EXTERNAL SCIENTIFIC REPORT

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Animal Consciousness

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Abstract

After reviewing the literature on current knowledge about consciousness in humans, we present a state-of-the art discussion on consciousness and related key concepts in animals. Obviously much fewer publications are available on non-human species than on humans, most of them relating to laboratory or wild animal species, and only few to livestock species. Human consciousness is by definition subjective and private. Animal consciousness is usually assessed through behavioural performance. Behaviour involves a wide array of cognitive processes that have to be assessed separately using specific experimental protocols. Accordingly, several processes indicative of the presence of consciousness are discussed: perception and cognition, awareness of the bodily-self, self-related knowledge of the environment (including social environment). When available, specific examples are given in livestock species. Next, we review the existing evidence regarding neuronal correlates of consciousness, and emphasize the difficulty of linking aspects of consciousness to specific neural structures across the phyla because high-level cognitive abilities may have evolved independently along evolution. Several mammalian brain structures (cortex and midbrain) are involved in the manifestations of consciousness, while the equivalent functional structures for birds and fishes would likely be the pallium/tectum and midbrain. Caution is required before excluding consciousness in species not having the same brain structures as the mammalian ones as different neural architectures may mediate comparable processes. Finally, specific neurophysiological mechanisms appear to be strongly linked to the emergence of consciousness, namely neural synchrony and neural feedback. Considering the limited amount of data available and the few animal species studied so far, we conclude that different manifestations of consciousness can be observed in animals but that further refinement is still needed to characterize their level and content in each species. Further research is required to clarify these issues, especially in livestock species.

Key words: Animal, consciousness, awareness, behaviour, neurobiology, philosophy, adaptation

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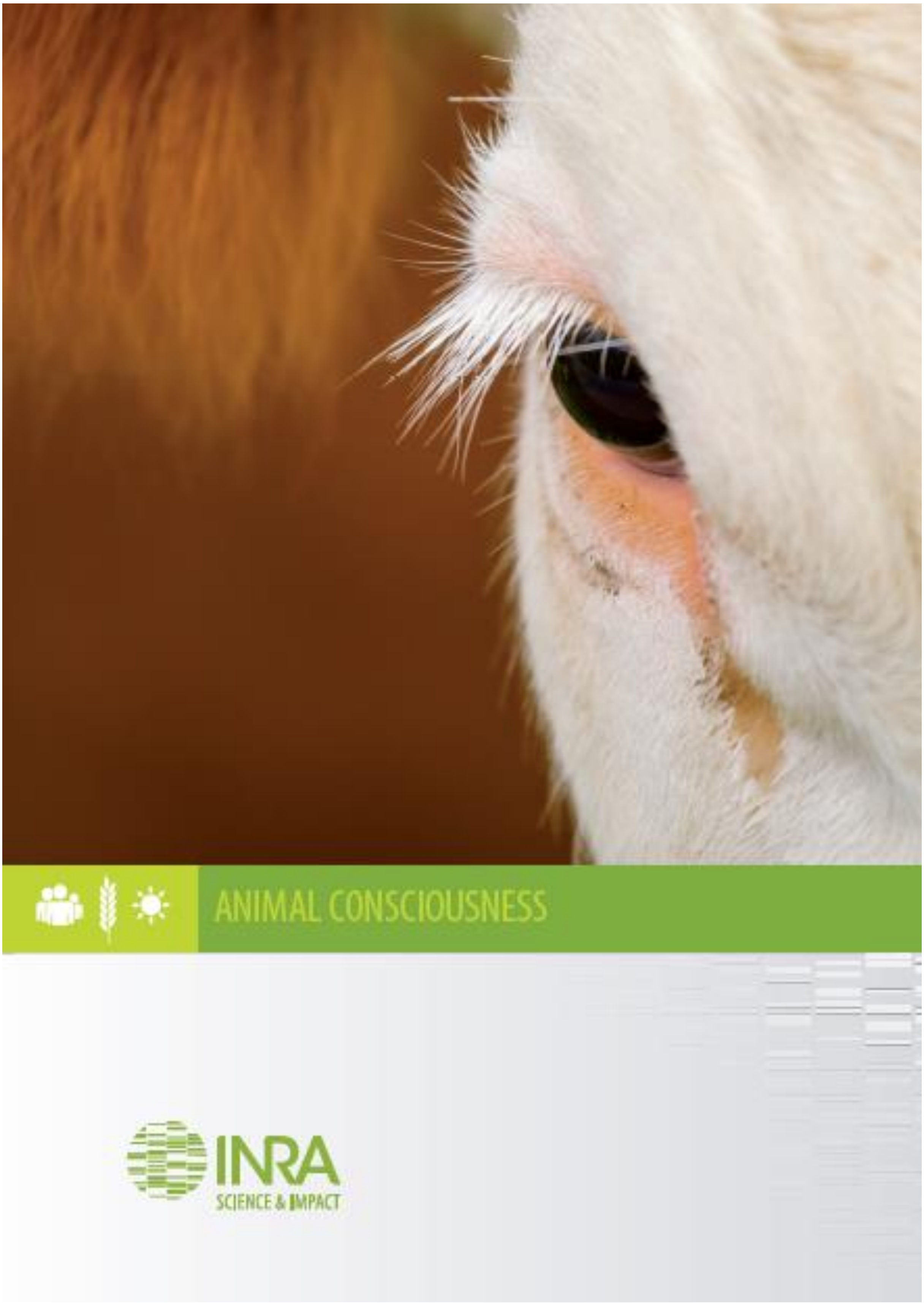
ANIMAL CONSCIOUSNESS
INRA
SCIENCE & IMPACT

Summary

The current report is based on a corpus of publications partly retrieved from databases (WOS) after an extensive bibliographic search. It provides the latest information on consciousness and related key concepts in animals, particularly in vertebrates. It provides the available information on consciousness in livestock animals.

Animal consciousness has been a topic of research by philosophers for many centuries. Their views from antiquity to modern times are detailed in chapter 1.

Research on biological and psychological issues came much later with several major conceptual innovations that established that consciousness is an outcome of brain processes and that it is a valid scientific topic.

As most research on consciousness has been, and still is conducted in humans, we found relevant to start with an overview of the current knowledge on human consciousness before addressing it on non-human species. This starting point to study the question of consciousness in animals is valid for non-human mammals due to their close phylogenetic relations with humans. However, we acknowledge that interspecies comparisons and extrapolations require cautiousness, especially when considering species other than mammals.

Human consciousness is private and subjective. In adults, it is accessible by others mainly through language, although non-verbal expressive means are far from negligible. In contrast, states of animal consciousness are accessible only through behavioural or neural markers. In adult humans, several levels and contents of consciousness have been defined, which are described in chapter 2.

Studies used in the report deal with a wide range of animals within the phylogenetic spectrum. However, most of them have been conducted on a few laboratory models, or on some privileged wild species, studied in the wild or in captive conditions. Very few studies have been done on domestic livestock.

It may be noted that, for the sake of clarity, the term consciousness is used in the report to characterize the phenomena evidenced in animals. We are fully aware that this term may not cover exactly the same components in animals as those observed in humans.

The following questions were more specifically raised by EFSA:

Question 1: what is the current knowledge on the different dimensions of consciousness and the scientific methods that can be used to determine whether an animal is conscious?

Chapter 2 describes several phenomena that are indicative of consciousness in humans. Distinct notions were considered: the levels of consciousness, with several vigilance states ranging from being fully awake to coma, and the contents of consciousness, with different cognitive processes including perception, cognition, and metacognition. Most of these processes have also been characterized in non-human animals as described in chapters 3 and 4. Answering the question "is there consciousness in animals?" with a simple yes or no is thus inappropriate. There are multiple levels and contents of consciousness in animals just as they are in humans. Recognizing this acknowledges clearly the heterogeneity of conscious processing in animal species. While cognitive processes that arguably involve a form of conscious access could be characterized in most animal species covered in this report, others seemed to be species-specific not requiring compulsory consciousness. A major obstacle is that consciousness in non-human animals is inferred from behavioural performance that by definition involves several types of cognitive processes.

Methods combining behavioural and neurophysiological approaches on animals are important for understanding cognitive processes such as metacognition, episodic-like memory, self-recognition and theory of mind. Ethological studies on animals in their familiar environment can lead to useful hypotheses concerning the type of cognitive process that is involved in their behaviour. However, these hypotheses still need to be tested using more sophisticated experimental paradigms, such as those developed in experimental and cognitive psychology. Such approaches have been recently designed to test hypotheses on emotions, social relationships, metacognition and episodic memory, all processes that involve some degree of consciousness.

It is clear to us that case studies and single published paper on a given phenomenon are not sufficient to conclude on whether animals, and more particularly livestock animals, can have conscious experience of their environment, self or conspecifics. However, the overall picture obtained from the large range of species considered strongly provides evidence for different types of consciousness in both livestock and fish.

Questions 2: Which types of consciousness, level and content, are present in vertebrate animals, specifically in livestock species, including farmed fish? and question 4: What is the content of different livestock species specific consciousness?

Because of similarity between questions 2 and 4 and the fact that the content of consciousness has not been thoroughly studied in animals the answers to these two questions have been merged.

Consciousness-related phenomena are extremely variable between species and between individuals within a same species. Thus, drawing general conclusions from a few individuals of a few studied species in a variety of specific environments is scientifically weak and should be done with great caution. This is especially the case when results gathered on wild animals or on animals studied in specific experimental environments are generalized to all domestic livestock.

We provide a few examples of higher levels of consciousness in domestic livestock: in poultry, hens can judge their own state of knowledge suggesting they are conscious of what they know or do not know. Pigs can remember what events they experienced, where, and when. Several other examples of cognitive capacities potentially underlying consciousness in domestic livestock are also available, such as recognition of individuals in sheep and cattle. Collectively these studies and those on wild and laboratory species, clearly support the hypothesis that domestic livestock species are capable of complex conscious processing.

Question 3: What are the neuronal correlates of consciousness in different livestock species?

At the theoretical level neuronal substrate of consciousness can certainly be measured in a wide variety of species, but for these measures to be fruitful, they need to be validated by being linked to behavioural patterns indicative of some degree of consciousness.

There is no single "centre of consciousness" in the brain. Several structures in the cortex and the midbrain are involved in conscious processing, but others are not involved at all. Two important mechanisms have been identified for consciousness to emerge: the synchronous coupling of oscillatory electrical signals and the re-entrant activity (broadcasting feedback) signals between different brain areas. These two mechanisms are compatible with current theories, such as the global workspace, the integrated information theory, and the predictive coding theories of consciousness.

It is difficult to link the expressive patterns of the various types of consciousness to specific neural pathways. Most neurophysiological studies have been conducted on animals that are phylogenetically close to humans. It is still possible that conscious processes may have arisen independently on many occasions during the evolution of vertebrates and invertebrates, specifically in cephalopods and arthropods.

In conclusion, extensive behavioural and cognitive capacities that have until recently been thought to be exclusive to humans and some primates have been identified in non-primate animal species. Among the most elaborate capacities, there is evidence that animals have knowledge of their own state (bodily self). They have the capacity to know and deal with their own knowledge, and also to evaluate the psychological state of their conspecifics, potentially leading to some form of empathy. One important outcome of this work is that the present report may be used for designing future ways of rearing animals.

We still need to emphasise that these conclusions are based on results from very few experiments on few species. To strengthen them further research is necessary, particularly to increase our understanding of the levels and contents of the different types of consciousness.

A pragmatic approach could be to adapt to livestock species experimental protocols that have been found useful in laboratory animals.

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BACKGROUND AND TERMS OF REFERENCE AS PROVIDED BY EFSA ANIMAL AND PLANT HEALTH UNIT

They will be detailed in 0.2.2 in chapter "Introduction and Objectives"

This contract was awarded by EFSA to INRA:
Contractor: Institut National de la Recherche Agronomique (INRA) /French National Institute for Agricultural Research
Contract title: Animal consciousness
Contract number: EFSA/INRA/2015/01

INTRODUCTION AND OBJECTIVES

0.1. History of the mandate

The current report aims to give a critical updated scientific review of literature on animal[1] consciousness, mainly in vertebrates. The question of human consciousness has been for a very long time dominated by very strong opinions based on religion and philosophy before becoming more recently a scientific issue. The question becomes even more complex when it comes to animal consciousness. Some authors start from the ideological position of emphasising the sharp frontier between human and animals, as described in chapter 1 of the report. Others authors question the importance of those frontiers and the wide range of cognitive abilities among animals and their levels of consciousness. In this report, we adopt the second position because we consider that ideological perspectives have no place in this debate.

The status of the animal consciousness is so controversial that a group of leading scientists decided to publish a manifesto calling for more research on the topic: the "Cambridge Declaration on Consciousness" (Low, 2012).

Box 1: The "Cambridge Declaration on Consciousness"

Publicly proclaimed on July 7, 2012, at the Francis Crick Memorial Conference on Consciousness in Human and non-Human Animals, at Churchill College, University of Cambridge, UK, the Declaration was signed by the conference participants that very evening and the ceremony memorialized by the CBS programme "60 Minutes". They declared the following: "*The absence of a neocortex does not appear to preclude an organism from experiencing affective states. Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviours. Consequently, the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Non-human animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates.*"

The scientific community recognises that a better understanding of animal consciousness is an important preamble for increasing knowledge of animal behaviour in particular when animals are facing difficult and stressful situations (Evola *et al.*, 2015; Matignon, 2013). Moreover calls for new research projects or conferences have been made (Allen and Trestman, 2015). Scientists propose that new research should bring a better knowledge on animals. In the meantime some scientists raise public awareness on the issues of animal cognition and consciousness *via* popular books (de Waal, 2016). Moreover, that subject receives an increasing attention in the media.

An INRA collective expertise on pain in farm animals was carried out at the request of the French Ministers of Agriculture and Research and published in French in 2009. The main outputs were a full report and a review, (Le Neindre *et al.*, 2009), an English summary is also available (Le Neindre *et al.*, 2014), available on INRA website (*http://institut.inra.fr/en/Objectives/Informing-public-policy/Scientific-Expert-Reports/All-the-news/Pain-in-farm-animals*). That report provides a scientific review of what was known in 2009 concerning pain in farm animals and the way it can be minimized.

Some of the experts who were involved in the expert group felt that the question of animal representation of pain and by extension the question of animal consciousness had not been sufficiently analysed despite its importance, due mainly to lack of time. Knowledge on this topic is indeed important, for the scientists involved in that field as for many stakeholders (breeders and animal welfare associations). It should allow to better understand how animals are able to perceive and represent their own world. In fact, most of the studies on animal welfare are based on the implicit assumption that animals perceive the situation they are experiencing. In addition new data on pain have been published since the 2009's report. It was considered therefore timely to revisit the subject.

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[1] The term "animal" means in that report "non-human animal".

A new development is that the French civil code was modified in February 2015. The legislators introduced the wording "*animal sentience*" (Legifrance, 2015). Animal welfare associations have taken a great interest in that change to better mobilize public opinion. French media promoted the issue since 2015 and animal right activists took advantage to advance their views. As French public opinion has become increasingly aware of the question, we felt important to discuss the new French legislation in this introduction section.

In addition, the joint ethic committee (Comité consultatif commun d'éthique pour la recherche agronomique, 2015) of two important research French institutes, INRA (French National Institute for Agricultural Research) and CIRAD (French Agricultural Research and International Cooperation Organization working for the sustainable development of Tropical and Mediterranean regions) released a report on animal welfare asking for more research on the subject.

The Animal Health and Animal Welfare Panel and unit (AHAW) of the European Food and Safety Authority (EFSA) has found interest in the development of that original multidisciplinary expertise and funded the project *via* the contract EFSA/INRA/2015/01.

As a consequence, INRA decided in 2015 to launch a scientific collective expertise on animal consciousness, as an extension of the INRA collective expertise on animal pain (Le Neindre *et al.*, 2009).

0.2. Organisation and mandate of the collective expertise

0.2.1. Organisation of work

INRA's Delegation for Scientific Expertise, Foresight and Advanced Studies (DEPE) provided the necessary scientific (senior scientist for coordination) and administrative support for the expertise work to seventeen French experts from different scientific fields and origins, in 2015 and 2016. Reference material such as publications and books was collected with the help of an INRA librarian (see statistics in 0.5).

DEPE was responsible for the certification of the expertise and independence of the experts who were chosen, and transparency of procedures following a standard INRA guidance. Their declaration of interest was carefully checked to avoid any conflict of interest.

DEPE was also responsible for contract negotiations, organization of monthly meetings, and management of the budget. The experts are solely responsible for their scientific contributions. The main selection criterion regarding choice of experts was their scientific expertise (assessed by their list of peer-reviewed publications) and for most of them scientific administration and leadership activities at French and international level, membership in governmental committees, and/or participation in governmental committees or evaluation of projects.

The seventeen scientific experts involved were identified from different disciplines related to the multi-faceted scientific domains in biology from neurobiology to ethology, and in social sciences from philosophy to law. Their affiliation is INRA (for 10 of them), CNRS (for 3), and Universities (for 4). Nine of those experts were previously involved in the INRA collective expertise on "Animal Pain" (Le Neindre *et al.*, 2009), including the project leader who had also been the project leader of the previous expertise.

The current report also reflects the comments and suggestions of external reviewers: an ANSES (Agence Nationale de Sécurité Sanitaire Alimentaire, Environnement, Travail) scientist and three English speaking referees from USA, Australia and Sweden.

0.2.2. The mandate, term of references as provided by EFSA

The terms of reference of the expertise as mandated by EFSA were the following:

"INRA, together with EFSA, is preparing an interdisciplinary scientific expertise on the subject of: Animal consciousness. The scientific expertise will be prepared through a comprehensive analysis of the relevant current scientific knowledge in this area in a series of meetings of a multidisciplinary team of experts organised by and held at INRA. The scientific expertise will address the following issues:

1. What is the current knowledge on the different dimensions of consciousness and the scientific methods that can be used to determine whether an animal is conscious?
2. Which types of consciousness are present in vertebrate animals, specifically in livestock species, including farmed fish?
3. What are the neuronal correlates of consciousness in different livestock species?
4. What are the components of consciousness in different livestock species? "

Answers to those questions are summarized in the "Summary" section (pages 4–5 of the report) and developed in the report, in the form of a critical analysis of the available scientific and philosophical academic knowledge found in published literature.

In the first chapter the main philosophical developments in history are presented. Philosophical questioning began with authors such as Aristotle and the French philosopher Descartes who dealt extensively with the question of consciousness. Scientists pondered on the issue of consciousness much later and some scientists were even very reluctant to consider it as a valid scientific question.

Chapter 2 is an overview of the current knowledge on human consciousness from which the main concepts have been developed. This chapter presents the main concepts that are important to understand data available on animals.

Chapter 3 presents what is known concerning consciousness in animals. This knowledge is presented with an emphasis on the main approaches – behavioural and neurophysiological – that have been used to generate it. Because only a few reports on consciousness of livestock species are available and they do not cover the main discoveries from the more recent years, we decided to consider other animal species when necessary (wild, laboratory animal, invertebrates as honeybees, considered as domestic animals).

Chapter 4 discusses the importance of consciousness in the adaptive abilities of animals especially from a phylogenetic perspective.

Chapter 5 presents how taking animal consciousness into account can lead to a better understanding of welfare, suffering and pain. For this last aspect, we made use of the additional evidence that has been made available since the publication of the Animal pain expertise. How knowledge of consciousness impacts on ethical issues is also considered in this chapter.

The most important definitions related to consciousness found in the literature search are presented in a glossary at the end of the report.

0.3. Legal aspects related to the 2015 modification in the French Civil Code referring to animal as “sentient beings”

On 16th February 2015 the French Parliament adopted a new piece of legislation: law n°2015-177, introducing article 515-14 in the French Civil Code and defining animals as “*sentient beings*”. This new provision may be the sign of a significant move regarding the status of animals in French Law. That change made in the Civil Code[2] takes place in a complex set of regulations, for which other pieces of legislation are relevant but are perceived as less symbolic.

The new article states in french: « ***Les animaux sont des êtres vivants doués de sensibilité. Sous réserve des lois qui les protègent, les animaux sont soumis au régime des biens.*** » (free translation: « *animals are sentient living beings. Apart from specific regulations that protect them, animals have to be legally treated as properties* ». “Beings” seems a more accurate translation compared to “creature”, taking into account the idea that creatures have a creator and that secularism is a very important piece of French legal order. In short, the law acknowledges that animals have their own sentient nature but confirms that they can be legally managed as properties and that legal persons can own them.

Other countries, including Germany, Austria, the Netherlands, Switzerland and Brazil, have introduced similar provisions in their legislations (Antoine, 2005; Blay-Grabarczyk 2015). In the Canadian province of Quebec an amendment very similar to the French one has been adopted in December 2015 (Recueil annuel des lois du Québec 2015, chap. 35; Gaillard *et al.*, 2015; Paradis, 2015; Lachance 2015). In Belgium, a proposal filed in 2012 is currently under discussion following the “French example”.

In France, various interpretations of the same text are proposed. Among legal scholars, some claim that nothing has changed and that the new legislation is simply “cosmetic” (Malinvaud, 2015; Mallet-Bricout and Reboul-Maupin, 2014). For others, the new article 515-14 c. civ. opens up a new

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[2] For historical reasons, the Civil Code is a major part of French law. For more than two centuries, the Civil Code has recorded legal solutions about the legal status of persons, property and contract law. It gathers in one legal book some of the most important concepts of the French legal order.

era in the French legal order. Marguénaud (2015) argues that article 515-4 c. civ. is the ultimate outcome of a shift in the French legal order: animals being defined as sentient is one of the most important pieces of the French legislation, animals can no longer be legally demeaned by simply integrating them into the legal category of goods or property. His position is not about considering animals as "persons" at the same level as "human beings", but rather creating a new category of legal persons, using a mixture of technical tools used for corporations and fundamental rights used to protect human beings (Marguénaud, 1998). However this line of argument is only one among others. In French Law Schools several propositions coexist. One of them may consider the possibility of refining and branching out the vast category of "legal things" (or "goods") by distinguishing "living" from "not living" things, natural from artificial or human made, things or property from non-appropriable things (*res communes*) (Desmoulin-Canselier, 2009; Desmoulin, 2005; Loiseau, 2006). Another suggests to abandon the latin *summa division* between "persons" and "goods", and to create a third category (Farjat 2002; Martin 2015).

Philosophers and ethicists are also involved in the debate but are more concerned by moral values. Strong views are defended but no prevailing paradigm obviously pervades the legal sphere. Consequently, it is difficult to link philosophical essays with changes occurring in the legal domain.

Bitter discussions are not confined to the academic world. The 2015 Article is the result of a long debate involving non-governmental organizations (NGO) and stakeholders. On one hand, some authors and stakeholders close to the agricultural industries consider that the current regulations were already sufficient to protect animals (Inchauspé, 2014). They consider that the change could have a profound effect on future relationships between humans and animals, (Denis, 2015; Hernandez-Zakine, 2014) in particular on the Agribusiness. On the other hand, groups in civil society claim that better protection of animals still requires a major modification of our lifestyle and of our legal system.

This preamble is important to understand the context and the symbolic weight of article 515-14 c. civ. It helps to shed some light on what interpretation can be expected at this point. In short, we may be seeing – between the lines of an apparently purely symbolic text – the birth of a new legal principle in French law. The European Union already recognizes a legal principle designed to protect animal welfare (art. 13 TFUE). This concept of "animal welfare" has to be distinguished from "animal protection" and from "animal health". In France, new legal provisions may announce the coming of a *general* principle dedicated to the protection of "sentient beings" (compared to current *specific* provisions).

The capacity for suffering is at the core of the debate (Libchaber, 2014). However, the notion of "sentient beings" is not really *per se* a subject of discussion. A report from the ethical committee for agricultural research states that "*recognizing the animal as a sentient creature means that the animal is able to think and experience emotions and has the ability to assess situations*" (Comité consultatif commun d'éthique pour la recherche agronomique, 2007-2015[3]). Before the change in 2015, Lesage (2013) already wrote that animals in French Law were defined using two principles: i). they have to have a centralized brain which is sensitive to pain and with some cognitive ability; ii). they have to have a level of interaction with humans.

However, without any demonstration to support it, this proposal appears more intuitive than scientific. No official, clear and complete classification referring to cognitive or sentient capacities is used to organize the legal protection of animals. For instance, the protection given to roosters used in public fights is stronger than the protection granted to bulls in public bull-fighting (French criminal code, art. 521-1, Conseil constitutionnel 21 sept. 2012, QPC n° 2012-271; Conseil constitutionnel 31 juillet 2015, QPC n° 2015-477). To provide a strong and scientific conclusion on this topic, it would be helpful to have a systematic and complete review of European and national jurisprudence as the cultural context is important in this matter. However this work has still to be done and is difficult due

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[3] http://institut.inra.fr/Missions/Promouvoir-ethique-et-deontologie/Tous-les-dossiers/Comite-d-ethique

to lack of centralized jurisprudence repository. Furthermore, a careful reading of the new art. 515-14 c. civ. reveals some ambiguities. Stating that “animals are sentient beings” may be interpreted in a provocative manner: one might say that the French legislator evicted from the animal family all living creatures unable to feel pain. Of course, it would be more exact to say that on the question of animal protection, the law does not take into account living creatures unable to feel pain and, for that reason, does not categorize them as animals. Consequently, the word “animal” may be defined differently depending on the purpose of the law. The situation is even more complicated with the use of the words “sentience” and “consciousness”. They are not legally defined. Is it because there is no need for a legal or judicial definition to mete out justice? Is it because the issues of “animal sentience”, “animal intelligence” and “animal consciousness” occurred only recently, with new developments of scientific knowledge? Is it because the scientific vocabulary on this matter is still equivocal? The definitive answer has still to be found and would probably mix these different elements. Some clues may be found in court rulings. Most of the judicial decisions on animal protection concern pets, horses and cattle, animals already granted the capacity of suffering. Neither forensic expertise on their peculiar emotional characteristics nor comparison between their neurological systems is necessary to pronounce a sentence of cruelty, abandonment or ill-treatment. Factual reports describing wounds, health problems or lack of care are sufficient to draw legal conclusions. The judicial reasoning assumes or presupposes that animals are sentient beings and admit, most of the time implicitly, that the suffering is a consequence of the described conditions. Nevertheless, all presupposed sentient beings are not equally treated. The level of interaction with human beings, especially with the animal owner plays a crucial role. For instance, an animal owner shall receive compensation for the moral injury due to the loss of a “dear being”. In 2015, a ruling of the *Cour de cassation* (French Supreme Court regarding civil and criminal law) stated that a pet is “unique” for its owner and that the consumer law shall be adapted to take this into account (Cour de cassation civile chambre civile, 2015). However, what is really at stake when a judge takes into consideration the relationship between man and animal is still unclear. Does the judge recognize the active participation of the animal, emotionally implicated in the relationship or does he acknowledges human emotions, without necessarily taking nature of the animal into account (without distinguishing between animal species depending on their cognitive capacities)? We still do not have a complete and systematic analysis of court rulings to describe the situation more precisely and act as a basis for strong opinion.

The only clear point at the moment is that a lot of information is still missing regarding the meaning of the word “sentience” which is polysemous and ill defined.

0.4. Assembling the bibliographic corpus

An INRA librarian developed the search terms, the gathering and handling of the bibliographic *corpus*, and the supply of documents regarding this collective scientific expertise to experts. The librarian likewise incorporated the bibliographic references into the final report and performed the quantitative and qualitative analysis of the referenced *corpus*.

0.4.1. Information sources and methodology

The librarian used the interdisciplinary bibliographic database Web of Science™ Core Collection (WOS), which indexes 12,000 journals. The search simultaneously queried the following databases: Science Citation Index Expanded (1975-present[4]); Social Sciences Citation Index (1975-present); Arts & Humanities Citation Index (1992-present); Conference Proceedings Citation Index-Science (2000-present); and Conference Proceedings Citation Index-Social Science & Humanities (2000-present). The corpus was created through an iterative process between the experts and the librarian.

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[4] Years only available to INRA.

An initial list of approximately fifty articles and books was drawn up by the project leader based on searches of the bibliographic database known as Scopus® (Elsevier). These references were then imported into an EndNote® file. EndNote's *Subject Bibliography* function was used to do a frequency analysis of the terms in the *keywords* field for these publications.

In this manner we were able to refine and validate the keywords supplied by the project leader for the initial search. The resulting corpus lay at the intersection of the terms: [_animal_] AND [_arousal OR *conscious* OR *aware* OR wakeful*_] AND [_cognit* OR metacognition OR empathy OR imitation OR "social learning" OR etholog* OR behavio$r*_].

These terms were searched in the title, abstract, or keywords of the first set of references gathered; it corresponds to a search of the *Topic* field within the Web of Science™ Core Collection.

Since the expertise request did not apply to all animal species, certain keywords corresponding to families or other grouping of animals were excluded: _["marine mammal*" OR seal OR llama OR moose OR "guinea pig" OR "guinea pigs" OR invertebrate OR drosoph* OR insect*_]. The search was validated by verifying the correspondence of the initial corpus with the preliminary list of references provided by the project leader.

0.4.2. Tools used for bibliographic management and document sharing

The decision was made to work with EndNote® online, a lighter and simpler bibliographic software tool than EndNote's® "desktop" version. The full bibliography for the project was made available to all experts on the Web, with links to full-text versions of publications facilitated by an SFX resolver link (present for each reference). One folder was created for each expert, with shared "read" and "write" access provided to all members of the working group. The Silverpeas platform was used to share the full texts of publications not accessible *via* subscriptions held by INRA (45% of the corpus). Working documents for the group, including the bibliographic lists, analytical grids of the publications, and draft chapters of the report during the writing process, were also shared in this way.

0.4.3. Refining the corpus

The initial *corpus* of over 3,000 references was reduced to include only articles, proceedings, papers, reviews, book chapters, editorial materials, and book reviews.

Even after these adjustments, publications outside the core expertise area were still present. Study of the titles and abstracts of a dozen or so publications yielded a list of terms to exclude: _pharmaco*; disease; zoonotic*; child*; brucellos*; "sexual behaviour"; "feeding behaviour"; "sexual behavior"; "feeding behavior"_.

This refined *corpus* of 2,300 results was submitted to the project leader, who retained 18% of the total based on a review of the titles, abstracts, and references.

0.4.4. Adding to the corpus

The experts then found necessary to conduct an additional survey with respect to the concepts "episodic-like memory," "sentience," AND consciousness" (excluding the same words as for the initial search):

Episodic like memory: TS=(_"episodic$like memor*" OR "episodic memor*_") AND _conscious_* AND _animal_

Sentience: TS= (_animal_ AND _sentience_).

A corpus of approximately 500 publications was obtained, validated and divided up among the members of the group. In reviewing the publications, the experts noted the key elements of their analysis on a customised form; these forms were classified by author and by report chapter into the Silverpeas platform.

During the course of the bibliographic analysis, some supplementary relevant documents were added to the corpus, including books, courses, and publications in journals not indexed by the Web of Science$^{\underline{TM}}$ Core Collection.

Finally, bibliographic monitoring of each of the searches was conducted monthly throughout the period of the project, resulting in the addition of further publications to the corpus.

0.4.5. Statistical analysis of the literature used in the report

Nine per cent of the papers retrieved from the first request in the WOS were finally referenced in the report. Half of them dealing with animals were published after 2010, among them 15% in 2015, 3.4% in 2014, and 12% in 2012, etc…..

A total of 659 references are cited, the distribution per chapter is shown in Fig 1

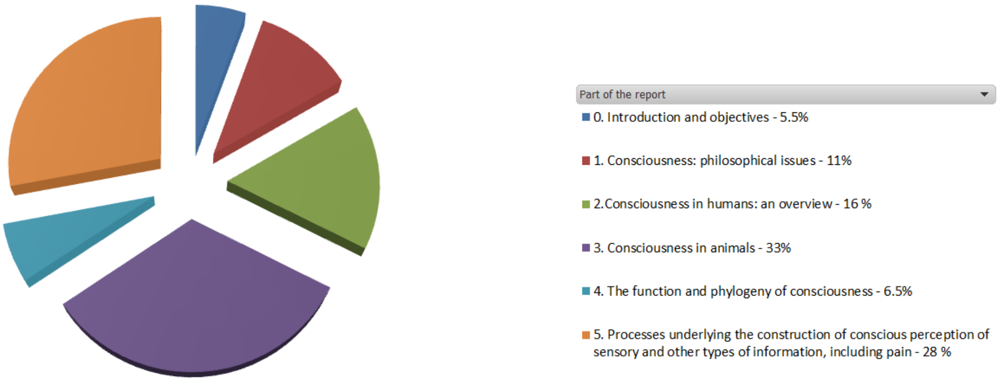

Fig 1: Distribution of references cited in each chapter

The majority of cited articles (Fig. 2) were published in international scientific journals (75%), which is consistent with the request of the mandate. Books and chapters of books (16+7 %) were cited in majority in Chapter 1 in philosophical discussions, including 60 books published before 1900.

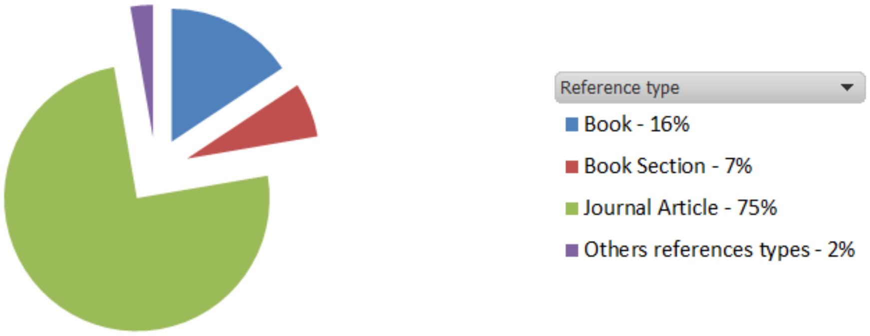

Fig 2: Percentage of cited references from various categories of publications

One third of total references were published after 2010, 60 books were published before 1900 on earlier philosophers (Fig 3).

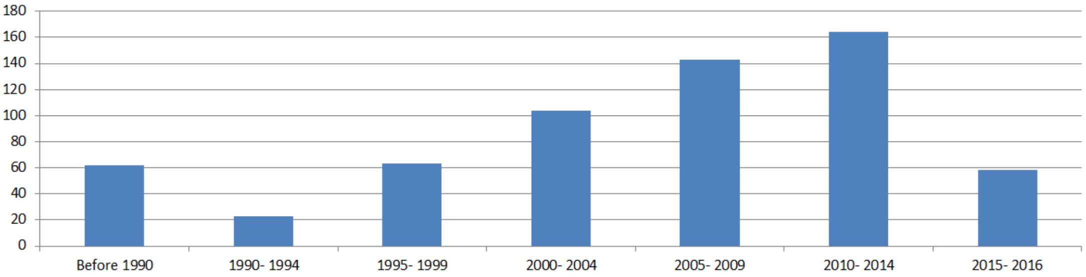

Fig 3: Publication year of references cited in the report

Journals in wich cited articles are published	**Number of cited articles**
Applied Animal Behaviour Science	26
Trends in Cognitive Sciences	20
Animal Cognition	18
Science	18
Nature	15
Proceedings of the National Academy of Sciences of the United States of America	15
Nature Reviews Neuroscience	13
Animal Welfare	11
Consciousness and Cognition	11
Behavioral and Brain Sciences	10
Pain	10
Animal Behaviour	9
Frontiers in Psychology	9
Journal of Neuroscience	8
Behavioural Processes	7
Cerebral Cortex	7
Journal of Neurophysiology	7
Current Biology	6
Journal of Experimental Psychology-General	6
Neuroimage	6
Philosophical Transactions of the Royal Society B-Biological Sciences	6
Plos One	6
Nature Neuroscience	5
Neuron	5
Neuroscience and Biobehavioral Reviews	5
Recueil Dalloz	5
Trends in Neurosciences	5

Table 1: Scientific journals in which more than 4 occurrences were published

The main journals cited in the report are presented in Table 1 ranked in number of occurrences order, 6 of them are cited more than 15 times.

Fig. 4: Word cloud depicting the relative frequencies of occurrence of words appearing in the titles of the cited references.

A frequency analysis of the words appearing in the titles of publications was performed with the program wordle.net (*http://www.wordle.net*) as shown in Fig.4. It portrays the correspondence between the major themes treated in titles, the size of words is proportional to their frequency.

Among the publications retrieved from the systematic analysis in the web of science containing **animal** in title, summary or key words (15% of the total list), the more frequent keywords are in decreasing order : metacognition; memory; humans; consciousness; cognition; awareness; brain; animal welfare; monkeys; behaviour. They are issued in majority from the fields of behavioural sciences (24%), zoology (15%), neurosciences (13%), veterinary sciences (10%), agriculture and dairy (9%), biology (7%), etc..;.

Meanwhile 48% of publications referenced in the report, retrieved from the WOS do not have **animal** in title, summary or key words. Among them the more frequent keywords in that sub corpus are in decreasing order: cortex; attention; consciousness; positron-emission-tomography; brain; pain; perception; prefrontal cortex; memory; awareness. Those papers are originated in majority from the fields of neurosciences (59%), psychology (24%), behavioural sciences (16%), etc….

A grid with main information contained in the paper was prepared by the experts for each one of the refined corpus, and available for all of them in the Silverpeas platform, the aim was to be able to share key information without a systematic reading of the whole paper.

To summarise the method used is not a systematic review as such, but it is quite close to it.

0.5. Major societal questions regarding animal consciousness

Over many centuries science and philosophy have debated the question of human and animal consciousness – their similarities and differences –, often in polemical terms. What impact have these debates had on our shared life with animals? Matignon (2013) wrote: "*in modifying the representations we have of animals, science invites us to take their interests into consideration, to redefine our relations with them and to ask ourselves what obligations we have toward them*."

Human beings have long sought to classify the world around us into grand categories, many of which are deeply anthropocentric, as our vocabulary testifies: "pest species," "animal companions," "livestock," etc. (Gouabault and Burton-Jeangros, 2010). Other classification systems seek to group animals based on the characteristics of the creatures themselves, whether these are anatomical or behavioural characteristics or (increasingly) on the basis of evolutionary proximity (Lecointre and Le Guyader, 2006). Scientific classifications have sought to move beyond a merely anthropocentric perspective, one based entirely on the similarities and differences between non-humans and humans. For many centuries, however, all the differences between humans and animals were the main force that motivated philosophical, religious, and scientific speculation and, as a result, helped to justify granting animals a merely instrumental value and using them accordingly (Digard, 2009). Comparative physiology made possible great advances in human medicine and thus justified experimentation on animals (Bernard, 1865). Comparative and experimental psychology and cognitive ethology made possible to approach animal psychology from a more scientific perspective. They seek to combat anthropomorphic assumptions that can impede our understanding of the distinctive world belonging to each animal species (Campan and Scapini, 2002). Some animals are raised only to be used by humans; others share their lives (we have relationships with them). We are engaged in a continuous exchange of information, services, and affects with domestic species (Boivin *et al.*, 2012; Porcher, 2001), therefore we need to better understand their behaviour than for other animals. Behind the theme of animal cognition lies the ethical issue of our responsibility to animals; that is, our responsibility for their physical and mental integrity, and to their self-interest (Boisseau-Sowinski, 2015). This responsibility is often expressed in terms of our obligation to ensure animals' well-being: "*Respect for the well-being of animals is becoming an important social demand*" (Veissier *et al.*, 1999). After the Second World War, "social demand" was focused on to producing increasing quantities of animal products at prices within reach of modest household budgets. Research in animal science concentrated on increasing the productivity of livestock operations. Once the goal of ensuring a plentiful supply of affordable livestock products was achieved, "social demand" began to concentrate on other attributes, including healthiness and good organoleptic properties. Livestock farms that pollute the environment could be disapproved, and the conditions in which animals were kept and how they were treated were considered. To respond to this transformation in "social demand," a range of different scientific disciplines have contributed to the development of new production standards and new production practices intended to meet these public expectations (Guillaumin *et al.*, 2008).

When economists speak of "social demand," they mean demand validated at the market place. Social demand in this sense changes according to consumer preferences and is expressed in terms of the price consumers are willing to pay for specific characteristics of a product, service, or good. What type of "demand" is expressed when we talk of animal "well-being"? Should we understand that consumers are willing to pay more for products from animals raised in conditions certified to an animal welfare standard? Or that an opinion poll would show that most of the public disapproves the conditions to which animals are subjected in industrial livestock production systems? Or can we consider that this "demand" is expressed by a vaguely defined group of animal rights organizations? In fact, what we refer to as "social demand" is defined less in terms of the preferences of consumers and is more a heterogeneous, multiform, and more or less informed expression of a shared unease. Individuals do not necessarily translate this unease into their behaviour as consumers, but they may express it as citizens since they have become sensitive to the idea of *sentience* as it is defined in the current report. Sentience is usually defined as common to humans and animals, it precedes characteristics that distinguish us from animals (like speech, reason, symbolic and thinking, etc.). The theory of evolution, the neurosciences, and ethology show that there are phylogenetic, neurological, and behavioural links between humans and many animal species (see the following chapters). It is thus likely that what matters to animals is rather similar to what matters to humans. We believe that human sentience is the capacity to suffer and to feel empathy for the suffering of others, and deserves ethical recognition (Boisseau-Sowinski, 2015). Therefore, the same should apply to non-human beings supposed to possess a "sentience-like".

The level of respect due to the animals is driven by the understanding of the forms of consciousness accessible to different animal species. Broadly speaking, we can say that the development of the cognitive sciences has resulted in the recognition of cognitive capacities in many species of animals (particularly mammals and some birds), including the capacity to experience a range of mental states and thus the possession of a mental universe much richer than that of mere existence as a sentient being. And yet this scientific development has coincided with the development of contemporary livestock production systems in which animals are, in the view of animal welfare advocates, increasingly treated as mere machines. In laboratory research, animals are likewise treated as though they were nothing but tools. Inquiring into the cognitive capacities and forms of consciousness manifested by various animal species thus results in a tension between a *"thing to respect"* in animals, which tends to expand, and a human behaviour that in practice respects the animal less and less, at least insofar as the public opinion understands it.

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CHAPTER 1. CONSCIOUSNESS: EPISTEMOLOGICAL AND PHILOSOPHICAL ISSUES

1.1. Introduction

For more than 2000 years, humans have been thinking and writing about animals and *ipso facto* comparing their behaviour to that of humans. Obvious dissimilarities between humans and animals and related religious beliefs led to the opinion that humans are fundamentally different from animals *sensu lato*. Therefore comparisons between human and animal behaviour and the mechanisms that control such behaviour are found in both philosophy and biological sciences. Philosophy, more or less imbibed with theology, has dominated over biological sciences for centuries. However it has been progressively forced to face the evidence of biology as scientific research has become feasible and available. This chapter explores this progressive shift and partitioning of philosophy and biological sciences in relation to the central issue of consciousness. In fact consciousness has been a major feature in the claim that there is a discontinuity between humans and other animal species, even when both are considered to adhere to Darwin's conception of the evolutionary continuity of mental states.

This chapter presents an epistemological view on mental states from Aristotle to modern philosophers, who, in contrast to Aristotle, have had the opportunity to take into account the development of different scientific fields dealing with consciousness. The philosophers we have selected include French philosophers from Descartes to those of the "Century of Enlightenment". Our selected biologists are naturalists including Lamarck, who forged the very term of biology, Darwin and Romanes and, later, comparative psychologists and ethologists like Morgan and Griffin. The last sections of this chapter presents views of contemporary philosophers and a synthesis of the different meanings given to the concept of « consciousness » and/or the different terms used to cover the phenomenon of « consciousness » in different species or according to different physiological and mental states.

1.2. First considerations

The idea that humans have interior forces, or an "interiority", that distinguish them from animals has long been proposed. These forces are characterised by representation, intentionality, reflexivity, moral sentiments; in short, consciousness. However there is nothing exceptional about humans relative to other organisms in terms of biology – what Descola (2005) termed naturalism – and this concept gained ground in the West beginning in the seventeenth century. Elsewhere in the world, and prior to that period in Europe, other ideas about the similarities and differences between humans and non-humans may be found. For example, animist ontologies are found in the Amazonian region, in Sub-Arctic America, in Siberia and elsewhere, as well as in the thinking of Greek antiquity with Plato. It is the exact opposite of naturalism which asserts that humans and non-humans have the same kind of interiority, but each living species "inhabits" a body that is specific.

If we were Amerindians or animists (in the sense given to animism by Descola : the animists attribute the same kind of intentionality to all beings, humans and non-human animals), the question of animal consciousness would not even arise. We would consider that these non-human creatures, so called animals, have "interiority" identical to our own. On the other hand, we would recognize that each animal species has its own body *sui generis*, with sensory and motor organs, and thus capacities of perception and movement, as specific to its kind as its dietary habits. This is undoubtedly also what makes animals seem mysterious to us: we cannot grasp what they are thinking (in the first person). We could be both convinced that bats possess the same mental capacities as our own, but we nevertheless adhere to Nagel's declaration in "*What is it like to be a bat*? " (Nagel, 1974) that knowing what it is to be a bat will remain forever inaccessible to us. With its wings and its sonar giving it the power of nocturnal flight and its need to hibernate in winter, the bat opens its eyes on a world of its own, a world that will never be known to us.

But we as Westerners are progenies of modernity. So, we are convinced that we have a physicality identical to that of all living beings (the same physico-chemical processes, the same type of functioning of cells and organs). However, at the same time, we are convinced that we have a distinctive mind that is unique to humans, and which animals do not possess at all or, at best, only in a rudimentary form. From the moment biology adopted this dualist ontology (Descola describes it as "naturalist") it engaged in observational and experimental research on animals as a means of comprehending our own physiology and behaviour. Philosophy, meanwhile, has shown little interest in animal nature, focussing instead on human nature, the mind that is thought to separate us from non-humans (Burgat, 1997).

This ontology has been important for the development of the sciences. However, it does not correspond to the experience of those who live in close contact with animals and who raise or hunt them. Some followers of Descartes went beyond the initial animal-machine concept proposed by Descartes himself (see section 1.2.2. on Descartes) and posited that the animal was nothing but a body and that a body was nothing but a machine. What they achieved, as G. Canguilhem (1969) observed, was simply a radicalising of modern dualism. Nevertheless, when, a century later, Leroy (1994) challenged the analogy between animals and machines, he did so, not by making reference to a tradition coming down from Greek antiquity *via* Plutarch (46-125), but by referring to a tradition taken from a sceptical perspective by philosophers M. de Montaigne (1533-1592) and P. Charron (1541-1603). Charron was lieutenant of the royal hunts at Versailles and Marly when he wrote his *Letters on Animals*. In his text and later in an article in the *Encyclopédie méthodique* – initially titled "Animal Instincts" – he drew particular attention to animals' "intelligence" and their "perfectibility."

The philosopher and theologian N. Malebranche (1638-1715) pushed the "theory of the animal machine" to the point of denying sentience to all animals (see section 1.3.5. C.L. Morgan) – hence his declaration, "*Thus animals have neither intelligence nor soul, as ordinarily understood. They eat without pleasure, cry without pain, grow without being aware of it: they desire nothing, fear nothing, know nothing*" (B. de Fontenelle, 1751-1761).

Animists do not hesitate to interpret what animals think, and base their interpretation on their own ways of thinking, their own desires, as a sort of extension of the theory of mind that they use of with human companions. This way of understanding what goes on in animals' heads was called anthropomorphism by modern dualists who stigmatised it as a miscomprehension. Each of us knows our own perceptions, emotions, intentions and thoughts. We can generally understand the perceptions, emotions, intentions, and thoughts of our human companions because we communicate with them by language. However, we are ignorant of those of animals, even those of the animals with whom we share work or everyday life. So, seeking to understand animals' minds by analogy with our own is doomed to fail. Scientists who study animal behaviour or cognitive abilities share this ontology in full, condemning those who pretend to project into non-humans' capacities, capacities that are like our own. It is no accident that some authors mentioned in our reference list, strongly adhere to Occam's principle (also known as the principle of simplicity, of economy, or of parsimony) when describing the existence of forms of consciousness in animals. In so doing they deny that animals have an internal procedure of their own as the tenants of behaviourism often did.

Nevertheless, this "anthropomorphic illusion" is a common way of interpreting what the animals, with whom we, in a sense, share life, have in their minds. What we interpret in this way is certainly not scientific and has no heuristic value, but such anthropomorphism has proven to be of impressive practical utility over a long time. It is thanks to this anthropomorphic, and in a way animist, inclination towards common sense, this way of interpreting the mental state and the intentions of animals as roughly analogous with our own, based on experience gained through trial and error, that humans have been able to raise animals, to live with animals, to train certain animals and to hunt others.

What do we know of animal "interiority"? Can we gain access to animals' mind, to the forms of consciousness that are exclusive to them (in the third person to be sure, because even an animist knows that one cannot speak for an animal in the first person, unless he is a shaman)? These are the crucial questions for anyone who regularly spends time with animals, who works with them or studies them. What we know about animals determines the interactions we have with them, our behaviour towards them (and theirs towards us), as well as how we decide how they should be treated.

1.3. Historical perspectives from Aristotle to the eighteenth century – An epistemological view

1.3.1. Animal consciousness according to Aristotle[5]

The notion of "consciousness" did not exist for the Ancient Greeks. The emergence of the concept is generally attributable to Augustine (354-430) and his notion of *voluntas*. The Greeks, from Homer (8th century BC) onwards, made use of two terms to designate what we now think of as consciousness: *aisthêsis* ("sensation") and *nous* ("thought") in the very broad sense of "perceive" ("awareness"?). Thus, the absence of the idea of consciousness in general entailed the absence of an idea of "animal consciousness"! On the other hand, many Greek philosophers, from Pythagoras (6th century BC) to Porphyrus (3rd century AD), were interested in the issue of animals (Labarrière, 2005), expressed for instance in the idea of vegetarianism: how can we eat our fellow creatures? Apart from these moralising notions, Aristotle remains our most important "scientific source" of Ancients' knowledge about animals. It should be remembered that between a quarter and a third of the works of Aristotle that reach us are treatises in zoology, commented on and even rewritten at least as late as Albert le Grand (Albert from Cologne, 1200-1280). Aristotle's principal argument about animal intelligence relates to the "practical intelligence" of what he refers to as the "other animals". This latter statement suggests that we are also animals. This is not the least thing we can learn from Aristotle! Nonetheless what Aristotle called *phronêsis* (practical wisdom) in certain animals has nothing to do with practical wisdom in humans, but refers rather to their capacity to recall past events and to anticipate new ones. One of Aristotle's favourite examples of this is that of the red deer doe teaching its fawn to hide in a safe place: thus demonstrating a power of memory as well as a strong capacity for learning and teaching. But, he cautions that all animals are not equally endowed with this form of practical intelligence: some do not have it at all, while others manifest it only in very specific contexts. Such is the case with the "industrious" bee, but also with large mammals living in family groups, such as lions and dolphins. But while animals are certainly endowed with a form of "practical reasoning", we should not conclude from this that they possess any sort of "theoretical reasoning". This remains the domain of humans, who alone possess the *logos*; and it is this form of reasoning, much more than "practical reasoning" or "political life", that radically distinguishes us from the "other animals" (Labarrière, 2004).

1.3.2. Animal consciousness according to Descartes

René Descartes' views (1596-1650) on animals are famous. It would be more accurate, however, to speak of his views on "beasts", since in Descartes' time the word "animal" referred to both beasts and men. Emblematized by the idea of the "animal-machine", Descartes' thoughts serve both as an indispensable point of reference and as a readily available set of ideas to argue against. The figure of the animal from his point of view is considered to amount to a disfiguration, the fullest expression of a general human tendency, and more specifically a modern one, to deny the reality of animals' cognitive capacities. Recent scientific research is generally thought to have closed this Cartesian chapter, recognising the complex nature of animal reality as long understood by those who work or live in close contact with animals, or by Eastern and ancient philosophers. The reasons for this blindness are

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[5] JL Labarriére contributed to this paragraph.

attributed to our deep-seated human arrogance, exacerbated by a scientific and technical culture and, according to some, by Christian anthropomorphism.

In fact, the Cartesian point of view is much more subtle than this. To understand it we must better appreciate its historical context – the questions and objectives that underlay this way of thinking about animals. His preoccupations were: 1) scientific – to establish an objective knowledge of physical reality; 2) methodological – to reflect critically on human thinking about animals so as to produce reliable and verifiable knowledge; and 3) ethical, and even theological – to understand and establish the values governing our relations among ourselves and with the various other beings with whom we live. It should be added that, in Descartes' thoughts, the idea of the animal is bound up with two other fundamental notions: that of the body, and that of the mind. This is the theory known as the body-machine: the living organism is approached as if it were a machine, something that can be disassembled and thereby understood without the intervention of mysterious forces such as the soul. The mind, on the other hand, obeys an entirely different set of reflexive and non-mechanical principles. The animal is thus understood as a body-machine, but as such it also serves as a model for all living organisms, including, specifically, human beings. In human beings, however, we also observe the existence of a mind, which, thanks to our use of language, cannot be reduced to the mere expression of emotions but which amounts to processes of reflection, of thought. Thus, when we engage in conversation with another person, we exchange thoughts and ideas. Our minds adjust themselves to the various subjects brought forward, even incorporating the unexpected – and in this way manifesting themselves as minds, as thoughts. It is not so with a machine, which, though as perfect as it is, follows a programmed series of actions; nor with an animal, for whom communication – assuming animal communication expresses only emotions governed by a stimulus reaction – does not amount to actual language or thought processes. Hence, Descartes concluded that the animal is most likely nothing but a body without a mind. But he stopped short of professing this as a certainty, since one cannot enter into the animal's being to verify the point. He supported this conclusion with other arguments, the most important of which was drawn from the predictability and strictly appropriate nature of animal behaviour. Descartes thus dismissed the common assertion of animals' remarkable abilities, arguing that such capacities were on the one hand mechanical – to admire such performances was like admiring the precision of a watch – and on the other hand species-specific. Given the unity of the mind, it is incomprehensible that a reflective capacity could be exercised within a specific domain and not be extendible to all aspects of a being's activity. Thus, Descartes' philosophy might have marked an end to a certain tradition ascribing much wider capabilities to animals (sometimes obviously too much), but his writings do not reflect the dogmatic and definitive point of view commonly attributed to him – and which in fact is more characteristic of one of his followers, Malebranche (1638-1715).

Descartes' approach was essentially methodological, seeking to assume nothing with respect to the animal and to draw conclusions based on the animal's external behaviour alone, in a quasi-ethological fashion. Reflecting his own position as much as reflecting the animal itself and grounding his approach on observation, Descartes thus declared himself ready to modify his conclusions in the case of exceptional animal behaviours: "*As for dogs and monkeys, if I were to attribute thought to them, it would not therefore follow that the human soul is not distinct from the body, but rather that in other animals mind and body are similarly distinguished*" (Descartes, 1641). Precisely because of his methodological rigour, then, and in light of current research, the relevant question now is to ask what point of view Descartes would adopt today with regard to the animal (Guichet, 2011).

Logically speaking, there is no reason – under the strict condition that animal communication could be established as being a true language in certain species – that a truly Cartesian perspective would refute the idea of some sort of animal consciousness.

1.3.3. Philosophers' views before Darwin: the question of animal capacities in the eighteenth century

In the eighteenth century, a variety of factors combined to bring about a profound re-evaluation of animal capacities (Guichet, 2006). In philosophy, these factors included first of all the reaction against

Cartesianism, crystalized in the idea of the animal-machine. Equally important was the new interest in empiricism advanced by Locke (1632-1704) at the end of the seventeenth century and further developed by Condillac (1715-1780) near the middle of the eighteenth. Then, to these two currents of thought were added the increasingly aggressive arguments of the materialists, beginning with Offray de la Mettrie (1709-1751), who engaged in a tug of war using a materialist view of animals as a critical spade with which to uproot the spiritualist idea of man and, by extension, theology. In the scientific domain, the increasing power of the natural sciences and their associated spirit of observation and experiment made animals an increasingly important focus of study. Fed by travellers' accounts of new lands, new creatures, and new observations, the natural scientists became interested in animal behaviour as well as in animals' biological characteristics. Increasingly taken up by the philosophers, natural scientists also entered the background of "enlightenment's men", as documented in Diderot (1713-1784) and d'Alembert's (1717-1783) in a vast synthesis of human knowledge and expertise, called the *Encyclopedia*. Thus, from every direction, new elements emerged to challenge the boundaries laid down in the previous century between spirit and flesh, man and animal, God and Nature. In the second half of the eighteenth century this process accelerated despite challenges from major thinkers who sought to qualify the new perspective. Thus, Buffon (1707-1788), while recognising more in animals than was allowed by the strict Cartesian vision, reasserted the idea of an incontestable human superiority. Buffon tended towards a minimalist view of the capacities of animals in accordance with a rigidly mechanistic model despite some contrary examples in the descriptions of species in his massive *Natural History*. In the work of Jean-Jacques Rousseau (1712-1778), man and animal were brought closer together in a decisive manner. Rousseau argued that when men and animals were regarded as natural beings, no external distinction could be made between them: "*In considering man [in the pure state of nature], as he must have emerged from the hands of nature, I see an animal*…." Furthermore, by attributing fundamental common characteristics to man and animals on the basis of sensibility, Rousseau made the animal into an object of genuine moral obligation: "*It would seem indeed that if I am obliged to do no harm to my equal, it is less because he is a reasonable being than because he is a sensitive being; and this quality being common to man and beast, it should at least give the latter the right not to be needlessly mistreated by the former*."(Rousseau, 1755). However, Rousseau distinguished sharply between man and beast in terms of intellect: considering only humans capable of free will and self-improvement, Rousseau developed a new concept of "perfectibility"; while representing animal understanding as largely limited to instinctive behaviours. Diderot, following a materialist logic that allowed for perfectibility in all species, pushed the re-evaluation of animal capacities as far as it was possible to go; although at the same time he regarded such capacities as an aspect of each species' bodily organisation (the brain, the sensory organs) and identified language as the defining threshold of the human. Other writers sought to place more emphasis on the idea of a genuine animal intelligence, although their works are less well known, for example, Georges-Charles Leroy (1723-1789). Thus, by the end of the eighteenth century, a decisive shift had taken place in favour of the idea that animals had mental capacities; while in terms of method, answers were increasingly sought at an empirical rather than at a metaphysical level. On balance, however, the record shows some ambivalence. This ambivalence would be extended into the nineteenth century, with a more limited conception of animal consciousness again coming to the forefront. The idea of the transmutation of species, embraced by Maupertuis (1698-1759), Diderot (1713-1784), and Lamarck (1744-1829), reached its full development in the work of Charles Darwin (1809-1882). By suggesting a phylogenetic link connecting all living creatures, these perspectives utterly and decisively modified the scientific basis of consciousness.

1.3.4. Historical perspectives from Lamarck to Griffin: the question of consciousness

1.3.4.1. Jean-Baptiste Monet, chevalier de Lamarck

Lamarck (1744-1829), at the onset of nineteenth century, adopted the evolutionist vision of some of his contemporaries, for example the anatomist G. Cuvier (1769-1832). He hypothesized a continuous relation between species, ranging from the simplest organisms to the most complex along a « *Scala naturae* » of complexity (Lamarck, 1809). In his work on classification, he considered four different degrees of how behaviour is triggered and/or controlled: the need, the instinct, the industry and finally the reasoning. What could be called his « behavioural classification », again along a gradient of complexity, is fundamentally based on the faculty to move or not to move. For Lamarck (1809) whatever the category, the behaviour is initiated by what he called an « irritability ». Lamarck (1809, 1815) then differentiated animals that do not move (« apathetic») which, while being « irritables », do not have any feeling from animals which possess a nervous system- able to move (arthropods)-, and so are sentients. This category of animals have « feelings » while not being aware of what they are doing (Lamarck 1809, 1815). Finally Lamarck distinguished the « most perfect » animals (the vertebrates from fish to mammals) which possess at the « highest degree » the faculties he did not recognized in the « lower groups ». These animals may have an intimate feeling of their existence and may form « *…clear ideas, and compare and combine them…* ».

Therefore Lamarck already envisioned an evolutionary as well as a mental continuity between species. All these attitudes were framed into an increasing complexity which developed over time – the simplest forms being the most « primitive », the most complex ones appearing the latest. Lamarck (1815) recognized that the faculties of movement, feeling and thought are very different and independent from each other. He clearly assumed later that there are differences in the degree in which animals perceived their world, in intelligence and feeling as it can be found in the whole process of nature.

1.3.4.2. Charles Darwin

Within the 19th century momentum of evolutionary ideas, or even before, Darwin endorsed some of Lamarck's ideas about continuous gradation of species and some processes underlying this gradation (Lamarck, 1809). However, Darwin and Wallace clearly formalized the fundamental process of natural selection by which species evolve (see Darwin, 1859). Darwin contended this continuous gradation should apply « to instincts as well as to corporeal structure... » (Darwin, 1859) using, according to Aristotle's terminology, the canon of natural history "*natura non facit saltum*". Darwin pointed out that the behaviours of simple « *very low in the scale of nature* » animals may involve « *judgment or reason*» (Darwin, 1859). He also assessed that human beings may perform many « *habitual actions* » unconsciously while displaying « *conscious will* ». Therefore Darwin contended that precursors of complex control of behaviours already exist in simple organisms and that, in the same way, human behaviours may range from the unconscious as found in lower species to behaviours controlled by conscious will or reason. These assumptions were much more developed in later books by Darwin (1871, 1872). Therefore, this issue was still very present in the framework of Darwin's evolutionary theory even though mental continuity was not the main issue of Darwin's thinking. So, Darwin recognised the gradation in bodily structure changes, but assessed that there were great differences between man and « *all other animals* » as far as « *mental power* » was concerned (Darwin, 1871). The « *interval in mental power* » *between ape and man was much less than that between fishes and apes. However, this interval was still* « *immense* », *and represented* « *an impassable barrier* » and, as Darwin's vision of evolution implies, it « *is filled up by numberless gradations* » (Darwin, 1871). He warned about the « *facade analogy* » between actions performed by lower animals and those performed by higher animals. He referred to actions by lower animals « *having been gained, step by step, through the variability of the mental organs and natural selection without any conscious intelligence* ». On the contrary, actions by higher animals were « *founded on the memory of past events, on foresight, reason, and imagination…*» (Darwin, 1871). In addition, Darwin recalled that it was well established at the end of the 19th century that « *lower animals were excited by the same emotions as us* ». Although man and non-human primates possess «*the same faculties of imitation, attention, memory, imagination, and reason* », they differ in the degree of their development. From this point, Darwin discussed at length what may be the « *mental powers* » specific to man, at least in their highest degree of development. The most important difference was the development of « *the moral sense or conscience* » Darwin (1871) uses very rarely the term « conscience » apparently in synonymy with « moral sense » and apparently uses even more rarely « consciousness ». For him this « conscience » might have been a faculty common to any animals that possessed « *well-marked social instincts* »: a social animal might always take into account a « *fellow* ». The dynamic of social interactions implies that « *images of all past actions and motives would be incessantly passing through the brain of each individual* » (Darwin, 1871). Therefore, as Darwin contended, sociality might be a trait quite favourable for the development of a moral sense that can be equated to some degree to a kind of « consciousness ». As we report above, Darwin maintained that there was a huge gap or « *impassable barrier* » between the mental powers of man and those of even apes, but he insisted that « *the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind* » and, as a consequence, there « *is no justification for placing man in a distinct order.* » (Darwin, 1871)

So Darwin clearly recognized that as far as what he referred to as « *mental powers* », there is both continuity and huge differences in the degree of development while not in kind, between man and « *all other animals* ». After assessing the importance of sociality in the development of « *highest* » mental powers, Darwin tackled the issue of communication which is central to a social life. Darwin wondered « *how far the will and consciousness have come into play in the development of the various movements of expression* » (Darwin, 1872). As already noted for other kinds of behaviours, Darwin assumed that some expressive movements, such as imitation, were « *unconscious* » though others, such as gestures « *employed as a means of communication* », were or became dependent on « *consciousness and will* » (Darwin 1872).

Therefore, from the many works of Darwin, we gleaned that some behaviours, communicative or not, may be performed consciously or unconsciously. These behaviours may be similar in both lower and higher animals. They only differ in the degree of control brought by the degree of development of « *conscience and will* ».

1.3.5. Georges Romanes

Romanes (1883) wrote « Animal Intelligence », 11 years after Darwin's last book, (Expressions of emotions in man an animals, 1872). Romanes placed this large review of behavioural performances in various animals within the framework of Darwin's evolutionary continuity in structures as well as in a framework of « *instincts* ». However, Romanes clearly expressed a hierarchical continuity of living beings because he repeatedly used evaluative terms such as « higher than » or « lower than » when he compared the intelligence of animals. For example, he wrote about fish intelligence: « *Although we here pass into the sub-kingdom of animals the intelligence of which immeasurably surpasses that of the other sub-kingdoms, it is remarkable that these lowest representatives of the higher group are psychologically inferior to some of the higher members of the lower groups (especially ant or bee)»*. Further he wrote « *Passing on to the general intelligence of reptiles, we shall find that this also, although low compared with the intelligence of birds and mammals, is conspicuously higher than that of fish and batrachians*». Further he stated « *The marsupials are as low in the scale of mammalian intelligence as they are in that of mammalian structure; so that, except the above, I have met with no fact connected with the psychology of this group that is worth quoting…* », (Romanes, 1883). This « hierarchical » view evokes the old « *Scala Naturæ* ». Romanes' method is based on anecdotal reports of observations made by himself and others, among them Darwin himself, in which Romanes had confidence, or anecdotes recounted by several other people.

However, Romanes recognized that there is a fundamental difference between man « contemplating » his own mind or that of other organisms. In the case of other organisms « …we can only *infer* the existence and the nature of thoughts and feelings from the activities of the organisms which appear to exhibit them » (Romanes, 1883). He also stated that mind has two fundamental features – consciousness and choice. However, he believed that mind implies consciousness and that choice may be « mindless », i.e. being unconscious, and much behaviours are performed « *without the intervention of consciousness* » (Romanes, 1883). He also recognized that there is a gradient in a requirement for cognitive function, from the reflex which requires no mental process – a so-called « non-mental activity », to instinct that « *involves mental activity*» (Romanes 1883) and finally to « reason ».

Romanes suggests that « *… instinct passes into reason by imperceptible degrees…* ». This process of gradation underpins the comparison between species within the animal kingdom and also within behavioural performances of individuals during ontogeny. However, he did not distinguish clearly between an action that involves consciousness and one that involves no consciousness. Pushing this argument further, Romanes assessed that the knowledge of the means-ends relationship is the critical feature that distinguishes reason [or intelligence] from instinct, as « *instinct is reflex action into which there is imported the element of consciousness* » without that knowledge. Therefore from Romanes' point of view «*no distinct line can be drawn between instinct and reason* » (Romanes, 1883)

The inference of « mind » that Romanes made from the behaviour of animals was based on analogies with human behaviour so within an evolutionary framework of continuity. Therefore, when recounting a second-hand anecdote from Darwin about what is interpreted as a « permanent attachment » between snails (*Helix pomatia*) as well as sympathy and 24-hour memory of direction in snails, Romanes considered that the interpretation went beyond « *that we should have reason to expect of snail intelligence* » (Romanes 1883). The phylogenetic distance between snails and humans, associated with huge differences in organization makes analogy with human behaviour more than suspect. Romanes, in his broad zoological review, systematically explores emotions, memory and « general intelligence » in the different orders or species. Under the heading « emotions », Romanes talked about what is often referred to as « feelings » or other terms such as affection, sympathy (« fellow-feeling »), pugnacity, anger, jealousy, curiosity, pride, vindictiveness, sense of injustice, sense of dignity, « sense of ludicrous », self-esteem, self-respect.

Examples of « intelligent behaviours », for which Romanes did not state whether they were conscious or not, but which were like analogous behaviours in man, were drawn from orientation behaviours. That included homing – « *…actions …of a nature unquestionably intelligent*» (Romanes1883), recognition – which implies also memory, self-recognition, discrimination, imitation. Other examples were drawn from social behaviours which imply communication. Romanes especially mentions « *intentional concealment of wrong-doing* », and deception, which are examples of social strategies - « manipulations » of other's understanding. As a consequence, retaliation and revenge is a prominent feature of social behaviour in monkeys. Considering that Romanes' methodology was to report anecdotes, it is not surprising that, as far as mammals are considered, the richest examples were drawn from domestic animals, especially dogs. The « natural intelligence » of these animals has « *greatly changed, by persistent contact with man coupled with training and breeding* » (Romanes 1883).

Incidentally, Romanes reported that « intelligence » is a feature of animals that moved, which is reminiscent of Lamarck‘s distinction. Though Romanes was impressed by the performances of insects, especially ants and bees (210 pages out of 498, Romanes, 1883), he mentioned that « *truly intelligent actions* » are individual « *adaptive movements to meet the exigencies of novel and peculiar circumstances*», contrasting with all individuals of a species reacting behaviourally to a common stimulus. Consequently intelligence emerges from an ability to learn by experience.

Romanes' anthropomorphic stance, which he himself called « analogy », leads to many contradictory statements. For example, as fish are concerned, Romanes dared assessing "*I have not evidence of sympathy […] but sympathy may nevertheless be present*". In addition, it is difficult to discern from his work which behaviours in animals have the greatest chance of involving « consciousness » at least some of the times. Even more so, Romanes assessed that even in humans some behaviours that appear to be intentional might be expressed without the « *intervention of consciousness* ».

1.3.6. Conwy Lloyd Morgan

In contrast to his contemporary Romanes, Morgan (1852-1936), being well aware of his colleague's work, based his approach to understanding behaviour in animals on systematic investigations and experiments (Morgan, 1898). Morgan thus looked for evidence, whereas Romanes stated concerning emotions in fish for example: « *… I have not evidence of sympathy […] but sympathy may nevertheless be present.* » (Romanes, 1883). In his book Morgan (1898) made consciousness a central theme. Like Romanes, he considered that it was not necessary to define consciousness in humans as all humans experience it, but he assumed that « *in man and mammal the brain, or some part of it, is the specialized seat of consciousness.* » (Morgan, 1898). Morgan considered consciousness to be a « *wave* » that dealt with representations of both past and future events occurring at the same time as a present moment of consciousness. Morgan speculated that consciousness was the result of the highest level of « *disturbances in cerebral hemispheres* ». As a consequence, he postulated other forms of consciousness that would be too low to reach the threshold of consciousness in the cerebral hemispheres. He named these lower levels « *unconscious consciousness* » (Morgan, 1898). Though all humans only experience their own states of consciousness, they may easily infer similar states of consciousness in their human neighbours based on a similarity of « mind ». It is obvious that this operation is not possible when one investigates « *other minds than ours* ». In obvious contrast to Romanes' use of anecdotes only, and then most often only second- or third-hand ones, Morgan set the bases of an experimental way of establishing the kind of consciousness that animals may experience. Morgan considered that Romanes' anthropomorphic interpretations may be acceptable for the practical needs for humans who deal with animals. However, those humans who wanted to compare psychical lives in man and animals, in this case confined to birds and mammals, should use scientific methods.

The results of these investigations might lead to opting for the most relevant level to control the performance of an animal instead of always choosing a level identical to that subjectively experienced by humans. Morgan himself called this proposal a « canon » to which he was especially attached as he repeated it thrice throughout his *Introduction to comparative psychology* (Morgan, 1898). For Morgan, consciousness was present in all animal species as a consequence of « accepting evolution » so that « *the community of nervous mechanism and its physiological functioning* » yielded to a « *community of psychical nature and psychological functioning* ». However, the role of consciousness in controlling animal actions and/or choices varies greatly. In the lowest organisms, Morgan considered that actions are controlled by reflexes – « *consciousness as mere spectator* », while, especially in higher vertebrates, actions may be entirely controlled by conscious processes. Morgan differentiates « *sense-experience* », which he also calls « *consentience* », where consciousness is expressed through trial-and-error learning processes, to a truly conscious process which allows perception of cause-effect relations or other kinds of relations between objects or, more precisely, between representations of objects. These highest levels of control of consciousness allow conceptual thought or « reasoning » that Morgan considered to be rare with a very low probability of it existing in animals. Though Morgan noticed that, in human thought for example, self-consciousness is just one feature and it is not always used to guide human action. In that case, humans may be « *nearest the condition of the animal at the stage of mere sense-experience* ».

To Morgan, the question was not « *does consciousness in animals exists?* » but « *How did it come to exist?* ». He answered that question by assuming that consciousness evolved from « *infra consciousness.* » (Fig. 5).

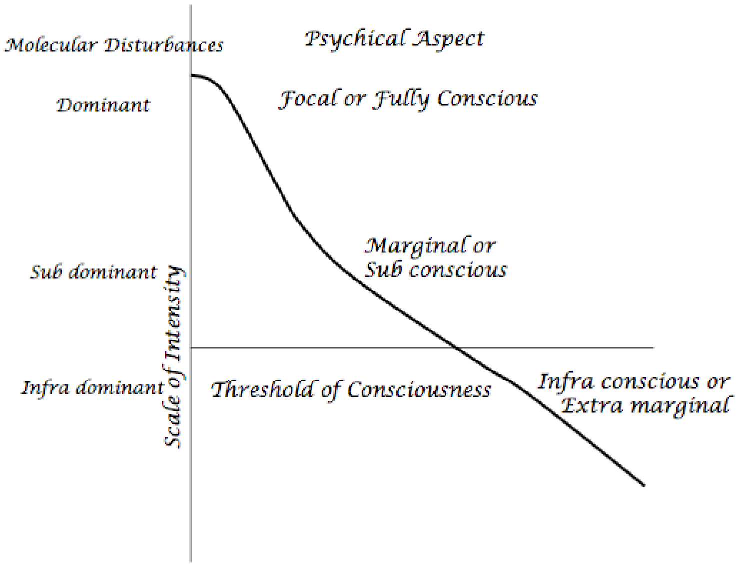

Fig. 5. The different levels of consciousness: According to Morgan, states of consciousness are induced by molecular disturbances of different intensities in the nervous system. The different intensities of molecular disturbances induce different levels of consciousness. (*modified from Morgan, 1898*)

Morgan considered continuity in mental evolution and distinguished three levels of « *consciousness* » in different species along the path of evolution: i) « *mere sentience* », ii) « *consentience* », which he also called « *sense-experience* », and iii) « *reflection* ». Morgan then suggested that there are breaches in that continuity between these three levels.

Morgan contended that only an experimental approach would allow us to determine different levels of « consciousness » which may be a universal property of nervous systems. He defended Darwin's concept of continuity in mental capacities throughout evolution, but he could not avoid considering some discontinuities based on the way behavioural actions were controlled. Morgan set the border between man and « animals » (in his case, birds and mammals) at perception of relations and conceptual thought which animals do not have. Modern research into comparative psychology and cognitive ethology prove Morgan's « border » theory to be wrong. As a result, animals appear to have higher levels of consciousness than Morgan assumed.

1.3.7. Donald Redfield Griffin

The American ethologist, Griffin (1915-2003), studied animal behaviour, especially orientation behaviour. Griffin was impressed by the complexities of animal behaviour. In 1976, he stated that ethologists and comparative psychologists and biologists involved in the study of animal behaviour had unravelled behaviours of increasing complexities, even since Romanes, Morgan and others (Griffin, 1976). On the one hand, in line with Thorndike's (1874-1949) work (Thorndike, 1898), Skinner (1901-1990) contended that there was a relationship between a stimulus (**S**) and a behavioural response (**R**). The association between **S** and **R** is set and maintained when a particular stimulus gives a rewarding response. On the other hand, Tinbergen (1907-988) and Lorenz (1903-1988) designated ethology as the biology of behaviour analysed in species especially in their natural world, maintaining the adaptive aspects of behaviours in an evolutionary framework. Griffin identified particular domains where significant progresses had been made. These domains were related to the evolutionary continuity of cognitive functions controlling behaviours in man and animals. Griffin (1976) talked of social organization, individual recognition, altruistic behaviour, biological clocks and navigation. In so doing, he assumed that ethology had ignored questions that he believed were fundamental, particularly mental experiences, mind, awareness and intention. All these terms actually referred to « *objects or* *events that are remote in time and space from the immediate flux of sensations* » (Griffin, 1976). Consequently, he tentatively defined awareness as « *the whole set of interrelated mental images of the flow of events* » (Griffin, 1976). These mental images that are used to control behaviour provided a provisional definition of consciousness. The distinction that Griffin made between awareness and consciousness seems to be a question of control. Consciousness was what guided actions of animals and awareness seemed to be a prerequisite of mind leading to « thought », « free will », and, ultimately, « consciousness » (Griffin, 1976).

Griffin's definition of consciousness is reminiscent of that of Morgan, which was discussed previously. Griffin argues against denying mental experiences to animals because it is not possible to show their reality. He points out that this is also the case for human mental experiences. The only difference as Morgan suggested, is that by introspection, we are aware of our own consciousness. However, being aware of our subjective consciousness, we humans have only indirect evidence of other humans' consciousness. This is another argument for not denying *a priori* that animals have consciousness. Because mental experiences might be linked to neurophysiological processes, and considering the evolutionary continuity of these processes, it would be difficult to assume a difference in nature between animal and human consciousness. Comparative neurophysiology might provide the best evidence of consciousness in both humans and non-humans. However, « *it certainly is not necessary to assume that [] mental experiences are at all similar to those which a person [human] might have under analogous circumstances* » (Griffin, 1976). Awareness is based on mental images, so we can compare them with stored images to recognize and/or to categorize many objects in the external world. Griffin considered being too simple to assume that these complex processes are based on « conscious awareness » rather than postulating complex chains of other kinds of processes. This approach might have revealed an adaptive aspect of consciousness that had been selected for along evolution in many species.

For Griffin, animal communication was a field in which what was observed made the « *denial of mental experiences to animals [] become an act of faith* » (Griffin, 1976). Griffin raised the paradox of ethologists creating the term « intention movement » while at the same time, not considering that these movements are controlled by «conscious intention». He also pointed out a circularity in arguments: « *conscious intention is ruled out a priori and then its absence taken as evidence that animal communication is fundamentally different from human language* » (Griffin, 1976). To explore levels of consciousness or « *conscious awareness* » in animals and compare it with humans, communicative processes might be a primary target because language, in all its features, could be considered a uniquely human adaptation (as brachiation is for lesser apes' locomotion). Communication has its greatest development in social species because social organization is based on interactions involving recurrent dialogs and negotiations, so Griffin suggested that animal communication might be a domain in which to explore intentional behaviours and other processes that could be under conscious control.

Griffin's suggestions extend those of Morgan, although Griffin puts more emphasis on neurophysiological studies to assess conscious processes more objectively in many animals, including humans. However, Morgan had already postulated the material aspect of consciousness in neural function. These assumptions provided guides to research to be performed or arguments to be polished in favour of a widespread consciousness which would differ with the characteristics of the different "Umwelts" (German word meaning: world as subjectively perceived) of the species and other specific adaptations – such as language.

1.4. Contemporary philosophical considerations

1.4.1. The subjectivity of consciousness

Perceptions are subjective experiences: it "*feels like something*" to see a rose, and this feeling is qualitatively different from touching or smelling it, or from seeing an orchid. The term '*qualia*' (singular '*quale*') is nowadays often used to refer to the introspectively accessible aspects of our mental lives. The term "phenomenal experience" is used to refer to the first person subjective experience of the surrounding world or of one's body. Phenomenal experiences are indescribable, in the sense that one can only share a subset of the myriad of details one consciously perceives and most others remain unreported (Block, 1995). In a famous experiment on thought, Nagel (1974) proposed that subjective experiences are not expressible in objective terms: understanding the principles governing echolocation does not tell us what is it like to have the sonar capabilities of bats.

Our mental life is essentially private because we alone have access to it, but our physical bodies are publicly observable. This perception of a non-physical mind in a physical body gave rise to dualism (Descartes, 1641 see § 1.2.2). How mind and body do interact remains a topic of heated debate. Alternative ideas suggest that mental and physical events are not connected (see Box 2). Later, monism took over dualism, arguing that the physical and mental worlds are made of one unique substance. One version of monism, idealism, affirms that only the mental substances exist, leading to the view that there is no universe beyond the mental realm. This stance is generally considered a dead end for scientific investigations (Grim, 2008). Another form of monism is materialism, the position that conscious experiences directly result from specific brain activity patterns (Damasio, 2006; Dennett, 1991). This is the view we will take up later in this review, as it remains the only one that treats consciousness as a scientifically tractable issue.

1.4.2. Current philosophical views

Nowadays, most philosophers and neurobiologists adopt materialist accounts of consciousness, assuming that subjective conscious experiences have a material substrate, usually a specific level of the architecture of the brain (see, e.g., Churchland, 1995; Damasio, 2006; Dennett, 1991 for influential accounts). Some particular cognitive functions, like other biological phenomena are easily interpretable in terms of cellular or systemic mechanisms. For instance, there is no debate about the role of neurons for visual recognition or motor execution. Yet, how neurons, or groups of neurons, give rise to phenomenology is less evident. The philosopher David Chalmers highlighted this issue by studying consciousness as two distinct problems. The first problem was to decipher the mechanisms responsible for the brain’s capacity to process information and produce appropriate actions. Chalmers considered this as the *easy* problem of consciousness because even though it encompassed the whole field of cognition, it did not constitute an insurmountable scientific obstacle. By contrast, the second problem, the study of subjective experiences, he considered to be *hard*. It involved understanding how neural processing was accompanied by *qualia*, the phenomenal aspects of our mental lives. In other words, the hard problem boiled down to determining why the complex behaviours considered under the easy problem would not exist in the absence of *qualia*. Chalmers used the example of philosophical zombies, hypothetical agents behaving exactly like conscious humans but with no *qualia* as an argument that the hard problem is beyond the scope of science (see Box 1 below).

Another influential distinction exists between access and phenomenal consciousness (Block, 1995). Access consciousness is akin to the easy problem of consciousness and includes all information processing functions used to control perception, reasoning and behaviour in general. Beyond that, Block (1995) referred to phenomenal consciousness as an experiential form of consciousness, the feeling of “what it is like”. Even today, it is not clear whether phenomenal or access consciousness have any functional role for information processing, as a myriad of cognitive processes occur despite unawareness (see section 2.2.2). These different concepts have stirred debates among philosophers and scientists, but they have not (yet) reached a consensus when it comes to encompass the whole issue of consciousness. In the following sections, we focus on access consciousness and adopt a working hypothesis according to which nothing will be left unexplained once all aspects of the easy problem of consciousness are resolved.

Box 1. What is it like to be a zombie?

"No explanation given in wholly physical terms can ever account for the emergence of conscious experience. How can we argue that consciousness is not logically incidental to the physical? There are various ways. The most obvious way (although not the only way) to investigate the logical incidental dependence of consciousness is to consider the logical possibility of a *zombie:* someone or something physically identical to me (or to any conscious being), but lacking all conscious experiences. At the global level, we can consider the logical possibility of a *zombie world:* a world physically identical to ours, but in which there are no conscious experiences at all. In such a world, everybody is a zombie. So let us consider my zombie twin. This creature is molecule for molecule identical to me, and identical in all the low-level properties postulated by a completed physical being, but lacks conscious experience entirely. To fix ideas, we can imagine that right now I am gazing out the window, experiencing some pleasant green sensations from the sight of the trees outside, having pleasant taste experiences through munching on a chocolate bar, and feeling a dull aching sensation in my right shoulder. What is going on in my zombie twin? He is physically identical to me, and we may as well suppose that he is embedded in an identical environment. He will certainly be identical to me *functionally:* he will be processing the same sort of information, reacting in a similar way to inputs, with his internal configurations being modified appropriately resulting in indistinguishable behaviour. He will be *psychologically* identical to me [ ]. He will perceive the trees outside, in the functional sense, and taste the chocolate, in the psychological sense. All of this follows logically from the fact that he is physically identical to me, by virtue of the functional analyses of psychological notions. He will even be "conscious" in the functional senses described earlier — he will be awake, able to report the contents of his internal states, able to focus attention in various places, and so on. It is just that none of this functioning will be accompanied by any real conscious experience. There will be no phenomenal feel. There is nothing it is like to be a zombie." (Chalmers, 1996).

1.4.3. Other contemporary philosophical notions of consciousness

Consciousness, along with the so-called mind-body issue, has been called "the hard problem" in the philosophy of mind (Chalmers, 1996). Defining consciousness — in a philosophically interesting and empirically operationalized sense — is challenging insofar as it involves both philosophical and scientific questions. What is consciousness, what is it like to be conscious, which animals experience consciousness? These questions can only be answered by drawing from many empirical sciences and techniques — neuro-imagery, neurophysiology, comparative, cognitive and developmental psychology, cognitive ethology, animal behaviour and animal welfare science. These questions arise across a wide taxonomic range of animals. They also require philosophical investigation into the epistemological, metaphysical and phenomenological aspects of consciousness. In contemporary philosophical discussions, consciousness raises at least three sorts of issues:

- First, there is a **definitional** problem. What is consciousness? What are its features? How is it related to the body, the brain, and the environment including conspecifics?
- Second, and relatedly, there is a problem of **scope.** What are the criteria for consciousness, and which animals meet them? This problem is compounded by an additional epistemological problem: how can we learn about consciousness in other minds, especially across species and across developmental stages within a same species?
- Third, there is a problem of **variety**. What are the forms and/or degrees of consciousness?

Philosophical disagreement about these issues involves larger issues about the so-called mind-body problem (i.e., relationships between physical and psychological states), as well as, more specifically, relationships between the brain and mental states.

Few contemporary philosophers deny that animals can be conscious, but most disagree as to exactly what forms, or degrees, of consciousness are open to them (e.g., self-awareness, autonoetic consciousness, i.e. 'mental time travel', metacognition, theory of mind). Still, there are exceptions. Dennett (1991, 1995) argues that consciousness is unique to humans, although many other organisms are minded or intentional to some degree. Dennett defends a form of anti-realism about consciousness. On his instrumentalist view, "*the very idea of there being a dividing line between those creatures 'it is like something to be' and those that are 'mere automata' (is) an artifact of our traditional assumptions.*" (Dennett, 1995). Mental properties are usually attributed to animals from the "intentional stance," primarily as it suits our predictive/explanatory purposes rather than as a way to describe reality. But insofar as many organisms can be described as intentional systems without sophisticated forms of consciousness, there is no reason to presume that other animals are conscious like we are. Consciousness, Dennett argues, is a sort of "fiction" (1991) or "user illusion" (1995). It is constructed through people's narrative descriptions: "What there is, really, is just various events of content-fixation occurring in various places at various times in the brain" but there is no "actual phenomenology" (1991). In other words, Dennett argues, against Nagel, Chalmers, and Block, among others, that there is no such thing as phenomenal consciousness, or an irreducibly *subjective* aspect of experience. Because consciousness is storytelling, which requires language, only linguistically competent beings (i.e., some verbal humans) might be conscious.

Carruthers (2000; 2005) also denies that animals have consciousness based on a 'higher-order thought' (HOT) theory, according to which, phenomenal consciousness requires the capacity to think about one's own thoughts. Such thoughts require, on his view, a theory of mind. And since, he claims, we lack evidence that animals have a theory of mind, except for perhaps chimpanzees (see Lurz, 2011 and Andrews, 2012, for detailed reviews), few animals are conscious by Carruthers' definition. But of course this denial of consciousness is no more compelling than the HOT theory of consciousness, which few philosophers consider plausible.

HOT theories can be contrasted with 'first-order representations' (FOR) theories, which are friendlier to attributions of consciousness to animals, insofar as it is uncontroversial that animals have first-order states with the requisite representational properties (e.g., Dretske 1995; Tye 2000). FOR theories make phenomenal consciousness inseparable from the capacity to perceive and respond to features of one's environment. On such accounts, consciousness even extends to invertebrates, including many social insects, which arguably have representational states.

Common sense seems to assume that animals are conscious in that consciousness lets them know about relevant features or events of the environment, or relevant bodily states. HOT theories of consciousness make sense of the claim that animals may be "conscious" in some loose sense without being technically conscious (i.e., phenomenally or reflectively). While animals are no doubt "conscious" in the sense of mere awareness (i.e., detection and sensation) of environmental or bodily features or events, this common sense view tells us nothing about genuine consciousness in nonhumans. Nevertheless, it is now widely accepted that a wide range of animals are conscious despite they do not meet the demanding criteria of human-like cognitive sophistication.

- ***Consciousness*** is indeed often used in the ordinary sense of being awake rather than asleep, or in a coma. Another ordinary sense of consciousness refers to the basic ability of an organism to perceive and respond to specific features of their environments — commonly referred to as "awareness". Both of these senses are attributable to most animals across a wide range of taxa, but they are not the sort of consciousness — '*conscious* awareness' — that matters here. Philosophers have identified more technical concepts of consciousness to pick out different functions or aspects that perhaps not all animals share and which fulfil distinct roles in an animal's life. Three main notions of consciousness are usually identified. There are potentially more different senses of consciousness, but given their overlap, interrelations, and the widespread philosophical discussions of the three meanings discussed below, we have decided to narrow down the pool of candidates.

- ***Access consciousness***, introduced by Block (1995), refers to mental representations cognitively available for use in rational control of action or speech. A given (e.g. visual) state is conscious when it is available to interact with other states and its content is accessible. Consciousness is here defined by its *functional* role in cognitive life. Block believes that many animals possess access consciousness (since language is not a requirement). This *functional* sense of consciousness is different from the *qualitative* aspect of other conscious states, which we describe below ("*what it is like*"). The *functional* sense refers more specifically to whether or not it and the visual information that it carries is generally available for processing by the subject. In so far as the information in a state of consciousness is richly and flexibly available to the organism in which it emerges, then it counts as a conscious state in the relevant respect, whether or not it has any qualitative or phenomenal feel in Nagel's (1979) sense of "*what it is like to be……*"

- ***Phenomenal consciousness*** refers to the qualitative, subjective, or phenomenological aspects of conscious experience, sometimes identified with *qualia* (experiences such as colours, tastes, noises and other sensations with their own distinctive character). Godfrey-Smith (2016) uses the phrase "*subjective experience*" more broadly than consciousness. A system undergoes subjective experience when there is something it feels like to be that system, and the mental states that are subjectively experienced have qualitative features. Consciousness, on the other hand, is more than just subjective experience, something more sophisticated and more recent in the evolution of animal life. So, some creatures might be sentient (in the sense of having subjective experience) without being conscious in that sense. The two processes may in fact come apart. Godfrey-Smith cites Dehaene's survey of divergences between complex cognitive processing and subjective experience (Dehaene, 2014). Much of our sensing and thinking is done in a way that feels like nothing at all. On this view, what we are conscious of is information made available in a "global workspace" (see 2.3.1) that integrates information from various sources through memory, attention, and executive control.

On this widely shared understanding, conscious animals are also *sentient* (see next paragraph). Varner (2012) writes, "*Phenomenal consciousness is simultaneously extremely important and deeply mysterious […] — mysterious because it is so hard to define and characterize clearly*". Therefore, subjective consciousness cannot be directly observed in others, although each of us can directly experience our own phenomenally conscious states. "*At the same time (…consciousness is…) important, because we each value our own lives in large measure as a function of the positive (and negative) phenomenally conscious experiences they contain.*" (Varner 2012).

- ***Sentient*** is derived from the Latin present participle *sentient-em* (from *sentire*), which means "to feel." Etymologically therefore, it means "*conscious of something*", but in animal ethics the term is used to refer to the ability to feel pain or pleasure, or the "*capacity to suffer and/or experience enjoyment*" (Singer 1990). Suffering and pain are not equivalent, though (see e.g., psychological suffering; enjoyable pain; pain experienced without the feeling of suffering; or suffering of patients with congenital insensitivity to pain). DeGrazia defines "*suffering*" as "*a highly unpleasant emotional state associated with more-than-minimal pain or distress*" and "pain" as "*an unpleasant or aversive sensory experience typically associated with actual or potential tissue damage*" (DeGrazia, 1996).

Varner (2012) construes "pleasure" as including all "pleasant" states of mind, from those associated with physical pleasures arising from drinking, eating and sex to those associated for instance with intellectual endeavours or a sense of accomplishment, "*in summary sentience refers to the capacity for phenomenally conscious suffering and/or enjoyment.*"

Sentience for Nagel (1979) roughly corresponds to subjective experience, i.e., there is something it feels like to be that animal. The existential question of *whether* animals are conscious in this sense or another is distinct from the experiential question of *what it is like* to be them. He never questioned the fact that many animals were conscious, as hard as it is to imagine the subjective, qualitative side of that datum. As human beings are homologous in terms of physiology and behaviour, they can compare detailed introspective descriptions of experience of others. This allows to draw analogies between our behaviours so as to draw inferences about their consciousness. Without a common language with animals, we cannot compare our descriptions with self-reports they could give us. We are thus restricted to drawing analogies based on behaviour, physiology and phylogeny, which arguably is a rather weak form of argument. Allen and Bekoff (1997) refer to this issue as "*the other species of mind problem*" but Sober's (2000) proposes an evolutionary parsimony approach as a solution to the attribution of mental properties across species.

With respect to pain in particular, the problem translates into one of finding evidence for the *experience* of pain, as opposed to *physiological* substrates for nociception (damage detection) and *behavioural* adaptive responses to it, since the responses can occur without pain being experienced. Moreover, organisms shown to be capable of complex learning and problem-solving are not necessarily sentient, since one can occur without the other. But it is likely and plausible that at least some forms of learning and problem-solving are closely linked to (or even require) consciousness. Evidence of conscious pain is usually associated with *flexible*, *adaptive* responses to damaging stimuli: e.g., seeking analgesics when, and only when, tissues are damaged; protection or nursing of injuries; learned avoidance of painful stimuli.

- ***Self-consciousness*** (or ***self-awareness***), is the third technical notion of consciousness after access and phenomenal consciousness, it is usually meant to capture an organism's capacity for second-order representation of its own mental states. Because of its higher order character, this capacity is often tied to the possession of a theory of mind (see chapters 3, etc…). The notion of self-consciousness usually encompasses several distinct abilities, including self-recognition, episodic memory, metacognition, and mindreading (implicit, for instance, in deception, imitation and complex social understanding). These abilities may not be in a bundle but rather distributed separately in some species.

DeGrazia (2009) distinguishes three forms of self-awareness: bodily, introspective, and social, and he argues that some animals may be self-aware in the bodily sense but not introspectively or socially. So even if self-awareness in some sense requires sophisticated underlying cognitive capacities, it might still be possible that animals lacking concepts, language and higher-order thoughts are self-aware in some other sense.

> ***(i) Bodily self-awareness*** is "*an awareness of one's own body being substantially different from the rest of the environment – as directly connected with certain feelings and subject to one's direct control*." DeGrazia suggests that the range of bodily self-aware animals may include all sentient animals, or those that have the capacity to feel pain and pleasure, desires, intentions, and emotions, such as fear.
>
> ***(ii) Social self-awareness*** is "*awareness of oneself as part of a social unit with differing expectations attaching to different positions*", "*is present in highly social creatures*", and "*presupposes bodily self-awareness since deliberate social navigation is possible only in creatures aware of their own agency*".
>
> ***(iii) Introspective awareness*** is "*awareness of at least part of one's own mental states such as feelings, desires, and beliefs*", and is probably not exclusive to language-users. The "*mental reflexivity*" of such awareness might require "*the conceptual rocket of language*", but it is also plausible that bodily self-awareness may implicate a basic sort of introspective awareness "*insofar as bodily self-awareness rests partly on having various sensations, and noting their connection with one's body*." (DeGrazia, 2009).

These three notions of consciousness (access, phenomenal, and self) are distinct and fulfil distinct functions in an organism's mental life and in the regulation of its behaviour. Because they are distinct, it is not surprising that some animals do not possess all three sorts of consciousness.

With respect to animal welfare, we suggest in Chapter 5 that phenomenal consciousness is what matters most in how we treat animals.

1.5. How Consciousness is defined or not defined

1.5.1. How to define consciousness?

The word consciousness is derived from the Latin word *conscientia*, or earlier, *cum-scire*, indicating "with knowledge". It could be used with different meanings; to indicate the experience of having done something wrong (e.g., Cicero, 52 BC) and to indicate the experience of self that is not immediately given but is reconstructed in recollection, recapitulation, and memory (Cassin *et al*., 2014). Today, many dictionaries provide a range of definitions for consciousness including terms of being awake, awareness, understanding, thinking and knowledge (Table 2). Defining consciousness in terms of "being aware of" may seem circular, because often, the terms consciousness and awareness are used interchangeably. In fact, these same dictionaries define "aware" in the same terms as they use to define "conscious": knowing, understanding, feeling, experiencing, noticing, perceiving, discerning or being informed.

Consciousness	Awareness
Merriam Webster[1] (*www.merriam-webster.com/dictionary)*	
The state of being awake and able to understand what is happening around you	Knowing that something (such as a situation, condition, or problem) exists
The upper level of mental life of which the person is aware as contrasted with unconscious processes	Feeling, experiencing, or noticing something (such as a sound, sensation, or emotion)
A person's mind and thoughts	Knowing and understanding a lot about what is happening in the world or around you
The state of being characterised by sensation, emotion, volition, and thought	
Cambridge dictionaries online[1] (*dictionary.cambridge.org/fr/dictionnaire/anglais/)*	
The state of understanding and realizing something	Knowing that something exists, or having knowledge or experience of a particular thing:
The state of being awake, thinking, and knowing what is happening around you	Having special interest in or experience of something and so knowing what is happening in that subject at the present time:
Oxford dictionaries[1] (*www.oxforddictionaries.com/fr/definition/anglais/)*	
The state of being aware of and responsive to one's surroundings	Having knowledge or perception of a situation or fact
A person's awareness or perception of something	Concerned and well informed about a particular situation or development
The fact of awareness by the mind of itself and the world	
The free dictionary[2] (*www.thefreedictionary.com)*	
Full activity of the mind and senses, as in waking life	Having knowledge or discernment of something
The mind or the mental faculties, characterized by thought, feelings, and volition	Attentive and well informed
Awareness of something for what it is; internal knowledge	
The mental activity of which a person is aware contrasted with unconscious thought.	

Table 2.: Definitions relative to "consciousness" and "awareness" provided by various online dictionaries

1. British English, 2. Type of English not specified

These dictionaries refer to two aspects of consciousness, sometimes within the same definition: the **level** of consciousness and the **content** of consciousness. The level of consciousness refers to the level of vigilance, or arousal, or of being wakeful. The content of consciousness refers to the conscious perception of internal and external sensory information, of thought, or decisions, or metacognition. They are related as rich contents of consciousness are usually observed during wakefulness, except for dreams and specific neurological disorders (see Chapter 2).

Most scientists reflecting on consciousness refer to the content of consciousness. They not only aim to define it, but also to understand how and why it appears and how it functions. They develop the ideas and hypotheses on consciousness in much more details than a simple definition in a dictionary, but their vision is compatible with many of the terms found in Table 2.

For example, the terms “mind” and “knowledge” are used by Damasio (2010): “*Consciousness is a state of mind in which there is knowledge of one’s own existence and of the existence of surroundings. Consciousness is a state of mind — if there is no mind there is no consciousness; consciousness is a particular state of mind, enriched by a sense of the particular organism in which a mind is operating; and the state of mind includes knowledge to the effect that the said existence is situated, that there are objects and events surrounding it.”*

Damasio distinguishes three stages of consciousness:

- The first stage is the establishment of the **protoself**, the most basic level of consciousness marked by a collection of neural patterns that are representative of the body's internal state and allow homeostasis to be maintained (Damasio, 2010). The *protoself* is not a traditional sense of self. Rather, it is a pre-conscious state containing a coherent collection of neural patterns, gathering of images that describe relatively stable aspects of the body and generate spontaneous feelings of the living body that map moment-by-moment the state of the physical structure of the organism (Damasio, 1999, 2010).

- The second stage is the **core self**. It results from the relationship established between the organism (as represented by the *protoself*) and any part of the brain that represents an object-to-be-known. The *core self* is associated with the feeling of knowing and attributing attention to one particularly object rather than others. These processes lead to the engagement of the body relative to the object that caused these changes in the body, the creating of the feeling of knowledge and of salience of the object (Damasio, 2010).

- The third stage is the **autobiographical self**, which gives us our sense of person and identity. The *autobiographical self* is built on the *protoself* and the *core self*, as well as from memory. It allows moving beyond the here and now and may activate language centres of the brain. Damasio (2010) concludes: “*Consciousness is a state of mind with a self process added to it*.”

Like Damasio, Tononi and Laureys (2009) see also simple or basic representations as the building stones for consciousness. The most basic form, which they describe as the feeling of ownership, is close to the *protoself* of Damasio (Damasio, 2010). It is based on the representations that the brain has of the body, which are not necessarily perceived consciously, but they lead to the experience of ownership (“*this is me*”). At a higher level, there is the feeling of agency, the experience that one is the source of one’s actions (“*it is I doing this*”). The experience of agency is not necessary for consciousness. Finally, the narrative *autobiographical self* is the self that characterises in a fundamental way who we are. It may be present without any specific input; it is present for example when awakening, before a person is totally reconnected to the inputs from the surroundings (Tononi and Laureys, 2009).

Tononi (2004; 2012) defines consciousness as the capacity of a system to integrate information: “*The integration of information in conscious experience is evident phenomenologically: when you consciously ‘see’ a certain image, that image is experienced as an integrated whole and cannot be subdivided into component images that are experienced independently. For example, no matter how hard you try, you cannot experience colours independent of shapes, or the left half of the visual field of view independently of the right half. And indeed, the only way to do so is to split the brain physically in two to prevent information integration between the two hemispheres.”* (Tononi, 2004).

The resulting experience has additional value; it is specific and unique, because the integration process confers a new informational content to it with respect to all the subsets of elements that were combined. Tononi indicates that how the brain works is fundamentally different from how, for example, a digital camera works. Each of the sensors of a camera captures bits of information independently and the final picture combines all the information cleverly, using smart software. The camera does not have consciousness, however, because each element of information remains independent of the other, and no information can be integrated among them (Tononi, 2004). The final content of the information of the picture is not greater than the sum of the separate initial elements, because there is no conscious processing in the camera. The degree of connectivity between brain structures is important for the integrated output. Too low a connectivity decreases the amount of integrated information because of the lack of shared information. But a very high connectivity lowers it also, because the elements lose specificity, resulting in less effective information being generated. This aspect of the theory explains why certain brain networks (e.g., the cortico-thalamic network) have the capacity to generate high levels of integrated information, while other brain structures (e.g., the cerebellum or basal ganglia) do not (Tononi, 2004).

Dehaene and Changeux (2011) define the content of consciousness as a piece of information subjected to conscious access and/or conscious processing. They indicate that: *"At any given moment, only a limited amount of information is consciously accessed and defines the current conscious content, which is reportable verbally or by an intended gesture. At the same time, many other processing streams co-occur but remain non-conscious"*). According to them, when a piece of information is conscious, it is treated at a high level in the brain, that is, by widespread interconnected areas involved in perceptual, motor, attentional, mnesic and value processes. In these interconnected areas, information is broadly shared and broadcast back to lower-level processors, allowing conscious processing or access. The processes leading to consciousness involve the amplification of brain signals that treat sensory information, followed by synchronised activation of related cortical areas leading to widespread ignition of cortical areas involved in consciousness (Dehaene and Changeux, 2011).

Lamme (2010) considered also that synchronised and recurrent (back and forth between brain areas) activities are central to conscious processing. He indicated however, in contrast to Dehaene and colleagues that the hallmark of consciousness is more than the "*cognitive access to the information, and the ability to cognitively manipulate that information, and combine it with information stored in working or long-term memory, or with inputs from other senses* ", because consciousness also includes phenomenological aspects. Lamme focused on processing of visual information and identified four stages of processing. The first is a superficial fast feedforward sweep, within the visual cortex. The second is a fast feedforward sweep reaching relevant additional cortical areas (e.g., those related to motor responses and decision making). The third stage is superficial recurrent processing and the fourth is widespread recurrent processing. These two latter stages reach much higher levels of integration than the earlier stages. The fourth stage is equivalent with a conscious experience that is attended to. The early stages may allow short-lived, conscious visual experiences that are quickly overwritten by other experiences and thus, forgotten and unreportable.

Thus, Damasio (2010) and Lamme (2010) described the attribution of attention to certain objects or events as part of the construction of a lasting conscious experience, but the German philosopher Thomas Metzinger considered that the attribution of attention is the central role of consciousness: "… *in essence, consciousness is the space of attentional agency: Conscious information is exactly that set of information currently active in our brains to which we can deliberately direct our high-level attention. Low-level attention is automatic and can be triggered by entirely unconscious events. For a perception to be conscious does not mean you deliberately access it with the help of your attentional mechanisms. On the contrary: most things we're aware of are on the fringe of our consciousness and not in its focus. But whatever is available for deliberately directed attention is what is consciously experienced.*"(Metzinger, 2009).

Dennett (1991) indirectly addressed the question of attention, when he indicates that consciousness allows us to identify things "that matter": "*So the conscious mind is not just the place where the witnessed colours and smells are, and not just the thinking thing. It is where the appreciating happens. It is the ultimate arbiter of why anything matters. Perhaps this even follows somehow from the fact that the conscious mind is also supposed to be the source of our intentional actions. It stands to reason — doesn't it? — that if doing things that matter depends on consciousness, mattering (enjoying, appreciating, suffering, caring) should depend on consciousness as well*". Here, he referred to the fact that what distinguishes a human from a machine, even a very cleverly built machine, is that humans are able to appreciate things and to make decisions. A machine would merely be able to yield "*at best the illusion or simulacrum of appreciation*".

Graziano (2013) made a distinction according to the degree with which someone can be conscious of information (he is using the term "aware" for the specific act of experiencing and consciousness as a more general term referring to the whole personal experience at any moment, the information about which I am aware and to the process of being aware of it.): "*The first component is the information about which I am aware. I am aware of the room around me, the sound of traffic from the street outside, my own body, my own thoughts and emotions, the memories brought up in my mind at the moment. All of these items are encoded in my brain as chunks of information. I am aware of a great diversity of information. The second component (…) is the act of being aware of the information. That, of course, is the mystery. Not all information in the brain has awareness attached to it. Indeed, most of it does not. Some extra thing or process must be required to make me aware of a specific chunk of information in my brain at a particular time.*" The first component described by Graziano contains the primary information captured by the senses and internal sensors of the body as does the *core self* proposed by Damasio. However, this component is more elaborate than Damasio's term as it also includes more complex forms of information, such as thoughts, emotions and memories, which for Damasio (2010) are part of the *autobiographical self*. The second component described by Graziano calls for higher-order processing, likely similar to the one described by Damasio (2010) for the *autobiographical self*.

The notion of *time* is an integrated part of conscious experiences. This is because the brain needs to represent and integrate time in the general picture, otherwise the integrated experience would not be organised methodically. Mammals have an excellent capacity for timing (Parker, 2015). According to Dennett (1991), the brain does not lay down a flow of events in a fixed manner. A subjective 'time line' is produced for each narrative of a course of events constructed in the brain. Time lines may be compared with each other and the temporal order perceived may not be precise.

Observations by Gazzaniga (2012) on split-brain patients confirm that the brain, specifically the left hemisphere, makes logical interpretations. In split-brain patients, different pieces of information obtained by the left and right hemispheres do not connect, as the two hemispheres are no longer linked. The patients can perform certain tasks well; for example, making correct choices from pictures presented to the left, the right or both visual fields. In most persons, the left hemisphere is in charge of speech. When patients are asked why they made certain choices, the answering left hemisphere has only partial information as it does not have access to the information of the right hemisphere. Generally, the left hemisphere "invents" an explanation that seems least illogical

"*We showed a split-brain patient two pictures: a chicken claw was shown to his right visual field, so the left hemisphere only saw the claw picture, and a snow scene was shown to the left visual field, so the right hemisphere only saw that. He was then asked to choose a picture from an array of pictures placed in full view in front of him, which both hemispheres could see. The left hand pointed to a shovel (which was the most appropriate answer for the snow scene) and the right hand pointed to a chicken (the most appropriate answer for the chicken claw). Then we asked why he chose those items. His left-hemisphere speech centre replied, "Oh, that's simple. The chicken claw goes with the chicken," easily explaining what it knew. It had seen the chicken claw. Then, looking down at his left hand pointing to the shovel, without missing a beat, he said, "And you need a shovel to clean out the chicken shed." Immediately, the left brain, observing the left hand's response without the knowledge of why it had picked that item, put it into a context that would explain it. It interpreted the response in a context consistent with what it knew, and all it knew was: chicken claw. It knew nothing about the snow scene, but it had to explain the shovel in his left hand. Well, chickens do make a mess, and you have to clean it up.(…) What was interesting was that the left hemisphere did not say, "I don't know," which truly was the correct answer. It made up a post hoc answer that fit the situation. It confabulated, taking cues from what it knew and putting them together in an answer that made sense. We called this left-hemisphere process the interpreter.*" (Gazzaniga, 2012).

1.5.2. Animal consciousness

For Damasio, language is not a prerequisite for the existence of consciousness although higher order processing may trigger language centres in the brain. He proposes "*that consciousness begins to occur* *when the brain generates a non-verbal account of how the organism's representation is affected by the organism's processing of an object, and when this process enhances the image of the causative object, thus placing it saliently in a spatial and temporal context*." (Damasio and Meyer, 2009).

Thus, in his view consciousness begins well before the highest-order processing and potentially, before the start of verbalisation. There is much evidence that human brains may process information to a higher degree of complex integration than animal brains, as well as subsequently using this integrated information better by cognitive or memory processes. Nevertheless, Damasio indicated that many fundamental aspects of consciousness may be constructed by animal brains: "*Most species whose brains generate a self, do so at core level. Humans have both a core self and an autobiographical self. A number of mammals are likely to have both as well, namely wolves, our ape cousins, marine mammals and elephants, cats, and, of course, that off-the scale species called the domestic dog."* (Damasio, 2010). Later in his book Damasio writes: "*No one can prove satisfactorily that nonhuman, non-languaged beings have consciousness, core or otherwise, although it is reasonable to triangulate the substantial evidence we have available and conclude that it is highly likely that they do. The triangulation would run like this: (1) if a species has behaviours that are best explained by a brain with mind processes rather than by a brain with mere dispositions for action (such as reflexes); and (2) if the species has a brain with all the components that are described in the chapters ahead as necessary to make conscious minds in humans; (3) then, dear reader, the species is conscious."* (Damasio, 2010).

In summary, the issue of consciousness has received and still receives much attention. Increasingly, science tries to elucidate the processes and brain mechanisms through which consciousness appears. Prominent scientists who deal with these questions come from different scientific fields. For example, Damasio is a neuroscientist specialising in behavioural neurology and experimental neuroanatomy. Tononi is a neuroscientist and psychiatrist with, amongst other attributes, specialised knowledge of large-scale computer models of sleep and wakefulness. Dehaene was originally a mathematician and computer scientist and now constructs computational neuronal models of human cognition. Lamme is a medical scientist, specialising in cognitive neuroscience and visual perception. The philosophers Dennett and Metzinger contribute through thought experiments and reflections on coherence and reliability of scientific theories. Although the terms used by these scientists are often different, the basic ideas are often compatible and complementary, showing similarities on essential points.

They agree on the existence of a feeling of self ('*this is I*"), considered pre-conscious, and a feeling of agency ("*I am the one doing this*"), considered as a lower stage of consciousness. More elaborate states of consciousness or extended consciousness are considered to need attentional processing and more complex, more widespread and above all, recurrent processing. This processing allows a widespread sharing of information; the more widespread it is, the larger the content of consciousness. This widespread processing may include cognitive processing and memory, as well as narrative or autobiographical consciousness, going beyond the here and now.

Finally, consciousness comes in different forms, degrees and contents and it is highly likely that many animals have conscious experiences. Consciousness is probably best viewed as a multidimensional state, where contents and levels are connected and vary in a continuum. Many scientists try to distinguish different forms of consciousness, but it may be difficult to distinguish between different but close and connected states of consciousness.

1.6. Conclusion

Amazingly, when confronting the different views of former, even ancient, naturalists, biologists and philosophers to the contemporary views and thoughts about consciousness, it seems that little significant progress has been made and that philosophers still have a role in the debate about consciousness because of the subjectivity of this phenomenon.

So far, the materiality of consciousness has not been scientifically established in either humans or animals though, as the next chapters will show, important progress has been made in humans. As subjectivity of consciousness remains an obvious inference in humans, this subjectivity will always be difficult to reach in animals. However, when materiality of consciousness would have been established in animals as well as in humans, it would be difficult not to infer « consciousness » or some forms of consciousness in animals. This would in fact confirm the position commonly held for about the last 300 years that, according to their behavioural performances, from the overt to the less visible, and whether complex or not, it was difficult for the different authors to deny that nonhuman animals had consciousness.

Humans have a particularly potent means of communication, verbal language. This adaptation gives humans the capability to put names on real as well as abstract items, especially on phenomena that we experience but do not see. One of these phenomena is called « consciousness ». It covers many meanings and very diverse interpretations. This label seems to cover all cognitive capacities, including the most complex ones observed in humans. The term « consciousness » coined by philosophers several centuries ago, is still resistant to experimental investigation but there is increasing evidence that « consciousness » has indeed its deepest roots into our evolutionary past. This accumulated evidence shows that « consciousness », from the simplest to the most complex expressions, might be present in at least some, if not most, nonhuman animals.

As assessed even by 19th century evolutionary biologists and philosophers, verbal language puts a wedge into the psychological evolutionary continuity while not altering the physiological one. Humans then have a unique way of benefiting from a unique kind of referential communication unequalled by any other species. Giving names, conceptualizing is one way to apprehend phenomena. Developing a scientific approach is another way to apprehend phenomena, quite much more difficult to achieve. However, these two ways of « seeing the world » need to merge. Scientific evidence from the behaviour of a large variety of animals suggests that consciousness may exist in many non-human species. This evidence might be found in studies of “animal intelligence” or many fields of “animal cognition” or social life, instead of explicitly tackling the issue of “consciousness”. The fact that the term “consciousness” has been rarely used or most often not used indicates that scientists who study animal behaviour are cautious about what kind of consciousness non-human animals *MAY* have while assuming that non-human animals *DO* have consciousness. Amongst many authors, Morgan and Griffin repeatedly claimed that to exist in animals, consciousness does not need to be the same as ours.

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CHAPTER 2. CONSCIOUSNESS IN HUMANS: AN OVERVIEW

Here, we provide an overview of the science of consciousness in humans, based on a literature review of 88 articles published between 1967 and 2016. We focused our efforts on the most prominent articles, based on bibliometric indices such as citations and journal impact factors. We start this overview by defining the issue of consciousness, focusing on its level and its content. For the level of consciousness (section 2.2.1), we discuss the cases of sleep, anesthesia and several altered states of consciousness including coma and seizures. For the content of consciousness (section 2.2.2), we define the contrastive approach, illustrate how it applies to perception and cognition, and discuss more complex levels of consciousness including metacognition and the sense of self. At the neural level, we describe the quest to find the neural correlates of consciousness, that is, the minimal set of neuronal mechanisms that, together, allow a specific conscious percept to occur (section 2.3). Finally, we consider the reviewed knowledge within the global workspace and integrated information theories of consciousness, two influential theoretical frameworks for human consciousness (section 2.4).

2.1. Dissecting the problem: the levels and contents of consciousness

A pitfall all scientists and philosophers in the field are facing is that the word “consciousness” refers to different concepts and different phenomena. According to Searle (1995), “*Consciousness refers to those states of sentience and awareness that typically begin when we awake from a dreamless sleep and continue until we go to sleep again, or fall into a coma or die or otherwise become 'unconscious”*. Here, sentience or awareness are taken as synonyms of consciousness that is any form of subjective phenomenal experience. Although this definition has the merit of being simple, one can further simplify it by considering two of its distinct components. Consciousness can be considered as a function of its content**,** and as a function of its level. The content of consciousness can be described as the conscious experience of something external like the smell of a rose, or something internal like the perception of bodily states and the feeling of self, that is the ability to perceive oneself as distinct from the outside world. The level of consciousness can be described as levels of vigilance or arousal of the brain, which fluctuates due to internal factors, such as circadian rhythm, or external events (the sight of a lion *vs* the sight of a rose). Level and content are usually positively correlated (i.e., a high state of vigilance is needed to experience a content), but several physiological or pathological conditions reflect dissociations with rich content under low vigilance states, such as oneiric activity during sleep, or low content under unusual vigilance states, such as epileptic seizures (Tononi *et al.*, 2016) and somnambulism.

The neurological systems underlying the content and level of consciousness overlap only partially, which is expected considering the modular architecture of the brain in which different parts of the cortex deal with specific functions (Fodor, 1983) (*N.B.: non neuro-cognitive trained readers can be referred to two textbooks offering a broad overview of basic functional neuroanatomy used in present report : Gazzanica et al., 2013 and Kandel et al., 2013.*). The cerebral cortex is thought to be central for elaborated neurological functions including the perception of exteroceptive signals like light, sounds and smells and interoceptive signals, such as those of visceral or cardiorespiratory origin. But, it is also important for motor behaviours, and several executive functions such as control of attention, planning, working memory, or problem solving. At the perceptual level, primary cortices are involved in the early stages of the encoding of sensory signals such as visual orientation, sound frequency and tactile location. At later stages of analysis, associative cortices participate in conceptualization of the information and their integration in a wider context. Therefore, the conscious perception of the environment is believed to require good functioning of both primary and associative cortices to process and give a sense to what is perceived (Crick and Koch, 1995).

At the subcortical level, the reticular formation is essential in regulating states of vigilance, also known as consciousness level, awakeness, or arousal. It is located in the brainstem and consists of many neural networks. The reticular formation and certain structures of the dorsal pons project to the cortex to activate it and allow it to function correctly. These projections are called the ascending reticular activating system. This system consists of two major pathways. One passes *via* the thalamus located just above the brainstem which in turn projects massively onto the cortex. The other runs ventrally *via* the hypothalamus among others before projecting onto the cortex. Consequently, lesions at the level of the reticular formation or the ascending reticular activating system can have consequences at the cortical level, and are usually responsible for altered states of vigilance, but also various interrelated functions like motivation, attention, learning and memory (Damasio, 2010; Zeman, 2001). The reticular formation is further involved in the sleep cycle during which it reduces its stimulating effect on the cerebral cortex provoking a decrease of the level of arousal (Brown, 2012).

In the following sections, we provide details about the brain mechanisms associated with different levels of consciousness, including sleep, anesthesia, and several disorders of consciousness such as comatose states and seizures. We then turn to the mechanisms enabling the content of consciousness to be formed at the perceptual, cognitive, and metacognitive levels.

2.1.1. Levels of consciousness

2.1.1.1. Sleep

The most common demonstration that the level of consciousness changes on a rhythmic basis along the day-night succession is provided by the existence of sleep. Thus, this daily state of unconsciousness can be a powerful tool to understand better the mechanisms that decrease the level of consciousness. Moreover, sleep is common to many living organisms, so a complementary approach to sleep phylogeny can provide complementary views of consciousness in different animal species. In laboratory conditions, it is possible to awake human subjects during different stages of sleep and ask them to report what was going through their minds just before waking up. Interestingly, sleepers report different conscious contents depending on the sleep stage from which they emerge. Sleep stages are typically defined in terms of electrophysiological signs recorded with a combination of electroencephalography (EEG, measuring electric fields from neural activity at the scalp level), electro-oculography (EOG, measuring electric fields induced by eye movements) and electromyography (EMG measuring electric fields engendered by muscle contractions). In mammals, two types of sleep are observed and characterised by fast and slow EEG waves with the presence or absence of rapid eye movement (REM) *vs*. non-REM, and modifications of muscular tonus. REM sleep, also called ”paradoxical” sleep, is characterized by wake-like activity in the EEG (high-frequency beta and gamma waves between 13 and 80Hz), individual and clusters of REMs in the EOG, and very low muscle tone (atonia) in the EMG. The fast, high frequency waves are associated with increased vigilance/arousal, and reflect a fast depolarisation/repolarisation cycle of neurons needed for efficient information processing in the active awake brain. Slow waves (delta and theta waves, between 1 and 8 Hz) reflect a slow depolarisation/repolarisation cycle, and are associated with somnolence, sleep or anesthesia, which are situations where information processing is very slow or absent.

As stated already, consciousness can be evaluated as a function of its content and level. The contents of consciousness, defined as the conscious experience of external and internal stimuli, are abolished during non-REM-sleep and transiently distorted during REM-sleep. The most noticeable feature of subjects’ recollections is that conscious reports are rarely observed during awakenings from non-rapid eye movement (NREM) sleep, especially early in the night, when EEG slow waves are prevalent. When present, reports from NREM sleep early in the night are often short and thought-like. However, especially later in the night, reports from NREM sleep can be longer, more hallucinatory and more “dream-like. Forced awakenings during REM sleep-high frequency waves, almost always yield reports of mental activity (Nielsen, 2001), often but not systematically associated to “dreams—vivid conscious experiences” and sometimes organized within a complex narrative structure (Bernardi *et al.*, 2015; Hobson and Pace-Schott, 2002; Pace-Schott and Hobson, 2002; Siclari *et al.*, 2014).

As reviewed by Hobson and Pace-Shott (2002), brain structures participating in the control of waking cognitive skills, perception and consciousness are not strictly localized centres but distributed networks. Describing the networks subserving sleep is not the main topic of our report, but it is worth mentioning them considering that some structures are involved in both sleep and other aspects of consciousness.

This is particularly relevant for a comparative perspective in non-human species. When animals are awake, activation of the forebrain in REM-sleep occurs through ascending (or feed-forward) arousal systems (areas 1, 2 in Fig. 6), starting in the brainstem reticular activating system and basal forebrain. During REM-sleep, activated thalamic nuclei (area 6 in Fig. 6), which occupy key sites in sensory-relay, transmit endogenous stimuli that lead to the sensory phenomenon of dreaming. In non-REM-sleep, intrinsic thalamocortical oscillations suppress, but do not completely extinguish, perception and cognitive processes. Medial forebrain structures (area 3 in Fig. 6) are selectively activated during REM dreaming. So too are limbic structures, including the amygdala, which is an indication for potential drivers of dream emotions and the social nature of dreaming (Pace-Schott, 2001). Activated structures also include the anterior Cingulate (linked to emotion-related cognition such as conflict monitoring, or affect-related premotor functions), parts of the medial orbito-frontal and insular cortices. In particular, these areas are recruited by emotional and social processing, which are important for phenomenological aspects of dream experience. The hippocampus collaborates with the amygdala to mediate the storage of emotional memories in waking; reactivation of these areas is supposed to allow the readout of emotionally-salient memory fragments in REM-sleep. Strong activation of basal ganglia (area 5 in Fig. 6) may also mediate the fictive motion in dreams. Areas of the medial occipital and temporal cortices that mediate higher visual processing (area 11 in Fig. 6) generate the visual imagery of dreams.

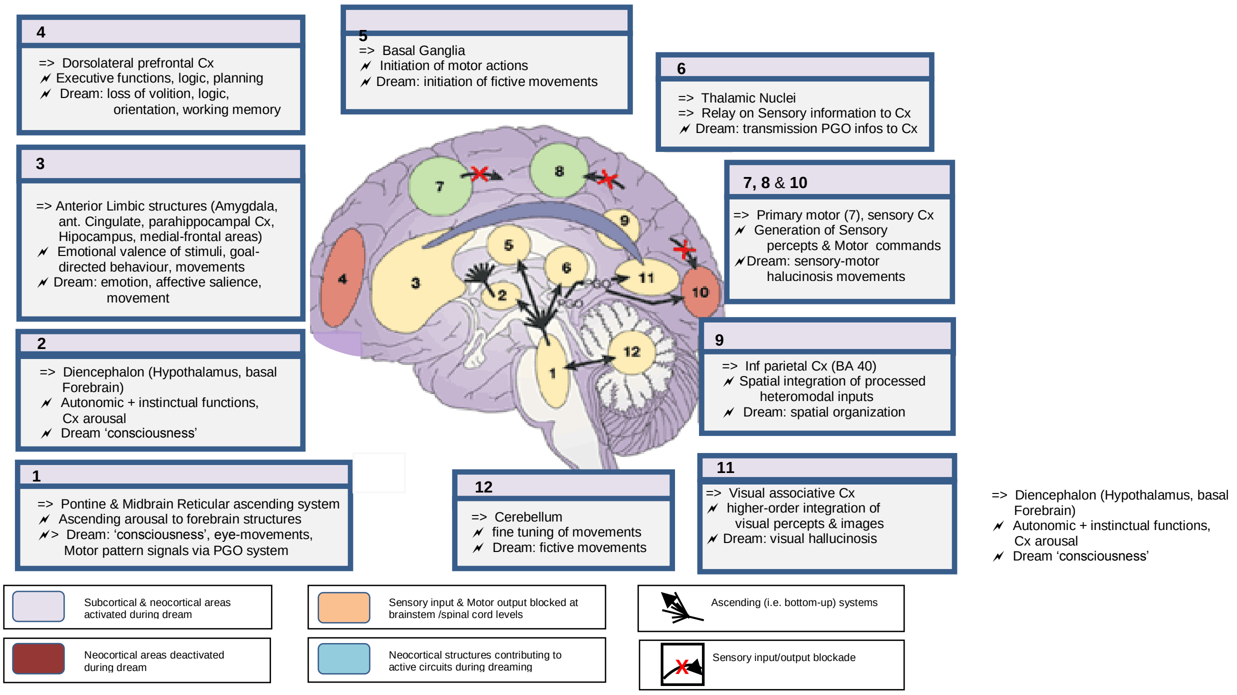

Fig. 6: Brain structures involved in Wakefulness, Sleep regulation and Mental process
numbers from 1 to 12 are indicative of successive steps of information processing
in various neuronal structures. Cx: Cortex; ant: anterior; inf: inferior.
=> structures. ⌿ functional role

The deactivation of executive areas in the dorsolateral prefrontal cortex (area 4 – in Fig. 6) during non-REM sleep is responsible for the prominent executive deficiencies of dream mentation, including disorientation, illogic, impaired working memory and amnesia for dreams.

In addition to this anatomo-functional description, general rules about dreaming in terms of network function have been proposed by Pace-Schott and Hobson, (2002):

(i) **ascending arousal systems** (often called feed-forward) activate the forebrain regions that are involved in dream construction in a manner that is chemically and anatomically different from waking arousal processes,

(ii) **REM dreaming** preferentially activates cortical circuits situated rather medially. They link posterior association and para-limbic areas, rather than circuits that include the primary sensory cortex and/or frontal executive regions, which are not activated in REM. The absence of any feedback from frontal executive areas, as normally occurs during awakeness, might explain why dreaming is so emotionally salient, but also shows profoundly deficient working memory, orientation and logic;

(iii) **subcortical circuits** involving the Limbic structures, Striatum, Diencephalon and brainstem regions are selectively activated in REM. Thus, dreaming often involves a suite of emotional (limbic subcortex), motor (striatum) and instinct-like elements (diencephalon).

Bringing together developmental and clinical case studies with the recent imaging data, Nir and Tononi (2010) proposed an integrated review to understand further how the human dreaming brain can elaborate conscious experiences during sleep and '*'why the subject is largely disconnected from the environment and whether dream state is more related to mental imagery or to perception''*.

Nir and Tononi conclude that dream consciousness can somehow be considered similar to waking consciousness, although there are several intriguing differences such as reduced attention and voluntary control, lack in self-awareness, altered reflective thought, occasional hyperemotionality and impaired memory. In spite of this, Mason *et al.* (2007) proposed that most dreams are perhaps similar to mind wandering or stimulus-independent thoughts.

Neuropsychological evidence indicates that dreaming and REM-sleep can be dissociated. For instance, forebrain lesions can abolish dreaming and spare REM-sleep, while brain stem lesions can almost eliminate overt features of REM sleep without abolishing dreams. Recalling that dream reports can be elicited during any stage of sleep and, conversely, some awakenings can yield no report, no matter of the sleep stage, Nir and Tononi (2010) pointed to a need to move beyond the REM/non-REM sleep dichotomy and traditional sleep-stages correlates. Their point is that the use of sleep-stages is still useful but it treats brain activity as if it were uniform in space and in time. In fact, more subtle features of brain activity, as demonstrated by brain-imagery techniques, are likely to influence the presence, degree and reportability of consciousness, but such data are still missing. When considering the mechanism of the flow of brain activity during dreaming versus slow wave sleep and versus awakeness, recent observations demonstrated that dreaming largely involves top-down connections in the human brain, akin to what happens during mental imagery data. By contrast, awake perception involves both bottom-up and top-down neural regimes. Such “top-down mode” during dreaming might disrupt the encoding of new memories and impede the processing of incoming stimuli, thereby explaining dream amnesia and the disconnection between the dreamer and his or her environment.

Although sleep is not primarily considered as a state of consciousness but merely linked to unconsciousness, it is important to consider it as a physiological process having important functional roles for the body (i.e. improvement of muscular efficiency) and as a conditional status for several cognitive functions such as regulation of memory and emotion. Sleep has been identified as a state that optimizes the consolidation of newly acquired information in memory, depending on the specific conditions of learning and the timing of sleep. Consolidation during sleep promotes both quantitative and qualitative changes in memory representations. REM-sleep consolidates cortical representations of memories through consolidation of synapses, favored by specific patterns of neuromodulatory activity and oscillations in electric field potential. By contrast, slow-wave sleep plays a role of coordinating the re-activation and redistribution of hippocampus-dependent memories to neocortical sites, notably through electrical activities such as slow oscillations, spindles and ripples (Diekelmann and Born, 2010). REM-sleep results from the interaction of brain stem cholinergic, aminergic, and GABAergic neurons which control the activity of glutamatergic reticular formation neurons leading to phenomena associated with REM-sleep such as muscle atonia, dreaming, and cortical activation. Strong activation of limbic regions during REM-sleep also suggests a role in emotion regulation, often associated with awakening bouts or long-lasting feelings after awakening (Brown *et al.*, 2012). Finally, and this is covered more fully in the next chapter, we should note that REM sleep in different species is very variable. So we find the absence of REM sleep in dolphins and short duration of REM sleep in birds in comparison to that of humans and rodents, the absence of penile erections in REM sleep in armadillo, as well as specific patterns in EEG signal during REM sleep, in platypus and ostrich (Brown *et al.*, 2012).

Before concluding this section, we stress that Rhythmic daily fluctuations of awakeness and related changes in levels of consciousness must take into account autonomic circadian fluctuations (biological rhythms with a periodicity close to 24 h). Indeed, circadian signals originating from the hypothalamic central clock are integrated with natural day-night signals and information on the need for homeostatic sleep originating from nuclei in the anterior hypothalamus. These nuclei interact with arousal systems in the posterior hypothalamus, basal forebrain and brainstem to control the onset of sleep (Fig. 7).

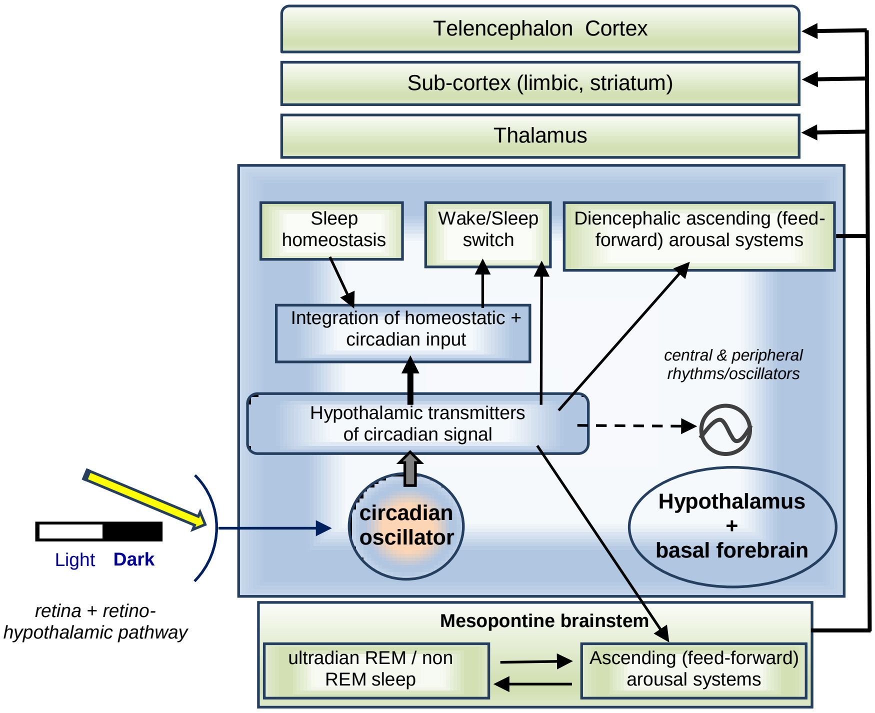

Fig. 7: Brain circuits regulating sleep-wake changes and REM/non-REM transitions.

Arrows → indicate main inputs/outputs. EEG: electroencephalogram; REM, non-REM: rapid/non rapid eye movements. Ultradian= rythms with a Period less to 24h, Circadian= rythms with a period close to 24h. (*modified from Hobson and Pace-Schott, 2002*).

An ultradian oscillator (biological rhythms with a periodicity of less than 24 h, 90-min REM–NREM cycle of the adult human) is located in the meso-pontine junction. It controls the regular alternation of rapid eye movement (REM) and non-REM sleep. Sleep cycles are accompanied by neuro-modulatory influences on thalamocortical networks. Such inputs diminish under the influence of circadian and homeostatic signals from the hypothalamus that are linked to sleep–wake switching mechanisms (Saper *et al.*, 2001).

2.1.1.2. Anesthesia

The key goal of anesthesia is to prevent the aversive experience of surgery by decreasing the level of consciousness. Anesthesia is used routinely but the mechanisms by which it triggers unconsciousness remain to be fully elucidated. If we could understand these mechanisms better we could have more efficient and secure use of anaesthetics but also potentially it could open a better understanding of consciousness *per se*. Over the last decade, explanations of the induction of consciousness-loss shifted from a focus on molecular targets of anaesthetics (mainly lipids and proteins receptors membranes, see Mashour, 2015) to paradigms rooted in neuroscience such as impaired cortical dynamics. In line with the current theories on consciousness, this new approach extends the understanding of mechanisms and casts new light on key structures involved in the process of consciousness. This section presents a short list of anatomical structures involved as targets of anaesthetics and complex functional interactions involved in the level of consciousness. Those structures are: i) brainstem and hypothalamus nuclei, known to mediate states of wakefulness/arousal and which have been primarily identified as targets of general anaesthetics; ii) thalamo-cortical ("vertical") and cortico-cortical ("horizontal") networks, considered to complement the conscious experience itself (see Box 1 for details).

Box 1. Anatomical targets of anesthetics (detailed data can be found in Mashour, 2016)

- Brainstem

The *locus coeruleus* (LC) located in the *pons* has wide cortical projections. Its activity is highest during waking consciousness, decreases during non-rapid eye movement (NREM) sleep, and is at its lowest during rapid eye movement (REM) sleep. LC is associated with cortical arousal during wakefulness, suggesting a role in consciousness, particularly of the environment.

The laterodorsal and pedunculopontine parts of the *Tegmentum*, located in the *pons* and with the basal forebrain, project to the hypothalamus and thalamus and generate electrical signals (slow oscillations, sleep spindles). The activity of *locus coeruleus* is high during wakefulness and low during NREM sleep, but in contrast to the *Tegmentum*, it is also active during REM-sleep. These neurons constitute the brain's source of acetylcholine. Cortical activation across the sleep-wake cycle is associated with higher activity in cholinergic neurons. Sleep spindles occur during halothane anesthesia and are associated with decreased cholinergic transmission to the pontine reticular formation.

The *Pontine Reticular Formation*, part of the reticular activating system, is essential for cortical arousal. Although GABA is associated with neuronal depression across the sleep-wake cycle, levels of GABA in the *Pontine Reticular Formation* are positively associated with cortical arousal (Vanini *et al.*, 2011). Lower levels of GABA in this structure are concomitant with isoflurane-induced unconsciousness. GABA appears to be involved in the neurobiology of anaesthetic induction but not emergence from anesthesia, implying that different mechanisms underlie these two phenomena.

The *Ventral Tegmental Area*, located in the midbrain contains dopaminergic neurons. These neurons do not change greatly during wakefulness and are not considered central to sleep-wake control. Nevertheless: anaesthetic-induced unconsciousness can be reversed by electrical stimulation of this area. Dopamine agonists can reverse the effects of isoflurane and propofol, further indicating that these dopaminergic neurons act as "trigger-awaking" cells.

- Hypothalamus

The *ventrolateral preoptic nucleus*, located in the anterior hypothalamus, transmits GABA and Galanin to neuronal populations which are most active during NREM and REM sleep (Sherin *et al.*, 1996). As one of the few "sleep-ON" neuronal populations, this nucleus has been viewed as the target of general anesthetics. Recent results suggest beyond being responsible for promoting natural sleep, VLPO has a more complex function like translating the physiological effects of preexisting sleep deprivation upon resulting anesthetic hypersensitivity (Eikermann *et al.*, 2011; Moore *et al.*, 2012; Nelson *et al.*, 2002). Although highly responsive to GABAergic anesthetics, this nucleus is now described as neither necessary nor sufficient for anaesthetic-induced unconsciousness, although it may play a contributory role.

The orexinergic neuronal subpopulation located in the lateral Hypothalamus innervates arousal centres in the brainstem and basal forebrain, transmitting orexin A and B. These cells fire maximally during the waking state. Their firings are suppressed during NREM sleep, and they may exhibit occasional bursts during phasic REM-sleep. Orexin infusion in the basal forebrain leads to cortical arousal and attenuate the effects of anesthetics like isoflurane, propofol, ketamine and barbiturates. Orexins are believed to play a role in emergence from unsconsciousness and not as simple on/off switch-anaesthetic drugs.

The *tuberomammillary nucleus* located in the caudal Hypothalamus, transmits histamine. Its activity and the levels and release of histamine are high during wakefulness and low during sleep, and it is considered as an "arousal- factor". Histamine release is depressed by gaseous halothane anesthesia. Systemic administration of propofol, pentothal and the GABA-agonist muscimol are believed to depress its activity.

- Thalamic and Thalamo-cortical systems in anesthetic-induced unconsciousness

In mammals, the Thalamus is subdivided into approximately 50 nuclei and subnuclei. Some of those nuclei receive lower-order sensory input primarily from the periphery while others primarily receiving inputs from the cortex. They subserve higher-order, or multimodal, integrative functions.

Given the importance of the thalamus, acting as a "hub" in sensory perception and sleep-wake neurobiology, this structure was examined for its likely key-role in anesthetic-induced unconsciousness. It has even been proposed that the thalamus could act as an ON/OFF "switch" for transitions within the anaesthetic state (Alkire *et al.*, 2008). This switch-like function would work by anaesthetics inducing hyperpolarization of thalamic neurons and then shifting neural electrical activity (i.e. from tonic emission of action potentials or tonic firing, to burst firing) which would prevent afferent sensory stimuli from arousing the cortex.

Evidence supporting this proposal comes from animal experiments in which stimulation of the centro-medial thalamus led to reanimation despite continued delivery of general anaesthetics. A similar observation in humans using brain imaging demonstrated that activation of the thalamus is correlated with recovery from anesthesia.

Nevertheless, in spite of coherent experimental data, it is not yet clear whether depression and reactivation of the thalamus is the trigger or the consequence in a mechanistic loop. In the effect of general anaesthetics, the closely integrated function of thalamus and cortex suggests that these two structures are a single thalamo-cortical system. This functional system undergoes state-dependent changes across the sleep-wake cycle and is thought to play a critical role in consciousness. The higher-order nuclei of the thalamus have been suggested to act as a “computational blackboard” for the cortex; these nuclei primarily receive cortical inputs and are probably responsible for stabilizing or facilitating cortical communication (Saalmann, 2014).

Recent brain imaging studies are beginning to clarify the role of impaired functional thalamo-cortical connectivity under anaesthetic-induced unconsciousness. In fact, cognitive impairments are more severe when they involve thalamo-cortical disconnections between higher-order (integrative) thalamic nuclei and the cortex than when they involve disconnections between sensory nuclei and cortex (Liu *et al.*, 2013). This might explain why some anesthetics still allow sensory cortical responses. These results were challenged by other studies that showed more significant functional disconnections between the cortex and putamen under unconsciousness induced by high concentrations of propofol. Furthermore, functional disruptions between the cortex and basal ganglia during general anesthesia are also observed in rats (exposure to isoflurane) and humans (exposure to propofol). This suggests that the cortico-cortical or thalamo-cortical nature of disconnections vary depending on the kind of anesthetics.

Over the last decade, different patterns of disrupted functional connectivity across the cortex were observed during anaesthetic-induced unconsciousness in humans. As a general trend, primary sensory networks remain relatively intact under drugs, such as propofol or sevoflurane-induced unconsciousness while higher-order cortical networks become functionally disconnected.

Recent studies also suggest that cortico-cortical rather than thalamo-cortical disconnections are critical for unconsciousness (Monti *et al.*, 2013), which strengthens the idea of a “top-down mechanism” for general anesthesia (Mashour, 2014). More importantly, another study combining several methods for brain imaging in humans under general anesthesia (Jordan *et al.*, 2013) suggested that functional directional connectivity is reduced across the cortex with functional disconnections across anterior-posterior (known as “re-entrant”, “recurrent” or “feedback connectivity”) and interhemispheric axes. Multiple recordings in isoflurane anesthetised rats produced similar data, with disruption in anterior-to-posterior communication, but maintained postero-to-anterior communication (“feedforward” connectivity).

Overall, the recent data which we reviewed tend to clarify the mechanisms involved in anesthesia-induced unconsciousness although they have been routinely used in medicine over more than a century. The detailed analysis of the actions of anesthetics at each critical level of the brain pathways, from brainstem and hypothalamus nuclei, to thalamo-cortical (incoming or “vertical” pathways) and cortico-cortical (“horizontal”) networks, profoundly help to understand the mechanisms underlying the levels of consciousness. Such a systemic approach (Brown *et al.*, 2011) aims to identify the processes of altered arousal states induced by five classes of intravenous anesthetics and relates behavioural and physiological features to the molecular targets and neural circuits at which these drugs act. The five different altered states of arousal are: sedation-unconsciousness, sedation-analgesia, dissociative anesthesia, pharmacologic non-REM sleep, and neuroleptic anesthesia. Each state results from the action of an anesthetic drug on multiple targets in the central nervous system which allows us to identify anatomical structures and how neurotransmitters are involved in different aspects of conscious states.

2.1.1.3. Disorders of consciousness

Due to traumatic, toxic, metabolic, or epileptic causes, **coma** is an acute disorder of consciousness characterized by a disruption of consciousness levels and contents (see 2.2) for at least one hour. During coma, patients do not respond to any stimulation and keep their eyes closed (Bateman, 2001; Laureys *et al.*, 2004). Coma can be caused by widespread deficiencies in both hemispheres, or by local deficiencies in the reticular formation or the ascending reticular activating system. The depth of coma is defined according to several scales at the behavioural and neural levels that rate the patient's reactions and reflexes, as well as the extent of brain damage (Laureys *et al.*, 2004).

Following coma, patients can enter a **vegetative state** (Laureys, 2005). Compared to coma, vegetative states are characterized by the presence of a sleep-wake cycle, including periods where the eyes are open and periods where the patient seems to be sleeping. The existence of this cycle is explained by the intact or virtually intact state of the brainstem including the reticular formation. The brainstem also continues to ensure vital functions such as breathing, cardiovascular functioning and those functions related to the maintenance of homeostasis allowing survival in a medical sense (Laureys, 2005). Although such patients may move spontaneously they do not react coherently or in a voluntary manner to stimuli from the environment, and they are considered as unconscious. This state is systematically associated with bilateral impairment of the associative cortices involved in complex cognitive functions.

A vegetative state can be permanent, or can lead to a **minimally conscious state**, in which one can measure the presence of repeatable, albeit partly inconsistent, behavioural reactions that are sustained over longer periods indicating that they are not reflex movements (Giacino *et al.*, 2002). The use of glucose by the brain is reduced, but it is on average slightly higher than that of patients in a vegetative state (Laureys *et al.*, 2004). Neurological studies show the presence of cortical activity in response to personalised narratives suggesting that they have a certain level of consciousness (Schiff *et al.*, 2005). Today, the proportion of patients considered vegetative but who are in reality in a minimally conscious state is estimated to be one-third.

Properly diagnosing disorders of consciousness is still a major issue, as about 40% of patients with disorders of consciousness are erroneously assigned a diagnosis of being in a vegetative state (Schnakers *et al.*, 2009).

Brain seizures. Besides coma states, other brain disorders are responsible for altered states of consciousness. During epileptic seizures, brain activity is characterized by massively synchronized abnormal oscillations (Blumenfeld, 2005). Depending on the brain areas affected, a seizure can cause a more or less lasting state of unconsciousness. When subcortical structures are involved in the crisis, the term, "generalized seizure", is used, even if this concerns in reality only part of the brain structures, such as the cortex and related subcortical structures and/or the ascending activating system arising from the brainstem (Blumenfeld and Taylor, 2003). There are other forms of seizures with more subtle impairments of consciousness. In "absence seizures" for example, patients, mostly children have momentary lapses of consciousness and are unresponsive for a few seconds. Generalized convulsive seizures are characterized by tonic and clonic phases with specific motor behaviours such as stiffening, and jerking of arms and legs, loss of consciousness during the tonic phase, and a state of lethargy following the seizure.

During a seizure, the brain consumes two to three times more oxygen than normal. The blood supply also changes, with increases in some areas and decreases in others. These changes lead to the production and accumulation of lactate in some brain areas which is responsible for the acidification of brain tissues. Epileptic seizures are further associated with an increased release of neurotransmitters, including GABA (gamma-aminobutyric acid) which plays a central role in the induction of seizures via its effect on the flow of ions across neuronal membranes (Blumenfeld, 2005). All these disturbances, if sufficiently widespread, may be associated with loss of consciousness. Besides the effects on consciousness, massive discharges in the brain can cause generalized muscle contractions (convulsions), hyperactivity of the peripheral nervous system and hypersecretion by the endocrine glands.

2.1.2. Contents of consciousness

Even though we experience life as a succession of subjective events, most processes governing our mental and bodily capacities are performed unconsciously. For instance, we are not aware of regulation of our digestive or cardiac systems, or of all the computation underlying perception of speech or execution of complex movement. Thus, a critical issue for understanding how the content of consciousness is formed is the distinction between conscious and unconscious processes. This “contrastive analysis” originally put forward by Baars (1988) involves comparing situations in which consciousness occurs with closely matched situations in which there is no conscious content (i.e., unconscious processing), so functional and neural specificities can be studied. Three main approaches are used to render a stimulus unconsciously to a subject: the first is to disrupt sensory signals (e.g., presenting an image very briefly, in the presence of visual noise), the second is to deplete attentional resources to be deployed on sensory signals, for example by distracting observers by having them performing a dual task, and the third is to reduce vigilance states, for example by studying perception/cognition during sleep or anesthesia, (see above). These methods have been reviewed by Kouider and Faivre (2016).

The contrastive study of consciousness has not only been motivated by the need to understand the specificity of consciousness, but also to characterizing unconscious processes in their own right. As such, a large part of the work on the content of consciousness consists of determining the limits and extent of unconscious processes. Unconscious perception is inferred when a stimulus influences behaviours and/or neural activity while the subject reports that they are unaware of it. This issue has been mainly addressed through the use of subliminal stimulation methods, in which a stimulus is presented below the threshold for conscious perception. The predominant experimental approach for validating unconscious processing of a stimulus is to establish a dissociation between its processing and its conscious access. Such dissociation involves the joint uses of direct and indirect measures. The direct measure allows researchers to assess awareness of the stimulus, by asking the observer to focus directly on the stimulus or one of its dimensions of interest, and to report its content. Note that those reports can be done verbally or by using button presses or any other means. In contrast to the direct measure which serves to assess awareness of a stimulus, the indirect measure allows the researcher to estimate the influence of the stimulus on behaviour and/or on brain activity. Unconscious perception is demonstrated when the indirect measure reveals a positive effect. This is the case when the stimulus influences the processing of a subsequent target, or when it elicits specific patterns of brain activity. Direct measure confirms the absence of conscious access when the subject cannot consciously report the feature of interest. Later, we briefly review the demonstrations of various unconscious processes, all of them being based on a dissociation between direct and indirect measures.

2.1.2.1. Perception

Experimental studies on consciousness have been largely confined to the domain of visual perception, because the methodologies are well-established and the long tradition of psychophysics has produced many sophisticated tools (Kim and Blake, 2005). The mere existence of subliminal influences at the perceptual level has been one of the most controversial issues in psychology (Holender, 1986). Today, the existence of subliminal perception is no longer denied. There is compelling evidence that visual, auditory, tactile, or olfactory stimuli can be detected and discriminated within a few hundred milliseconds even though participants deny perceiving them consciously, and perform at chance-level when asked to guess their nature. In other words, it is largely accepted that simple forms of processing (e.g. motor reflexes, sensory analysis) do not necessitate perceptual awareness. The controversy has shifted to understanding the depth of processing in the absence of awareness; that is, to what extent unconscious perceptual information can be processed. Bluntly stated, research over the last few decades has focused on whether the unconscious mind involves basic or complex cognitive processes

(Loftus and Klinger, 1992). Understanding the depth of unconscious perceptual processing is still the topic of on-going research.

2.1.2.2. Cognition

Whether or not there are unconscious complex computations involving higher processing levels (e.g. executive functions including action planning and inhibition, problem solving, etc.) remains largely debatable. Recent studies brought new evidence that there are high-level unconscious processes involving parts of the brain such as the prefrontal cortex that are traditionally associated with conscious access. In particular, these studies showed that unconscious stimulus processing is not necessarily restricted to perceptual systems, but can also trigger activations in prefrontal regions under certain circumstances, such as when cognitive control and executive functions are heavily involved. For instance, invisible cues that predict which of two tasks is to be performed by an observer can modulate neural activity in premotor and inferior prefrontal cortices (Lau and Passingham, 2007). Unconscious cognitive control was also studied using go/no-go paradigms, in which participants are asked to respond as fast as possible to a target if it is preceded by a go cue (e.g., a square), but to inhibit that response if it is preceded by a no-go cue (e.g., a diamond). In several experiments, invisible no-go cues were shown to slow-down responses on the target, reflecting an incomplete activation of the inhibition to the response, and therefore suggesting that cognitive control is enabled in the absence of awareness (van Gaal *et al.*, 2008). This effect involved the Pre-Supplementary Motor Area, a region typically associated with cognitive control, including unconscious control of actions that suppress motor decisions. Finally, another cognitive function that is typically believed to require consciousness is working on short term memory, whereby newly formed or stored information is transiently processed to meet current goals. The finding that masked stimuli can be discriminated above chance-level performance a few seconds after their display while observers report no conscious experience of the stimulus suggests that information does not need to be accessed consciously to enter working memory (Soto and Silvanto, 2014). Interestingly, such unconscious working memory was found to involve the superior frontal and dorsolateral prefrontal cortices, regions of the brain that are typically linked to the global neural workspace for consciousness (see below for theories of consciousness). Apart from short term memory, the role of consciousness for other forms of memory is poorly understood. Indeed, the field of memory is subdivided in many domains, according to its temporal properties and capacity (e.g., short term memory as described above vs. long term memory, which stores large quantities of information for long durations), or according to the type of information being stored (spatial for places, declarative for events, procedural for skills, etc.). At a more fundamental level, it is still unclear how consciousness interacts with the encoding, storage, and retrieving of information, three of the main mechanisms involved in memory. Overall, the links between consciousness and memory in humans are complex, and still largely unexplored.

Beyond executive functions such as action planning or episodic memory, the question of unconscious integration of information has triggered a lot of interest recently. Based on the phenomenological observation that conscious objects of perception are experienced as wholes rather than sums of disparate features, several theories consider that consciousness and integration of information are tightly linked, if not mutually dependent. Conversely, these theories hold that integration of unconscious information should be limited, if not absent. Yet, it has been shown that unconscious integration is possible, because stimuli made up of physical features spread in space, and time, semantic domains or sensory modalities can be integrated even when not accessed consciously (Mudrik *et al.*, 2014). However, the literature also indicates that the scope of unconscious integrative processes is more limited, and the sizes of the effects are smaller than conscious ones, suggesting that consciousness still plays a role in integrative processes in accordance with prominent theories in the field. We will come back to the issue of information integration and consciousness when describing the integrated information theory of consciousness (see section 2.3.2).

To conclude this section, it is important to note that evidence for unconscious effects does not rule out the possibility that consciousness might play a functional role in executive functions, particularly when it comes to applying them in a flexible manner, within a novel, non-stereotypic context (Dehaene and Changeux, 2011).

2.1.2.3. Self-consciousness and metacognition

A fundamental property of consciousness is its link with the self, defined as the subject of conscious experience. The sense of self and its close link to neural body representation has been termed bodily self-consciousness (BSC) and has been a target of recent research (Blanke *et al.*, 2015). BSC is commonly thought to stem from the integration of signals coming from the environment (exteroception, including tactile, visual, olfactory or auditory signals), as well as from the body (interoception, including cardiac, visceral, proprioceptive or vestibular signals). Based on the multisensory integration on these signals, BSC involves self-identification (the experience of owning "my" body), self-location (the experience of where "I" am in space), and first-person perspective (the experience from where "I" perceive the world) (Blanke, 2012). The scientific study of bodily self-consciousness has expanded over the recent years, benefiting from the examination of neurological patients with altered states of BSC and from virtual reality coupled with work on robotics to induce well-controlled states in the research laboratory. For instance, altered states of BSC of neurological origin may be experienced from a location and perspective that are not centred on the physical body of the observer: in these so-called out-of-body experiences, the subject or centre of consciousness is experienced as being displaced to an elevated and down-looking first-person perspective and location.

The sense of self is not limited to the feeling of owning a body and to the feeling of perceiving the world from this body. Indeed, we have the capacity to introspect and reflect upon our own memories (e.g., autobiographical memory), as well as our immediate objects of perception or decisions (Fleming *et al.*, 2012). Metacognition is the ability to report (through verbal reports or other means such as pressing a button) our own mental states, or in other words "to know how much I know". Akin to the private aspect of consciousness (see Chapter 1), metacognition occurs from a first-person perspective and as such has unique access to internal signals: only I know what goes on in my mind. This capacity allows us, amongst other things, to form a sense of confidence about any decision we make in our life (Yeung and Summerfield, 2012), and to seek more evidence before committing to one option if our confidence is low.

According to the influential framework of signal detection theory (MacMillan and Creelman, 2005), metacognition includes all processes that monitor one's certainty in a response. One simple way to measure metacognitive performance is to have participants first make a perceptual judgment and, in a subsequent trial, report their confidence in the correctness of their own response. Participants who are able to assign high confidence to all (and exclusively to) correct trials are said to have high metacognitive ability. The key principle under signal detection theory is that a single stimulus in the environment elicits an "internal signal" in the brain. This internal signal is not fully deterministic, but is associated with a bell-shaped probability density. Thus, when participants decide which of two possible stimuli (each associated with a probability density) was present in the environment, they place a decision criterion along the internal signal axis. If the internal signal falls above the threshold of this criterion, participants will answer that the stimulus that they perceived is the one with the higher mean. In the same way, to report their confidence in their own response, participants compare the internal signal to multiple confidence criterion thresholds, one for each confidence level. Metacognition is not always optimal, and metacognitive failures have a great societal impact; overconfidence correlates with aggressive attitudes, and is also observed in several psychiatric disorders, including schizophrenia.

2.1.2.4. Attention and consciousness

There is a strong correlation between the contents of consciousness and attentional states: in high vigilance states we are usually conscious of what we are attending to. Attention is defined as the cognitive function that allows us to amplify relevant signals and inhibit irrelevant ones. The nature of the links between attention and consciousness remains debatable, some researchers arguing that consciousness and attention are two dissociable functions (Koch and Tsuchiya, 2007; Lamme, 2003), others that consciousness requires attention (Cohen *et al.*, 2012), or that consciousness actually consists of a perceptual reconstruction of attention (Graziano and Kastner, 2011).

A variety of methods has been used to manipulate attention and consciousness (Box 2). Attention may be influenced further by cueing, when a visible or auditory cue indicates the place where the target will appear (Kentridge *et al.*, 1999; van den Bussche *et al.*, 2010). Some authors indicate that attention is necessary (De Brigard and Prinz, 2010; Merikle and Joordens, 1997) and according to some it is even sufficient for consciousness (Posner, 1994). Others indicate that consciousness and attention are not necessarily linked. Specifically, Koch and Tsuchiya (2007) and van Boxtel *et al.* (2010) propose a fourfold classification of states of attention and consciousness (Box 3). They list examples where apparently, attentional processes and consciousness are dissociated. Thus, a study using the attentional blink paradigm (see Box 4; Olivers and Nieuwenhuis, 2005) showed that participants paradoxically improved second target recognition when they were concurrently engaged in distracting mental activity, such as free-associating on a task-irrelevant theme or listening to music. Koch and Tsuchiya (2007), van Boxtel *et al.*(2010) have interpreted these findings as indicating that top-down attention and consciousness can have opposite effects, and therefore they must be different processes. Similarly, these authors indicate that consciousness seems to exist with little or no attention because subjects can accurately perceive the category of the object (a face, a natural scene or a letter) or distinguish between male and female faces flashed in the (unattended) periphery (Reddy and Koch, 2006; van Boxtel *et al.*, 2010). With only a 30 ms exposure to natural scenes, followed by a mask, observers can clearly perceive their gist (Biederman, 1972; Li *et al.*, 2002) even in the absence of any expectation about what type of scene will be flashed. van Boxtel *et al*. (2010) also pointed that for some scientists, within these 30 ms, top-down attentional bias could not have taken effect and therefore, this is an example of consciousness without attention.

Taking all of this into account, van den Bussche *et al.* (2010) set out to create the 4 processing states in a 2 x 2 factorial design, manipulating attention and consciousness (see Box 3). To do so, masked and unmasked priming paradigms were used, to manipulate attention and consciousness independently. The stimulus strength was manipulated by presenting the primes either subliminally (i.e. for a very short duration and masked; see Box 4), or clearly visible (i.e. for a longer duration and unmasked), in which case these primes reached consciousness. Top-down attention was manipulated by directing the subjects' attention either towards the primes or away from the primes, using a cue which predicted target location on each trial. The primes could either be presented at the same location as the target; hence they also received top-down attention, or at a different location, in which case they did not receive attention.

Box 2. Experimental paradigms to manipulate attention and/or consciousness

Inattentional blindness: participants perform a few trials of a primary task (e.g., visual search, multiple object tracking, etc.), and on a critical trial, a new and unexpected stimulus is presented, while participants are focused on the primary task. Participants routinely fail to notice the unexpected stimulus.

Change blindness: changes to natural images are difficult to detect when they occur during a blank gap, eye-movement, or camera cut. If properly masked, a single item can change (e.g., by appearing and/or disappearing), without observers noticing.

Load-induced blindness: participants perform a visual search task, in which perceptual working-load is manipulated, while attempting to detect the presence of a meaningless task-unrelated figure, referred to as the critical stimulus. There is a reduction in the critical stimulus detection rate and detection sensitivity, when the search task is of high perceptual load, compared to a low perceptual load.

Motion-induced blindness: when a perceptually salient stationary visual stimulus is superimposed on a field of moving distracters the stationary visual stimulus repeatedly disappears and subsequently reappears.

Attentional blink: when a pair of targets is presented in rapid serial visual presentation, observers often fail to notice the second target when it comes 200 to 500 ms after the first (see Box 5).

Dual-tasks: two tasks, requiring visual search and working memory, are performed separately and then concurrently. The attentional requirements of each task can be determined by measuring the difference between performances in the task in single- and dual-task settings. Typically, performance drops in dual-task conditions. However, in certain cases the addition of a second task has no effect; this is cited as an example of consciousness without attention.

Box 3. The 4 categories of combinations of attention and consciousness[1] proposed by Koch and Tsuchiya (2007) and used by van den Bussche *et al.* (2010).

Attention with consciousness: subjects become conscious of objects or events that they attend to

No attention, no consciousness: objects or events do not receive top-down attention and therefore remain unreported

Attention without consciousness: subjects attend to a location, but still fail to see one or more attributes of an object at that location

Consciousness in the near absence of attention: even though no or very little attention is dedicated to a certain object or event, subjects are still able to report partially.

[1] *The last 2 combinations can be considered as controversial.*

Box 4. The attentional blink paradigm

Subjects have to detect two target stimuli, T1 and T2; T1 appears first and is followed by T2, which may appear immediately after T1 or at some other point in the sequence after T1, with distractors presented between T1 and T2 (that is, the temporal lag between T1 and T2 can vary). The blink effect refers to a decrement in detection of T2: the basic finding is that the decrement is often greatest when T2 occurs not immediately after T1 (position n +1), but instead somewhere around positions n +2 through n +5 (that is, when there are one or more distractors between T1 and T2). The performance improves with a higher number of distracters and reaches an asymptote around n +6 or n +7. A possible explanation for the attentional blink is that processing of T1 takes up attentional resources which are limited: as a result, either access to these resources is denied for T2 or the representation of T2 is so vulnerable that it easily suffers from the interference of temporally surrounding distractors (Marchetti, 2012).

To elicit priming, the prime needed either to be attended to or to be visible. This means that both attention (prime attended or not) and visibility (prime reaching consciousness or not) significantly modulated priming effects. The combination of top-down attention and visibility boosted the priming effect. According to several scientists, these results confirm the hypothesis that consciousness and attentional processes depend on at least separate processes and therefore on different neural mechanisms (Koch and Tsuchiya, 2007; Lamme, 2006; van Boxtel *et al.*, 2010; van den Bussche *et al.*, 2010).

Box 5. The priming paradigm

In the priming paradigm, participants are asked to discriminate a target. It is known that prior exposure to another stimulus (the prime) influences the performance of the task. For example, participants are faster in categorizing a target word when it is preceded by an associatively or semantically related prime. For example, the target NURSE is categorized as a medical term faster when following the prime DOCTOR than following BREAD.

In the masked priming paradigm, the prime is presented very briefly (< 50 ms), preceded and/or followed by visual patterns. Due to the short duration of the presentation and the presence of the masks, the prime becomes invisible, and is not accessed consciously.

Despite this, the idea that attention and consciousness are separate processes is still controversial (Bor and Seth, 2012; Cohen *et al.*, 2012; De Brigard and Prinz, 2010; Marchetti, 2012; Posner, 2012). For example, Posner (2012) and De Brigard and Prinz (2010) indicate that the complex paradigms recruit various pathways that process information in the brain which may partly overlap. Hence, the complexity of the experimental paradigms may create bottlenecks in information processing, particularly in the frontal cortex. Thus, while Koch and Tsuchiya (2007) and van Boxtel *et al.* (2010) found that the results of the study of Olivers and Nieuwenhuis (2005) corroborate the hypothesis that consciousness and attention are different processes, Posner (2012) indicated that alternatively, they may suggest the implication of different neural networks competing for attention.

Furthermore, the hypothesis that attention and consciousness involve different mechanisms are often based on paradigms manipulating only top-down attention (Koch and Tsuchiya, 2007; van Boxtel *et al.*, 2010). Marchetti (2012) indicated that, unintentionally, bottom-up attention may have occurred in these paradigms, thus explaining the conscious perception despite absence of top-down attention. In addition, different forms of top-down attention may exist, ranging from focused to more diffused attention, and different levels of attention may exist, ranging from low to high (see also Keller, 2012). To explain the improved performance of the observers when they were distracted in the study of Olivers and Nieuwenhuis (2005), Marchetti (2012) postulated that attention may have become more diffuse while at the same time increased attentional capacity may have been recruited. In accordance with this idea, theories based on neurophysiological studies and brain-imaging suggest that attentional processes depend on the task and the brain area being studied (Posner and Dehaene, 1994).

Most of the work on the links between attention and consciousness was conducted using vision, since it is the system we know the best (Dehaene *et al.*, 2006; Koch and Tsuchiya, 2007; Lamme, 2006; van Boxtel *et al.*, 2010). Yet, knowledge on other sensory modalities is worth mentioning. For example, in the auditory modality, the brain response elicited by the presence of a deviant within a sequence of otherwise regular stimuli has been extensively studied. For example, when a tone is repeatedly played, with 90% of high pitch tones and 10% of low pitch tones, low pitch tones elicit a specific brain response, with two main components (Chennu and Bekinschtein, 2012). There is an early component, named P3a, at frontal locations, and a later one, more posterior, named P3b. P3a is present even if subjects are concomitantly presented with another distracting task that demands attention. As it is assumed that subjects in these conditions have no conscious access to the deviant sounds, P3a is believed to be elicited in a bottom-up, unconscious manner (Chennu and Bekinschtein, 2012). The later component P3b, is only elicited when subjects are phenomenally conscious of the discrepancies, and the response is typically not present in disorders of consciousness such as the vegetative state (Bekinschtein *et al.*, 2009). P3b is also of bigger amplitude when subjects are asked to pay attention to the deviant stimuli (Schnakers *et al.*, 2009). Although this may be an example where a single process is related to both attentional and conscious processing, the authors indicate that it may be too early to conclude that in auditory processing, attention and consciousness are inseparable, and conclude that further research is needed (Chennu and Bekinschtein, 2012).

Keller (2011) explored the relationships between attention and consciousness in olfaction. Olfaction is very different from vision in several aspects; it is diffuse (lack of spatial specificity), and does not have a distinct intrinsic connection with an object. In addition to spatial aspects, there are also differences in temporality, as odours typically appear and disappear slowly. By contrast to insects that use their antennae to detect odours, olfaction in mammals is not constant, but interrupted according to the sniffs. Importantly, olfactory pathways bypass the thalamus and connect directly to several cortical areas, as opposed to other sensory pathways which involve thalamocortical connections. Olfaction and vision also have similarities. For example, like vision, olfactory attention can be shifted in space by orienting the nose differently, or covertly, by recruiting more attentional processing to a specific odour, for example. This may also allow the source of the odour to be identified. As with vision, attentional processes may speed up task performance in olfactory paradigms. When an auditory cue preceded an olfactory stimulus, subjects had a shorter response time to the odour (Spence *et al.*, 2001). It is also clear that olfactory stimuli can reach consciousness through bottom-up processes. In contrast to other modalities, odours are unable to wake up sleeping subjects; when volatile compounds wake up subjects they do so by stimulating the trigeminal nerve in the nasal cavity (Keller, 2011). This would suggest that during states of low consciousness, intrinsic properties of an olfactory stimulus cannot trigger bottom-up attention. In conclusion, the relationship between attention and conscious processing of olfactory cues also needs further research.

2.2. The quest for the neural correlates of consciousness

There is still no consensus as to whether a neural theory of consciousness can explain how phenomenal experience arises from physical events in the brain (the hard problem, or phenomenal consciousness), or simply characterize the mechanisms supporting cognitive functions (the easy problem, or access consciousness) (Aru *et al.*, 2012). To circumvent the problem of reducing mental states to elementary brain structures, Crick and Koch (1998) proposed to leave that issue aside for the time being, and focus on “correlating” mental and neural events to find out about their relationship. This search for neural correlates of consciousness (NCC) is known to have its limitations but it is believed to lead ultimately to a better understanding of neural processes that support consciousness. An NCC is defined as the minimal set of neuronal mechanisms jointly sufficient for a specific conscious percept to occur. In practice, defining the NCC implies a contrastive analysis, in which researchers compare the neural and behavioural responses elicited by perceived vs. unperceived stimuli, in order to characterize the neural and cognitive features that are specifically involved during conscious vs. unconscious processing. A valid NCC would thus be found only during conscious experience and never in its absence.

Regarding the level of consciousness, the quest for NCCs has benefited from the study of sleep and anesthesia, as well as the different clinical conditions reviewed above. Regarding the content of consciousness, most data and greatest detail regarding NCCs comes from visual psychophysics and brain imaging, where an arsenal of techniques allow the display of subliminal, invisible images in various manners (Kim and Blake, 2005). These studies led to a better understanding of visual consciousness but the interaction of conscious and unconscious visions with other senses remains to be explored (Deroy *et al.*, 2016). This interaction is crucial considering the multisensory nature of perception, and the relevance of touch, olfaction, audition, or nociception in the field of animal consciousness. The sense of touch or olfaction constitutes a promising model to study perceptual consciousness, considering its rather ‘‘primitive’’ attributes, with both phylogenetic and ontogenetic roots preceding those of vision (Gregory, 1967). Accordingly, its functional organization and the computational steps underlying tactile or olfactory consciousness are likely to be simpler compared to vision, and therefore more accessible to empirical investigations and theoretical interpretations. Below, we review some of the main neural correlates of consciousness.

2.2.1. Neuroanatomy

Over the years, clinicians and scientists have noticed that widespread damages in parts of the nervous system may have no or little impact on the level of consciousness (e.g., spinal cord, cerebellum) but other, more limited damages can cause severe disorders of consciousness (Koch *et al.*, 2016). This loss of consciousness is usually associated with lesions of the grey or white matter of the cortex and, most of the time, with the involvement of the thalamus. Other structures, particularly in the brainstem (e.g., ascending reticular activating system, see above), are necessary to enable consciousness since coma is likely to follow lesions in these regions, but in themselves are not sufficient for conscious experience. These structures should therefore be considered as enablers of the level of consciousness, rather than of generators of consciousness *per se*.

One focus of research on the contents of consciousness concerned the role of primary cortices for subjective experiences. Crick and Koch (1995) first suggested that the primary visual cortex is not part of the neural correlate of consciousness, in the sense that activity of these neurons does not contribute directly to phenomenal experience. This claim was comforted at least in part by electrophysiological, neuroimaging studies, and clinical studies. At the clinical level, the role of the primary visual cortex for conscious vision is illustrated by the phenomenon of "blindsight", resulting from a lesion in the primary visual cortex (Weiskrantz, 1986). When blindsight patients are asked to discriminate two stimuli (e.g., a grating tilted to the right or to the left), they deny having any experience of the visual stimulus (i.e., they claim to be blind), even though their performance in discriminating the stimulus exceeds what would be expected from a blind person (i.e., random, chance-level performance). Even though the rest of the visual system (qualified as extrastriate) of these patients functions normally, visual information does not reach consciousness. This could be due to insufficient activation of extrastriate areas following a lesion in the primary cortex, or insufficient activity in the primary cortex *per se*. Since patients with damaged extrastriate areas and intact primary cortices also suffer visual unawareness, primary areas are unlikely to contribute directly to conscious experiences, and the role of higher-level areas is held to be greater. One should note that not all extrastriate areas play a role in visual consciousness. An influential model for visual processing (Goodale and Milner, 1992) distinguishes two main pathways, a ventral stream involved in object processing and recognition, giving rise to conscious percepts, and a dorsal stream involved in spatial processing and visual control of skilled actions, with little or no contribution to the contents of consciousness. Besides visual consciousness, several lesion studies highlighted the role of other cortical regions for the content and level of consciousness. Of note posterior prefrontal regions are believed to play an important role for consciousness, because lesions in these regions are usually responsible for hyperkinetic mutism (Inbody and Jankovic, 1986), in which patients produce uncontrolled motor activity, and seem unconscious of themselves and of their environment. By contrast, lesions in more anterior parts of the prefrontal cortex seem to have a low impact on consciousness. This distinction, as well as others, are reviewed elsewhere (Tononi and Laureys, 2016).

2.2.2. Neurophysiology

The last twenty years have seen a surge of interest in the electrophysiological mechanisms associated with the level and content of consciousness. This work has provided a finer level of detail than the neuroanatomical descriptions provided above. We summarize the vast corpus of studies of these mechanisms in two main categories: neural feedback, and neural synchrony.

When presented with a visual stimulus, two main waves of neural activity occur. First a so-called “feedforward sweep”, starting from early visual areas and ascending to higher level areas, responsible for the encoding of basic visual features (see Box 6). Second, a re-entrant wave of activity, either from horizontal connections within visual areas, or originating from high level areas. The high level areas can be seen as high-level cortical areas sending feedback signals to low-level visual areas. Work in macaques and humans has shown that feedforward activity is associated with unconscious processing of visual features, and does not result in conscious visual experience. By contrast, the secondary, descending neural feedback modulates the tuning of neurons in low-level areas. It enables complex visual processing such as figure/ground segregation, and is thought to instantiate access to visual consciousness. This suggests that the feedforward sweep of information processing is mainly involved in unconscious vision, whereas recurrent processing is required for visual awareness. In summary: in coherence with the attention *vs* consciousness distinction (Koch and Tsuchiya, 2007; van Boxtel *et al.*, 2010, Lamme (2006; 2010) proposes that shallow feedforward processing leads to an *unattended, unconscious* experience. Widespread feedforward processing that reaches higher cortical areas, such as prefrontal and motor cortices, leads to an *attended, unconscious* experience. Shallow recurrent processing which does not reach such higher cortical areas, leads to an *unattended conscious* experience that does not influence behaviour, cannot be reported and which is quickly overwritten by other phenomenal experiences. Finally, widespread recurrent processing from the visual cortex to high level areas in the temporal, parietal, motor and/or frontal cortices leads to an *attended consciou*s experience, accessible to cognitive operations (Lamme, 2006; 2010).

Box 6. The feedforward sweep in visual processing

Typically, cells of the primary visual cortex start to respond 40 ms or more after the onset of a stimulus while other areas of the visual cortex (extrastriate areas) respond with successively, slightly longer delays. At about 80 ms most visual areas are activated, at 120 ms visual activation can be found in all cortical areas, including the motor cortex (Lamme and Roelfsema, 2000). During the feedforward sweep, early visual areas extract simple features of the image such as orientation, shape, colour, or motion (Bullier, 2001; Lamme and Roelfsema, 2000), but also complex features, because cells in the inferior temporal cortex distinguish between face and nonface stimuli with their first spikes (Oram and Perrett, 1992; Rolls and Tovee, 1994). Motor responses are initiated when the feedforward sweep reaches motor regions (Dehaene *et al.*, 1998), while control centres are activated in the prefrontal cortex. The feedforward sweep thus enables a very rapid categorization of visual stimuli, probably into relevant categories (Lamme, 2006).

Besides neural feedback, some authors have proposed that neural synchrony is a key element for consciousness. Indeed, the synchronization of oscillatory neural signals has been proposed to shape the content of consciousness by supporting integration and by joining distributed sets of neurons into coherent sets during visual or multimodal processing (Lamme and Roelfsema, 2000). Moreover, neural synchrony is thought to play a role for aspects other than perceptual consciousness such as working memory (Engel and Fries, 2010). Neural synchrony is a mechanism well-suited to enabling any given content in working memory to be maintained, notably by stabilizing neural assemblies in some reverberatory state, and thereby preventing the occurrence of temporally disorganized activity. It is also commonly assumed that maintaining high levels of consciousness implies enhanced thalamocortical synchrony in high oscillation frequencies. Importantly, regarding both the content and the level of consciousness, coupling between oscillatory neural signals must be specific in order to be potent: unspecific global synchronization throughout the brain is observed in sleep, epilepsy, or anesthesia, which, as we saw previously, are counterproductive to consciousness.

2.3. Theories of consciousness

The various theories that emerged from the quest for NCCs state that consciousness requires either integration of information throughout the brain, involvement of mechanisms such as short range or long range feedback connections, or neural synchrony. As of today, there is no general consensus and no unified theory to explain the different aspects of consciousness outlined above. We chose to present briefly two of the most influential theories — the Global Workspace and the Integrated Information Theories of consciousness.

2.3.1. Global Workspace. Theory of consciousness

The idea of a “global workspace” for consciousness combines several consensual aspects of existing theories on the easy problem of consciousness, or access consciousness (see chapter 1). Baars (1988) initiated the idea of a model where the current conscious content is represented within a distinct mental space called global workspace, with the capacity to broadcast this information to a set of other processors. A global workspace is defined as an information exchange system that allows specialised processors in the nervous system to interact with each other, and is thought to be located in prefrontal regions of the brain (Baars, 1988; Dehaene and Changeux, 2011). In this framework, specialised unconscious processors compete or cooperate for access to that global workspace. Once having gained access, specialized neurons of the global workspace can send back information to all other specialised processors through long-distance projections, resulting in an “ignition” of brain activity. Thus, conscious access is thought to occur when incoming information is made globally available to multiple brain sub-systems through a network of neurons with long-range axons, densely distributed in the prefrontal cortex. Converging neuroimaging and neurophysiological data indicate objective neural measures of conscious access: late amplification of relevant sensory activity, long-distance cortico-cortical synchronization in the high frequency range (β and γ at 13-80 Hz), and “ignition” of a large-scale prefronto-parietal network. Plus, the selective loss of re-entrant/feedback connectivity during general anesthesia tends to confirm the proposed role for feedback connection in consciousness (Dehaene and Changeux, 2011). At the behavioural level, the global workspace theory accounts for many properties specific to conscious processing, including information integration, flexibility, temporal maintenance, and additional amplification of information (Dehaene and Naccache, 2001). Today, it is one of the most influential theories for the neurocognitive bases of consciousness. Within this framework, selective attention and conscious access are considered to be related but dissociable concepts. Attention is seen as a ‘‘gateway’’ that regulates which information reaches the global workspace, and therefore conscious access. Without attention, a stimulus, even if salient, is not consciously perceived, and remains “preconscious”. Preconscious refers to salient stimuli which could reach consciousness if attention were paid to them. Hence, attention is a selection process where some inputs are processed faster, better or are more widespread than others, increasing the chance of producing or influencing a behavioural response and conscious access (Lamme, 2010).

2.3.2. Integrated Information Theory

The Integrated Information Theory (IIT) identifies consciousness with information integration, so that the level and content of consciousness of a system are equivalent to the ability of that system to integrate information over and above the information that is integrated by the union of its parts (Tononi, 2010). IIT starts from phenomenology, by noting that subjective experiences are both informative (i.e., conscious experiences are extremely diverse and rich), and integrated (i.e., one experiences the world as a unified whole rather than a sum of disjoint features). IIT is grounded on six axioms, which are thought to capture the essential properties of experience. A mathematical framework is derived from these axioms, producing a measure termed *phi*, which measures the level by which a system integrates information over and above the sum of its parts. Put simply, if a system can be broken into multiple independent parts without altering its function (e.g., several photoreceptors of a camera chip), its value of phi will be null, and so will be its conscious state. By contrast, other architectures such as thalamo-cortical loops cannot be broken down in such way, and are characterized with high values of phi, and therefore conscious. At the roots of IIT is the assumption that consciousness is a basic constituent of our physical universe, similar to mass or to an electric charge. This leads to panpsychist views, according to which all living and non-living complex systems (e.g., robots, networks, particles) could in theory be conscious, along a continuum. However, IIT also provides strict criteria for consciousness to occur, so that any non-living complex systems are unlikely to be characterized by high values of *phi* (Tononi and Koch, 2015) (but see Aaronson, 2014) for a criticism), and acknowledges that *phi* values greater than that of humans could be found. Thus, since consciousness is described for non-zero values of *phi*, one crucial aspect of IIT is that it is directly applicable to animal consciousness, as the estimation of *phi* is substrate-independent. In its current form, the estimation of *phi* for human brains is computationally intractable, and only rough, empirical estimations are available. At the empirical level, researchers have used an approach based on perturbation to infer the level of integration enabled at a given level of consciousness. For example, during wakefulness or REM sleep, external perturbations such as those induced by strong magnetic fields (i.e., transcranial magnetic stimulation) were found to induce changes in activity patterns across distant interconnected brain regions, indicating that connectivity between distant brain areas during wakefulness is enabled. By contrast, during non REM sleep or anesthesia, the response evoked by transcranial magnetic stimulation remains either local (loss of integration), or spreads not specifically (loss of information). This kind of experimental data gives strength to the hypothesis that the level of consciousness is linked to the capacity of the brain for integrating information.

2.3.3. Predictive coding and consciousness

As we described above, both the global neuronal workspace and the integrated information theories state that information is processed hierarchically to generate conscious experience. However, we should not consider the brain as a passive processor. Instead, a prior internal model of perceptual reality precedes perception, as put forward by the predictive coding framework. In short, predictive coding is a bayesian perspective of brain function, in which “priors” (i.e., pre-existing models built from experience and stored in memory) are permanently updated and revised according to new information from the environment (Moutoussis *et al.*, 2014). In this context, sensory information received by the brain is not used to generate consciousness *per se*, but rather to detect errors between what is expected by the internal model (i.e., the prior), and what is being actually perceived from the environment. Thus, according to this scenario, key perceptual information is not ascending in a bottom-up manner (for instance from primary visual to prefrontal cortex) but are rather descending in a top-down manner within a hierarchical cognitive architecture. When prediction errors between priors and the internal model are detected, the model is revised and updated accordingly. In fact, it is precisely these prediction errors that need to be coded in order to adjust the model. Accordingly, events that remain stable and consistent within the model do not require much conscious attention, while events associated with high prediction errors (e.g., novelty, surprise, awareness of potential threat, pain, etc.) account for much of the conscious content. Consciousness may thus be described as the interplay between the internal predictive model and external reality (Clark, 2013).

Further developing this concept, the Predictive Interoception Coding model proposed by Barrett and Simons (2015) and; Oosterwijk *et al.*, (2016) takes into account the interoceptive information flow from internal bodily organs. According to this model, the permanent flow of signals issued from the body is supposed to « prepare », or set the « tone » according to which further incoming sensory inputs from the external world will be interpreted. In other words, interoceptive signals act as a basis for interpretative anticipation.

2.4. Conclusions

This chapter is a brief overview of the issue of human consciousness. We split the problem into two parts, focusing on its level and on its content. We started by reviewing the behavioural and brain correlates of situations in which levels of consciousness are low (sleep, anesthesia, coma, seizures), highlighting the importance of enabler systems for maintaining a high-level of arousal. Next, we turned to the contents of consciousness, and described recent results in three of its main components, perception, cognition, and metacognition.

Following this two-dimensional analysis of levels and contents, we briefly reviewed the neuroanatomical bases of consciousness, and discussed the role of the thalamo-cortical system, as well as early and high-level cortical areas. In more detail, we also described neural feedback and neural synchrony as two important mechanisms for the level and content of consciousness. Finally, we outlined two of the main theoretical frameworks attempting to make sense of many empirical results. These were the global workspace theory, stressing the importance of fronto-parietal neurons for sharing information across the brain, and the integrated information theory, which assumes that the essence of consciousness is the capacity of a complex system like the brain to integrate information.

One common aspect of most of the work we reviewed is that it relies on a contrastive analysis: the key approach to study the level and content of consciousness is to compare situations in which level/content are low or absent with situations where the subject is fully aware. This is the logic that guided the quest for a definition of the neural correlates of consciousness in humans, and, as we will see in the next chapters, the same logic will be applied to animals. Studying the levels of consciousness in animals does not pose immediate concerns, as sleep, seizures, and disorders of consciousness are all observed in many animal species as well as in humans. Thus, contrasting high and low arousal states in animals does not seem out of reach. Studying the content of consciousness in animals might seem more challenging, as most studies we reviewed in humans rely on reports by the subjects themselves, either verbal or measured with button presses. As described in the following chapters, training animals to obtain subjective reports is also possible for many species. To what extent we can trust these subjective reports is an open question that will be addressed in the next chapters. In this context, we note that relying on subjective reports to study the content of human consciousness can also be problematic. With such approach, it is hard to know whether what is measured is the pure content of consciousness, or whether the measure is contaminated by the way in which the content of consciousness was reported. In other words, it is hard to not overestimate the neural correlates of consciousness, so that they include only the neural mechanisms directly generating the experience, and not those necessary to report it. Recently, some researchers have attempted to tackle this issue by relying on the so called no-report paradigms (Tsuchiya *et al.*, 2015). In a nutshell, those paradigms consist in bypassing the need of subjective reports to infer whether contents are conscious or not. Typically, bypassing is performed by decoding physiological measures including brain imaging but also eye movements or pupil size. One challenge in the absence of a report is to make sure that the decoded contents reflect conscious experience and not mere unconscious processes. In case this distinction is not perfect, the measured neural correlates of consciousness including unconscious neural processes will also be overestimated. This is the very same risk one takes when attempting to decipher conscious contents in infants, non-communicating patients, or animals. One always faces the possibility that what is measured reflects unconscious processing rather than consciousness *per se* (see the notion of philosophical zombies in chapter 1). Although these paradigms are still under active development, they are very relevant in studying consciousness in non-communicating patients, infants, or animals.

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CHAPTER 3: CONSCIOUSNESS IN ANIMALS

3.1. Introduction

The philosophical and biological questions about consciousness in humans were covered extensively in the first two chapters. However, there are good reasons for extending our biological questioning on consciousness towards animals. First there is no strong scientific argument to deny *a priori* the presence of consciousness in animals. Second, due to fundamental and practical implications, it is relevant to investigate whether and how different levels and contents of consciousness also exist in non-human species. Griffin (1976) argued that evidence for the complexity and sophistication of animal behaviour in cases, such as use of tools, communication and problem solving, is increasing and has revealed unsuspected capacities that in turn suggest conscious awareness. Such capacities should help animals to integrate the information they receive into a larger picture, allowing them to summarize relevant information making it accessible for high level cognitive treatments and for responding adaptively in novel situations. The question of whether the emergence of levels and contents of consciousness should be linked to increasing behavioural complexity in phylogenesis will be discussed in Chapter 4.

The existence of some forms of consciousness in animals has already been acknowledged in the literature in restricted ways. Thus, theories and questions related to visual consciousness have been extended from humans to monkeys. For example, blindsight is the inability of people who are cortically blind to respond to visual stimuli that they do not consciously see (cf. 2.2.2). It has been used to demonstrate similar processing of visual information in monkeys as in people. Visual consciousness and different levels of such consciousness are now well established in monkeys (Stoering and Cowey, 1997). The existence of sleep with changes in the level of consciousness throughout the day-night cycle has also been reported in animals, with functional characteristics resembling those of humans (cf. 2.2.2). Two types of sleep (REM and non-REM) have been observed in terrestrial and marine mammals as well as in birds (Vorster and Born, 2015; Beckers and Rattenborg, 2015). Researchers have also applied novel neurobiological and neuropsychological approaches to study animal cognition with the goal of using animals as models for the study of neuropsychiatric disorders in humans. This strategy presupposes convergence of emotional and other conscious states between humans and these model species, which include not only mammals but also birds and fish. Accepting the presence of consciousness in animals implies a reconsideration of the relationships between them and humans. For instance, handling procedures for domestic animals used for meat production, among others, has been extensively reconsidered from this new perspective. Overall, all these reasons explain the recent increase in publications and debates on consciousness in animals.

As a following to the state-of-the-art information on human consciousness presented in chapter 2, we will now discuss published information, which will extend such discussion on various aspects of consciousness to animals including mainly vertebrates, but also some invertebrates.
There are at least three challenges that complicate this task:

1) As consciousness is private and inherently linked to one's own experience, the absence of narrative language in animals impairs communicating their experience. This prevents us from having direct access to an animal's experience. However, we will show how overcoming this difficulty may be partially possible based on appropriate behavioural tests to which humans are commonly exposed in studies on consciousness. Similarities in performance, which may not necessarily prove that underlying mechanisms are similar, may help interpreting the levels of information accessible and interpretable to animals. Moreover, combining investigations on behaviour, comparative brain anatomy and physiology, as well as considering phylogenetic relationships between species, is also an important approach when discussing consciousness in animals.

2) The term "animals" includes a large diversity of species, vertebrates and invertebrates, living in very different environments and arising from different evolutionary histories. In that context,

one might anticipate that consciousness would vary greatly among species, and would differ from that in human. Moreover, if we take an evolutionary perspective, most people would argue that this capacity appeared late in evolution, after the split of human ancestral lineage from that of non-human relatives. Yet, so far, this view has never been demonstrated. Comparative analysis of brain structures along the evolutionary pathway has not completely solved the question. We will show that different authors have argued that consciousness is probably associated with different brain structures that vary with the species considered. Moreover, the information available in vertebrates and invertebrates on the relationship between the mind of animals and the anatomical and physiological organizations of their central nervous system is limited and does not help to solve these issues. On the contrary, if we assume that consciousness is an emergent property of the nervous system, the question of animal consciousness becomes evident as animals, like humans, have typically specialized sense organs and nervous systems that allow them to respond adaptively to environmental stimuli. The relevant question would be then, not whether only humans possess consciousness, but rather, from which nervous system complexity consciousness can emerge.

3) Most of the studies on animal cognitive abilities have not been designed to analyse consciousness in animals (as noted in a recent recension by de Waal, 2016), which drives us to discuss these studies in relation to consciousness according to criteria established in humans. In this chapter, we focus on the behavioural components of animal life and discuss whether or not characteristics of human consciousness can be extended to animals.

In this context, this chapter will start by analysing the relationships between consciousness and five important components of animals life—emotion, metacognition, episodic memory, social behaviour and human-animal relations. These behavioural and cognitive processes in animals will include a description of neuronal correlates. However, we have not set out to be exhaustive and do not cover such behavioural and cognitive components of consciousness as the ability to integrate the relations between the means and the ends, the sense of agency or the use of tools by animals.

We acknowledge that consciousness in animals has not been demonstrated so far to be equivalent to the consciousness as described in humans, and consequently we could have used another term. However, for the ease of reading, we have kept the term “consciousness” along when applying it to behavioural, cognitive or neurobiological investigations in nonhuman animals. We focus our discussion along a two dimensional analysis of consciousness involving levels and contents (see Chapter 2) that is most often described in humans.

3.2. What emotions can tell us about consciousness in animals?

Emotions are intense, short-lived reactions to specific events or stimuli which can be characterized by two main dimensions (Russell, 1980; Kron *et al.*, 2015): arousal (bodily activation or excitation) and affective direction (positive, or pleasure, and negative, or displeasure). An emotion is usually described by behavioural and physiological expressive components and by a subjective component, which, strictly speaking, is the emotional experience (Dantzer, 1989). In animals, the subjective component can be only inferred from the behavioural and physiological components. There are clear similarities between humans and animals in the behavioural and the physiological components, at least for vertebrates. The subjective component is obviously more difficult to access in animals than in humans as they cannot verbalise. However, even if animals cannot tell us in words what they like and dislike or what they want or want to escape from, their behaviour can be used as a convincing substitute of verbal reports. Several methods have been employed for accessing an animal’s perspective. Choices can be quantified in preference tests (first choice and repeated choices) to assess the information guiding such choices. Animals can be induced to work for reinforcements to determine what they like or dislike and to assess how much or how little they want (Dawkins, 2015). Also, from an ethological point of view, it is sometimes possible to study the body language of the animals and thus to get insights into their emotional experiences.

This section aims to discuss consciousness together with emotions experienced by the animal. Part 3.2.1 summarizes the approach developed in animals, which is based on appraisal theories originally developed for human psychology. Part 3.2.2 considers the increasing body of studies in animals that explore alterations of emotional experiences and their impact on elementary cognitive functions, such as attention and judgment, which can change their perception of the environment and, in turn, modify emotional reactions. Part 3.2.3 explores animal consciousness from the perspective of the conscious processing that is involved in human emotional experience.

3.2.1. Animal emotions and cognitive psychology: when cognitive processes elicit emotions

The study of animal emotions has been the subject of increasing interest in the past decades. It was at the origin of a new discipline referred to as "affective neuroscience" (Panksepp, 1998).

Among many studies produced by 'animal affective scientists', some focus on appraisal theories used in cognitive psychology to understand human emotions. They provide a strong framework enabling to understand the nature of emotional experiences in animals (Mendl and Paul, 2004; Boissy *et al.*, 2007 a; Veissier *et al.*, 2009). According to these theories, human emotions result from an individual evaluating a triggering situation, beginning with an evaluation of the situation *per se* and followed by the responses to that situation (Lazarus *et al.*, 1970; Scherer, 2001). A fourth component, named cognitive component, is added to the three components (subjective, behavioural and physiological components) that characterize emotions. Scherer (2001) stated that the evaluation follows a sequence of checks (assessments) grouped into four classes:

i) The relevance of the situation, including the check for novelty (suddenness, familiarity and predictability), the check for intrinsic pleasantness, and the check for relevance to the individual's own goals;

ii) the implications of the situation for the individual, including a check of the probability of the expected consequences and a check for consistency with the individual's expectations;

iii) the coping potential, including a check on the possibilities of coping within the environment, (its controllability) and abilities within the individual; and

iv) the normative significance, including a check for internal standards (if I fail to respond correctly, will that affect my self-esteem?) and a check for external standards (are there responses that are preferable or compulsory according to the social group I belong to?). These checks do not necessarily need high-level cognitive processes.

According to Scherer (2001), the outcome of the checks controls the psychological component of an emotion, which in turn affects physiological and behavioural responses. Typical human emotions, such as fear, anger and happiness, are linked to the outcome of the evaluation. Sander *et al.* (2005) report links between human emotions and the individual's evaluations that triggered them. For instance, fear is experienced by an individual when he/she is exposed to an unpleasant event which is sudden, unfamiliar, unpredictable and inconsistent with his/her expectations. Rage is experienced in similar situations, except that the individual's evaluation is that he/she cannot control this situation. The appraisal theory developed by Scherer (2001) appears to encompass other appraisal theories that emphasize either the nature of the checks (Smith and Kirby, 2001), the levels of cognitive processes (Philippot *et al.*, 2004), or present slightly different descriptions of checks (Frijda, 1986).

A comprehensive study used paradigms derived from appraisal theories and adapted them to sheep. This study was developed to understand better how the animal evaluates its environment and responds to it emotionally (for reviews; Boissy *et al.*, 2007a; Veissier *et al.*, 2009). Sheep were exposed to situations designed to enhance the prominence of a certain check. It was postulated that if the outcome of checks that require cognitive processes has an impact on emotional responses, then the animal would not only express emotional responses but also feel emotions. It is important to note that such emotional responses suppose conscious and high-level cognitive processes and cannot be seen as mere stimulus-response processes. In that context, sheep exhibit distinctive profiles of behavioural and physiological responses to different events defined according to the checks. For examples, the sudden presentation of a familiar object induces a startled response and a brief cardiac acceleration, but the presentation of an unfamiliar object elicits a behavioural orientation towards the object and a transitory increase in the variability of heart rate. These evaluative processes appear to be automatic and non-conscious. However, going beyond these stimulus-response reactions, sheep are also able to anticipate events and their emotional response to an event can be affected by its predictability. Sheep are also able to form expectations. A discrepancy between their expectations and the current situation itself induces behavioural agitation and cardiac acceleration. Similarly, sheep are able to control their environment in such a way that the emotional response to a given event depends on the extent to which the animal can act on it. In an experiment, researchers applied to sheep the check of compatibility with the social norms in using the typical dominance hierarchy in this species. The emotional responses of individual sheep to a disturbing situation varied according to its position in the dominance hierarchy: A sheep expresses more internal, often physiological, reactions when it is dominated by a partner. It expresses more overt behavioural reactions when it dominates the partner.

These findings indicate that emotional responses of sheep involve cognitive processes. Sheep not only have emotion-related responses, which could be considered to depend on stimulus-response processes, but they also experience complex emotional states. Similar results have been described in other animal species such as quails (Valance *et al.*, 2008), even if in less detail. Sheep may experience a wide range of emotions including fear, rage, despair and boredom *via* their sensitivity to suddenness, unfamiliarity, unpredictability, and discrepancy from expectations, controllability, and social norms (Veissier *et al*., 2009). Therefore, emotional processing in animals must now be regarded as having not only behavioural, physiological and subjective components, but also a cognitive component that forms the basis of the emotional experience.

Other recent investigations in rats suggest that the anticipatory behaviour of an animal to a positive event is linked with positive emotional states. Indeed, specific behavioural responses are observed in the period between a signal that predicts a reward and the delivery of the reward both in classical and operant-conditioning protocols. In these experiments, male rats were conditioned to anticipate transfer to various environments: an enriched cage, sexual contacts with a female, transfer to a standard cage or to their home cage (van der Harst *et al.*, 2003). Rats waiting to be transferred into an enriched cage or for sexual contact with a female engaged in more behavioural transitions compared to rats waiting for their transfer to a standard cage or their home cage. In other studies, minks increased locomotor activity following exposure to the conditioned stimulus of a positive reward (Hansen and Jeppesen, 2006). Likewise, laying hens stood more alert, with their neck stretched and eyes open, after a conditioned stimulus signalling forthcoming mealworms (Moe *et al.*, 2013).

Taken together, these studies provide strong evidence that modified activity may be associated with positive emotions. Anticipation is commonly assumed to represent the appetitive, or “wanting” phase of positive emotions (Spruijt *et al.*, 2001; Boissy *et al.*, 2007b; Mendl *et al.*, 2010). Overall, one could anticipate that in all these examples, animals have developed some affective conscious state through expression of emotion triggered by the process of evaluation.

3.2.2. Emotional states and cognitive psychology of animals: when emotions alter cognitive processes

Our better understanding of how emotions influence cognitive functions has enabled us to develop new frameworks to assess prolonged affective states in animals. Here again, the concepts underlying these frameworks are derived from a significant body of psychological research in humans. This research has shown how emotional responses can bias the cognitive capacities of the individual. The bias involves changes in learning and memory, and also in attention and judgment of the situation that are involved in the selection of the stimuli that the individual prioritize. For instance, emotionally-loaded events are more readily remembered than neutral ones (e.g., Reisberg and Heurer, 1995). Likewise, moderate to strong emotions improve memory, while extreme emotions have a deleterious effect on memory (Mendl *et al*., 2001). These effects are well-known but current emotions may also affect attentional and judgment processes. For example, anxiety induces an attentional shift towards potential threatening information (Bradley *et al.*, 1997). Likewise, participants exposed to negative events tend to interpret all subsequent ambiguous events negatively (Wright and Bower, 1992). The overall emotional modulations of the cognitive processes are interpreted as having adaptive value by helping a fearful or anxious individual to pay attention to, to memorize and to make judgments on threatening circumstances (Mendl and Paul, 2004; Fiacconi *et al.*, 2015).

Modulatory effects of emotions on learning and memory have been frequently reported in animals (Paul *et al.*, 2005). For example, heifers subjected to strong stressors are unable to extinguish a previously learned behaviour that is no longer rewarded which prevents them from acquiring a new, more appropriate behaviour (Lensink *et al.*, 2006). In contrast, a moderate stressor facilitates learning and rats that have received a catecholamine injection, mimicking the physiological component of a moderate emotion, pay more attention and display improved memory (Sandi *et al.*, 1997). Similar modulatory effects have been described in zebrafish (Perathoner *et al.*, 2016).

More recently, studies have investigated the effects of emotions on attention and judgement in animal species. They were made possible through the development of a judgement-bias test in rats (Harding *et al*., 2004) which has been adapted and used in a range of species including starlings (Matheson et al., 2008), dogs (Burman *et al.*, 2011), sheep (Doyle *et al.*, 2010; Destrez *et al.*, 2012) and pigs (Douglas *et al*., 2012).

In sheep, the test is based on a spatial discrimination task (Doyle *et al.*, 2010; Destrez *et al.*, 2012). Sheep were trained to associate a bucket in one side of a pen with a reward (food) or another bucket at the opposite side of the pen with a negative reinforcer (a dog or a noisy blower). Once trained to respond in this go/no-go task, sheep were exposed to several ambiguous cues. The bucket was located in various positions between the positively and the negatively trained locations, and the animal's response was measured. The response to these ambiguous cues is thought to reflect the animal's positive or negative emotional state or mood. An 'optimistic' judgement-bias is suggested when ambiguous cues elicit responses resembling those elicited by positively reinforced cues. A 'pessimistic' bias is shown when the animal treats ambiguous cues as being similar in outcome to negatively reinforced cues. With this methodology, Burman *et al.* (2008) elicited a 'pessimistic' bias following negative past experiences such as removal of environmental enrichment. Doyle *et al. (*2011b) and Destrez *et al.* (2013) observed such a bias after repeated exposures to unpredictable and antagonistic events. Pessimistic biases have also been suggested in conditioning experiments in honeybees where variation in the ratio of components of odour mixtures can create ambiguous stimuli, closer or distant from rewarded and not rewarded odour combinations (Bateson *et al*. 2011). Yet, simpler explanations have also been suggested to account for these performances based on simple discriminative processes that preclude emotional arguments (Giurfa, 2013).

Other types of cognitive bias measures, such as attention bias or threat perception (Brilot and Bateson, 2012), reflect states such as anxiety as shown by increased attention and vigilance in response to a threat. All in all, these findings suggest that cognitive biases may participate in the development of long-lasting affective conscious states in mammals and birds. However, supplementary experiments will be necessary to consolidate this view.

3.2.3. How the relationships between emotions and cognition help to access consciousness in animals

The experimental proof of the existence of an emotional component in animals does not imply that they are conscious of their own emotions. However, improvement in the knowledge of the relationships between emotions and cognition provides new insights into the existence of consciousness in animals (Mendl and Paul, 2004).

As reported in the earlier sections of this chapter, many animal species, including fish, are capable of the same evaluative processes as those known to trigger emotions in humans. Anticipation, expectation and ability to control, all assume that the individual has some mental representations of the outcome. Studies on expectation clearly show that animals not only respond to the intrinsic value of a reward, but also respond according to their previous experience of the reward. Crespi, in a pioneering work in 1942, reported that rats walked more slowly or more quickly to the site of a food reward if the reward was smaller or larger than the reward they were accustomed to receive. He concluded that these results were evidence of a form of "expectation" in rats, so that rats receiving a reward below the level of expectation were "frustrated" while rats receiving a reward above the level of expectation were "elated". Similar results have since been shown in a number of animal species, including insects confronted with variable rewards, using incentive contrast paradigms in studies that were not designed to tackle the issue of consciousness (Flaherty, 1982).

So, evaluative processes are biased by the emotional past experience in animals as well as in humans, but the evaluative checks defined by Scherer (2001) for humans require different levels of cognitive processes. Some are fairly automatic and subconscious, especially within the first check of relevance, while others are more complex (Kappas, 2006) and need conscious access. Evaluative checks operate at several levels according to the cognitive complexity of the situation. Leventhal and Scherer (1987) distinguish three levels: i) a sensorimotor level that involves automatic processes, ii) a schematic level requiring the individual to memorize emotional experiences and which involves conditioned responses, and iii) a conceptual level that is voluntarily and consciously activated, for example by comparing the present situation with conscious plans or self-representation. Within the check of relevance, suddenness seems to require only automatic processes while familiarity and predictability require at least schematic processes. Likewise, assessing a situation in terms of expectations and controllability requires schematic processes, while the check of normative significance is likely to require higher-level cognitive processes (Leventhal and Scherer, 1987).

Conscious emotional experience in animals can also be supported by the concepts of "empathy" and "emotional contagion" particularly in the case of social animals. As it will be developed in section 3.4 on social behaviours, expression and perception of emotions play a crucial role in the regulation of social interactions (Panksepp, 2010; de Waal, 2016). The perception of emotion can trigger the same emotions in the receivers than in the senders. This phenomenon is termed "state matching" or "emotional contagion", and is the foundation for empathy, which is the ability to be affected by, and to share the emotions of others (Preston and de Waal, 2002). Emotional contagion improves transfer of information through state sharing between individuals, resulting in higher coordination among members of a group and stronger inter-individual bonds (Špinka, 2012; de Waal, 2008). For example, emotional contagion of negative emotions like fear within a group enables rapid defensive behaviours towards predators. By contrast, the transmission of positive emotions through play (Boissy *et al.*, 2007b) enhances a positive long lasting affective state, resulting in stronger bonds between individuals (Špinka, 2012). Emotional states that lead to emotional contagion can be expressed in many ways; through olfactory signals (Boissy *et al.*, 1998; Amory and Pearce, 2000), visual signals (Mineka and Cook, 1993), vocalizations (Buchanan *et al.*, 2012), or a combination of these (Langford *et al.*, 2006; Edgar *et al.*, 2011). Familiarity, social affiliation, sociability and past experience play a crucial role in emotional contagion.

3.2.4. Conclusion

Emotions are reactions which deeply modify and shape many aspects of physiological, cognitive and behavioural functions. Modern studies have investigated emotional reactions and experience in animals by using frameworks originally developed in human cognitive psychology. Most animal species investigated so far show behaviours that have functional parallels with human conscious cognitive processes. The studies now bring ample support to the hypothesis that animals do experience a wide range of emotions, including fear, anger, rage, despair, boredom, disgust, and happiness that might be consciously experienced. Thus, the same gradient of consciousness in emotional experiences may be transposed from humans to animals, depending on the level of the cognitive processes used to appraise the eliciting situation. The original frameworks developed in human cognitive psychology offer promising new ways for the scientific exploration, even if indirect, of consciousness in animals. However, further progress in emotion-cognition-consciousness links in animals will also need to consider developing original theoretical frameworks and experimental methods that are tailored to the specific conditions that given animal species meet in the adaptive challenges of the everyday lives (e.g. de Waal, 2016).

3.3. Metacognition in animals

Metacognition is usually defined as the ability to monitor one's cognitive processes. For example, the ability to monitor the state of one's own memory is referred to as metamemory. In humans, metacognition is linked to consciousness and self-awareness. Thus, because metacognition is considered to be one of the most complex forms of cognition it has been often reported as exclusively human. While in humans the study of metacognitive abilities is mainly based on verbal reports, assessing metacognition in non-verbal animals is a much greater challenge. Experiments testing for metacognition may differ in both design and rationale. Two kinds of paradigms are widely used: those that evaluate metacognitive monitoring (the ability to judge one's own state of knowledge), and those that are designed to measure metacognitive control (the ability to seek information when a lack of knowledge has been detected).The first experiments in animals adhered to the first category; they exploited the possibility offered to experimental subjects to decline or opt-out from a choice situation when the discrimination proposed is difficult. By declining choice in such conditions, subjects can reveal whether or not they monitor their own knowledge and thus their probability of success in the proposed task.

This rationale was used in the pioneer study in dolphins by Smith *et al.* (1995). In this experiment, a bottle-nosed dolphin (*Tursiops truncatus*), was first trained to respond to a left paddle when a tone of 2100 Hz was played and to respond to a right paddle when a tone of any lower frequency (ranging from 1200 to 2099 Hz) was played. As expected, the dolphin's accuracy decreased as tested tones became closer to frequency of 2100 Hz. Then, a third paddle was introduced, which allowed the animal to decline the trial when discrimination was difficult. The dolphin indeed declined more often to make a choice when tone discrimination was difficult. Interestingly, humans, tested in a similar psychophysical discrimination, responded in a similar way and declined to respond whenever they felt uncertain. This study indicates that some animals may monitor their own knowledge similarly to humans. But we need to be cautious in concluding this, as metacognitive tests may sometimes present experimental caveats as we will see below.

3.3.1. Methods of assessing animal metacognition

3.3.1.1. Assessing metacognitive monitoring: the uncertainty-monitoring and confidence-rating paradigms

Uncertainty-monitoring and confidence-rating paradigms are generally based on three types of tests: perception, memory or foraging. The principle of the perception test is to discriminate stimuli according to their psychophysical (usually auditory or visual) properties in a given dimension. For instance, in the study by Smith *et al.* (1995) cited above, a dolphin had to classify an auditory tone according to its frequency (low vs. high frequency). In another study by Shields *et al*. (1997), monkeys had to classify a visual stimulus as either sparsely or densely pixelated. Memory tests, on the other hand, are generally based on a "matching-to-sample task". A sample, for example a picture, is first presented to the subject at the beginning of the trial. Then, after a short delay, the animal has to select among different pictures those that match the sample presented earlier. Here the potential difficulty is the possibility of correctly matching the stimulus perceived with the sample memorized. This paradigm has been frequently used in monkeys (e.g. rhesus monkeys: Hampton, 2001). In the foraging test, also called the food concealment test, the subject has to search for a reward hidden by an experimenter. Examples of foraging tests are those of Call and Carpenter, (2001) who used apes and of Watanabe and Clayton, (2016) who used western scrub jays.

Whatever the tests, once the subject is able to perform the feasible task by making a correct choice, the difficulty of the task is then manipulated. During the perception task, the two stimuli presented to the animals become more difficult to discriminate. During the delayed matching-to-sample task, the delay between the presentation of the sample and the moment animals have to select the matching sample among different items is increased. In the foraging task, the experimenters can hide the bait, move it to induce confusion, or can extend the delay after baiting. Then, if a subject is capable of judging its own state of knowledge (metacognitive monitoring), it should be able to detect the level of difficulty of the task, and to differentiate the choice for which it is certain to know the answer from those for which it is uncertain and to act accordingly. Depending on the timing of the judgment (before or after making the choice) this evaluation is called prospective or retrospective judgment. Two different kinds of paradigms have been developed to measure these two judgments and these are called the uncertainty-monitoring paradigm and the confidence-rating paradigm.

- ***Uncertainty- monitoring paradigm (prospective metacognitive judgment)***

  In the uncertainty-monitoring task, the subject may choose to accept or decline to perform one of the tasks presented above. To do this, an “opt-out option” is given to the animal. This option results in a higher value of reward than the reward given for an incorrect response, but lower than the reward given for a correct response. The prediction is that an animal capable of metacognitive prospective judgment will proceed to the test when it is certain of the answer, but will choose the opt-out option when it is uncertain.

  Species such as dolphin (Smith *et al.*, 1995), rhesus monkeys (Morgan *et al.*, 2014), orangutans (Suda-King, 2008), chimpanzees (Neldner *et al.*, 2015) and rats (Foote and Crystal, 2007) selectively declined the most difficult tasks suggesting they were all capable of prospective metacognitive monitoring. Recently, an experiment on honeybees reached a similar conclusion, although the authors proposed alternative associative mechanisms to account for the bees’ opting-out of a maze upon difficult visual discriminations (Perry and Barron, 2013). On the other hand, prospective metacognitive abilities were not seen in large-billed crows (Goto and Watanabe, 2012) or capuchins monkeys (Beran *et al.*, 2009).

- ***The confidence-rating paradigm (retrospective metacognitive judgment)***

  This paradigm was designed to evaluate a form of retrospective metacognitive judgment: the confidence judgments (“*Am I sure that I was right?*”). The paradigms are similar to those described above except that there is no “opt-out option” because the animal cannot decline the task and must make a choice. However, once the subject has completed the test it has to evaluate its confidence rating, In other words, it has to rate how well it has answered (Shields *et al.*, 2005). For that, after making a response but before a reward is given, the subject is required to select one of two icons: one being a low-risk icon, the other being a high-risk icon. If the subject selects the low-risk icon, it obtains a small but guaranteed reward whether it gives the correct response or not. If the subject selects the high-risk icon, it obtains a large reward in the case of a correct answer but an equally large loss when the response is incorrect. The hypothesis is that an animal that is capable of retrospective metacognitive monitoring would select the high-risk icon for test trials in which it was confident that it had responded correctly and the low-risk icon for those in which it had responded incorrectly.

  This paradigm has been tested in rhesus macaques (Shields *et al.*, 2005; Morgan *et al.*, 2014), large-billed crows (Goto and Watanabe, 2012), pigeons and bantams (Nakamura *et al.*, 2011). These species used the “risk icon” appropriately, suggesting that they would be able to make retrospective judgments.

3.3.1.2. Evaluation of metacognitive control: the hint-seeking paradigm

The hint-seeking paradigm is based on the same tests used in the uncertainty-monitoring paradigm: perception, matching-to-sample or foraging tests. However, in the hint-seeking paradigm, the “opt-out option” is replaced by an option to collect more information to help the subject choose the correct answer in the test. If the animal can monitor its own knowledge of what is and what is not stored in its memory and can control its knowledge by complementing missing information, its hint-seeking behaviour should positively correlate with its level of uncertainty. The paradigms vary slightly depending on the kind of test.

In the delayed matching-to-sample test, the information about the sample was unavailable before the display of the matching stimuli. The aim was to investigate whether animals would choose to go directly to the test or to study a sample stimulus before trying to choose the shape that matched the sample. To obtain this information the animal had to touch a “reveal samples” icon (pigeons: Roberts *et al.*, 2009; capuchins and rhesus monkeys: Beran and Smith, 2011). In another memory test, initially developed in pigeons by Roberts *et al*. 2009, subjects could get a reminder when memory of the sample was weak. In monkeys and rats, some studies have also developed a “play it again paradigm”. Monkeys had to recall and reproduce the location of two squares on a touchscreen, but the target stimuli were no longer visible during the response period (macaques and baboons: Basile *et al.*, 2015; Malassis *et al.*, 2015). In rats, the subjects had to classify a brief noise as short or long (Foote and Crystal, 2012). In this case, they could repeat the stimuli (the noise or the location of the squares) before responding. The general prediction was that an animal capable of cognitive control would preferentially use the “reveal samples” or the “repeat key” icons to obtain more information when it considered its response to be uncertain. Paradigms can also be based on foraging tests during which the animal has to search for a reward hidden in multiple tubes. The experimenters vary the level of uncertainty as explained above (western scrub-jays: Watanabe and Clayton, 2016). The prediction is that animals capable of metacognitive control would look into the tubes more often when they are uncertain of the location of the bait.

The hint-seeking paradigm has been tested with success in rhesus macaques (Hampton *et al.*, 2004), lion tailed macaques (Marsh, 2014), chimpanzees (Beran *et al.*, 2013; Call and Carpenter, 2001), orangutans (Call and Carpenter 2001) and western scrub jays (Watanabe and Clayton, 2016) which suggests that cognitive control exists in these species. In the “play it again paradigm”, rats, baboons and macaques used the repeat key more frequently in difficult trials, in accordance with the prediction (Foote and Crystal, 2012; Basile *et al.*, 2015; Malassis *et al.*, 2015). This clearly supports the idea that these species are capable of metacognitive monitoring, but in certain cases does not provide unequivocal evidence of metacognitive control. For instance, in baboons the use of the repeat-key does not improve performance, so there is no clear evidence of their being able to collect and use the supplementary information efficiently. Moreover, this capacity has not yet been clearly confirmed in capuchin monkeys, dogs, or pigeons, which in some cases present only a rudimentary version of metacognitive control compared to that seen in great apes and humans (Brauer *et al.*, 2004; Basile *et al.*, 2009; Roberts *et al.*, 2009; Beran *et al.*, 2014; Vining and Marsh, 2015). Further studies are required to improve understanding of metacognitive control abilities in these species.

3.3.2. Interpreting metacognitive responses

From the experiments presented above, it is clear that some animal performances meet the criteria for metacognition. Animals can adaptively decline difficult tests, they are able to judge their past performance in a cognitive test, and can collect additional information when uncertain about the outcome of their choices. However, as animals cannot report verbally about uncertainty, their feelings or their mental state, the extent to which their responses are based on processes that are conscious is still debated. In summary, many investigations have been conducted to assess whether uncertainty responses can be simply explained by low level, associative processes that do not involve consciousness. In the following section, we will describe the main scientific criticisms of the view that animals are metacognitive.

3.3.2.1. *Influence of environmental and behavioural cue association*

Some authors postulated that most of stimuli that are used to train an animal during a metacognitive task can acquire an associative value that does not necessarily imply high-level metacognitive processes. The processes of acquiring these associations may guide the metacognitive responses. For example, animals may be able to learn that stimuli of a specific magnitude or range of intensity, given after a certain delay, are associated with a low chance of getting a reward. Such an association may thus guide the animal to decline the test, and to make its response when confronted to these stimuli without requiring any explicit knowledge of the uncertainty. Also, difficult stimuli may become associated with a high likelihood of punishment because of the high error rate in these trials; although not itself rewarding, an opt-out response would still also have a strength of conditioned response because it provides a way to avoid punishment. These assumptions alone, based on associative theories, are sufficient to predict that animals will opt-out more for hard than easy trials, and that performance should be better in unforced than in forced hard trials. In order to exclude these possibilities, Hampton (2009) proposed testing the capacity of the animal to transfer metacognitive responding across different experimental conditions. That author postulated that demonstrating that animals are able to maintain metacognitive performances across situations would indicate that animals can give metacognitive responses on a more abstract and cognitive level, and discount the concept of a metacognitive performance driven by simple stimulus associative concerns. Kornell *et al*. (2007) found such a transfer in macaques.

A second way of explaining metacognitive performance without involving conscious processes is based on the idea that the subject’s behaviour may guide the metacognitive performance (see Hampton 2009). For instance, in several experiments it was reported that a subject’s latency of response is longer for difficult than for easy trials. Then authors discussed the possibility that animals could use this behavioural cue for their response in metacognitive tasks. Indeed, when confronted to difficult trials, subjects may use their experience of a long latency to decline the test or to seek complementary information. Similarly, in many experiments designed to assess metacognitive abilities in animals, they receive a food reward when they give response that indicates uncertainty. Some authors interpreted this as meaning that the experimental procedure can reinforce the uncertainty response without requiring a high-level or conscious metacognitive process. However, this possibility was discarded in experiments where the reward contingency for the uncertainty response was removed (i.e., prospective or retrospective metamemory). In these experiments, the animal still made uncertainty responses and declined response selectively for the difficult trials.

3.3.2.2. *Behavioural competition*

In many experiments on animal metacognition, the secondary metacognitive response option (e.g., decline the test, collect more information) is given simultaneously with a primary discrimination trial. However, animals can only give one response. This procedure has been called concurrent metacognition. As expected, the frequency for a metacognitive response increased when the discrimination trial became more difficult. It was postulated that a non-conscious competition between the two responses may guide the metacognitive response. Indeed, when the primary trial is easy, the primary response may automatically dominate the metacognitive response. On the other hand, when the primary trial is difficult, the metacognitive response may dominate. To exclude the possibility that metacognitive responses may be based on a competition between the two possible responses, the secondary metacognitive response option can be presented either before or after the primary trial (Hampton, 2009; Terrace and Son, 2009): this is called prospective and retrospective metacognition. As reported above, some animals are capable of these forms of metacognition.

3.3.3. Overview of the neurobiological bases of animal metacognition

Many brain imaging studies in humans clearly demonstrated that metacognition involves the frontal and the prefrontal cortex. This confirms the general view that these brain areas are generally required for high-level, conscious cognitive processes in humans. However, in animals, few studies have investigated the neurobiological bases of metacognition.

In one study conducted in rats (Kepecs *et al*., 2008), animals were trained on a two-choice discrimination task involving a mixture of odours. When the odour mixture contained more of compound A than compound B, the animal was rewarded when inserting its nose into a port placed on the left part of the cage. When the odour mixture contained more of B than A the rat was rewarded when inserting its head into the right-side port. To increase the difficulty to discriminate between the two odour mixtures, the proportion of compound A and B varied across trials. To explore the neural correlates of uncertainty, single neuron activity was recorded in the orbitofrontal cortex, a region of the brain implicated in decision making under uncertainty in humans. The firing rates of some single neurons located into the orbitofrontal cortex (OFC) was higher on difficult (when the proportion of A and B compounds in the odour mixture were relatively similar) than on easy trials. Interestingly, cells fired before the outcome of the trial suggesting that cells encoded the confidence estimates, previously suggested to require metacognition. This finding was confirmed in a recent experiment by the same group (Lak *et al.*, 2014). However, in these second experiments animals were not trained to provide metacognitive responding (to decline the test or seek additional information) and it is not possible to exclude totally the conclusion that firing of OFC cells reflects only an expectancy of the outcome.

In another study, monkeys were trained to make decisions about the direction of motion in a dynamic random-dot display (Kioni and Shadlen, 2009). The difficulty of the task was influenced by varying the duration of viewing and the percentage of coherent moving dots. After the phase of presentation of the moving dots, the monkeys were tested and invited to give their choice of direction by making an eye movement. On half random trials monkey were given the option to decline the test. The authors observed that monkeys declined the test more frequently after difficult trials than after simpler trials. They also observed that neuron firing in the parietal cortex was associated with the decision about direction and the degree of uncertainty underlying the decision to decline.

Therefore, the neural mechanisms that underlie metacognitive responding may be similar in humans and some mammals. Nevertheless, more information is required about the precise neural mechanisms specifically underlying each metacognitive process (confidence judgment and collection of additional information). So far, there have been no investigations on the neural substrates of metacognition in other species, such as birds, fish or invertebrates.

3.3.4. Conclusion

It is important to consider that studies in animals provide strong evidence that, like humans, animals exhibit controlled, flexible, abstract use of metacognitive responding. These components are core symptoms of conscious metacognition in humans. So, overall it is possible that metacognition in animals reflects their conscious evaluation of their own knowledge and uncertainty.

Metacognitive responding has been mainly demonstrated in those animals that are usually used in cognition research like rodents, primates, corvids and pigeons. Investigations provide evidence that metacognitive-like processes may be present in many animal species from invertebrates to vertebrates. However, metacognitive responding still needs to be considered in farm species which display many cognitive capacities and do possess neurobiological substrates that may underlie metacognition. Interestingly, the recent studies on animal metacognition presented above provide a solid scientific framework and behavioural tests specifically dedicated that could tackle this outstanding issue in farm animals. Moreover, the development of neurobiological investigations on animal metacognition may contribute to the fine characterization of the neurobiological substrates that subserve specific metacognitive processes in non-human animals.

3.4. Episodic memory in animals

Mental time travel in humans has been described in Chapter 2. It allows humans to access to events or episodes that they have personally experienced. It is different from the semantic memory that stores knowledge extracted from an event (Tulving, 1972, Suddendorf and Corballis, 2007). The neurobiological structures involved in episodic memory have been also described, and include the hippocampus and different parts of the cortex. Humans can also plan for the future using past events. Suddendorf and Corballis (2007) state that "*mental time travel is a term we coined to refer to the faculty that allows humans to mentally project themselves backwards in time to re-live or forwards to pre-live events*". It supposes that the subject possesses a sense of self-identity and an autonoetic (self-knowing) consciousness (Suddendorf and Corballis, 2008). However, Berntsen and Jacobsen (2008) found that mental time travel can also be involuntary.

Remembering the past and planning for the future can be characterized verbally by humans. Suddendorf and Corballis (2008) state that such capacity "… *exists only in human brains*" and that "…*we must use all our scientific artifice to protect it*." A definition of mental time travel based on verbal reports is useless for falsifying its existence in animals or in non-verbal humans (MacPhail and Bolhuis, 2001). In 2002, Roberts hypothesised that animals are "stuck in the present" (Roberts, 2002) and further supposed that they can neither remember the past nor plan for the future as humans do. Suddendorf and Busby (2003a, 2003b) and Suddendorf and Corballis (2008, 2010) have also defended that point of view.

However, an operational definition has been proposed for discovering whether animals have episodic memory. It is based on experiments addressing the question of whether animals can characterize what, where and when (WWW) after experiencing specific events. This multiple information should be gathered into a single representation and expressed in a flexible way to support adaptation to the situation (Clayton *et al.*, 2003). It should not be instinctual or associatively learned, and even it should be part of the repertoire of animals just as verbal abilities are specific to the repertoire of humans.

As some authors have suggested, even if the behaviour of some animals is consistent with the "what, where and when" notion, it does not completely satisfy all the characteristics of episodic memory observed in humans, including long term effect, flexibility and that it is not learned through associative or instinctual processes (Suddendorf and Busby, 2003 a, b). To overcome this objection, Shettleworth (2007) and others decided to define this memory as "episodic-like memory" in animals. Some authors also suggested that the observed WWW behaviour could be explained by other mechanisms, such as a mere stimulus-response processes or mechanisms that do not necessitate an episodic memory such as the travelling salesman problem path, which consists of "constructing the shortest route possible that will take the traveller to all locations exactly once " (Sulikowski and Burke, 2015).

The first useful insight into the question of episodic memory in animals was provided by a study of the western scrub-jay, a corvid that is well-known for its food-hiding abilities (Clayton and Dickinson, 1998; Raby *et al.*, 2007; Raby and Clayton, 2009; Shettleworth, 2007). WWW responses were thoroughly assessed in these birds by observing them outdoors and by subjecting them to specific tests in the laboratory (Clayton *et al.*, 2001).

For example scrub-jays were allowed to hide worms, a preferred but time-dependent perishable food, or food pellets, a less preferred but unperishable food. The jays chose to visit first the locations where the worms had been hidden for a short time but the pellet locations if the worms had been hidden for a longer time. The authors concluded that jays used information about where (the locations of the hidden food), what (worms *vs*. pellets) and when (short *vs* long period) components, characteristic of episodic memory. Further experiments by the same group demonstrated that birds are able to use this form of memory flexibly.

Since these pioneering experiments, episodic-like memory has been studied in food-hiding corvids, including magpies (Zinkivskay *et al.*, 2009). Other species use this type of memory in other contexts.

For example, Jelbert *et al*. (2014) showed that hummingbirds have WWW abilities when choosing flowers where they can harvest nectar, although the authors acknowledge that these birds also use semantic rule-learning to remember the identity of rewarding flowers. Eacott *et al.* (2005) described episodic-like memory in rats that use their innate tendency to explore new items (see also Babb and Crystal, 2005; Freitas Barbosa *et al.*, 2010; Binder *et al.*, 2015. In meadow voles, males used their episodic-like memory to optimize their visits to females and increase their sexual efficiency (Ferkin *et al.*, 2008). Pigs also recall memories of events and their performance is consistent with WWW abilities (Kouwenberg *et al.*, 2009). Even honeybees exhibit WWW abilities in a foraging context (Pahl *et al.*, 2007).

3.4.1 Neural bases of episodic memory

Experiments on the neurobiological mechanisms underlying episodic memory highlight the role of the hippocampus (Crystal, 2009; Eacott and Easton, 2012). Binder *et al.* (2015) showed that destroying the hippocampus disrupts the episodic-like memory of rodents. In parasite cowbirds, the size of that brain region changes seasonally, being larger during the season when they have to find nests of other birds in which to lay their eggs (Clayton *et al.*, 1997). Seed caching birds show an enlarged hippocampus compared to non-caching relatives (Sherry and Hoshooley, 2010). All of these studies confirm the functional importance of the hippocampus for WWW memory.

In humans, it is classical to differentiate between remembering and knowing. One simple example is the “tip of the tongue” phenomenon when we know that we know something but cannot remember it. One approach used in animals to differentiate episodic recollection (remembering) from familiarity (knowing) is to use the “receiver operating characteristics approach” or ROC (Fortin *et al.*, 2004; Eichenbaum *et al.*, 2010, Koen and Yonelinas, 2011). Eichenbaum *et al.* (2010) measured the responses to olfactory stimuli of rats that had their hippocampus damaged, a procedure that showed the differentiation between remembering and knowing in the rat. They showed that it is possible to distinguish in intact animals independent components of recognition that are associated with features of recollection and familiarity in humans. Furthermore, damage limited to the hippocampus results in a selective deficit in recollection and not in familiarity. These results show that the dynamics of memory revealed by ROC analyses in rats converge with anatomical findings and studies on humans that assign to the hippocampus a critical role in binding event and context information in support of episodic recollection.

3.4.2 Planning the future

Related to episodic memory is the ability to plan the future. In the case of animals, the question is not to prove if they can predict the future, but rather if they can plan scenarios or make simulations taking into account the past — in particular the content of their episodic memory. One condition for demonstrating such ability was outlined by the Bischof-Köhler (B-K) hypothesis which proposes that “any demonstration of future planning should be independent of the animal’s current’s motivation state” (Eacott and Easton, 2012). Suddendorf and Corballis (2007) argue that this capacity has been established only in humans and that only humans can flexibly anticipate their own mental states of need and act to secure them. But, they also agreed that new research on animals could change their conclusions.

Recent results seem to confirm their misgivings. For instance, scrub-jays are able to hide the type of food they foresee as not being available in the future (Shettleworth, 2007; Raby *et al.*, 2007). Soley (2011) studied Tayras, a South American mustelid, which hide immature plantain when it is not eatable. These animals come back to eat this food when it is ripe enough and eatable. This ‘satisfies’ the condition in the B-K hypothesis since is does demonstrate future planning as Tayras appear to perform preparatory activities for the later consumption of food for which they feel no hunger at the moment in which they hide it. Other works with black-capped chickadee and western scrub-jays have dealt with this question and reached the same conclusion, i.e. that future planning can be independent of the animal’s current motivational state (Raby *et al.*, 2007; Roberts, 2012).

Several authors raised the question of the adaptive relevance of such abilities. For example, Paxton and Hampton (2009) explain the inability of rhesus monkeys to demonstrate future planning by “the species-specific motivation to diversify food availability”. In the same species, Hampton *et al.*, (2005) found that the monkeys had a “robust memory of what and where but not when”.

Some authors are still sceptical about the conscious nature of these processes and the impossibility of confirming this issue based on the paradigms that have been used up to now (Eacott *et al.*, 2005). In fact, Shettleworth (2007) suggested that the fact that psychological and behavioural components of mental time travel in animals are ill defined should promote more research, and even a “moratorium” in this type of research (Suddendorf and Cordallis, 2007).

3.4.3 Conclusion

The existence of an episodic-like memory in animals and the resulting capacity to plan the future have been recently proposed following the development of new behavioural paradigms. An episodic-like memory has been identified in a broad spectrum of animals ranging from insects (bees) to birds and mammals. It was first demonstrated in animals which hide food and related to a specific feeding ecology (Raby and Clayton, 2009). However, it was also found in other contexts such as gathering food or finding sexual partners. It is not clear if this trait has developed *de novo* in each species, as a result of convergent evolutions, or if it belongs to the animals’ default state and is expressed more specifically when the context is demanding. The characteristics of the episodic-like memory of animals have many similarities with episodic memory in humans, from both behavioural and neurobiological perspectives. Crystal (2009) proposes, therefore, that research on this topic in animals may help studies on human neurological problems. Easton *et al.* (2012) also propose that animal research on episodic-like memory could be a useful tool for the study of episodic memory of nonverbal humans, such as infants (Haynes and Imuta, 2011).

3.5. Consciousness and social behaviour

Animals often live in groups of variable composition and size. These collective formations are categorized in terms of the mechanisms underlying the association (Aron and Passera, 2009). Thus, some crowds of animals are gatherings of individuals temporarily attracted to the same resource, such as abundant food or shelter. In other cases, animals congregate only for reproduction or to dispense parental care (e.g. colonial birds). In others, named “gregarious” species, individuals are attracted to each other without necessarily developing inter-individual discrimination. Still other species form more or less permanent associations where individuals are selectively attracted to conspecifics, with which they interact in a coherent, generally hierarchized, organization. The epitome of such organized social groups is seen in certain mammals (anthropoids, some rodents) or in insects where the society is sometimes divided into specialized subclasses or castes that fulfil complementary functions to the benefit of the whole society (*e.g.,* Wilson, 1975; Aron and Passera, 2009). These different types of social organisation do not imply the same level of social cognition among members of a same species. While crowds or aggregations do not necessarily rely on individual recognition, stable social groups or subgroups within larger societies are obviously based on recognition at the individual or kin-categorical level.

Three main concepts have been articulated in the context of the behavioural analysis of sociality: “interaction” and “relationship” between individuals, and “group structure” (Hinde, 1976). Reliable affiliative or agonistic *interactions* with particular conspecifics define the *relationship* between individuals; and from such relationships emerges what is called the *social structure of the group, i.e.* who belongs to the group and how the group is structured. For millennia, scholars have been interested in the individual *vs*. collective mechanisms, underlying the success of individuals in their social enterprise (*e.g.*, Wilson, 1975, 2012). The various forms of social organization and between-species similarities or dissimilarities fuelled abundant theorizing about causal processes in social behaviour and cognition (Wilson, 1975; Campan and Scapini, 2001; Aron and Passera, 2009). In the XXth

Century, the debates first revolved, in the objectivist current of ethology, around the existence of communication loops based on evolved processes, illustrated in the concepts of “innate releasing mechanisms” and “fixed-action patterns” (*e.g.*, Campan and Scampini, 2002). A strong theoretical current (developmental psychobiology and comparative psychology) emerged in response to this “inneist” approach, investigating social behaviour through its physiological causes as well as through experience and learning in various animal species. Another approach, often based on mathematical models, assessed the existence of auto-organizational processes based on local and simple individual exchanges between group members, such as in avian flocks, fish shoals or insect societies (e.g.: Camazine *et al.*, 2001; Sumpter *et al.*, 2009; Bialek *et al.*, 2014). Finally, an active cognitivist current stimulated by Griffin (1976) dared to investigate the more sophisticated processes, such as emotions, self-cognition, metacognition and theory of mind (Griffin, 1976; Premack and Woodruff, 1978; Bekoff *et al.*, 2002).

For the purpose of this chapter on the phenomenon of consciousness in non-human species, we will concentrate on one important aspect of the concept of inter-individual relationships: the fact that individuals need to know each other to build a reliable pattern of relationship. Indeed, the concept of relationship questions the degree to which each individual can predict the outcome of present interactions from the outcome of previous interactions, and even to plan future interactions into a given strategy. In other words, to what degree do relationships involve automatic and unconscious interactions, or alternatively, but not exclusively, to what degree do they depend on subjective and conscious mental representations of social partners? We present here some unconscious or conscious processes underlying social behaviour to ultimately discuss whether individuals form mental representations of conspecifics, as assessed through individual recognition, and of their willingness to act.

3.5.1. Do individuals living in large groups behave as automatons or as integrated entities?

Some animals as diverse as insects (especially “social insects”), fish, birds or mammals live in “swarms”, shoals, flocks or herds comprising many individuals (e.g.: Couzin and Krause, 2003). These collective arrangements have a high adaptive value in that they reduce predation, increase foraging success, and at the same time reinforce individual fitness. Scientists are particularly interested in how these collections of individuals are coordinated in space, time and activities. Explanatory models test either the need for leaders to have control over the whole group or the occurrence of distributed high-level cognitive abilities in all individuals (e.g. Campan and Scampini, 2002; Couzin and Kraus, 2003; Sumpter, 2009; Bielak *et al.*, 2014).

In the context of large groups, it is difficult, if not impossible, for an individual to know its exact position among all its group-mates. This may question whether and how an individual perceives the group as a whole. Auto-organisation theories (Couzin and Krause, 2003) suggest that local information and interactions at an individual level influence the behaviour of the whole without necessarily engaging individual perception of the whole group. For example, mathematical models applied to starling flocks or fish shoals predict that individuals can detect group behaviour based on simple interactions, such as attraction, avoidance of collision and keeping the direction constant (Campan and Scapini, 2001; Couzin and Krause, 2003). These computational approaches do agree excellently with observational data and are « *mathematically equivalent to statistical physics models for ordering in magnets* » (Bialek *et al.*, 2014). In addition, a minority of individuals who are strongly motivated to orient in a particular direction can influence the whole group, for example in increasing the speed of movements; “leading can occur in the absence of knowledge of or communication about the needs of other group members and without the assumption of altruistic cooperation” (Conradt *et al.*, 2009). For this reason, some authors excluded interpretations referring to selective inter-individual relationships (as defined above) and potential conscious phenomena.

Nevertheless, in some species, a subjective perception of the individuals of the group has been demonstrated. For example, Hager and Helman (1990) found that, in the presence of a predator, fathead minnows chose to associate with the larger of two shoals. Thus, not only can the fish discriminate the “mass effect” of the group, but the stronger this effect the more individual fish are attracted to the group. Moreover, Krause *et al.* (2000) showed that individuals prefer to join shoals of familiar or genetically related fish than shoals exclusively composed of unfamiliar, unrelated conspecifics. Accordingly, the mass effect alluded to above is modified by the composition of the group, highlighting the ability of fish to detect cues from individuals or categories of individuals. Such abilities are not specific to fish as similar phenomena can be found in other large group-living species. For example, ungulates prefer herds composed of familiar individuals (*e.g*. sheep: Dumont and Boissy, 2000). Long-lasting inter-individual relationships are common in ungulates (*e.g*., sheep: Rowell, 1980). That primatologist even suggested that sheep should be studied in the same way as primates: i.e., hey should be considered as individualities rather than just anonymous “Panurge’s sheep” behaving like automata.[6]

In summary, even if mathematical models, essentially based on reductionist appraisals excluding any reference to consciousness, fit well with field data on large moving groups, cognitive fine-tuning of movement decisions seem to occur at the individual level. Indeed, Bode *et al.* (2011) stated that *future models in ecology should take inspiration from empirical observations and consider different mechanisms of how social preferences could be expressed in collectively moving animal groups*.” The coherence of social groups is indeed facilitated through the process of discriminating in-group from non-group members, and possibly by recognizing group members at the individual level. The ability to recognise, through all possible sensory channels, is also basic to the formation of dominance hierarchies within groups (e.g. Bouissou, *et al*., 2001).

3.5.2. Individual recognition in animals

According to Hinde (1976), inter-individual relationships result from regular interactions between partners in the relationship. But this definition “*does not exclude a case in which a pair of animals have a series of predictable interactions without even being able to identify their partner*” (Rowell, 1980). So, in this section we intend to evaluate whether social animal species have developed individual recognition. Recognition implies previous knowledge about one or more individuals and might be achieved along unimodal or multimodal “representations” of one or more conspecifics. Such representations rely on complex perceptual, memory, and motivational abilities, and allow for an individual to anticipate the nature of relations with conspecifics and somehow predict their outcome (*e.g*. Galistel *et al.*, 1990).

For example, the social hymenoptera paper wasps (*Polistes fuscatus*) form seasonal colonies. When these colonies are established, a stable dominance hierarchy is formed through fights after which inter-individual aggression decreases dramatically (West-Eberhard, 1969). Paper wasps have complex patterns of coloured marks on the face and abdomen, which operate as visual signatures used in individual recognition (Tibbetts, 2002). When these marks are experimentally altered, the manipulated wasps receive more aggression from nest-mates in comparison with intact wasps. Thus, paper wasps do perceive each other as different and recognize nest-mates by means of their complex facial and abdominal markings.

Other illustrative examples of individual recognition come from domestic gregarious ungulates. Cattle of different dairy breeds are ideal for such studies as they can have contrasting coat patterns and colours. Heifers trained to discriminate pictures of cow heads from different breeds presented from different angles of view, grouped all different visual representations of a given conspecific, even from the same breed into the « *same individual* » category (Coulon *et al.*, 2009). Sheep are able to recognize up to 50 different faces from familiar individual sheep (Kendrick *et al.,* 2001). Such impressive socio-cognitive abilities are interesting in the context of the previous discussion on individual roles within large social groups. Probably, animals use an “analytic” mode to recognise social partners, focusing on

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[6] François Rabelais invented the figure of Panurge’s sheep to mock the ovine, and in fact the human, tendency to blindly follow their conspecifics (Rabelais, 1552, quart livre, publie.net classique).

particular individuals within the group at the same time as they use a "configural" mode of recognition of the whole group, its activities, direction of movement and boundaries. Both modes of recognition would be highly adaptive to keep cohesion of the whole group, in the same time as structuring it in sub-groups where recognition is more effective. Such social sub-sets have been described in social insects as well as in ungulates. Ungulates are indeed organized in matriarchal groups with strong affiliative ties between mother and offspring (Bouissou *et al.*, 2001). Correspondingly they seek proximity and synchronization with certain conspecifics, as well as with the relative leadership of the experienced matriarch (e.g. Veissier *et al.*, 1998). Thus, multiple levels of awareness may mobilize nested levels of social cognition, in particular at the individual or group levels.

The ability of non-human species to recognize individuals was first investigated through experiments in which cues were presented in only one sensory modality as referenced above. But, real interactions always involve multiple sensory cues, and progressively studies began to assess how multiple sensory cues provide complementary and redundant information (Johnson and Peng, 2008). Thus, related individuals, as well as in-group versus out-group individuals, may be assessed and recognized through different sensory modalities as a consequence of exposure to group members during ontogeny. Experiments that assess this multi-sensoriality are numerous. Visual cues are easily matched to vocal or olfactory cues. Such intermodal transfers are normal in social cognition, leading an individual to record multiple sensory signatures of individuality or categories of conspecifics (*e.g*. male *vs*. female, immature *vs*. adult, dominant *vs*. subordinate). For example, grey-cheeked mangabeys (*Lophocebus albigena*), when exposed to computer images of familiar group-mates and the vocalizations of one of these individuals, identify most easily the face that is congruent to vocalization (Bovet and Deputte, 2009). This shows that mangabeys are more proficient at recognizing familiar individuals when their choice is based on multiple cues of individuality.

Taken together, this section highlights that the ability to recognise conspecifics is essential for maintaining successful and adaptive social performances.

3.5.3. Social animals adjust their behaviours according to what other group members know

3.5.3.1 From interactions to relationship: the representation of the social partner

Social life is the result of the activity of several individuals engaging in preferential relationships, reflecting selective affinities and the operation of a common code of communication signals, beyond solely sexual relationships (Campan and Scapini, 2002). The specificity of social interactions is that each partner exerts a mutual influence on the other one (Hinde, 1976). Even when the basics of communication systems have been set up evolutionarily, mutual experience based on repetition and learning fine-tunes the relationship (Campan and Scapini, 2002; Scott, 1992). Proximity and sometime synchronization have been observed among individuals in many species ranging from fish to primates (Aron and Passera, 2009; Campan and Scapini, 2002; Veissier *et al.*, 1998). Through inter-individual relationships several adaptive roles are made possible for individuals within the group. This is the case for alternate watching for predators and protection (giving alarm), collective food seeking and tolerance during competition for food (Veissier *et al.*, 1998). Nonetheless, competition for resources can lead to agonistic interactions that need strong regulation to maintain group cohesion. Hierarchical relationships are often observed in social groups which allow the animals to predict agonistic interactions and reduce their harmful consequences at both individual and collective levels. These examples demonstrate the importance of inter-individual relationships in the formation of social bonds and social groups.

The initial adult–young (usually mother-young) relationship is the basis for the socialisation process in many vertebrate species. When growing, young animals interact more in quantity and in quality as the number of interactants increases, involving first, apart from the mother, siblings or peers, if any. Afterwards, they interact with other young and adults which allow them to build their social network. Scott (1992) suggests that socialisation is formed through attachment-like processes from an early age. That attachment may be subsequently adjusted between individuals. In the extensive literature on primates and ungulates, social attachment is defined as an affective (emotional) state in the presence or absence of a particular partner (Kraemer, 1992; Scott, 1992; Cassidy, 2008; Veissier *et al.* 1998; Nowak and Boivin, 2015). Infants form attachments to any caregiver who is socially sensitive and responds to them (Ainsworth, 1979). In attachment theory, different attachment relationships could exist in the same individual but within a hierarchical system headed by one figure. Individual recognition, which we highlighted in the previous section, is essential to the formation of this process.

Attachment is viewed as an internal mechanism involving regulation of behaviour towards others. Several studies in birds, farm herbivores or primates describe how an animal can express behavioural distress during a short separation test with a particular individual and calmness in its presence (Gubernik, 1981; Tzschentke and Plagemann, 2006; Nowak and Boivin, 2015). Following research on humans, Cassidy and Shaver (2008) insist that the “attachment object” can serve as a secure base for exploration of the environment. In ungulates, Veissier *et al.* (1998) and Nowak and Boivin (2015) showed how the presence of particular conspecifics can affect exploration of new objects or foods. However, this concept of a secure base needs more research in other species. This functional conception of social relationships clearly suggests the existence of subjective mental representations as defined by Vauclair (1990): ”*Representation is an individual phenomenon by which an organism structures its knowledge with regards to its environment*.”

Attachment behaviours appear to be similar in form and function in humans and in a diversity of animals studied so far. Such a functional similitude suggests that emotional feelings and conscious phenomena may exist in the social transactions of non-human animals. Nevertheless, applying the principle of parsimony, we cannot exclude that unconsciously learned processes might explain the early formation of affiliative behaviours towards social partners. Emotional behaviours have a communication value: alarm signals could elicit “reflexive” avoidance and flight, while distress signal of a conspecific might elicit automatic approach responses. So, we cannot be sure that an individual consciously associates its own or others’ signals to others’ or its own responses (*cf.* section 3.2 on Emotion and Consciousness). However, the complexity and flexibility of some social behaviours in non-human animals could also lead to the hypothesis that animals have high-level socio-cognitive abilities, such as conscious feelings of self and others’ mental states (*e.g.*, de Waal, 2016).
In the last part of this section some specific social abilities of animals are described.

3.5.3.2 About “theory of mind” in animals?

In comparative psychology, an individual is said to have a “theory of mind” if it is able to impute a mental self to itself or to conspecifics (Premack and Woodruff, 1978). In psychology, it refers to understanding oneself and others in terms of mental states: desires, emotions, beliefs, intentions, and other inner experiences that result in explicit behaviour. Field studies suggest that audience effects can influence an individual’s behaviour, questioning how an individual perceives others being attentive to it. For example, cocks vocalize when they find food in the presence of a hen, but not in presence of another cock (Marler *et al.*, 1986). Hyenas and capuchin monkeys have a very complex social life and seem able to discriminate between the social ranks of two individuals engaged in a fight (Engh *et al.*, 2005, Perry *et al. 2004*). They would aid the higher-ranking combatant, regardless of their own social rank in relation to those of the fighters. It has been previously emphasised that animals, especially young animals, learn which conspecifics belong to their group and how to adjust their own behaviour to the behaviour of other group members. During this early formative period, young animals could build social representations of group-mates. The « theory of mind » is therefore relevant in this context, implying that an individual may behave towards another conspecific according to what that conspecific sees, hears, or even to what the other « knows ». This question has been discussed for animals, mostly for primates, but recently in many other taxonomic groups (*e.g.* de Waal, 2016). We will now consider examples in situations where individuals compete for food, but also in situations where altruism and empathy might also be involved.

Premack and Woodruff (1978) were the first to tackle the issue of the inferences that chimpanzees can make about non-observable goals (as manifested by human demonstrators). Instead of applying a solution to a problem induced by the human experimenter, the chimpanzee itself had to identify a relevant means to reach the solution. A chimpanzee was exposed to videotapes of a human being confronted with a more or less complex problem; the videotape was stopped before its end and the chimpanzee was then given a box containing several photos of items, one of which was part of the solution to the problem (Vauclair, 2000). The chimpanzees chose the correct object in most cases in order to get a reward, thus showing a capacity to infer the nature of the problem and its potential solutions. Later, instead of confronting chimpanzees with a human, the same issues were investigated when pairs of chimpanzees were put in competitive situations. For example, when dominant and subordinate chimpanzees had to compete for food that was visible to both or only to one of them, the subordinate got most of the food that was visible to it and invisible to the dominant (Hare *et al.*, 2000). The authors concluded that subordinate chimpanzees derive knowledge from what dominant individuals can and cannot see. Reviewing 30 years of studies on chimpanzee's "theory of mind", Call and Tomasello (2008) suggested that chimpanzees understand both the goals and intentions of other individuals, as well as the perception and knowledge of others (including humans). They claimed that chimpanzees certainly have a "theory of mind". However, to be similar to human's "theory of mind", chimpanzees should understand « false beliefs » (i.e., actions that do not correspond to reality). That has not yet been demonstrated.

Several recent papers also investigate these aspects in corvids suggesting "convergent intelligence" with primates (Emery and Clayton, 2004). For example, ravens are social scavengers who cache for later use surplus food or food contested by others (Bugnyar and Heinrich, 2005). Several experiments addressed the question of whether ravens are able to differentiate between potential competitors who have or have not had the opportunity to observe their action of caching.

They allowed the « storers » to retrieve hidden food in three different contexts:

i) in private,

ii) in the presence of a subordinate competitor who has seen food being hidden,

iii) in presence of a subordinate competitor who has not seen the food being hidden. The storers retrieved more food in the second situation, *i.e.* when paired with an observer than when paired with a non-observer competitor. Moreover, storers only retrieved the hidden food when an observer moved towards a cache. If observers did not move towards caches, the storer's recovering rates did not differ in any of the three contexts. To assess tactics of pilfering, a human experimenter served as the storer and maintained a constant number of caches to be potentially recovered. In these conditions, subordinate and dominant ravens were tested together to address the question of behavioural flexibility in pilfering. The observing birds delayed their pilfering significantly more when paired with a dominant non-observer than when paired with a dominant co-observer. Thus, ravens can display sophisticated skills in competitive contexts to recover hidden food: storers selectively recovered hidden food when in the presence of informed, potentially competing observers; pilferers also recovered food faster in the presence of co-observers perceived as potential competitors. Ravens therefore appear capable of « perspective taking », a pre-requisite considered as one of the strongest criteria of consciousness in humans.

These abilities are not limited to ravens. Another corvid, the Western scrub jay also showed different strategies for hiding food depending on the audience. It was also able to remember who was present during earlier caching events (Dally *et al.*, 2006). These birds also moved the hidden items more often when they were being watched, suggesting that they were able to employ confusion tactics and cache protection strategies (Dally *et al.*, 2005). Such tactics are not limited to corvids because grey squirrels also perform deceptive caching, *i.e.* the "*use of false signals to modify the behaviour of a receiver in a way that benefits a sender, at some cost to the receiver* » (Steel *et al.*, 2008). These mammals hid their food but also built dummy caches where no food was hidden. This deceptive tactic increased when the number of squirrels around them was large and when humans experimentally removed hidden food. Dally *et al.* (2006) suggested that these results provide converging evidence for "triangulation"; that is, consciousness of a third party, and for the possession of a "theory of mind" in animals.

The examples reported above investigated competitive situations among individuals. However, social behaviour also includes pro-social behaviour, which refers to actions that are intended to benefit conspecifics (Bartal *et al.*, 2011). One common force of pro-social behaviour in humans is empathic concerns: emotional responses elicited by and congruent with the perceived distress of another individual. Many observations in animals of this sort of empathy are single cases, often condescendingly referred to as anecdotal (Bové *et al.*, 2012). However, according to Mogil *et al.* (2012) who reviewed the current scientific literature in this topic, a "fairly robust demonstration of empathically motivated helping behaviour" has now been provided.

To test for empathically motivated pro-social behaviour in rodents, Bartal *et al.* (2011) placed a free rat in an arena with a cage-mate trapped in a restrainer. After several sessions, the free rat learned intentionally and quickly to open the restrainer and to free the cage-mate. Rats did not open empty restrainers or restrainers containing objects. They freed cage-mates even when social contact was prevented. When the act of liberating a cage-mate was pitted against a reward of chocolate in a second restrainer, rats opened both restrainers and typically shared the chocolate. Thus, rats behave pro-socially in response to a conspecific's distress, providing strong evidence for biological roots of empathically motivated helping behaviour. Mogil *et al.*, (2012) suggested that there should be confirmatory and complementary studies to understand the motivation of the rat to perform in this way but they particularly highlighted the simple experimental design and the fact animals were spontaneous and deliberate when opening the cage and sharing the chocolate.

3.5.4 Conclusion

The examples of social competences in this section are a small sample from a rapidly growing field that covers an increasing number of species, following Griffin's (1986) recommendations (cf. de Waal and Tayack, 2003; de Waal, 2016). The few studies discussed here were intended to illustrate the performances of social individuals in their daily social lives. Many studies concern birds, and non-human primates, and tackle issues related to the « theory of mind » such as deceptive behaviours, intentionality, and perspective-taking. Despite the wide variety of experimental protocols and species studied, there is consensus that animals, at least many vertebrates, are not simply reacting to visible signals or behaviours of others but use past experience and ongoing relationships to adjust their behaviour and reach immediate goals which may be outcomes of competitive situations or cooperation[7]. These performances very likely represent a form of «consciousness of important social issues ». This form of consciousness requires the mastery of more or less sophisticated means of perception and communication, though not a language in the human sense. It also requires a particular organization of the brain (see chapter 2).

3.6. Can the study of human-animal relationships bring insight into animal consciousness?

The analysis of the reciprocal relationships that humans establish with animals may be relevant to address the occurrence of consciousness in the later. Individual animals often show a large adaptive plasticity during interactions with their human partners, discriminating or generalizing their responses to them. Unfortunately, most authors studying interspecific relationships rarely discuss such processes explicitly in term of consciousness. Animals' relations with humans have long been held as a topic of lower interest (Davis and Balfour, 1992) and it is rather recently, with the intensification of studies on domestication and animal welfare, that animal-to-human relations have become a topic of scientific enquiry, justifying a separate section in this chapter.

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[7] Bear in mind that animals are more skilled in competitive situations than in cooperative ones; in social contexts that means with conspecifics (see Bugnyar and Heinrich, 2005, Call and Tomasello, 2008).

Despite ethology's relative disinterest for the mechanisms underlying animal-human relationships, some researchers have attempted to integrate intraspecific social relationships and human–animal relationships (e.g. Scott, 1992 ; Estep and Hetts, 1992 ; Hemsworth and Boivin, 2011). For example, Scott (1992) developed the concept of "socialisation" to address how animals build relationships with humans during their life-span. While evolved social behaviour guides individuals to organize into species-specific social structures based on inherited communication systems[8], these systems also contribute to the information exchanges occurring between individuals of different species. "Social" abilities of animals towards humans have indeed capitalized upon the former's predispositions to engage 'positive' relationships with the latter, specifically at the occasion of mutual exposure at given periods of life (*e.g.*, Faure and Le Neindre, 2009). By all means, we acknowledge that inter- and intra-specific relationships differ qualitatively: distinct species do not rely on the same sensory cues to direct their responses and, hence, they do apprehend their respective "Umwelten" along different dimensions (von Uexküll, 1909, discussed in Campan and Scapini, 2002). Further, different species use different ways to express emotions and their cognition operates along different adaptive criteria.

However, the extent humans and animals are sharing the processes that could be associated with "consciousness of the other" remains a constant ambiguity in the understanding of interspecific relations. For example, Konok *et al.* (2015) observed that dog owners are reported to perceive a wide range of emotions in dogs. These authors suggest that "humans represent dogs' emotions in a partly similar way to their own". These same authors evaluated their results not only from an anthropocentric point of view, but also along possible homologies in the expression of emotion and in communication between humans and dogs. Do animals react to human cues only because of unconscious associative learning and behavioural processes? Do humans only project their own conscious state within their animal partner? Or do animals experience more elaborate conscious representations of their human partner than humans do? Here, we aim to briefly summarize research on human-animal relationships along examples that question the phenomenon of animal consciousness.

3.6.1 Human- animal relationship: some theory

The study of relationships between humans and animals forms a recent, multidisciplinary field of investigation (Despret and Larrère, 2014). Anthropology and the biological sciences describe interspecific relationships in many cultures and in many circumstances (*i.e.*, work, food, pet, leisure, scientific investigation, and/or social support). Although multiple underlying theoretical backgrounds have been postulated, the theory we privilege here relies mainly on cognitive ethology and comparative psychology.

For example, to conceptualize the human-animal relationship, Estep and Hetts (1992) took inspiration from Hinde's (1976) theory of relationship (see section 2.5, above), according to which a relationship is based on regular, non-random interactions between two or more individuals. Such relationships can come in many, "positive" or "negative" forms ranging from the type of interactions occurring between predator and prey to the type of interactions occurring in symbiotic exchanges (*e.g.*, mother-infant bonds: Estep and Hetts, 1992). The balance between such "positive" and "negative" interactions affects the final quality of the inter-species relationship through familiarization processes and the conditioned reduction of fear. Following the principle of parsimony and according to the low-level learning processes potentially involved, one might suggest that unconscious associative processes are sufficient to explain the engagement of animal-to-human relationships.

However, recent studies on animal emotions and cognitive abilities (see section 3.2 in chapter 3) and on human-animal relationships indicate that the cognitive/emotional contribution of each partner should be taken into account (e.g. Boivin *et al.*, 2003; Waiblinger *et al.*, 2006; Rehn and Keeling, 2016). These studies suggest indeed that both the human and non-human involved in the relationship do perceive, interpret and remember the outcome of their reciprocal interactions. Further, Porcher

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[8] During the short history of domestication, in particular of domestication for tameness, the mechanisms facilitating tolerance of humans by animals have further been manipulated by genetic selection (Price, 1999).

(2002) considered that, for an in-depth interpretation of the relationships between humans and animals, it might be worthy to recognize that inter-subjective processes may occur. She based her proposal on arguments from phenomenology, from von Uexküll's *Umwelt* theory (von Uexküll, 1909), from Griffin's views on animal awareness and from the "theory of mind". Thus, research on human-animal relationships has finally opened to the study of the cognitive abilities and mental and conscious states that occur, or are thought to occur, between the animal and the human.

3.6.2 Human-animal relationships: experimental psychology perspectives on human effects on animals

The field of experimental psychology provides historical examples of studies questioning how animals can be influenced by their human partners. However and, much more important for our purpose, they eventually questioned how the animals involved are perceiving us.

Experimental psychologists Rosenthal and Fode (1963) evidenced the "Pygmalion effect", according to which the expectations of human experimenters before running a behavioural test can influence ensuing performances of experimental animals. When such "experts" were told that the rats in the experimental group will be better in a T-maze than those in a control group, Rosenthal and Fode (1963) did effectively note the higher performance of the experimental rat compared to the control rats. The biased "experts" also attributed better scores to the rats than unaware experts. According to the biased "experts", the control rats behaved differently than the experimental rats even when they did not move at all in the maze. Rosenthal and Fode explained that biased "experts" had a different attitude towards their "better" rats and they admitted they had handled them more gently than control rats.

When reporting this study, Rosenthal (1970) recalled the case of the horse "Clever Hans" (Pfungst, 1911). This horse was trained to perform arithmetic calculations, first after obtaining food rewards, but later without any (controlled and conventional) reward. To answer mathematical questions, the horse was trained to knock on the ground with a hoof. Clever Hans and its owner became famous worldwide until the psychologist Oskar Pfungst scrutinised how the horse could succeed in such an arbitrary task for a horse. He demonstrated that in fact Clever Hans relied on changes in the owner's behaviour at the exact time that he was expecting the correct answer. This famous example has become a paradigmatic illustration of Lloyd-Morgan's principle of parsimony. Indeed, unconscious mechanisms of associative learning were first hypothesised by Pfungst. But Rosenthal (1970), suggested to analyse which human cues were perceivable to the horse, inducing it to stop hoof-knocking in coincidence with the expected answer. The presence of a human knowing the answer appeared essential. He involuntarily transmitted his knowledge to the animal through body cues as subtle as minimal head inclination or nostril enlargement. However, in relation with animal consciousness issues, one cannot exclude that Clever Hans might additionally have been able to somehow please the human who required him to make calculations. This, indeed, questioned Clever Hans' motivation to perform the task despite the absence of (planned) rewards and despite the fact that different humans were involved. The horse was indeed able to generalize its responses to many other people than its owner. It is unfortunately impossible to further assess Clever Hans' emotional and cognitive abilities and his representation of humans beyond the data presented by Pfungst.

This classical example points, however, to the subjective point of view of the animal when facing communication with a human. We need to revisit animal behaviours, and their underlying mechanisms, in the context of relationships with humans (i.e., animals as partners of the relationship) with a modern concept of consciousness. The elusive human cues reported by Pfungst to be effective in influencing the horse's responses may be relevant in intraspecific communication among horses, but, as stated recently by McGreevy *et al.* (2009), « *the gulf in our ability to integrate the equid sociogram into riding techniques explains some of the difficulties faced by both species in equitation and has profound implications for rider safety and horse welfare* ». Although in different forms, such considerations may apply to animal from any other species when establishing a persistent relationship with humans.

In the next part, we will discuss recent studies published in several species of the underlying mechanisms of the human-animal relationship. Ethology as many other biological disciplines is comparative. This allows hypothesising mechanisms through comparisons between species including the human being. However, again, these studies did not discuss their results in term of consciousness and were not designed for it.

3.6.3 Human-animal relationships: comparative ethology perspectives on mechanisms involved

Within the last decade, the overlap between inter- and intra-specific communications has been studied more intensively in Primates and Canidae. In particular researchers have focused on the socio-cognitive skills of animals allowing them to follow the direction of gaze not only of conspecifics, but also of humans (e.g., Tomasello *et al*., 1998; Call *et al*., 1998), or to voluntarily follow communication cues conveyed by pointing, tapping or placing a marker on a correct container of hidden food (e.g., Hare *et al*., 2002; Barth *et al*., 2005).

Primates of many species appeared to be skilled to follow gaze direction expressed by humans. In natural conditions, such a skill normally allows the animals to detect food, predators, and on-going interactions among group mates. But, compared with dogs, chimpanzees and some other primates performed poorly in an object choice task on the basis of such gestural cues displayed by humans (Hare *et al*., 2004). Hare *et al*., (2004) and Riedel *et al*. (2008) demonstrated that the ability to rely on such human cues is acquired in dogs when aged few postnatal weeks, even in situations involving restricted human contact (kennel rearing). These authors also suggested that a dog's ability to use human gestural cues in choice tests could result from selection during domestication. Dogs' ability to rely on human cues to try to find a hidden object is impressive (Topál *et al*., 2009): dogs performed better alone in searching for a hidden object than in the presence of a person sending wrong cues about the position of the object. Like 10 month-old infants, they tend to wrongly follow human indications. These examples suggest a functional representation in dogs of their human partners through signals they can use to find a hidden goal. We are far from a simple unconscious and predetermined response to a stimulus. By contrast, human-reared wolves do not seem to have the same social-cognitive abilities, suggesting a possible effect of domestication (Topál *et al*., 2009).

Studies on human-dogs interactions also questioned the underlying mechanisms for acting together. In a recent study, Nagasawa *et al*. (2015) demonstrated the effect of oxytocin in the abilities of dogs and humans to follow a gaze that could contribute to the development of human-dog bonds, and therefore in one consequence of the domestication of dogs. Oxytocin is known to favour calmness, especially during social interactions, and the development of trustful affiliative relationship; it is indeed released in rats and dogs during tactile stimulation by humans (Uvnäs-Moberg, 1998; Gordon *et al*., 2011; Mitsui *et al*., 2011). Accordingly, a social rewarding effect was suggested in interacting humans and dogs. It appears in a loop mediated by oxytocin that would favour the development of affective bonds. These findings agree with those from studies showing specific emotional responses of domestic animals to different humans and to the presence or absence of their owners (Prato-Previde *et al*., 2003).

The aforementioned examples examined interspecific relationships in which the human and animal parties develop relationships based on intimate ties that start from early ontogeny and remain quasi-permanent during the life-span. Thus, the timing and degree of ontogenetic proximity between two particular human and animal individuals shape their system of meaning and of communication. In addition to these ontogenetic effects of exposure to the benefits of relationships with human, transgenerational tendencies based on genetic or epigenetic inheritance can reinforce the animal engagement into a trajectory of 'trustful' relationship with humans. As an example, we will summarize here research on human relationships with a species, sheep (*Ovis aries*) which is not often treated along individual qualities.

Sheep live indeed in flocks, with much less “personalized” interactions with their human keeper relative to horses or dogs. Lay preconceptions generally consider the ovine gregarious way of life as ‘non-adaptive’ and ‘automatic following’. Moreover, sheep are relatively inexpressive relative to dogs and horses, their facial expressiveness appearing rather “poor” and impenetrable to human observers (Boissy *et al*., 2011). However, sheep display perceptual abilities which appear adaptive in gregarious conditions. As stated before adult sheep are able to distinguish up to 50 individuals within a herd (Kendrick *et al*., 1996; Kendrick *et al*., 2001). This ability generalizes to humans and sets on early in development as lambs can distinguish their human keepers from at least 2 days of age (Nowak and Boivin, 2015). Beyond mere discrimination, such recognition ability appears adaptive as hand-fed lambs do calm down only in the presence of a familiar keeper after being isolated from the herd (Guesdon *et al*., 2016; Nowak and Boivin, 2015). In addition to facial configuration of humans (Kendrick *et al*., 2001), adult sheep can use visual cues from clothes to identify human individuals with whom they are interacting (Davis *et al*., 1998). Further, they show persistent memory of a person who is associated with painful experience even weeks after the event (Fell and Shutt, 1989). Finally, sheep were shown to generalize their responses to humans based on particular previous experiences. Accordingly, Destrez *et al., (*2013) exposed groups of ewes to humans consistently interacting in a negative manner and groups of sheep interacting in a positive one. Those persons were differently dressed. Then ewes were shortly tested with the same persons but also with a new one, differently dressed. Destrez *et al.*, (2013) showed that sheep differently generalized their responses to new people based on their previous interactions. Thus they performed more generalized responses in association with negative experiences (fear responses) compared to positive experiences (approach responses).

Thus, much like dogs, the above studies on sheep show evidence of both objective and subjective perception of human partners. We are only beginning to unravel the intraspecific and interspecific socio-cognitive abilities of sheep and other ungulates. They should be more systematically investigated along dimensions already scrutinized in other species (e.g. gaze-following abilities, contagion of stress, solacing effect of humans, social plasticity). As mentioned in section 3.2, the suddenness, novelty, hedonic valence, predictability, and controllability of social or non-social events are essential in eliciting adaptive (or maladaptive) emotional responses in animals. Our understanding of how animals respond to and integrate these properties of social contexts conditions our understanding of how animal-to-human relationships are being shaped in terms of non-conscious associative learning processes, as well as in terms of conscious processes.

3.6.3 Conclusion

In summary, several studies suggest that some animals, as different as primates, dogs and sheep, are able to mobilize cognitive and emotional abilities during human-animal interactions to build a mental and functional representation of their human partner. They highlight the potential momentum of the animals’ subjective experience in perceiving humans. These studies reinforce the usefulness of a theoretical framework, exploring not only animals’ responses to humans, not only animal-human interactions, but really animal-human relationship built from previous interactions and based on mutual perception from both the human side and the animal side. Life-experiences in addition to genetic predispositions appear determinant.

Studies underscore that distinct human partners are differentially perceived by the animals, resulting in plastic, predictable and consistent emotional and behavioural responses in the relationship, potentially ranging from avoidance to bonding. This indicates that conscious, rather than only predetermined and automatic, processes may occur in the development of animal-to-human relationships.

Results presented in this section were not interpreted in term of consciousness in relative publications, and in general these studies were not designed to analyse processes indicative of any conscious content of behaviour. However in the future, they could allow to question conveniently the different contents of consciousness involved as human-animal relationships could be more easily manipulated than intraspecific relationship.

3.7. Neural correlates of consciousness in animals

Most of the current knowledge on the neural bases of emergence of consciousness was presented in Chapter 2 (section 3.3.6-Neurophysiology) of the present report. This knowledge refers mostly to the properties of human consciousness and derives from studies carried out primarily on human subjects.

The parallel issue of assessing forms of consciousness in animals has long been, and still is, approached using behavioural observations interpreted in the light of proposed hypotheses on correlations with neural substrates underlying the performance of animals. Such performance can be described as a property of consciousness but the global approach is an attempt to identify the neural substrates of a given functional property. Elements for understanding properties of consciousness can be provided by comparative neuro-anatomy or functional tools like electrophysiological recordings, pharmacological manipulations of behaviour, or attempts to modify the expression of a target gene.

Taking this line, Mashour and Alkire (2013), for example, proposed a global picture of current knowledge and called for experimental models in which: (i) consciousness emerges from unconsciousness at a discrete and measurable point in evolutionary time, (ii) phenomenal consciousness and access consciousness (cf. Chap 2, section 2.2.1) are closely juxtaposed or mixed, and (iii) it is possible to assess neural structures and functions linked to consciousness. In practice, they proposed considering ‘top-down’ and ‘bottom-up’ approaches to consciousness and to extend this to non-human consciousness in order to highlight the cardinal role of information flow underlying the emergence of consciousness. Moreover, they also proposed to use the resumption of consciousness in humans from general anaesthesia (see chapter 2, section 2.2.1.2) as a model to study the evolution of consciousness in animals. We present the main conclusions of these approaches in the two following parts.

We compare human and vertebrate animal brain structures and highlight possible homologies in structures. Involvement of these structures in human consciousness is used as a guide for tackling “consciousness” in animals. We also briefly consider the brain of invertebrates which can exhibit some forms of consciousness (see previous paragraphs) but in which neural architectures are very different from those of vertebrates.

3.7.1. Top-Down approach to consciousness in animals

This approach aims to describe relationships between upper parts of the brain (telencephalic cortex and thalamus) and neural brain-stem structures in animals. Echoing what is described for human consciousness (see 2.2.1.1 and 2.3.6), several authors proposed three main physiological reasons supporting the importance of the neocortex for animal consciousness (Seth *et al.*, 2005; Mashour and Alkire, 2013):

(i) **Changes in EEG pattern mainly concern the neocortex**: EEG changes have been observed in neocortical (or neocortical-like) areas of virtually all mammals and birds when they shift from an awake state to depressed levels of consciousness. These changes indicate that firing properties of neurons across the neocortex depend on the level of arousal.

This finding has been used to support the idea that neuronal brain activity (particularly in the neocortex) is a necessary requirement for consciousness (Revonsuo, 2006). Yet, one may argue that such changes in EEG merely reflect a wakefulness/alertness state, indicative of a capacity for a given level of perception. Thus neocortical changes in EEG response patterns, even if commonly considered as an index of neural correlates of consciousness, may in fact involve other basic processes in addition to consciousness, rather than simply being understood as “being awake”.

(ii) **Thalamo-cortical loop activity**: Consciousness appears to be linked specifically with neural activity in the thalamo-cortical system. According to this view, the midline brain structures of the brain stem and midbrain are important for keeping the cortex in an awake state, whereas the cortical regions are thought to serve more specific cognitive functional modules contributing to the components of conscious experience.

(iii) **Conscious activity is correlated with widespread brain activity**: The spread of cortical activity is linked to sensory inputs and associated with multiple, or recurrent local feedbacks, followed soon after by long range feedback from anterior to posterior structures ('horizontal pathways'). These long-range connections are thought to be important for the experiential aspects of consciousness (Singer *et al.*, 1993). It is increasingly clear that the direction of cortico-cortical communications (i.e. direction of neural activity flow) is relevant for processing of consciousness. Information processing from the caudal to the rostral direction (feed-forward) is associated with sensory processing. It can occur in the absence of priming by consciousness, e.g. general anaesthesia. In contrast, information processing in the rostral-to-caudal direction (feedback or cortical reafference) is thought to be associated with experience of consciousness itself. General anesthetics preferentially inhibit these rostral-to-caudal flux of information (see the conclusion in section 2.2.1.2.).

Overall, these data suggest that the neocortex is important as one major player of consciousness in animals. Nevertheless, more accurate studies have provided a deeper understanding of the implications of the cortical telencephalic circuits, including associated thalamic nuclei (thalamo-cortical loops), and mesencephalic-brain stem reticular circuits. These brain stem circuits constitute the core of somato-sensing structures necessary for triggering the function of arousal. They act as "a gate for the core self to emerge" (see Parvizi and Damasio, 2011; Damasio, 2010; and the review from Fabbro *et al*., 2015). As a consequence, it is now understood that what is commonly designated as "consciousness" is a multicomponent property mediated by different neuroanatomical components.

A more complex and accurate view of consciousness indicates that different contents and levels of consciousness coexist and that "consciousness is not restricted to higher-complex dimensions such as self-consciousness or narrative-self, which were too often considered in former psychological studies as being the only dimensions corresponding to human consciousness.

Box 1: The interplay between segregation and integration of information is a fundamental element of the Integrated Information Theory of consciousness (ITT) proposed by Tononi (2012). This theory (described in section 2.3.6-Integrated Information Theory) includes a « metric index for consciousness » termed Φ (Phi), i) reflecting the amount of information generated by an integrated system beyond the information contained, and ii) meant to capture the emergent property of the system (i.e., level of consciousness). The capacity of the thalamo-cortical system to achieve both integration and differentiation is reflected in higher levels of Phi. Phi is predicted to decrease during sleep and seizures. Preliminary evidence suggests that it also decreases during anaesthesia, possibly due to impaired long-range coupling of neural spike activity.

The ITT of consciousness remains to be demonstrated. It is, nevertheless, a guiding paradigm that can provide information about the evolution of consciousness from a network approach. From an evolutionary perspective, creatures with elaborated brain network systems able to generate high values of Phi would likely be conscious (Edlund *et al.* (2011).

One remaining dimension is to estimate and test the validity of this metric theoretical paradigm in birds and fishes, and even invertebrates. For instance, the recent proposal of consciousness in insects (Barron and Klein, 2016) requires a challenging evaluation of Phi in this invertebrate class.

It has been claimed that consciousness, irrespectively of its level and content, emerges from a specific brain organization. It includes either cortical telencephalic circuits and related thalamo-cortical loops or mesencephalic-brain stem reticular circuits, all present in mammals. It should be assessed in other vertebrates. A recent study in parrots and songbirds emphasized the importance of numbers of telencephalic neurons in the pallium which provide a means of increasing computational capacity. It supports the concept these birds have advanced behavioural and cognitive complexity (Olkowicz *et al*., 2016). However, this claim about the emergence of consciousness from a specific brain organization ignores an important fact about the evolution of different nervous systems: these structures, absent in species evolutionarily distant from mammals or birds, such as invertebrates, could eventually be functionally substituted by other structures. Such structures, likely sharing similar neural architectures could support and regulate similar functions. One could argue that only the olfactory bulb is relevant for a certain cognitive capacities and therefore, this capacity would be the hallmark of vertebrates which have olfactory bulbs. But, in doing so, one would ignore the fact that insects possess an antennal lobe with a glomerular architecture, very similar to that observed in vertebrates, which performs an odour-encoding process similar to the one performed by olfactory bulbs in vertebrates.

This emphasises the need for careful consideration of neural architectures across species rather than defining borders between them based on whether or not they have a specific brain region.

Box 2: Examination of the differences between gross morphology of the brain across vertebrate species may suggest that the capacities of consciousness increased as brains evolved from a more primitive reptilian organization (with a comparatively major importance of limbic system) to a neo-mammalian organization, characterized by an intricately, folded and expanded neocortex. Such a conceptualization of the evolution of the brain has been popularized by Maclean (as "the triune brain"). It proposes to have occurred in linear stages through which more "advanced" brains - along with their expanded behavioural repertoire - were built on the structure of earlier forms. It has been recurrently used to explain cognitive and consciousness differences. More importantly, such a view of the evolution of the brain is now largely considered as over-simplistic since, for instance, it did not take fish brains into account. It now appears to be erroneous, as discussed for instance by Fabbro *et al.* (2015). Fabbro *et al.* indicate that fish have developed a basal subcortical system and may thus have a primary consciousness. Moreover, a precursor of neocortex is actually present in these earlier vertebrates. That claim is also based on some aspects of connectivity and homology of early transcription factor expression (Striedter, 2005).

3.7.2. Bottom-Up Approach in animals

The discovery of the ascending reticular activating brainstem established the fundamental role of active arousal in generating conscious states in all the vertebrates. A number of specific nuclei and cell types within the brainstem, midbrain, basal forebrain, and diencephalon send long-range axons throughout the cortex. They enhance arousal and generate the basic cortical neurochemical environment compatible with the energetic burden of a large cortex supporting, among multiple functions, consciousness (Lydic and Baghdoyan, 2005). The role of arousal in regulating overall levels of consciousness is also seen when comparing full awakeness to depressed levels of consciousness during sleep, coma (Laureys *et al*., 2004), or anaesthesia (also see section 2.2.1). Current research analyses how arousal circuits interact with consciousness, mostly by facilitation processes but also during more subtle cognitive and behavioural tasks. The study of arousal and its relationship to emotions is another topic of research that should also be considered, including a revival of Darwin's investigations on emotions (McGaugh, 2005).

Current studies of the emotional lives of animals show that affective reactions in animals and humans are supported by similar brain structures (Panksepp, 2011). Rather than consciousness resulting from a selective pressure to create an internal representation of the outside world, consciousness might be the indirect consequence of very basic primitive or primordial emotional influences. Such a hypothesis has been proposed by Denton (2006) who argued that the drive triggered by such emotions generates an arousal response in any living organism and prepares the brain for action. The basic behaviour of an organism is driven by a fundamental physiological need to maintain homeostasis. Thus, basic needs such as water, air, salt, food, and drive for reproduction, including its associated behaviour like maternal care and nesting, are considered to be the starting points for evolving a conscious brain (Denton *et al*., 2009). This proposal fits with the basic aversive primordial emotions experienced during pain (*cf*. Le Neindre *et al*., 2009 and 2014).

Box 3: Based on a recent work on the lamprey (Stephenson-Jones *et al.*, 2012), Mashour and Alkire (2013) stressed how the neuroanatomical and neurochemical needs for selecting an action can be crucial for survival. They suggested that the basic neurophysiologic mechanisms supporting consciousness in humans can be found early in evolution. The primitive lamprey's behavioural motor output system has similar complexity challenges to those of more recent vertebrates who regulate their behaviour *via* the selective activation of both direct and indirect motor output pathways at the level of the basal ganglia. This conclusion implies that the lamprey can selectively activate (implicit « intentionality »?) one motor output to perform and simultaneously inhibit other possible outputs. Thus, this primitive vertebrate seems to be able of making a choice depending on the situation confronting it. According to these two authors, such a "reduction of uncertainty" (*a standard definition in information theory*) through action selection, could be considered as the precursor to the more highly informative states of consciousness characteristic of humans. However, experimental demonstrations are still unavailable. It remains possible that many « motor choices » would only imply a cascade of integration of information and reciprocal inhibition in structures like the tectum (i.e. diencephalon) and pallium (i.e. dorsal parts of telencephalon). The build-up of complex motor responses could not necessarily imply any kind of consciousness. This is an interesting hypothesis but further studies are required to validate its operational role in the emergence of consciousness.

3.7.3. Another approach of consciousness in animals

To identify the different components and level of consciousness in vertebrates, a somehow anthropo-centered starting point has often been to look for recognized basic features of the different components of human consciousness. These studies implied identifying the emergence of elements that make up a "self" and the associated neural structures. Nevertheless the possibility of inferring from data collected in humans the equivalent neural structure associated with a dimension of consciousness in animals does not exclude the possibility that somehow a similar conscious dimension might have emerge along the phylogenic tree as based upon a different set of the neural architecture.

Box 4: In 2015, Fabbro *et al.* wrote "*Neuroanatomic, neurophysiological and neuropsychological data supporting the hypothesis that different levels of self and world representation in vertebrates rely on two things*" :
(i) a basal subcortical system that includes brainstem, hypothalamus and central thalamic nuclei and that may underpin the primary (or anoetic) consciousness that is probably present in all vertebrates; and
(ii) a forebrain system that include the medial and lateral structures of the cerebral hemispheres and may sustain the most sophisticated forms of consciousness [e.g. noetic (knowledge based) and autonoetic, reflective knowledge].
We postulate a mutual, bidirectional functional influence between these two major brain circuits. We conclude that basic aspects of consciousness, like primary self and core self (based on anoetic and noetic consciousness), are present in many species of vertebrates and that, even self-consciousness (autonoetic consciousness) does not seem to be a prerogative of humans and of some non-human primates but may, to a certain extent, be present in some other mammals or in birds.

The search for possible neural correlates of consciousness can be carried along a phylogenic perspective with reference to known dimensions of human consciousness since the studies and hypotheses have mostly been developed in this species. In the present case, we choose to refer to the four functional components of self as proposed by Damasio (2010) and already briefly introduced in chapter 1, section 1.5.1:

(i) A primary functional level, termed "**proto-self**", was defined as the most ancient form of coherent world and bodily representation (also referred as functional maps) for any organism equipped with a brain. This organizational level provides the possibility of focusing on the fundamental aspects of life (e.g., visceral and motor) and constitute an organizational unit providing elementary coordination for all sensations (Humphrey, 2011), including primordial emotions (Panksepp, 1998 a, b; Denton, 2006). It can be proposed that the proto-self is probably operative in most animals including invertebrates equipped with a nervous system capable of encoding different aspects of the environment and of organizing motor responses hierarchically and adaptively.

(ii) The second functional level called "**core self**" (Damasio, 1999, 2010; Parvizi and Damasio, 2001) provides a sense of ownership (feeling that the body is mine) and a sense of agency (the feeling of being the actor of one's own actions). These characteristics are pre-reflexive, implicit and a basis for tacit aspects of one's own experience. The core self is linked to affective systems. This basic form of self and world representations implies a sense of temporality as the two representations operate in the present moment (Edelman and Tononi, 2000). They are probably present in many vertebrate species. Based on neural architectures and behavioural and physiological evidence, it has been argued that they may also be present in insects (Barron and Klein, 2016). Mammals and birds are reported to be endowed with developed knowledge-of-the-world (semantic memory). They are able to be flexible in utilizing such information (Tulving, 2002 a). Some fish, reptiles and birds can encode the features of the environment in "map-like memory representations" (Bshary *et al*., 2002). This spatial representation has also been proposed for honeybees which are long-range navigators returning to the same place in space, the hive. Several experiments demonstrating short-cuts and travelling of novel routes support this idea (Menzel *et al*., 2005). In vertebrates, such spatial representation is encoded and stored in the hippocampus, while in teleost fish which have no hippocampus it has been proposed that the lateral pallium could play a similar function. Even in insects a neural correlate for spatial representation can be found: in the fruit fly, it resides in a central brain structure termed the central complex (Oftstadt *et al*., 2011).

> Associated behavioural manifestations of proto-self and core-self seem to be present in most vertebrate species and are suggested for some invertebrates. However, there are two other functional dimensions of a self which are still the subject of debate for most non-human species, since experimental proof for their presence is not established yet.

These two components are:

> (iii) **Self-consciousness.** It was initially explored in developmental and comparative psychology studies using mirror recognition tests. These studies explored how human babies, some primate species and bird species, and even a few molluscs, can react to surreptitiously introduced changes of their image reflected in a mirror. This test has been used with some positive results in several vertebrate species, such as chimpanzees over 28 months of age (Povinelli *et al.*, 1997), orangutans (Lethmate and Ducker, 1973), macaques (Rajala *et al.*, 2010), dolphins (Reiss and Marino, 2001), elephants (Plotnik *et al.*, 2006), and corvids (Prior *et al.*, 2008). However there are still vigorous arguments about the validity of this test as it may not provide definitive evidence for the presence or absence of self-recognition (de Veer and van Den Bos, 1999).
>
> (iv) **Narrative self.** Gallagher (2000), Boyd (2009), and Damasio (2010) refer to this notion as the capability of handling episodic-type (see section 3.4), declarative memories that unify the self into a coherent story. Prerequisites for developing a fully blown narrative self may include language (Gazzaniga, 2002, 2011; Baddeley *et al.*, 2009) and a neuro-psychic architecture that allows individuals to travel mentally in time (Wheeler *et al.*, 1997; Tulving, 2002 a,b; Corballis, 2012). Such an architecture makes possible not only to be aware of and recall past events (i.e., autobiographical memory), but also to imagine possible future events including one’s own death (Valentini *et al.*, 2014). The ability to travel mentally in time seems to be underpinned by several neural regions involved in memory, like the hippocampus and by the aware perception of the self in the mid-line prefrontal and parietal regions (Schacter *et al.*, 2007). These aspects are developed in section 3.3.4.

The components that make up a world-representation and a self-representation are mediated by neurobiological substrates that can be uncovered, both in humans and non-humans, by experimental and technological tools. These anatomical components can be pieced together according to the following view:

The vertebrate brain is composed of a basal and a forebrain system:

> (i) The **basal subcortical system** includes the spinal cord, the brainstem, the cerebellum, the hypothalamus, the central thalamic nuclei and the oldest portions of the telencephalon.
>
> (ii) The **forebrain system** includes the evolutionarily most recent parts of the thalamus, basal ganglia and the cerebral cortical hemispheres including medial and lateral parts.

The forebrain system is developed in vertebrate terrestrial animals, although with various degrees of complexity in amphibians and reptiles as compared to birds or mammals. Only the basal subcortical system is well developed in fish. Thus, a kind of primary consciousness, somehow equivalent to the functional proto and core-selfs, is already present in animals that have a nervous system mainly consisting of the basal subcortical system (e.g., in fish, Damasio, 1999, 2010, 2016; Chandroo *et al.*, 2004; Merker, 2007; Ward, 2011). These basal structures play an important role in the representation of self and the world (Panksepp, 1998 a; Merker, 2007; Damasio, 2010).

The main function of subcortical brain regions, with a variety of brainstem structures, is to coordinate and control both the cephalic segment, including eye movements, and the remaining parts of the body. They include mostly phylogenetically ancient brain regions such as the centromedial regions gathered under the name periaqueductal gray (Bailey and Davis, 1942; Panksepp, 1998 a, b). That last structure is of fundamental importance for the emotional-motor integration as it coordinates a large variety of emotion-related behaviours, such as defence, aggression, reproduction, voice, and pains, from fish to human beings (Parvizi and Damasio,2001; Merker, 2007, 2013; Panksepp and Northoff, 2009; Damasio, 2010).

Three other midbrain and brainstem structures play a critical role in the development of primary forms of consciousness:

(i) the **hypothalamus**, which is primarily involved in monitoring body homeostatic (e.g., hunger, thirst, and thermoregulation) and emotional states, and in regulating and integrating primary motivational states related to goal-directed behaviours;
(ii) the **central thalamic nuclei**, particularly the thalamic reticular nucleus, which are thought to be involved in maintaining the proto-self or primary conscious awarenesss (Ward, 2011);
(iii) the **roof of the midbrain** (superior colliculus or optic tectum), which represents a multisensory integration station where representations (simulations) of a “distal world” are generated.

The roof of the mesencephalon of vertebrates, or optic tectum, together with the hypothalamus, make up the mesodiencephalon, a structure with major integrative functions in all vertebrates.

It has to be noted that the mammalian superior colliculus, or the optic tectum in birds, has a special role in fish by controlling eye movements, probably the most complex movements present in those species (Stein *et al.*, 2002 a, b). The periaqueductal grey matter (PAG) is a complex mesencephalic structure that surrounds the cerebral aqueduct. It is intimately connected to the deeper collicular layers, and is also part of the emotional motor system. In mammals, PAG receives more than half of the ascending fibers related to perception of pain (Parvizi and Damasio, 2001; Damasio, 2010). It is strongly connected with structures of the basal subcortical system (hypothalamus, amygdala, raphe nuclei, and superior colliculus) as well as with structures of the forebrain group (insula and cingulate cortex).

Anatomical, physiological and behavioural evidence suggests that the basal subcortical system may underpin a primary self-representation. This system, present in all vertebrates, is made of neural circuits based on reciprocal connections between brain stem and central thalamic nuclei and phylogenetic old cortices (Meek and Nieuwenhuys, 1998; Mueller, 2012).

These connections may allow re-entrant interactions which is highly relevant since they are considered to be the basis of primary consciousness and proto-self (Edelman, 1992, 2004; Edelman and Tononi, 2000). Neurophysiological studies indicate that brainstem structures are endowed with a neural organization able to perform multimodal integration of sensory stimuli. They can create multisensory representations of the self and the body (Herrero *et al.*, 1998; Sparks, 2002; Luque *et al.*, 2005). Eventually, they integrate the world- (target selection), body- (action selection), and motivation-need cues to optimize decisions (Merker, 2007; Broglio *et al.*, 2011).

In addition, we must remember that the superior colliculus is the only structure outside the cerebral cortex where fast electrical oscillations (gamma frequency range of EEG) can be recorded. This kind of activity is known to be associated with the conscious perception of stimuli (Brecht *et al.*, 2001; Engel and Singer, 2001; Fries, 2009). In teleost fish, lesions of the tectum, but not of the pallium (often referred as “hippocampal” sub-part of pallium), impair the use of egocentric strategies for spatial orientation and generate a profound disorganization of exploratory patterns (Salas *et al.*, 2003; Burnett *et al.*, 2004).

This is reminiscent of some clinical observations on anencephalic humans that can exhibit minimal states of consciousness as indexed by affective interactions with other individuals and absence of seizures (Shewmon *et al.*, 1999; Merker, 2007).

The structures of the nervous system that researchers assign to the basal subcortical group seem to be capable of generating an elementary representation of the world and of the self in mobile animals. In particular, the superior colliculus and the periaqueductal gray may be involved in the creation of a self-consciousness that is crucial for generating a representation of the world (Stein *et al.*, 2002b; Panksepp and Northoff, 2009; Damasio, 2010). More precisely, consciousness can arise in particular from the interaction between the self and other individuals (Damasio, 1999, 2010; Revonsuo, 2006).

Thus, it is now clear that emotional consciousness is a property of subcortical circuits that humans share with the other animal species (Panksepp, 1998 a; Solms and Panksepp, 2012).

In conclusion, several main trends arise from this overview of the literature on processes and neuronal structures involved in the emergence of different dimensions of consciousness. As already stated in chapter 2, consciousness is not a unique homogeneous phenomenon. Attempts to link one dimension of consciousness to a single structure or a given single network were shown to be difficult and very hazardous.

In contrast to clinical observations in humans, where verbal testimony is often possible, there are few comparative studies aimed at directly providing a link between the behavioural performances of a species with its existing nervous substrate. Thus, we can only refer to the neuronal correlates of cognitive performances in human subjects or in a few non-human primates or rodents. Data on farm animals are mostly lacking, but some common basic functional neuronal correlates of consciousness can be drawn.

In mammals, telencephalic cortical areas are linked to the other parts of the brain *via*:

(i) Horizontal pathways insuring the spread of information between different cortical areas. They are also described as subserving feed-forward and backward functions;

(ii) Vertical pathways mainly corresponding to cortico-thalamic circuits. This subset of feedback loops seems to be mandatory for achieving higher conscious features.

Midbrain nuclei are present in all vertebrates and are involved in the basic dimensions of consciousness, they act as a gateway process before more complex functions can be completed. In birds and fish, functional structures subserving functions equivalent to cortex are likely represented by the telencephalic pallium or the mesencephalic tectum. Midbrain structures could be homologous to those present in mammals. However, the issue of assessing true homology of brain structures remains debatable. In addition to these architectural features, two specific neurophysiological mechanisms, described in chapter 2, are strongly linked to the emergence of consciousness. These are the neural synchrony between different brain structures and the neural feedback at each level of the processing of information.

3.8. Conclusions

In this chapter we have reviewed several aspects of animal behavioural and cognitive capacities, and where available, of its underlying neurophysiology to address consciousness in animals. This analysis is based on criteria validated in adult humans, where consciousness has been analysed by focusing on its level and its content. We only partly followed this approach in this chapter as most of the information collected in animals refers to the content of consciousness rather than on its level. We reviewed a series of behavioural findings in different cognitive contexts, from emotionality, sociality and animal-human relationships to metacognitive problem solving and the existence of episodic memory in animals. In doing so, we concluded that these cognitive processes analyzed from a behavioural perspective suggest the existence of different contents of consciousness depending on the animal species. We also provided information on the most important neural structures that are involved in animal consciousness. In vertebrates, we highlighted the importance of the forebrain system and basal subcortical system which seem to play a critical role in the development of consciousness in animals. However, we also stressed that caution is required before excluding consciousness in invertebrates that do not have these structures, as different neural architectures, resulting from distinct evolutionary histories, may be involved in comparable processes leading to some forms of consciousness.

These analyses do not fully demonstrate that all form of consciousness occur in all animals, but we now consider that the overall picture provided by this corpus of behavioural, cognitive and

neurobiological studies supports the notion that such forms of consciousness exist in the species studied so far.

All the cognitive processes reviewed in this chapter are based on perceptual, attentional, mnesic, emotional and evaluative competences which are the contents of the consciousness. As for humans, animal consciousness might be best described as the emerging product of interactions between different functional layers constituted by these competences which revolve around a central node supporting core regulations involved in vigilance and central rhythms. Upon the perception of a stimulus of interest, several of these layers are activated and do interact to ultimately produce interpretations and intentionality which are actualized through the expression of actions and, potentially, conscious actions. In this way, consciousness has to be regarded as a goal-directed dynamic system and is produced by the activity of interactive competences. **Thus, processes related to consciousness allow the emergence of responses which have greater complexity and content than the simple combination or addition of individual responses of separate systems.**

Depending on the animal species or the external factors which are considered, consciousness may fluctuate from lower contents (mobilizing less numerous brain structures and complexity levels and limited associative learning abilities) to higher contents (mobilizing numerous brain structures and complex integrative processes). As an over simplistic example, two situations are proposed:

> (i) **Low content of consciousness**: This consciousness would involve tasks which can be organized without a high degree of awareness but with the obligation of coordinated basic responses. Such situation would imply some kind of primary emotional drive, require the cooperation of simple memory components and involve sound-enough estimate evaluation of a given situation (i.e., the sequence of elementary motor responses involved in the decision to fight or fly). Beyond necessary basic feed-back neuronal circuits, responses of low- level of consciousness do not require much complex feed backs nor long range re-entrant processes within the brain, rendering self-awareness rather unlikely. This type of response is not only observed among « lower species » but can also occur in species equipped with complex brains and exhibiting highly elaborated complex behavioural repertoires.
>
> (ii) **High content of consciousness**: Such consciousness would imply an emotional component, require numerous, different memory components and complex estimates of potential responses with longer range consequences. Such kind of behavioural responses or even elaborated thoughts involve complex feed-back processes (long-range neuronal loops – now referred as horizontal feed-forward or backward interactions) that render self-awareness more likely to happen. Such kind of responses has been observed among species equipped with more « recent » and complex brains such as those of mammals and some bird species.

An important limitation of the studies presented in this section is that they were performed on a limited number of species. However, the range of species considered covers a broad phylogenetic spectrum, spanning from invertebrates to vertebrates, so that it seems reasonable to extend with caution the conclusion stated above beyond the study cases discussed in this chapter.

Reducing the answer to the question “Is there consciousness in animals?” to a simple yes or no answer is inappropriate due to the complexity of conscious processes and their diversity, both at the mechanistic levels and in terms of behavioural contexts where they are or may be expressed. Rather, there may be multiple answers which in all cases should acknowledge for the heterogeneity of conscious processing in animals. Studies on animal consciousness cover outcomes as different as attention in lampreys and perspective-taking in ravens to “theory of mind” perspective in primates, which is included in self-consciousness.

This heterogeneity is not surprising when considering animal evolution and the very large diversity of solutions that animals use to adapt to different environments. The question resulting from this consideration is whether consciousness is the result of evolutionary processes, and, thus, whether it may be considered as any other adaptive biological or psychological process (such as, e.g., locomotion or food specialisation). This question will be developed in the next chapter.

We conclude that most animals studied so far, ranging from some invertebrates to some vertebrates, exhibit some behavioural and neural properties that are compatible with the inference of some forms of consciousness. From the species which were unequally studied as yet, we might generalize that consciousness, at least in its basic forms, cannot be discounted to occur in the species which were not yet studied. Thus, instead of rejecting the existence of consciousness in animals, it seems more prudent not to exclude it so as to conceive better, i.e. animal-adapted, forms of animal handling, animal experimentation and animal-human relationships. This conclusion is enhanced by the findings that at least some non-primate animals exhibit performances that could express high levels of consciousness that were previously considered as a prerogative of humans and of some primates. This discovery highlights the importance of developing more accurate characterizations of consciousness using appropriate protocols for asking pertinent questions. Such studies should consider both specific experimental protocols and also experimentation of animals in their natural or familiar environments. Further work in this direction, coupled with the exploration of neural substrates in the animal brain, is necessary to appropriately characterize the levels and contents of animal consciousness

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CHAPTER 4: FUNCTION AND PHYLOGENY OF CONSCIOUSNESS

A major challenge to the study of consciousness in animals is to understand its function. After considering the possibility that consciousness has no function, we review the evidence about its role in adaptive processes, and in particular in the most complex situations involving the connexion that animals have with other members of the same species or group. The adaptive role of consciousness raises the questions of natural selection and the development of consciousness during evolution.

4.1. The adaptive function of different types of consciousness

Most authors interested in adaptive function propose that different forms (or degrees) of consciousness and their associated cognitive capacities may have been influenced by two imperatives.

The first is methodological, and holds that a scientific explanation should distinguish itself from what is commonly understood, which is all too likely to overestimate the importance of consciousness and, with respect to animals, to lapse into anthropomorphism. Hence it explains the importance given to the "principle of parsimony" in the conception and interpretation of systematic observations and experiments. The goal is to explain the most complex phenomena and behaviours by way of a minimum of simple causes.

The second imperative is programmatic. It is in fact a program of mechanisation (or computerisation) of mind. In this sense, this line of research belongs to the tradition of sociobiological interpretations focused on the emergence and function of emotions and of moral behaviour such as altruism (familial altruism as described by Hamilton (1964), reciprocity (Trivers, 1971), or the "tit for tat" or "win-win" strategies described by the prisoner's dilemma (Maynard Smith, 1982; 1989). It belongs to a project known as of the "naturalisation of mind". Seth (2009), in his introduction: "*A major challenge for the successful naturalization of consciousness lies in locating its biological function, or functions*".

4.1.1. Do the different types of consciousness have a function?

Some authors, concerned with the principle of parsimony, feel it is possible to argue that consciousness has no adaptive function, either because it is not essential (Flanagan, 1992), or because it is merely an epiphenomenon (Chalmers, 1996; Robinson, 2007). The lack of consistency of consciousness is said to be demonstrated through a series of experimental clones that together show that, even in the case of a voluntary action, awareness of having performed the action follows rather than precedes the movement itself. Humans (and thus *a fortiori* animals) will only become conscious of a voluntary movement after the movement itself has been completed unconsciously, and thus seemingly mechanically (Haggard, 2005; 2008; Haggard and Eimer, 1999; Libet, 1985).

Granted, consciousness may not be essential (or epiphenomenal) to certain simple voluntary acts, but this does not mean that it is not essential for the full range of behaviours that are likely to enable animals to adopt such behaviour to adapt to changing environments. The hypothesis holds for the simplest forms of consciousness. For example, an animal that is capable of forming a representation of a situation in which it finds itself, can act in accordance with an objective of survival, or out of a desire to reproduce, but might well be acting in a merely impulsive manner, as a simple expression of its emotions (that is, of the mental states induced by the representation it has formed of its environment). Its actions will thus follow a predetermined direction. But our conclusions must be different in the case of an animal capable of modifying its movements in light of new circumstances, or because it realizes that its initial representation of the situation is false (Proust, 1997). We may consider that such cognitive and behavioural capacities are likely to have a function in the interactions the animal has with its biotic and abiotic environment. By making reference solely to experiments conducted in stable environments and studying only simple behaviours combining consciousness and will, some authors seem to apply the principle of parsimony with a bit too much enthusiasm. While we can grant that spontaneous reactions (those that are unconscious or only reach the conscious level in retrospect) are most effective when the animal (human or non-human) is confronted with a habitual situation, such spontaneous reactions are insufficient when the animal is confronted with a changing environment or unfamiliar situations.

4.1.2. Adaptive functions that seem well established

The capacity to adapt one’s behaviour to unanticipated or ambiguous situations requires cognitive abilities that go beyond the capacity to form representations of the world and thus to identify the perceived objects and events and react as necessary. At a minimum, the animal must distinguish between the objects that surround it, the mental representation it makes of those objects, and the emotions that are triggered by that representation. It must therefore be capable of objectification. This higher level of consciousness that this involves supposes that the animal is able to identify, assign, and memorise the nature of these objects and events and to select those that are relevant to it or important to its survival. These capacities are present in vertebrates and octopuses. Equipped with this capacity, the animal can direct and adapt its behaviour to new or changing circumstances. A further step is attained when, even without exchanging information with other members of its species, the animal is capable of adjusting its initial interpretation and correcting its behaviour if it sees that it is mistaken.

This capacity for integrating and processing information and for the objectification and discrimination of objects according to their relevant qualities enables the animal so endowed to behave in a way that is flexible and adaptable to uncertain environments, to find solutions to ambiguous situations, and to cope with the unknown. Moreover, an ability to adjust mistaken beliefs quickly in a very short time is a considerable advantage for survival and therefore fitness, since the accuracy of the representations of the world that the animal forms for itself is essential to the adoption of a behaviour appropriate to a given situation. In this way, the animal can avoid threatening situations in its environment and take advantage of opportunities that can increase its chances of survival and reproduction.

Furthermore, the environment of any organism includes other members of its species, and the interactions it maintains with them will likewise play an important role in its fitness. Hence the importance of the signals animals exchange between themselves and of their social interactions, from the simplest forms of interaction, as studied by sociobiologists, to the most complex, such as the forms of cooperation and the division of labour present among highly social species.

The emission of a signal can be merely a reflex, with no meaning except that it indicates the mental state of the emitter. Among some species, however, a link exists between the production of a signal by one individual and a corresponding reaction among members of the same species that receive it. So, even in cases where such signals are very simple, they possess a semantic function. They can designate a mental state such as the quest for a sexual partner or the discovery of a food source, or point out an object or an event such as a predator, or unfavourable weather. It can communicate to other members of the same species or group, information relevant to their survival and prosperity. There are cases in which this equivalence between the signal produced and the interpretation made by those receiving it can be explained by the coordination of two automatic responses, without any need for primary-order forms of consciousness. However, some signals are intentional: these can be cooperative signals intended to alert fellow members of a species to important events; they can also be competitive, signals intended to deceive one’s fellows in order to gain some advantage. It is in the case of this kind of tactical deception, common among great apes, that we believe animals possess a “theory of the mind” which has already been introduced in chapter 3. In this case they are capable of representing to themselves the representations – and thus the beliefs and desires – of other members of their social group. The animal’s deception is intended to modify the mental state of its fellows (Proust, 1997; 2003; Whiten and Byrne, 1988). But the acquisition of a theory of the mind has many other functions for social species. Thus most primates (Premack and Woodruff, 1978), including the capuchin monkey (Perry *et al.*, 2004), are capable of identifying and recognizing specific characteristics of different individuals of their group; that ability also exists in animals from other phyla such as sheep (Kendrick *et al.*, 2001), hyena (Engh *et al.*, 2005), western scrub-jays (Dally, 2005; Dally *et al.*, 2006) and possibly some cetaceans. They are capable of remembering the nature of the interactions among members of their social group and can adjust their social behaviour according to what they know about these relationships (de Waal, 1992). Hence the surprising quotation made by Dennett (1995): "*Even in the case of non-human animals, inferring a genetic basis from an adaptation is risky when the adaptation in question relates not to an anatomical trait but to a behavioural schema that is in all evidence a 'good thing'. Because then there is another possible explanation: the general non-stupidity of the species.*" Even where one cannot assume cultural transmission, some species may very well "reinvent the wheel" whenever the trait proves itself to be a "good thing". This may be particularly so for certain primate species, among whom primatologists have observed forms – albeit simple – of technical culture.

4.1.3. Consciousness, adaptation, and natural selection

If different forms of consciousness can be favourable to adaptation, can we conclude that they result from natural selection acting on the corresponding behaviours over the course of evolution? Such a conclusion is tempting and this is in fact the fundamental hypothesis of sociobiology. If an observed trait is stable within a given species, the trait is presumed to be controlled by genetic mechanisms. One only needs to find an argument explaining the competitive advantage that the trait can provide in terms of reproduction, and thus fitness, to account for its presence by means of natural selection. In responding to the question, "Why does this trait exist in this species?" this approach searches for a theory of final causes, a mechanism that is blind, but teleological since it explains the trait by its purpose rather than by postulated causes (Godfrey-Smith, 1996; Gould and Lewontin, 1979; Seth, 2009). One has only to rack one's brains to come up with hypotheses of conferred advantage translating into improved fitness to explain why things are as they should be, all the while admitting, but without dwelling on the fact, that they could be otherwise. This applies to all traits, whether they be physical or behavioural, including the cognitive capacities necessary for what we recognise as forms of consciousness. However, this "machine for justifying that which exists" raises several problems (for example Bolhuis and MacPhail, 2002, as opposed to Hampton (2001) claim that neuronal structures cannot be explained by adaptive functions).

In the first place, it is simplistic, to say the least, to explain the existence of a trait on the basis of having observed competitive advantages and adaptive capacities of individuals exhibiting that trait under current conditions. There is no evidence that the current adaptive function of a trait is the same as the one prevailing at the time of its selection possibly millions of years ago, in conditions very different from those existing today. To accept such a hypothesis it is necessary to assume that the context of selection remained stable over geological time, whereas we know that "*the advantage conferred by a particular trait is… always relative – to a place and to a time – and is subject to change at any time*" (Morange, 2005).

Most traits (and, *a fortiori*, complex cognitive capacities) are controlled by an indeterminate number of interacting genes – some of which may also contribute to the control of other traits. Without having elucidated the complex mechanisms governing expression of the trait, we cannot know if selection acted on the advantage conferred by the trait or on other advantages derived from other traits genetically associated with it. Similarly, a complex trait could have been co-selected with capacities that are now found together in all the individuals of a species. Evolution is a mosaic of processes, as has been well established with respect to the origins of hominids (Chapouthier, 2001; Dutour *et al.*, 2005). In other words, just because a trait appears today as a functionally coherent ensemble does not mean that this ensemble lies at the phylogenetic origin of the trait in question. Often it is only an association of salient traits that have been selected for in different populations of the species based on a variety of functions and which have then been combined through subsequent crossings across populations.

Another difficulty relates to the fact that the question of what exactly evolutionary selection acts on is still controversial. Does it act on the genes, as Hamilton (1964) and Dawkins (1976) have hypothesised? In this case phenotypes are only “vehicles” created by the genes to transmit and spread themselves by interacting with the environment, thus the term “interactors” used by Hull (1980) to designate phenotypes? Other authors insist on the plasticity of phenotypes relative to their genetic inheritance and consider that selection also acts on phenotypic characteristics, and in particular behavioural characteristics (Bossdorf *et al.*, 2008). For sentient organisms this phenotypic emancipation is well accepted, *a fortiori* in cases where the animal is capable of perceiving and distinguishing within its environment those objects and events that are favourable or unfavourable to it – those elements that are likely to contribute to its fitness. Even if one subscribes to the individualist point of view, the phenotype’s environment includes other members of its species and their interrelations include cultural transmission. An example of this among the great apes is the transmission of how to make and use tools (Danchin and Wagner, 2010).

Finally, we can observe that selection also acts on populations making use of the same resources (or occupying approximately the same ecological niche), as well as on groups of closely associated species in cases where such associations are, in a sense, species-specific, to the point where we can consider that there has been a co-evolution between them.

4.2. The emergence of consciousness in phylogeny

The issue of the phylogenetic origin of consciousness is linked to that of its function. Consciousness may be seen as a fundamental feature of living organisms with corresponding ancient roots that was conceived as a global workspace (see 2.3.1.) to cope with the complexity of life (Merker, 2005). In this context, two main approaches have been used to search for the phylogenetic origin of consciousness, functional and neuroanatomical.

Functional studies usually focus on one process or other contributing to the global workspace, such as episodic memory which contributes to prospective cognition and gives the historic component of consciousness. However, due to the limited number of studies and the conceptual and methodological limits to study these mental processes, most knowledge has been confined to mammals and birds (Allen and Fortin, 2013; Raby and Clayton, 2009). Other functional approaches consider emotions (“affective consciousness”; Panksepp, 2005) as a core component of consciousness to be traced across evolution. In this case, maximizing sensory pleasure is the fundamental process when making decisions about selecting the final behavioural path (Cabanac *et al.*, 2009). For example, Cabanac (2009) concluded that consciousness emerged with Amniotes (including reptiles, birds and mammals) on the basis of the occurrence of physiological responses to handling, an emotion-eliciting stimulus, and other behavioural signs of emotion and sensory pleasure, such as play.

However, the neuroanatomical organization of the upper brainstem, a set of key structures forming a control system for the environmental guidance of motivated behaviour and decision making, suggests that this function devoted to consciousness may be extended to the whole phylum of vertebrates, although possibly only in limited form in the lower vertebrates (Merker, 2005). The extension to other phyla including animals with complex active bodies, arthropods and molluscs, is less likely because of their large differences in anatomy and physiology as compared to vertebrates. However, several studies on octopuses, squids and cuttlefish show that these coleoid cephalopods exhibit many behavioural indicators of consciousness (Merker, 2005; Seth, 2009). In arthropods, recent studies also described emotional-like behaviours in crayfish which were controlled by neurochemical (serotonergic) mechanisms (e.g. Fossat *et al.*, 2014).

More recently, Bronfman *et al.* (2016) described the transition of living organisms to minimal consciousness through the evolution of associative learning. They define *sentience* as the minimal state of consciousness, referring to the most basic form of sensory phenomenal experience, i.e. with subjective feelings. They propose the process of *unlimited associative learning* (UAL) as the marker of the evolutionary transition to minimal consciousness or sentience and describe the functional architectures of unlimited associative learning. They could find behavioural evidence of UAL and the structures implementing it not only in vertebrates, but also in arthropods and molluscs. It is therefore possible that consciousness may have arisen multiple times across evolution, alike winged flight, which appeared and evolved independently in insects, birds, bats, and pterosaurs, or eyes (vision) in vertebrates, cephalopods and arthropods (Allen and Trestman, 2015).

4.3. Conclusion

We should thus be cautious in accepting teleological interpretations of the adaptive functions of different forms of consciousness and the cognitive capacities they imply. Does this mean that we should renounce the common assumption according to which we assume that the emergence and increasing sophistication of forms of consciousness are the result of natural selection? Not entirely. Even if we restrict ourselves to the idea of competitive advantages in terms of fitness, we argue that one of the current functions of the cognitive ability to objectify the environment and correct erroneous notions is to enable behavioural flexibility. This flexibility may well have favoured the reproduction of individuals living in environmental contexts very different from ours. Animals with such capacities were able to fashion successful ecological niches for themselves within the biotic communities and wider environments in which they lived over the course of time.

Several authors subscribe to a neo-Darwinian concept of natural selection, typical of sociobiology. We can note that a focus on the competitive advantage of genes and phenotypes, that is, individual carriers of a genome, is consistent with the neoliberal economic view of society. In this view, it is assumed that interactions within a species are reducible to the competition to reproduce and ensure the prosperity of offspring, overlooking cooperative interactions and examples of the division of labour found among certain social species. It is as though inter-specific interactions were confined to predation, exploitation, and competition for limited resources. This view neglects forms of mutualism and the fact that certain species, either because of their behaviour or their structure, function as “ecosystem engineers”, creating habitats for a range of other species. The fitness of individuals and the reproduction of populations are also determined by these intra- and inter-specific relations, mutualism and cooperation. Cognitive capacities enable organisms to recognise the qualities of other beings and to organize them into categories. These forms of consciousness have enabled certain animals to organise themselves into social groups and, in company with competitive advantages, have played a role in the interactions that form the background to natural selection over the long term.

The phylogenetic origin of consciousness is linked to its function. The global workspace (GW) theory is compatible with consciousness being a fundamental feature of living organisms throughout their phylogeny. Functional studies of the GW components such as episodic memories, emotions and unlimited associative learning draw attention to conceptual and methodological difficulties in tracing these process across species. Neuroanatomical studies are limited to organisms related to humans. Therefore it is still possible that consciousness may have arisen independently many times during evolution in other vertebrates, cephalopods and arthropods.

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CHAPTER 5: PROCESSES UNDERLYING THE CONSTRUCTION OF CONSCIOUS PERCEPTION OF SENSORY AND OTHER TYPES OF INFORMATION, INCLUDING PAIN

The present chapter presents information on the conscious or unconscious processing of information by brains of animals and humans. It is organised in three parts.

The first section presents recent knowledge and theories on the brain processes and brain structures involved in the processing of information from the external world, while taking into account the internal needs and physiological state of the organism.

The second section is dedicated to pain perception and the integration of pain-related stimuli in general processing of information by the brain. Compared to other stimuli, pain-inducing stimuli have the largest potential to interrupt and reorient behaviour. The peripheral and central systems involved in pain are presented, as well as current knowledge and theories on the relationships between perception of pain and consciousness. Questions relative to processing of emotions are also addressed, but in contrast to pain, detailed information on animal emotions can be found in Chapter 3. The third and last section discusses the relevance of existing knowledge on consciousness of animals and how recent knowledge should be taken into account from an ethical point of view, given that humans rear and slaughter animals, or use them experimentally.

The articles cited have been selected based on their relevance to the subject. Due to the development of new brain image techniques, recent information is often, but not exclusively, based on human studies. When human subjects are used, we can simultaneously obtain information on specific brain activity and conscious perception. Other studies use non-human primates or other mammals and where available, these have also been cited. It should not be forgotten however, that many of the protocols used for recent work on humans and primates were conceived using the existing large body of neurological knowledge on animals of different species. For example, current knowledge of the anatomical and functional connectivity of the sensory system draws very largely on earlier, very precise animal studies. The implications of current knowledge based on human studies for hypotheses on animal consciousness, particularly with reference to pain, are addressed at the end of the second part.

5.1. Dealing with information

5.1.1. Introduction

Before addressing questions relative to consciousness we need to consider how complex organisms function. Humans and animals constantly adapt their behaviour to their internal state and the external environment. The decisions they take and the way they behave depend on how they evaluate these internal and external features. The information is collected through various modalities. The senses play an important role in the collection of exteroceptive stimuli containing information relative to the environment. Organisms are further extensively equipped with sensors to obtain interoceptive stimuli, with information on the body’s status. For example, oxygen and carbon dioxide sensors, baroreceptors and pulmonary stretch receptors inform the brain in real time on aspects of the hemodynamic status of the body, allowing constantly adjustments. Proprioceptors - sensors that provide information about joint angle, muscle length, and muscle tension-, nociceptors - sensors involved in pain perception-, and various chemical sensors in the gut provide information on the posture and spatial position of the body, of possible tissue lesions and of the digestive status. These and other sources of information related for example to memory, need to be compiled by the brain into an integrated image for further use (Barron and Klein, 2016; Damasio, 2010; Merker, 2007).

An adequate compilation of information and integration into a larger perspective, the correct identification of priorities, followed by relevant decisions and behaviours is indispensable for the survival of complex organisms in a multifaceted and changing environment (see Chapter 4). In practical terms, a behaviour must be interruptible when higher priorities arise, but there is also a need for behavioural persistence: if behaviour changes in response to each change in the internal or external environment, it would become chaotic and inappropriate. This chapter addresses current knowledge on the processes involved in the construction of behavioural responses to a challenging environment and changing internal needs.

5.1.2. Brain processes

Organisms with brains have the potential to collect very large quantities of information, of both the external environment and their internal bodily state, but brains have a limited capacity to process large volumes of information. One of the basic principles when dealing with these large amounts of information is "attentional selection"; in other words, attending only to the most relevant stimuli (Desimone and Duncan, 1995; see Chapter 2). Attentional selection refers to the separation of relevant versus irrelevant information, isolation of an object or of a spatial location. The information to which attention is directed may be regulated exogenously ("bottom-up") or endogenously ("top-down"). Top-down attention is goal-oriented and refers to the voluntary allocation of attention to certain features, objects, or regions in space. For instance, a person or an animal may search for food items or a companion. Bottom-up attention in contrast is stimulus-driven: salient stimuli can attract attention, even though the subject had no intentions to attend to these stimuli (Schreij *et al.*, 2008; Theeuwes, 1991). For instance, someone may be looking for red items, but an unexpected, sudden appearance of a non-red object may inadvertently draw her/his attention.

Different neural mechanisms underlie bottom-up and top-down attentional processes and they work in parallel. Bottom-up processes depend on neural substrates involved in recognition of an object, including its features, its location and the timing of appearance. Top-down processes depend on neural substrates involved in memory, cognition and determination of relevance. According to the most widely accepted theory, complete representations of objects and other stimuli are formed, before the neural competition for preferential processing takes place (Desimone and Duncan, 1995). From these competitive neural interactions, believed to be relatively slow, attention progressively emerges. The direction of the attention will depend on the result of the competitive interactions (Desimone and Duncan, 1995; Chica *et al.*, 2011; Corbetta and Shulman, 2002; Pinto *et al.*, 2013). This process is called "biased competition"; the attention given to an object is influenced or *biased*, by its intrinsic features and top-down processes to give priority to the most relevant stimuli (Desimone and Duncan, 1995).

Thus, through selective attention the brain identifies and treats the presumed most important pieces of information. Obviously this information must be made available to be used for subsequent decisions and behaviour. For this, it is believed that processes related to consciousness are needed. In this context, scientists refer to "phenomenal consciousness", the subjective experience, and "access consciousness", when it is poised for direct control of reasoning and action (see Chapter 2). While "attentional processes" aim to select information, processes related to phenomenal and access consciousness make it possible to integrate the information into a larger picture. The integrated picture is enriched because it gives a sense or content to the information; for example, it is not possible to experience visual shapes independently of their colour, or perceive the left half of the visual field independently to the right half (Tononi and Laureys, 2009; see Chapter 2). The integrated relevant information can be made accessible for detecting anomalies and errors, decision making, developing strategies, further planning, inferring the internal or motivation state of other animals and, at least in humans, setting long-term goals and strategies and rational thought (Barron and Klein, 2016; Damasio, 2010; Koch and Tsuchiya, 2007; Merker, 2007).

The question of how consciousness and attentional processes are related is currently receiving a lot of scientific attention (see Chapter 2). The existing ideas rely rather strongly on the functioning of the visual system, because this system is relatively well described, but there is also some information on other sensory systems. Briefly, organisms with brains have different needs at different times and deploy varying behavioural strategies to fulfil them. The activities allowing the animal to fulfil its goals or needs compete for its behavioural resources and these are often mutually incompatible. For example, searching for food or for a mate requires different strategies. Decision-making has to integrate both needs and opportunities. It involves action selection, target selection and motivational ranking (Merker, 2007).

In conclusion, the titration of input in terms of energy, time and priority involves complex processes that are not yet totally unravelled. Recent literature describes two main aspects of information processing by the brain. First, attentional processes are involved in the selection of those stimuli considered a priority. Second, processes related to consciousness help to integrate the information into a larger picture, allowing relevant information to be summarised and made accessible for higher level cognitive treatment. Some scientists, but not all, think that attentional processes and consciousness involve different brain mechanisms. The main brain structures involved in attention and consciousness will be presented next.

5.1.3. Brain structures involved in attention and consciousness

Current theories are essentially based on the effects of local lesions or temporary functional blockage of certain parts of the brain, using behavioural (task performance, verbal reports in humans) and physiological outputs, on anatomical studies of connectivity between areas, and on brain imagining techniques in relation to behavioural, cognitive or emotional status. In general, the prefrontal, parietal, and insular cortices and the posterior and anterior cingulate cortices are essential for complex conscious processing of information. It is believed that the anterior cingulate is involved in response selection and preparation, and that it functions in close interaction with the insular cortex (Medford and Critchley, 2010). For example, the insular and anterior cingulate cortices are often jointly activated in subjects experiencing emotional feelings (Craig, 2009). The central role of the insular cortex in complex conscious processing of information of very different sources has been repeatedly emphasised (Craig, 2009; Ibanez *et al.*, 2010; Nieuwenhuys, 2012). It is implicated in gustatory, olfactory, auditory, visual and somatosensory perception, and experiencing and recognition of the emotion of disgust. Lesions in this region may cause underactivity and tiredness and abnormal functioning of the autonomic nervous system (Ibanez *et al.*, 2010). In addition to the anterior cingulate cortex, the insular cortex presents multiple anatomical and functional connections with other cortical (orbitofrontal, parietal, occipital, and temporal cortices) and subcortical areas (thalamus, amygdala and ventral striatum) and could play an important role in the converging of different sources of information (Ibanez *et al.*, 2010). Similarities in the insular cortex have been found between humans and other mammals, including monkeys, apes, elephants, whales and walruses (Nieuwenhuys, 2012).

As indicated earlier, attention and consciousness are intimately connected but scientists do not agree as to whether they are separable or not. Currently there are no studies showing distinct brain activations formally illustrating distinct attentional and conscious processing (but see Lamme, 2003). However, several proposed models that build in various ways on the theories of attentional and conscious processes will be described next.

5.1.3.1. A central role of the cortical areas

Neural models of higher order information processing and access consciousness are often strongly cortically oriented. For example, Dehaene and colleagues propose that a subset of cortical pyramidal cells with long-range excitatory axons, particularly dense in prefrontal, cingulate, and parietal regions, together with the relevant thalamocortical loops, form a horizontal ‘‘neuronal workspace’’ interconnecting the multiple specialized, automatic, and nonconscious processors (see Chapter 2; (Dehaene and Changeux, 2011; Dehaene and Naccache, 2001). Lamme (2006; 2010) proposes that phenomenal visual experience occurs only if following the first feedforward sweep, recurrent interactions between areas take place, particularly between the primary visual cortex and other regions of the visual cortex (see Chapter 2). According to Lamme (2006; 2010) widespread feedforward is necessary to attend to a stimulus and widespread recurrent processing between primary and temporal, parietal, motor and/or frontal cortices leads to an attended conscious experience, accessible to cognitive operations. The progressive build-up of recurrent interactions proposed by Lamme (2006; 2010), first locally within the visual system and then, more globally, into parieto-frontal regions reflects the distinction between preconscious and conscious processings made by Dehaene and colleagues (cf. Chapter 2).

5.1.3.2. The central role of the subcortical areas

Models studying phenomenal consciousness suggest that a cortex is not necessary, but certain subcortical structures need to be present, particularly those that facilitate the creation of an integrated neural model of the organism and contain information on the state of self, self-initiated movement, environment and memory (Barron and Klein, 2016; Damasio, 2010; Merker, 2007). This processing would allow a very basic form of consciousness hallmarked by subjective experience, and is given different names including primary consciousness, core consciousness or phenomenal consciousness (Barron and Klein, 2016). More specifically, higher parts of the midbrain (superior colliculus) receive multimodal input, i.e. containing exteroceptive (external world) and interoceptive (bodily state) information to compute information of the organism as it moves in space. Lower parts of the midbrain (hypothalamus, pituitary, mammillary bodies) collect information on the physiological status. Other structures of the midbrain (thalamus, periaqueductal gray, reticular formation) and the basal ganglia (ventral *striatum*, *substantia nigra*) combine these sources of information into an integrated model. If present, higher cortical areas and the hippocampus do have a strong input in this system, but the functioning of the system does not depend on this input (Barron and Klein, 2016; Damasio, 2010; Philippi *et al.*, 2012).

The above suggested integrated neural model based on subcortical processing would thus allow basic forms of consciousness, particularly subjective experience or “core consciousness” (Barron and Klein, 2016; Damasio, 2010; Merker, 2007). Other observations (Philippi *et al.*, 2012) suggest that certain aspects of higher order conscious processing are possible if only small parts of the cortex are still functional. A patient with extensive bilateral damage to the insula, the anterior cingulate cortex, the medial prefrontal cortex and the medial temporal lobes had not only “core consciousness”, but also higher-order levels of consciousness. In this patient the autobiographical self, referring to the presence of a repository of autobiographical memories and representations of physical affective and personality traits, was largely intact. In addition, the patient was also capable of introspection, which relies on higher-order executive attentional and metacognitive functions and reflection on one’s own mental states. These capacities would thus emerge from distributed interactions among networks of brain regions that include the brainstem, thalamus, and posteromedial cortices, which had remained intact (Damasio, 2010; Philippi *et al.*, 2012).

Thus, theories of conscious processing of information agree on the central role of subcortical neural processes, particularly the essential role of the thalamus. The thalamus is placed centrally in the brain and receives input from the reticular formation in the brain stem, involved in the sleep-wake cycle and arousal, and it projects to and receives projections from the cortex. The thalamus is an essential relay station for visual, auditory and somatosensory information. It plays a role in attention and in attentional shifts within (e.g. within vision) and across modalities (for example between vision and audition) and participates in directing sensory and motor information to the cortex (Huart *et al.*, 2009; McAlonan *et al.*, 2008; McCormick and Bal, 1994; Rees, 2009). One exception is olfactory information most of which, in contrast to the other senses, bypasses the thalamus on its way to the neocortex (Keller, 2011; Box 1).

Box 1. Olfaction seems unrelated to the thalamus.

In contrast to the other senses, the majority of olfactory information bypasses the thalamus on its way to the neocortex, suggesting that the thalamus is not responsible for shifts of attention toward the olfactory modality (Keller, 2011). Possibly, attentional selection of olfactory information occurs in the olfactory bulb or the piriform cortex, but this needs investigation (Keller, 2011). The phenomenal experience of olfaction is possibly related to activity in the neocortical orbitofrontal cortex. A recent lesion study of a single patient showed that brain injury of the right orbitofrontal cortex completely abolished conscious processing of olfactory information (Keller, 2011).

The models also agree that cortical input allows more complete and complex processing. Hence, the thalamo-cortical circuit would permit the highest-order conscious processing. However, we lack information on the exact contribution of the cortex in lower-order conscious processing. In addition, from work on humans several scientists confirm even that the mere presence of subcortical structures allow basic forms of conscious processing, while complex conscious processing such as abstract thinking or introspection needs cortical structures.

5.2. Pain

The somatosensory system receives and treats sensory information coming from the surface of the body, or its internal organs and tissues. It has been proposed that, like vision, somatosensory processing involves an initial feedforward sweep of neural activity to the primary somatosensory cortex creating a fleeting unconscious image of the tactile sensation. Subsequently, recurrent processing between this and other cortical areas generates the conscious tactile experience (Azanon and Soto-Faraco, 2008).

Somatosensory receptors are specialised sensors responding to temperature (thermoreceptor), pressure and touch (mechanoreceptors), chemicals (chemoreceptors) and noxious stimuli (nociceptors). A stimulus is noxious if it is potentially capable of causing injury. Vertebrates have a sophisticated and specialised subsystem of the somatosensory system, the pain system, to identify and deal with noxious stimuli. Pain is multidimensional, involving different systems and processes. The International Association for the Study of Pain (IASP) states that pain is: “An unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage” (Merskey and Bogduk, 1994). As indicated by the definition, pain perception is associated with potential tissue lesion and danger and logically needs to be attended to. Pain is a very specific stimulus in that it generally interrupts attention to other stimuli and urges action (Eccleston and Crombez, 1999). It is difficult to ignore pain stimuli, especially those of high intensity. In an experiment by Crombez *et al.*(1994), painful stimuli captured attention involuntarily and impaired performance in auditory discrimination tasks as shown by increased reaction times. Behavioural responses, such as escape and defence reactions do not extinguish easily in response to repeated pain stimuli, even when they are predictable (Eccleston and Crombez, 1999). Iannetti *et al.*(2008) found that when a painful stimulus was applied repeatedly, the electroencephalographic (EEG) response diminished but the level of perception of pain remained the same. For these reasons, in the context of animal welfare, it is necessary that pain be avoided and treated wherever possible (Le Neindre *et al.*, 2009). The next section is a brief description of the main mechanisms involved in the elaboration of the pain signal (Le Neindre *et al.*, 2009), as well as brain processes involved in the treatment of pain perception. Table 3 summarises the different brain areas having a potential role in pain experience as will be discussed below as well as those involved in perception and discussed above.

Table 3: Role of different brain structures in processing of pain and other sensory information and their potential role in conscious perception.

part of the nervous system involved	input	connections	function	possible degree of consciousness in normally functioning humans and non-human primates	Section of Chapter
ascending system					
spinal level, interneurons	combined noxious and tactile stimuli	brain stem, subcortical and cortical areas	gating	unconscious	5.2.3
thalamus	combined noxious and other sensory stimuli	somatosensory cortices, anterior cingulate and anterior insular cortices	convergence of different types of sensory information and selective transmission	for some scientists, unconscious; for other scientists, potentially some degree of consciousness	5.1.3; 5.2.3
amygdala	visual, auditory, somatic sensory, visceral sensory, gustatory, and olfactory stimuli	prefrontal cortex and thalamus	convergence of different types of sensory information and emotional contents	being part of a neocortical circuit, potential access to conscious perception	Box 6
primary somatosensory cortex	combined noxious and other somatosensory stimuli	thalamus and higher processing areas	convergence of different types of somatosensory information	conscious perception	Box 2, 5.2.3
anterior cingulate cortex	reticular formation, insular cortex	prefrontal cortex	affective motivational component of pain; integration of negative sensory information of different origins	conscious perception	Box 2, 5.2.3, 5.3.1
parietal cortex	sensory stimuli, thalamic input	anterior insular cortex	convergence of sensory input, increasing processing rate of attended stimuli via the anterior insular cortex	conscious perception	Box 5, 5.2.3
anterior insular cortex	thalamus, ventral striatum, parietal and temporal cortices	anterior cingulate cortex, amygdala	depth of processing of different types of information depending on attentional selection	conscious perception	5.2.3, 5.3.1
descending modulatory pain system					
peri-aqueductal gray	amygdala, prefrontal cortex	spinal cord	pain modulation, connective interface between emotional and motivational brain systems and behavioural output systems	probably unconscious	5.2.3, 5.3.1
spinal level		brain stem, subcortical and cortical areas	modulation	unconscious	5.2.2

5.2.1. The afferent pain system and the pain matrix

Nociceptive stimulation may be caused mechanically, thermally or chemically. Such stimulation is perceived by nociceptors which are specialised nerves, capable of transforming nociceptive stimulation into a nervous message which travels from its peripheral origin via the spinal cord to the brain. According to the definition of pain by Merskey and Bogduk ((1994); see above), activation of nociceptors is neither sufficient nor necessary for pain to be experienced. For example, multisensory cues that only suggest injury can sometimes generate an aversive experience that has all the characteristics of pain. In one report by Fisher *et al.* (1995) a person expressed pain following a nail driven through a boot while in reality there was no actual injury. This suggests that the presence of actual nociceptive inputs is not necessary to experience the primary affective dimension of pain (Roy, 2015). Most often however, pain is associated with nociception, which is the neurophysiological manifestation generated by a noxious stimulus. The translation of the nociceptive stimulation into a nervous message involves the stimulation of Transient Receptor Potential (TRP) channels in the membranes of free nerve endings of the nociceptors. These TRP channels are stimulated by certain chemical substances, in particular ATP, protons, bradykinin, liberated by the cell due to lesions, by temperature changes or by changes in osmotic pressure following mechanical stimulation (Basbaum *et al.*, 2009; Julius, 2013).

Nociceptors can be found in many tissues. Pain emanating from the skin, joints and muscles is referred to as somatic pain and pain emanating from internal organs as visceral pain. Somatic nociceptive messages are transmitted by these specialised peripheral nerves, Aδ and C nerves, to second-order neurons located in the I, II and V layers in the dorsal horn of the spinal cord. Visceral nociceptive messages are transmitted via C-nerves to second-order neurons located in the V, VI, VII, and X layers in the dorsal horn of the spinal cord. Stimulation of Aδ nerves causes sharp pain, while stimulation of C nerves causes burning or dull pain. Aδ nerves carry in addition, cold and pressure signals, whereas C-fibres carry thermal and tactile signals. Other nerves of this group, the Aβ nerves, mediate only tactile information (Haggard *et al.*, 2013).

Part of the second-order neurons are nociceptive specific; they transmit either information only from Aδ nerves, or from both Aδ and C nerves. Others are “wide-dynamic-range neurons”; they transmit signals from Aδ and C but also from Aβ nerves. The spinal or second-order neurons transmit their signals to various brain structures forming a network which is called the “pain matrix” (Ingvar, 1999; Ossipov *et al.*, 2010; Peyron *et al.*, 2000). This matrix consists of brain stem and subcortical areas, including medullary structures, the periaqueductal gray, the midbrain, the thalamus, the amygdala, the basal ganglia, and cortical areas, including the insular and cingulate cortices, the primary (S1) and secondary (S2) somatosensory cortices, the prefrontal cortex, the posterior parietal cortex and the supplementary motor area (see Fig. 4). The brain stem and subcortical areas are involved in initial processing and relay information to cortical areas. The cortical areas then interpret the nociceptive stimulation. The primary and secondary somatosensory cortices and the posterior part of the insular cortices are involved in the sensory-discrimination of pain processing: they allow the interpretation of the signal in terms of the site of the body and the type and intensity of the input (Hofbauer *et al.*, 2001; Box 2). The anterior cingulate and the anterior insular cortices are involved in the affective qualities of nociceptive stimulation: when they are activated, the stimulation is experienced as unpleasant (Apkarian *et al.*, 2005; Hofbauer *et al.*, 2001); Box 2). As a consequence, pain normally causes negative emotions and therefore is considered a cause of stress in both animals and humans (Box 3). In addition to this ascending system, there is also a descending system from the pain matrix to the dorsal horn. It exerts modulatory effects on pain perception, by influencing the transmission between peripheral nerves and spinal neurons (see 5.2.2).

Box 2. The two components of pain

As indicated by the definition of pain (Merskey and Bogduk, 1994), the concept of pain refers to the situation where both dimensions, the sensory (somatosensory cortices) and motivational-affective (limbic cortices) dimensions of pain are perceived. The pain sensation represents therefore a nociceptive sensation associated with a negative affective sensation (Paulmier *et al.*, 2015). Low-level nociceptive stimulation may be insufficient to activate the limbic cortices and to cause negative affect, and in this case, will not cause pain (or stress).

Focal lesions may help to shed light on the roles of the respective cortical areas involved in the perception of pain. Ploner (1999) describes a patient with partial lesions of the primary and secondary areas of the somatosensory cortices. When pain stimulations were applied to regions of the body corresponding to the lesioned areas, the patient reported a clearly 'unpleasant feeling' without being able to characterise its cause or origin.

The role of the cingulate cortex in the emotional aspects of pain perception is illustrated by neurological interventions carried out on patients suffering severe incapacitating pain. This intervention involved the transection of the cingulum, a collection of fibres running from the cingulate cortex to other parts of the brain, including the hippocampus. When questioning the patients after the intervention, they reported that pain was still present, but no longer 'bothersome' (Foltz and White, 1962). More recent studies showed more specifically that the degree of pain-evoked activation of the anterior part of the cingulate cortex is correlated with the perceived unpleasantness (Rainville *et al.*, 1997).

Box 3. Pain as a cause for negative emotions

The insular and cingulate cortices are components of the limbic system, which encompasses several structures involved in processing of emotional states. Because pain is associated with negative emotions, it is considered to be a potential source of stress. Like any stressor, pain can cause activation of the HPA axis and a shift in the balance of the autonomic nervous system. Animals that perceive pain may adopt certain postures like abnormal lying or standing, in order to reduce the sensation of pain. They may remain prostrated, or may lick or scratch the painful site or vocalise (Grandin, 1998; Prunier *et al.*, 2013).

The spinal and supraspinal neurons reaching the different cortices involved in the processing of nociceptive stimulation show a specific spatial organisation. Three major routes have been identified: the spino-thalamic, the spinoreticular and the spinomesencephalic tracts (Calvino and Grilo, 2006; Millan, 1999; Treede *et al.*, 1999). The spinothalamic tract is phylogenetically the most recent of the three tracts (Millan, 1999). Neurons of the spinothalamic tract synapse in the medial thalamus and project to the cingulate and insular cortices and in the ventrobasal thalamus to project to the somatosensory cortices (Almeida *et al.*, 2004; Garcia-Larrea and Peyron, 2013). This tract is involved in the sensory-discriminative and motivation-affective aspects of pain, but also in modulating pain (Almeida *et al.*, 2004; Millan, 1999). Neurons of the spinoreticular tract synapse in different structures of the reticular formation, involved in pain modulatory mechanisms and motor control. They are involved in the motivation-affective aspects of pain, as well as in autonomic responses to pain and pain modulation (Almeida *et al.*, 2004; Millan, 1999). Neurons of the spinomesencephalic tract project in part on the periaqueductal gray and in part on the superior colliculus. They are involved in modulation of pain, but also in motor responses, autonomic, and motivation-affective responses (Almeida *et al.*, 2004; Millan, 1999).

Several other routes have been described: the spinoparabrachio-hypothalamic, spinohypothalamic, and spinocervical tracts and the postsynaptic dorsal column (Almeida *et al.*, 2004; Millan, 1999; Fig. 8). They are all involved in the motivational-affective aspects of the sensation of pain. The spinocervical tract and the postsynaptic dorsal column are further involved in the sensory-discriminative aspects of pain. There is no postsynaptic dorsal column in fish. The spinoreticular and the spinomesencephalic tracts exist in all vertebrates. The other tracts are specific only to mammals (Millan, 1999).

5.2.2. Mechanisms for modulating pain

The transmission of nociceptive messages can be altered before reaching the brain; it may be enhanced or partly or totally inhibited. Several pain-modulating networks operate in parallel. The nociceptive message may be enhanced at the level of the noxious stimulus due to the presence of various substances, particularly during injury. These substances include protons, bradykinin and ATP, released from lesioned cells, substances released by immune cells involved in inflammatory reactions and substance P, liberated by the free nerve endings of the activated nociceptors themselves. These substances may bind to the TRP channels and facilitate their activation (Basbaum *et al.*, 2009; Julius, 2013; Julius and Basbaum, 2001). Other substances may increase sensitivity at the peripheral level. For example, under certain circumstances, adrenaline and noradrenaline may increase the excitability of nociceptors. These hormones are excreted under stressful conditions, so it has been suggested that stress may contribute to the amplification of nociceptive messages (Le Bars and Willer, 2004; Melzack and Wall, 2003). Enhancement of the nociceptive signal may also occur during transmission from the nociceptive nerve to the spinal neurons. At this level, normally silent glutamate channels may become activated due to longer lasting stimulation, and consequently exacerbate responses to noxious stimuli (Basbaum *et al.*, 2009).

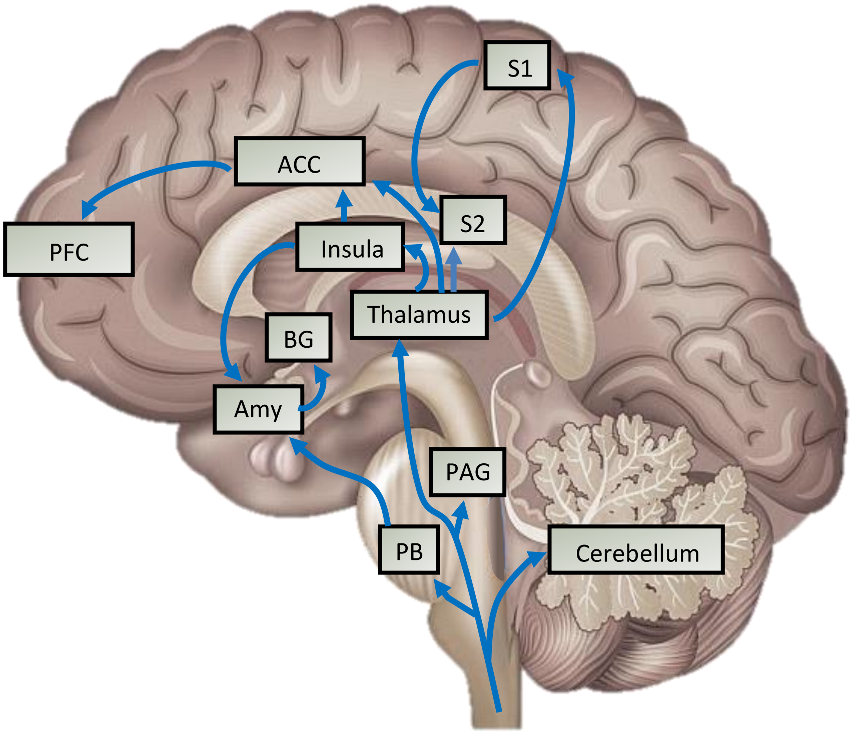

Fig. 8: Afferent pain pathways. Afferent nociceptive information enters the brain from the spinal cord. Nociceptive information from the thalamus is projected to the insula, anterior cingulate cortex (ACC), primary somatosensory cortex (S1) and secondary somatosensory cortex (S2), whereas information from the amygdala (AMY) is projected to the basal ganglia (BG). PAG, periaqueductal grey; PB, parabrachial nucleus; PFC, prefrontal cortex (after Bushnell *et al.*, 2013).

Opioids may inhibit transmission of the nociceptive message at the level of injury. Opioid receptors are produced in the cell body and transported to the peripheral endings of the nociceptor. Immune cells present at the site of injury are also capable of producing opioids, thus activating the opioid receptors and contributing to suppression of the pain (Melzack and Wall, 2003; Ren and Dubner, 2010). The opioid receptors are further transported to the synapse at the level of the dorsal horn, where their activation reduces the release of neurotransmitters from the peripheral nerve and thus, transmission to the spinal neuron. Opioid receptors are also found in brainstem, subcortical and cortical structures of the pain matrix (Rainville, 2002).

Interneurons play an important role at the level of transmission to the spinal neurons. Interneurons represent the majority of the neural population throughout the dorsal horn, and are particularly dense in laminae I, II and III (Todd and Koerber, 2013). Certain interneurons are inhibitory; they attenuate the transmission of nociceptive messages through the release of GABA or glycine (Foster *et al.*, 2015; Todd and Koerber, 2013).

The transmission to the spinal neurons can further be influenced by descending pathways, located in the brain stem. The effects of these pathways are bidirectional. Stimulation of the periaqueductal gray may enhance or inhibit the transmission from the peripheral nerve to the spinal neuron (Heinricher and Fields, 2013). Similarly, stimulation of another descending pathway arising in the tegmentum of the *pons* may have analgesic or hyperalgesic effects (Heinricher and Fields, 2013; Melzack and Wall, 2003). In addition, the rostral ventromedial medulla contains two populations of neurons, the ON and OFF cells, that project to the spinal cord. ON cells enhance transmission from nociceptors to lamina I neurons, while OFF cells depress it. ON cells are constitutively silent but are turned on by nociceptive inputs. OFF cells are constitutively active but are turned off by nociceptive inputs. These descending pathways do not act independently from higher brain structures. For example, the periaqueductal gray receives extensive inputs from the anterior cingulate and insular cortices, the amygdala, the hypothalamus and various brain stem nuclei (Heinricher and Fields, 2013).

Pain modulation is constitutional to the pain system, controlling perceived pain, but many stimuli not directly related to pain may also influence pain perception. Thus, sometimes, stress may enhance pain perception (Le Bars and Willer, 2004; Melzack and Wall, 2003), but certain stressful conditions, for example inescapable shock, may cause a hypoalgeic state (Bellgowan and Helmstetter, 1998; Flor *et al.*, 2002). The behavioural responses and hypoalgesic responses to these conditions involve the periaqueductal gray (Heinricher and Fields, 2013).

5.2.3. The larger picture: integration of pain and other processes

To produce continuously adaptive responses in a complex and changing environment, an organism monitors constantly all available relevant information from internal and external sources to produce an integrated picture. Among the senses, pain has a unique position in that it functions as a warning signal allowing detection, localization, and reaction to potential threats of the physical integrity of the body. To fulfil these functions, pain signals need to be integrated in a larger functional body image, including its spatial orientation and potential to react, and the environment. These processes involve subcortical and cortical processes, not all of which are necessarily conscious.

5.2.3.1. Pain and attentional selection

In common with all senses, different cognitive processes participate in nociceptive processing. Selective attention allows the individual to prioritize the processing of the most significant stimuli and action selection prepares the most appropriate motor action in response to the nociceptive stimuli (Legrain *et al.*, 2012). The high potential of pain to draw attention and disrupt ongoing behaviour highlights its relevance and illustrates that the high priority of pain signals (Bushnell *et al.*, 1984) (Eccleston and Crombez, 1999; Low, 2013; Miron *et al.*, 1989). The strongest disruptive effect is found when the painful experience is new, which is attributed to the higher salience of unfamiliar pain experiences (Eccleston and Crombez, 1999; Legrain *et al.*, 2009). When subjects were instructed to attend to the intensity of the painful stimulus, their ratings for pain intensity increased, but ratings for perceived unpleasantness of the pain did not. This leads to the hypothesis that attentional processes influence pain intensity preferentially (Villemure and Bushnell, 2009; Villemure *et al.*, 2003).

Despite the high potential for pain to disrupt ongoing behaviour, pain-related information has to compete for attention; that is, ongoing attentional processes may influence the processing of noxious stimuli and vice versa. In mice, the presence of cage mates decreases the expression of pain-related behaviour (Langford *et al.*, 2006). In monkeys, attending to a visual stimulus reduced reactivity to a heat stimulus (Bushnell and Duncan, 1989; Box 4). In rats, pain reduces cognitive function and attentional processes (Low, 2013). In humans, subjective ratings for pain intensity and unpleasantness were reduced if subjects were involved in a cognitive task, or presented simultaneously with another sensory stimulus, compared to when they were not (Eccleston and Crombez, 1999).

Box 4. Responses of thalamic cells to noxious stimuli depend on attentional processes
Rhesus monkeys performing a visual task received heat stimuli. When they were rewarded for ignoring these noxious stimuli, they did not respond behaviourally to it, but cells of the medial thalamus increased their activity. When they were rewarded for responding to the heat stimuli, that is, they were attending to them, the same cell responded more strongly. Hence, reactivity of these thalamic cells to noxious stimuli depended both on the presence of the stimuli and attention of the animal to the stimulus (Bushnell and Duncan, 1989).

This reduction in perception of pain was accompanied by a reduction in pain evoked activation of the peri-aqueductal gray, anterior cingulate, and posterior parietal cortices and somatosensory association areas, but also of structures related to contextualisation of pain and other stimuli, such as the orbitofrontal and insulate cortices (Brooks *et al.*, 2002; Frankenstein *et al.*, 2001; Petrovic *et al.*, 2000; Villemure and Bushnell, 2009; Villemure *et al.*, 2003). Reduced perceived pain intensity due to shifting attention away from the pain stimulus, was accompanied by less activity in the anterior insular and posterior parietal cortices (Brooks *et al.*, 2002; Seminowicz *et al.*, 2004; Villemure and Bushnell, 2009). This is coherent with existing information on the role of the parietal cortex in driving attentional processes in the context of other sensory modalities (Box 5). Thus, attending to a pain stimulus may enhance activity of the parietal cortex which in turns activates the anterior insular cortex, leading to better processing of pain stimuli and increased perceived intensity of the pain (Villemure and Bushnell, 2009).

Box 5. The parietal and insular cortices and attentional competition
In the context of visual and auditory stimuli, the posterior parietal cortex is believed to synchronise the spiking activity in those neurons processing the attended stimulus enabling more effective attentional competition reflected by increased activity of the anterior insular cortex (Liu *et al.*, 2003; Wu *et al.*, 2007).

5.2.3.2. Integration of pain signals at the level of the pain matrix

Before discussing the integration of pain signals with other signals of the body and the environment, it is important to note that the pain process itself has a strong integrative character, in the sense that experiences of pain result from the coordinated activity of a number of brain regions. Reviews and meta-analyses based on studies in humans and animals show that despite different types of pain stimulation and measuring techniques, six areas of the pain matrix are consistently activated: the anterior cingulate, anterior insular and somatosensory cortices, the prefrontal cortex and the thalamus (Apkarian *et al.*, 2005; Bushnell *et al.*, 1999; Craig, 2009). Several studies show a strong relationship between brain activity and pain perception. A study using the EEG responses to pain stimuli found that the pain ratings could be predicted using the pain-evoked EEG response with an 83% accuracy (Schulz *et al.*, 2012). Another study showed that the cerebral blood flow of the dorsal posterior insular cortex correlated with pain intensity ratings in humans (Segerdahl *et al.*, 2015).

The primary somatosensory cortex receives the nociceptive information before the anterior cingulate cortex. This probably reflects the different biological functions of these two regions. First pain signals provide precise sensory information for an immediate withdrawal, whereas second pain signals attract longer-lasting attention and motivate behavioural responses to limit further injury and optimize recovery (Ploner *et al.*, 2002).

It has become clear however that most of the structures of the pain matrix are not specific for pain. For example, most of the above mentioned areas responded in a very similar way to nociceptive and non-nociceptive somatosensory stimuli, auditory stimuli and visual stimuli (Mouraux *et al.*, 2011). In addition, in humans, stimulation of structures of the pain matrix, with the exception of the insular and the secondary somatosensory cortices, seldom causes the experience of pain, (Garcia-Larrea and Peyron, 2013; Mazzola *et al.*, 2012). Further, with exception of certain parts of the thalamus (posterior ventromedial nucleus) or insular cortex (dorsal posterior insular cortex) destruction of most areas of the pain-matrix does not cause analgesia (Craig, 2009; Garcia-Larrea and Peyron, 2013). Finally, anticipation of pain or empathy for pain caused brain activation in structures of the pain matrix, but showed a pattern that was distinct from the activation of pain itself (Lamm *et al.*, 2011; Ploghaus *et al.*, 1999; Sawamoto *et al.*, 2000). Overall, these results indicate that processing of pain is complex and occurs at multiple levels. At least at the macro-level of currently available techniques; certain brain structures appear to be consistently activated by nociceptive stimuli, although none of the brain structures appears to process pain exclusively.

5.2.3.3. Integration of pain with other types of information

- *Integration within the somatosensory system*.

Processing of pain signals needs to generate a higher-order representation of the source of the pain in relation with the body in its environmental context. Different levels and degrees of integration are believed to exist. First, integration at an early level was described as the “gating theory” several decades ago (Melzack and Wall, 1965): tactile stimulation may diminish certain pain sensations (i.e. rubbing the skin surface after a shock). In this case, stimulation of mechanoreceptors activates inhibitory interneurons in the spinal cord, thereby diminishing the transmission of the peripheral nociceptive signal to the second-order neuron (see 2.2 Pain modulatory mechanisms). Second, systems that process tactile and nociceptive information are believed to interact at higher processing levels (Haggard *et al.*, 2013). For example, at the anatomical level, the somatosensory cortical areas activated by selective tactile and nociceptive stimulation are very similar, at least at the macro-scale of current techniques (Haggard *et al.*, 2013; Mancini *et al.*, 2012). At the functional level, the response of the somatosensory cortex to nociceptive or thermal stimulation appears to integrate tactile information (Green, 1977; Haggard *et al.*, 2013; Ho *et al.*, 2010; 2011; Ploner *et al.*, 2004). For example, when subjects touch three plates simultaneously with the middle three fingers but only the outer two plates were cooled or heated, the central (neutral) plate is also perceived to be cold or warm (Green, 1977). Similarly, touching a grill consisting of alternate cool and warm produces a sensation of often painful heat (Craig and Bushnell, 1994). Finally, in humans and monkeys, the primary somatosensory cortex is less apt to treat tactile information if it receives simultaneously nociceptive information (Bushnell *et al.*, 1999).

- *Integration with other sensory systems*.

The above results illustrate that information from closely related systems (pain and touch) are integrated, both at the peripheral and brain level. Similar examples are found for other systems, such as the integration of visual information and body position in space, or the translation of sensory information into motor commands (Duhamel *et al.*, 1997; Sparks, 1991). This provides motivational systems with sufficient information to evaluate the threat level of the situation and to respond appropriately. Such integration of multimodal information occurs at many places in the nervous system. For example, the feline suprageniculate nucleus of the posterior thalamus contains many unimodal cells (responding only to one sensory modality) but 20 % bimodal and trimodal cells, responding to various combinations of visual, auditory, somatosensory and nociceptive information (Benedek *et al.*, 1997). Similar results were found for the *pulvinar* nucleus of the thalamus (Tyll *et al.*, 2011). Several studies have further shown that at the functional level, thalamic structures are involved in multisensory integration processes (Tyll *et al.*, 2011). For example, humans were more accurate in classifying emotional stimuli when these were presented audiovisually, compared to when they were presented by auditory or visual stimuli separately, and this was associated with increased activity in the thalamus (Tyll *et al.*, 2011).

Information is also integrated at the cortical level; multimodal convergence zones have been identified at the border of sensory specific cortices (Tyll *et al.*, 2011). In addition, it has been long known that the brains of mammals contain association areas, that is, areas where different sensory modalities converge. This occurs in certain zones of the parietal and frontal cortices. For example, in humans and primates, a subdivision of the parietal cortex (the ventral intraparietal area) contains neurons responding to different types of sensory information: visual, auditory and tactile information as well as relative to the position of the organism in space (i.e. vestibular stimulation; Avillac *et al.*, 2005; Bremmer *et al.*, 2001; Duhamel *et al.*, 1997). Other association areas are the temporal and frontal cortices and subcortical structures like the putamen and superior colliculus (Avillac *et al.*, 2005; Bruce *et al.*, 1981; Damasio, 2010; Rizzolatti *et al.*, 1981; Sparks, 1991). Neuroanatomical studies and neuroimaging studies in primates and humans showed that these association areas receive feedforward projections from brain structures receiving primary sensory input and, importantly, that they are interconnected to allow further integration of information (Damasio, 2010).

The integrative function of the associative cortices has been illustrated in several species including cats, monkeys and humans. For example, certain single neurons in the inferior temporal cortex of rhesus monkeys are specifically activated by the vision of monkey or human faces seen from the front, and others by the vision of the profile of faces. These neurons receive inputs from other brain areas containing specific visual information relative to frontal or lateral visual aspects of faces, respectively (Purves *et al.*, 2004). The delayed response task is used to study the role of specific neurons in the frontal cortex in planning. In this task, the monkey must wait in order to get a reward that the experimenter hides while the monkey is watching. Thus during the waiting time the monkey has to decide he wants the reward and keep all the information available until the end of the waiting time. Specific neurons in the prefrontal cortex are maximally active while performing the task while the performances of the monkeys are reduced if these cells are destroyed, which is in keeping with clinical observations in human patients. (Purves *et al.*, 2004).

- Pain and emotion.

Emotions are considered the driving force behind motivational states. Certain behavioural expressions of a motivational state increase the probability that positive emotions are produced, such as social or sexual behaviour, or the ingestion of palatable food. Other behaviours are driven by negative emotions. For example fear may induce fight or flight reactions, and disgust induces rejection of food. Emotions are processed by the limbic system (Damasio, 1998; Panksepp, 2005); (see Chapter 3 and Box 6).

The anterior cingulate cortex is part of the limbic system and, as indicated above, plays an important role in the negative affective component of the experience of pain. While pain influences emotional status, experimental modulation of the emotional status appears also to influence nociceptive processing. It was found that negative emotions increases perceived unpleasantness of pain, while declared intensity of pain was less influenced or not influenced at all, (Rainville *et al.*, 2005; Villemure and Bushnell, 2009; Villemure *et al.*, 2003; Zelman *et al.*, 1991). For example, painful and near painful stimulation caused more discomfort and anxiety if simultaneously fear-depicting faces were presented to the subjects (Phillips *et al.*, 2003; Ploner *et al.*, 2011). As the protocols of these latter studies may have influenced not only emotional status but also attentional processes or arousal, other studies set out to avoid these possible secondary effects by modulating emotions using odours. Presentation of pulses with pleasant odours (fragrance odours) induced positive emotions and decreased perceived unpleasantness of pain, while unpleasant odours (e.g. rotten fish) produced the opposite effect. The reduction in perceived unpleasantness of pain was associated with lower activity in the anterior cingulate, medial thalamus and somatosensory cortices (Villemure and Bushnell, 2009). In these experiments, emotional status did not influence intensity ratings, suggesting that emotional and attentional circuits influencing the processing of pain are different (Bushnell *et al.*, 2013; Villemure and Bushnell, 2009; Villemure *et al.*, 2003; Fig. 9). The Periaqueductal gray is an important hub for descending pathways mediating the effects of emotion on perceived pain (Bushnell *et al.*, 2013; Fig. 9).

Box 6. The emotional brain circuit

In addition to the anterior cingulate cortex, the limbic system includes the *amygdala*, the mediodorsal nucleus of the thalamus, the ventral basal ganglia*, hypothalamus, the orbital and medial frontal cortices. These regions play an important role in decision making. The amygdala is well known for its role in fear and recognition of fearful expression. The amygdala is also an important integration hub. It links cortical regions providing visual, somatic sensory, visceral sensory, and auditory information with hypothalamic and brainstem effector systems. This distinguishes the amygdala from the hypothalamus, which receives relatively unprocessed visceral sensory inputs. The amygdala is part of a circuit linking it to the orbital and medial prefrontal cortex and the thalamic mediodorsal nucleus (directly and indirectly *via* the ventral parts of the basal ganglia), allowing complex direct and indirect interactions between the amygdala and the prefrontal cortex. Furthermore, many neurons in the amygdala respond to visual, auditory, somatic sensory, visceral sensory, gustatory and olfactory stimuli. In addition to sensory inputs, the prefrontal and temporal cortical connections of the amygdala give it access to more overtly cognitive neocortical circuits, which integrate the emotional significance of sensory stimuli and guide complex behaviour (Damasio, 2010; Purves *et al.*, 2004).

Pleasant experiences are associated with relatively greater activation in various brain areas, including the *nucleus accumbens*, portions of the ventral striatum, hypothalamus, ventromedial prefrontal cortex and right orbital frontal cortex. Unpleasant experiences are associated with more consistent activation in amygdala, anterior insular cortex, left orbital frontal cortex and more posterior portions of the ventral striatum (Wager, 2008).

* *dorsal striatum (caudate nucleus and putamen), ventral striatum (nucleus accumbens and olfactory tubercle), globus pallidus, ventral pallidum, substantia nigra, and subthalamic nucleus.*

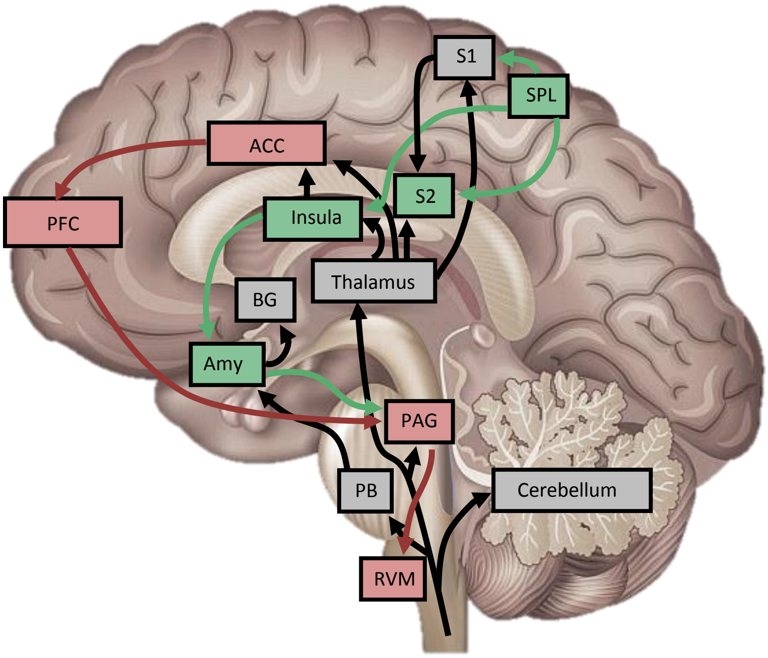

Fig. 9: Main structures of the pain matrix (grey coloured) and of the descending pain modulating system, mediating effect of attention (green coloured) and emotions (red coloured). Emotions (and placebo analgesia) activate circuitry involving the anterior cingulate cortex (ACC), prefrontal cortex (PFC) and periaqueductal grey (PAG), whereas attention activates circuitry involving projections from the superior parietal lobe (SPL) to the primary somatosensory cortex (S1) and insula. Grey regions show parts of the ascending pain pathways depicted in Fig. 1. Amy, amygdala; BG, basal ganglia; PB, parabrachial nucleus; RVM, rostroventral medulla; S2, secondary somatosensory cortex (after Bushnell *et al*., 2013).

5.2.3.4. Higher-order integration of pain: pain and consciousness

Recent data and ideas underline increasingly the large-scale architecture of the brain network involved in complex processing of information, including in the pain matrix. Thus, the anterior insular cortex may be involved in the pattern of activation of different parts of the pain matrix. For example, Ploner *et al.* (2011) found that attentional manipulations not only increased pain ratings but also functional connectivity between the anterior insular cortex and areas of the frontoparietal cortex. Manipulations of emotional status increased the functional connectivity between the anterior insular cortex and areas in the medial temporal lobe, classically known for its role in memory (Ploner *et al.*, 2011; Squire *et al.*, 2004). Subjects showing stronger activity in the anterior insular cortex before receiving a pain stimulus showed a stronger response of the pain matrix to a painful stimulus (Ploner *et al.*, 2010). These observations agree with the earlier suggestion (Box 5) that the anterior insular cortex plays a role in the orientation of brain processing, making processing of information by certain brain areas more likely and more efficient, and probably increasing the probability of making them available to consciousness. This idea agrees also with theories on the conscious processing of visual information (Lamme, 2006; 2010; see 5.1.3.1 of this chapter).

The thalamus appears also to have a central role in the interconnection between different brain areas. As for the conscious perception of other sensory information (olfaction excepted, see Box 1), thalamo-cortical processing of information is believed to be crucial for the conscious perception of pain stimuli. Particularly in animals and humans, the medial *pulvinar* nucleus of the thalamus receives nociceptive input and has a wide cortical connectivity. This part of the thalamus is believed to play a major role in synchronizing activities of relevant cortical areas (Box 7), thus contributing to the ultimate conscious perception of noxious input (Bastuji *et al.*, 2016).

Box 7. Cortico-thalamo-cortical connections and conscious perception of pain
The medial pulvinar nucleus has extensive cortical connectivity, involving parietal, frontal and temporal cortices ensuring cross-talk between remote cortical areas via the cortico-thalamo-cortical route (Cappe *et al.*, 2009; Cappe *et al.*, 2007; Shipp, 2003). These observations suggest a central role of this thalamic nucleus in the conscious perception of pain (Bastuji *et al.*, 2016).

The importance of interconnectivity between different brain areas in pain processing is further illustrated by observations on patients suffering from disorders of consciousness. In patients suffering from unresponsive wakefulness (i.e. vegetative patients), nociceptive stimuli activated the midbrain, the thalamus and primary somatosensory cortex, suggesting that these patients could process at least partly the sensory-discriminative component of pain (Laureys *et al.*, 2002). Another study on unresponsive wakeful patients found that electrical nociceptive stimulation activated not only both somatosensory cortices, but also parts of the cingulate and insular cortices, but many parts the pain matrix were not activated making it difficult to ascertain that conscious pain had been perceived (Kassubek *et al.*, 2003). Specifically, it was shown that in these patients, the different parts of the pain matrix lack functional connectivity, particularly backward connectivity between high-order associative cortices, that is, from the frontal to the temporal areas, which are necessary for integrative brain processing leading to consciousness, including for pain processing (Boly *et al.*, 2011; Schnakers *et al.*, 2012).

Certain patients are in a minimally conscious state, often confounded with the unresponsive wakefulness syndrome. These patients present fluctuating but reproducible signs of consciousness, such as emotional and oriented behavioural responses, object manipulation or visual pursuit (Schnakers *et al.*, 2012). In these patients, associative areas of the cortex show a normal level of metabolism and, importantly, correlations between activity in these areas and the thalamus, indicating that these brain areas are functionally connected. In these patients, the brain responses to nociceptive stimuli involve the thalamus, the primary somatosensory cortex, the secondary somatosensory or insular cortex and the anterior cingulate cortex, although somewhat differently from healthy controls (Boly *et al.*, 2008). Similar results were found using pain specific EEG responses to nociceptive stimuli (Naro *et al.*, 2015). The authors concluded that minimally conscious patients might show an elaborate and integrated level of noxious processing associated with conscious pain perception (Boly *et al.*, 2008; Naro *et al.*, 2015; Schnakers *et al.*, 2008).

The above section indicates that although much progress needs to be made to understand the organisation of interconnected pathways involved in integrated information processing, existing knowledge indicates that central pain mechanisms combine different components, including sensory-discriminative processing, general arousal, selective attention, orienting, affective-motivational and motor responses and memory. These processes are not exclusively involved in the generation of pain in the brain but more generally involved in the elaboration of motivationally driven behaviours towards meaningful stimuli (Legrain and Torta, 2015). The non-specificity of many areas of the pain matrix that are not specifically related to nociceptive processing, and their role in many other processes including attentional processes, behavioural and vegetative responses and decision making, is consistent with the notion that the final experience of pain integrates the continuous interaction between these subsystems (Garcia-Larrea and Peyron, 2013). Hence, many brain areas, not specifically or exclusively dedicated to processing of nociceptive information, participate in the processing of noxious stimuli and the characteristics of the process determine the characteristics of the pain experience.

In conclusion, current theories indicate that in humans and non-human primates, and probably all mammals (see section 5.3.1), conscious pain perception involves ultimately recurrent processing of nociceptive stimuli between the thalamus and cortical areas, necessary for the larger integration of all forms of relevant information (see Table 3). The implication of the cortical processes and the complex behavioural responses that pain may produce indicate that in awake evolved animals, the perception of pain is conscious. Some scientists believe that, in the absence of a cortex, thalamic processes may allow at least a certain degree of consciousness. It is also clear that an important part of the integrative pain processing occurs unconsciously at the peripheral and spinal level.

5.3. Conscious perception: ethical considerations concerning the use of animals by humans

5.3.1. Conscious perception of emotions and pain

5.3.1.1. Extrapolation to mammals other than humans and non-human primates

- *Emotions*.

Studies on the behaviour, physiology and functional anatomy of the brain have shown that not only humans but also many animals are capable of experiencing negative and positive emotions (Boissy *et al.*, 2007; Paul *et al.*, 2005; see Box 8). Specifically, humans and animals show largely similar behavioural and physiological reactions to positive or aversive events (see Chapter 3). Furthermore, it is well known that the limbic system, known for its involvement in emotions in humans, is also present in the brains of non-human mammals (LeDoux, 2000; see Box 8).

Today, there is much evidence that in animals, like in humans, the emotional, physiological and behavioural reactions to positive or aversive events depend on the integrated image that the brain has constructed from relevant information. Positive or negative events may have a further impact on subsequent behaviour or emotional states. For example, it is well known that events with a strong negative emotional impact may have long-lasting effects on emotional status, and physiological and behavioural functioning, not only in humans, but also in animals. A recent study by Destrez *et al.* (2013) illustrates this (see also Chapter 3), lambs were subjected to repeated, unpredictable and uncontrollable aversive events such as social separation, changes in the environment, noise, and handling. When subsequently tested, these lambs show increased reactivity to novelty and had altered learning or memory capabilities. They were further tested in a choice test. In this test, they received a reward if they made the correct response (for example, the response “left”) and were punished if they made the incorrect response (for example, the response “right”). Lambs that had been subjected to repeated negative events choose the ambiguous answer, “middle” less often than their unstressed counterparts. This indicates that the way the animal evaluates the situation, that is, the integrated image that was produced, has a negative or pessimistic bias (Destrez *et al.*, 2013).

Box 8. Dealing with emotions in animals: current status

Current practices take increasingly into account the fact that animals are sentient beings, that is, they are capable of experiencing positive and negative emotions, including those that arise from noxious stimuli. For example, efforts are made to conceive equipment that facilitates animal handling and management by taking into account the characteristics of the species and to reduce fear-inducing situations during animal handling. Particularly, remarkable progress has been made for cattle handling, particularly where herds are large (Grandin, 2007).

Efforts are also made to reduce pain. Veterinarians use analgesics* and anaesthetics** to limit pain due to pathologies or surgical interventions. More specifically, recently, it was indicated that pain in animals may be minimised using the "suppress, substitute and soothe" approach. Thus, first any source of pain that brings no obvious advantage to the animals or the producers and those for which potential benefits are exceeded by the negative effects should be suppressed. Second, painful techniques should be substituted by a less-painful method where possible. Third, in cases of "unavoidable" pain, pharmacological or other treatments should be used to soothe pain (Guatteo *et al.*, 2012).

In the slaughter context, the obligation to stun animals before bleeding exists in many countries. The objective is to induce unconsciousness to avoid the animal experiencing fear or pain. Different techniques exist. The stun gun uses a captive bolt that first causes concussion, followed by partial destruction of the brain, including the thalamus and/or reticular formation, when the bolt penetrates the brain. The principle of electrical stunning is to pass an electric current of sufficient intensity through the brain provoking a massive depolarization of neurons in both cerebral hemispheres. The principle of gas stunning is to immerse animals in an atmosphere containing high concentrations of CO_2 which after inhalation dissolves in the blood and reaches the brain. All these techniques result in brain dysfunction, either due to destruction of the reticular formation or the thalamus (captive bolt), depolarisation of the neurons (concussion, electrical stunning), or acidification of the brain cells (gas stunning; Terlouw *et al.*, 2016).

* *Analgesics act directly on the nociceptors or inhibit the propagation of the electrical signal in the peripheral or central nerves inhibiting the transmission of the information, or inhibit normal functioning of certain centers in the brainstem, the thalamus or relevant cortical areas.*

** *Anaesthetics block essentially the transmission of information through the thalamus, although structures in lower parts of the brain may also be influenced.*

Positive events may also influence the emotional status, behaviour and physiology of animals and have consequences for future behaviour. Young lambs given regular and tactile contacts with a human showed behavioural (relaxation posture) and physiological signs (decreased heart rate and increased parasympathetic tone) of a soothed state (Coulon *et al.*, 2015). They also showed a stronger attachment than controls to humans (Coulon *et al.*, 2015). Similar results were found for cattle; calves and cows are easier to handle and touch if the farmer has a positive attitude towards them (de Boyer des Roches *et al.*, 2016; Lensink *et al.*, 2001). Other studies show the implication of the brain; lambs raised in an enriched environment after weaning were less reactive and had less dendritic spines in the prefrontal cortex than controls (Coulon *et al.*, 2013 and 2014).

- *Pain*.

Animals other than non-human primates or humans show pain-induced changes in behaviour, such as a change in posture, licking and scratching the painful location or apathy (Prunier *et al.*, 2013). In addition, it was shown more recently that rodents, lagomorphs and large animals, such as horses and sheep, display measurable changes in facial expression (Dalla Costa *et al.*, 2014; Guesgen *et al.*, 2016; Keating *et al.*, 2012; Matsumiya *et al.*, 2012). Animals show also physiological changes similar to those in humans (McGrath, 1987; Prunier *et al.*, 2013). There is further a strong analogy between humans and animals in neuro-anatomical characteristics. For example, humans, monkeys, rats, and mice all possess anterior cingulate and anterior insular cortices, the major structures involved in the affective-motivational component of pain. They also have primary and secondary somatosensory cortices, which are involved in the sensory component of the experience of pain (Kobayashi, 2011; Rolls, 2015; Vogt and Miller, 1983). Research into pain uses animal models extensively, including rats, mice, dogs, cats, rabbits, and to a lesser extent guinea pigs, cows, pigs, sheep, birds, hamsters, frogs and reptiles (Mogil, 2009). Much of this research aims to increase our understanding of how humans process pain, indicating that the animal and human systems are considered to be comparable for many aspects (Di Giminiani *et al.*, 2013; Mogil, 2009). In addition to similarities in the peripheral wiring of the pain system, there are many examples showing the similarities in higher order processing of pain and other information between humans and primates, and rats. For example, like in humans and primates, in rodents, the cingulate cortex plays a central role in processing integrative sensory, motor and emotional information, as well as in the affective component of the pain experience (Johansen *et al.*, 2001; Vogt and Miller, 1983; Wang *et al.*, 2015). Similarly, in rats, specific neurons of the insular cortex respond to different forms of information, including tail pinch, gustatory and baroreceptor stimulation (Hanamori *et al.*, 1998).

- Conscious processing.

Widespread functional connectivity between different brain areas is necessary for higher order information processing leading to consciousness. Much remains to be done to be able to translate detailed knowledge of higher order processing from human and primate studies to other mammals. For example, despite some differences in size, monkey and human brains contain the same orbital and medial prefrontal cortex areas (Ongur and Price, 2000). In contrast, certain prefrontal cortex areas do not exist in rats making it difficult to establish which prefrontal cortex areas of the rat are homologs of certain prefrontal areas in monkeys and humans (Ongur and Price, 2000; Rolls, 2015). Despite differences between rats, monkeys and humans, areas of the prefrontal cortex make widespread connections with other cortical areas, the amygdala, the ventromedial thalamus, the hypothalamus, the periaqueductal gray and the striatum (Ongur and Price, 2000; Rolls, 2015). This suggests that animals have the necessary connections between the relevant brain areas to have at least some form of consciousness, even if it may be different and possibly less complex from certain points of view, from that of humans. For example, the absence of certain cortical prefrontal areas in some species, possibly all non-primate mammals, may indicate that in these species the conscious experiences including that of pain, have a different motivational-affective content. Alternatively, other brain structures may compensate for these deficient areas. Similarly, complex behavioural responses and cognitive capacities in many species, suggest also higher order complex processing.

In conclusion, the presence in these species of all the essential areas in higher order processing, including of pain, present convincing evidence that mammals are able to consciously experience sensory perception and emotions, including the negative affective component of pain.

5.3.1.2. Extrapolation to birds and fish

In contrast to mammals, the bird dorsal telencephalon does not include a morphologically identifiable cortex; it is, instead, a collection of nuclei. The central region of the bird dorsal telencephalon contains a pallial structure called the dorsal ventricular ridge (Dugas-Ford *et al.*, 2012). The mammalian neocortex is also a pallial structure and it is believed that the avian dorsal ventricular ridge and the mammalian neocortex have a common phylogenetic origin (Dugas-Ford *et al.*, 2012; Wang *et al.*, 2010). The dorsal ventricular ridge receives sensory projections from the dorsal thalamus like the mammalian neocortex. The connectivity patterns are remarkably similar (Wang *et al.*, 2010). Furthermore, analysis of gene-expression shows that avian pallial nuclei can express many of the same molecular markers as their hypothesized mammalian homologs (Dugas-Ford *et al.*, 2012). Finally, the activity patterns of the avian auditory pallium matches closely its mammalian counterpart. For example, in the mammalian and avian auditory cortex, adjacent and connected regions form a hierarchy in processing of information and the same two classes of neurons, excitatory principal cells, firing at relatively low rates, and inhibitory interneurons, firing at higher rates are found in the mammalian and avian auditory cortex (Calabrese and Woolley, 2015). Thus, the avian brain contains structures that are homologs to the mammalian neocortex, although much research remains to be done.

In addition, birds may express highly developed cognitive behaviour. For example, they are exceptionally skilled at discriminating between visual images. Such images can be categorized according to their perceptual similarities or may even be grouped together based on a human-like, abstract concept, such as same–different. Pigeons, for example, can discriminate between images of aerial photographs and pictures containing human beings and those that did not (Emery, 2006). All the stimuli were novel to the pigeons, the backgrounds were different, the people were either clothed or naked and the number of people in the photographs was not consistent across trials. Pigeons, chickens and quail are also capable of learning more complex problems that require the application of a rule;

however, they are outperformed by corvids and parrots (Gossette *et al.*, 1966). More specifically, members of the crow and parrot families have cognitive skills once thought exclusive to primates: the use of tools, impressive spatiotemporal memory, and apparent causal reasoning (Emery and Clayton, 2004). The relative size of the forebrain in these birds is significantly larger than in other birds, particularly those areas thought to be analogous with the mammalian prefrontal cortex: the nidopallium and mesopallium, possibly explaining their higher primate-like intelligence than other birds (Emery and Clayton, 2004; see also chapter 3: sections 3.3 and 3.4).

Finally, the pain system in birds shows many similarities with mammals. Different types of nociceptors have been identified, including thermal, mechanical and thermos-mechanical nociceptors. Their behavioural and physiological reactions are also similar to those of mammals (Gentle, 1992; Prunier *et al.*, 2013).

In summary, the avian brain contains homologs of mammalian neocortical structures with similarities in connectivity and functional organisation. Further, birds have remarkable cognitive performances, indicative of higher-order integrative processing of complex information. It is therefore highly likely that birds have at least some degree of conscious access to information processed in the brain.

It has been believed for a long time that that fish are unable to feel pain or negative emotions. This idea has been challenged by recent research. As with birds, fish lack the cerebral cortical structures that are involved in pain perception and awareness in humans. Recent studies, based on neuro-anatomical evidence and behavioural expression suggest that like mammals, fish do experience pain, and fear or other forms of negative emotions (Chandroo *et al.*, 2004; Mok and Munro, 1998). First, it was shown that trout possess peripheral nociceptors, that is, nerves equipped with receptors that respond to noxious stimuli including high temperatures and certain chemicals (Sneddon *et al.*, 2003). Further, trout that receive a painful stimulus change their behaviour, for example, by rubbing the painful site against available substrates (Sneddon, 2003; 2009). Similarly, lesions in the dorsomedial telencephalon affected emotional behaviour (avoidance of a painful stimulus) in goldfish (Portavella *et al.*, 2002). Glucocorticoids levels rise during crowding or handling in many fish species just as they do in mammals (Barton, 2002; Ramsay *et al.*, 2006). Behavioural observations indicate that teleost fish have a number of learning and memory mechanisms and basic cognitive capabilities, similar to those in mammals, birds and reptiles (Broglio *et al.*, 2005). The fish brain lacks some structures of the mammalian brain but other structures fulfil these functions. Thus, like the hippocampus in mammals, birds and reptiles, the teleost lateral pallium is essential for spatial cognition and trace memories and like the pallial amygdala in mammals, the teleost medial pallium is involved in emotional and fear conditioning (Broglio *et al.*, 2005).

In conclusion, research on brain functioning involved in processing of sensory and other information in fish is even less advanced than for birds. However existing information on brain structures and cognitive functioning suggests that at least some form of conscious perception and higher-order processing of information exists in fish.

5.3.1.3. Nociception and potential pain in invertebrates

All animal taxa, including invertebrates, seem capable of nociception, allowing rapid reflexes or responses to withdraw from noxious stimuli, which has an obvious advantage for survival (Sneddon, 2004, Crook *et al.*, 2014). Data on nociceptive capacity exist for example for insects, crustaceans (crab, crayfish, prawn) and mollusc cephalopods (octopus, squid, cuttlefish). Thus, studies found that fruit flies (*Drosophila melanogaster*) possess nociceptors that mediate behavioural responses to noxious stimuli (Tracey *et al.*, 2003; Kim *et al.*, 2012). Similarly, crayfish (*Procambarus clarkii*) possess sensory neurons that respond specifically to noxious high temperatures, while not to low temperatures, and these neural responses were accompanied by behavioural responses (Puri and Faulkes, 2015). Prawns (*Palaemon elegans*) rub their antennae when pinched or treated with certain chemicals (Barr *et al.*, 2008). Squids (*Doryteuthis (Loligo) pealeii*) and octopuses (*Abdopus aculeatus*) possess nociceptors that are sensitive to lesions and pressure and that mediate behavioural responses (Crook *et al.*, 2013; Alupay *et al.*, 2014).

It is much more difficult to determine whether invertebrates are capable of feeling pain, that is, whether they experience the negative affective state accompanying nociceptive perception in mammals. Their brains are very different from mammalian and even other vertebrates' brains, and today there is little knowledge on the specific functions of brain areas of most invertebrates. Of all, the octopus (*Octopus vulgaris*) brain is among the best described. Cephalopods have the most complex nervous system among invertebrates including a vascularised brain. Together with insects, their nervous system has the highest degree of centralisation which considerably reduces the time for information processing between stimulus reception and behavioural reactions (Budelman, 1995,). Like insects, cephalopods possess further an effective blood-brain interface, allowing a good control of the neuronal microenvironment which may explain their higher integrative functions of the brain, such as pattern vision and relatively complex social behaviour (Abbott *et al.*, 1986). Although the blood-brain interface of crustaceans is considered less effective compared to insects and cephalopods, it does have charge-selective and size-selective properties thus blocking selectively molecules from entering into the neural space (Otopalik *et al.*, 2012).

In coherence with their relatively complex nervous system, octopuses learn very rapidly, for example in visual discrimination tests where attacking a given object is rewarded with food and attacking a different object is punished with a painful shock. They have particularly good performances in observational learning tests, that is, learning by observing another octopus performing a task (Hochner *et al.*, 2006). These learning and memory capacities need an intact vertical lobe of the octopus brain (Hochner *et al.*, 2006). However, octopuses do not reach the level of performance of vertebrates in discrimination tasks. They do not seem to be able either to integrate visual and tactile stimuli, but they do integrate tactile and taste stimuli (Young, 1991). In addition, while taste stimuli stimulate the octopus to take an object, if nociceptive stimulation occurs, it will release the object, indicative of the integration of taste, tactile and nociceptive information (Young, 1991). In experiments using injury it was shown that following arm autotomy (shredding of the arm in response to arm crush) octopuses show coordinated behavioural responses, including wound grooming, holding the arm stump in the beak or close to the body, sometimes curling intact arms around the injured site (Alupay *et al.*, 2014). They display further a marked neural hyperactivity, both in the wounded and ipsilateral uninjured arms accompanied by coordinated protective movements upon light pressure on the injured arm (Alupay *et al.*, 2014). Squids show also neural hyperactivity after injury, but this occurs both at the ipsi- and contralateral body parts, suggesting that compared to octopuses, their nervous system provides less information on the locality of the injury (Crook *et al.*, 2013).

Prawns rubbed specifically the antenna that had been pinched or treated with chemicals, showing that they have precise information relative to the location of the noxious stimulus (Barr *et al.*, 2008). Despite a probably less complex nervous system, crustaceans are further capable of learning in contexts using rewards or punishment. For example, crabs (*Carcinus maenas*) were able to learn lever pressing for food (Abramso, and Feinman, 1990) and *Chasmagnathus granulatus* crabs and hermit crabs (*Dardanus arrosor*), were able to learn to avoid a localisation associated with electrical shocks (Cuadras *et al.*, 1978; Fernandez-Duque *et al.*, 1992).

Insects are capable to avoid noxious heat. When a fruit fly is suspended from the thorax in the middle of a cylindrical arena that allows the presentation of visual landmarks, the tethered fly flies stationary but if some of these landmarks are paired with an unpleasant heat beam the fly learns to orient itself toward a safe direction, avoiding the landmark indicative of danger of the beam (Heisenberg *et al.*, 2001). Fruit flies exhibit further second order conditioning. Specifically, fruit flies associated an odour with a shock and subsequently a second odour with this first odour: during testing, the trained fruit flies avoided both the first and second odour (Tabone and de Belle, 2011). At least some insects are also capable of observational learning. For instance, wood crickets (*Nemobius sylvestris*) learn to hide under leaves by observing experienced conspecifics in the presence of a natural predator, the wolf spider (*Latrodectus mactans*, Coolen *et al.*, 2005).

The perceptual and learning capacities of honey bees have particularly received scientific attention. Bees see colours, recognise a large range of odours, and perceive shapes and patterns as well as movements with a high temporal resolution. Mechanosensory perception is extremely rich including information on the body surface, due to thousands of hairs all over the body while proprioceptors give information on position and movements (Giurfa, 2003). Of particular interest is the honey bee’s capacity of conceptual learning in delayed match-to-sample or delayed no-match to-sample-tasks. In the first case, a bee is presented first a non-rewarded visual stimulus, for example a horizontal grating, and will be rewarded if it chooses subsequently the arm of a Y-maze marked also by a horizontal grating. In the delayed no-match to sample task, it should choose a different grating, for example vertical, to be rewarded. Honey bees were able to learn the concept of sameness or differentness: they responded correctly even when the stimuli changed (e.g. the gratings are replaced by signs of different colours; Avarguès-Weber and Giurfa, 2013). Although it is currently not known which brain area is involved in conceptual learning in bees, it is believed that the capacity to integrate different types of sensory information is essential albeit not sufficient. This integration takes place in the mushroom bodies of the bee brain (Avarguès-Weber and Giurfa, 2013). The capacity of conceptual learning in honey bees confers to them a more complex functioning than when based on a stimulus-response principle (Avarguès-Weber and Giurfa, 2013). For example, nematodes are able to integrate various forms of sensory inputs and exhibit basic forms of learning such as habituation and classical conditioning. However, their behaviour appears to be organised as responses either to the immediate sensory environment or to immediate interoceptive signals of physiological state; when hungry, they seem incapable to search for food in a coordinated strategic way, that is, beyond their immediate sensory environment (Barron and Klein, 2016). Other Hymenoptera (wasps, ants and solitary bees) also possess mushroom bodies capable of multimodal sensory integration, but it is presently unknown whether these insects are equally capable of conceptual learning. Brains of other insects, such as the fruit fly possess unimodal mushroom bodies, exclusively treating olfactory information and incapable to integrate multimodal sensory information (Avarguès-Weber and Giurfa, 2013).

The above data show that invertebrates such as insects, crustaceans and cephalopods possess nociceptors and that they are capable to avoid situations associated with nociceptive stimulation or other forms of threat. Most scientists feel that the existing data do not allow any firm conclusion on the presence or absence of a subjective negative affective pain experience in invertebrates (Alupay *et al.*, 2014; Puri and Faulkes, 2015; Stevens *et al.*, 2015; Adamo, 2016). Other scientists have suggested however, that the presence of a centralised nervous system that is protected by a blood-brain interface, and particularly, the rather complex behavioural reactions in octopuses and in mollusc cephalopods in general to various situations, including injury, would suggest at least the possibility of the presence of some degree of a negative affective experience in response to a nociceptive stimulation (Barr *et al.*, 2008). Similarly, the behaviours of crustaceans present a certain complexity and some scientists interpret their reactions to nociceptive stimuli as indicative of at least some degree of a negative affective experience associated with nociception (Magee and Elwood, 2013; Elwood and Adams, 2015).

Regarding insects, it has been suggested that mushroom bodies in their brain capable to integrate multimodal sensory information may be comparable to certain structures of the human midbrain (see 5.1.3.2.) and consequently, a neural substrate potentially allowing at least some degree of subjective experience (Barron and Klein, 2015). It has been pointed out however that adding the additional neurons necessary for the capacity of emotional experience to insect brains may be costly in terms of space and energy and it is not clear whether these costs outweigh the benefits (Adamo, 2016).

Current knowledge does not, however, exclude the possibility of subjective experience in insects either (Adamo, 2016). For example, the capacity of conceptual learning described in honey bees illustrates the potential of a motivational state (the choice of the second grating for a food reward) to be connected to experiences occurring at a different point in time (perception of the first grating), and vice versa. In these contexts, the storage and retrieval of information allows a certain degree of time independency and the integration of different forms of information (presence of the grating and the Y-maze, anticipation of the food reward) allows the generation of the additional informational content necessary for obtaining the food reward. These processes are totally coherent with current concepts of consciousness in humans and other mammals (see Chapter 1: 1.5.1). Therefore, the idea that at least some level of subjective experience, i.e. a very basic form of consciousness, exists in at least some invertebrates, is plausible and deserves further investigations.

5.3.1.4. Questions on animal consciousness meeting ethics

The preceding chapters and sections presented the existing knowledge and ideas on consciousness. Although much of the detailed knowledge of complex processing leading to consciousness is derived from studies on humans and non-human primates, specific reference is made to animals. It is clear that consciousness is a complex phenomenon (see also Chapter 2). Conscious functioning allows animals to adapt continuously to a rich and changing environment (Chapter 3 and 4) and is intrinsically linked with higher-order integrative processing of information, including detection of incongruent events, the access of information for higher cognitive processing and memory; and the notion of time and the timing of events (see also Chapters 2 and 3). Although human and non-human mammal brains show differences, characteristics of their peripheral and central nervous systems, essential for complex processing of information show many similarities. Brains of birds and fish are even more different from human brains, but they contain homologs for at least part of the mammalian brain areas essential for complex information processing.

Like humans, animals experience positive and negative emotions that add further to the complexity of the integrated image that the brain computes. Emotions are adaptive; they are the drive behind motivations, and thus orient motivated behaviour (see also Chapter 3). Pain is a complex phenomenon; it includes a physical sensation and a potentially strong negative affective state. Animals, including birds and fish, are equipped to detect and react to noxious stimuli. The brain structures involved in the complex affective processing of pain signals are those that are involved in the processing of other forms of complex information processing, including of emotions unrelated to pain. As indicated above, non-primate mammals possess many of the brain structures needed for the conscious perception of the aversive component of pain, while avian and fish brains have homologs for at least part of these structures, which makes it highly likely that birds and fish have at least to a certain degree a conscious experience of the negative affective component of pain. Consequently, when humans keep animals, they need to take into account all the causes of potential negative emotions, for example, treat pain during surgical interventions and use properly designed equipment when handling animals to avoid fear (Box 8 and 9).

In summary, vertebrates are equipped with nervous systems that are highly likely to be able to process consciously complex information, comprising positive and negative emotions, including those caused by noxious stimuli. At least some invertebrates are possibly capable of at least a basic degree of consciousness, related to subjective experience. Humans use animals extensively for many purposes. In this context, society, be it through habits, culture, or law imposes various rules. The next section discusses whether and how the recent knowledge delivered in the present document may contribute to reconsidering these habits and rules in the light of moral obligations that humans have when using animals (Box 9).

Box 9 Dealing with emotions in animals: which way further

Despite new regulations, improved training and increased awareness of the public and stakeholders relative to the sentient capacities of animals, many aspects need further improvement. For example, new well designed equipment may be expensive and their installation is progressing only slowly. Further, there are still many invasive interventions on animals, specifically farm animals, without any accompanying analgesic or anaesthetic treatment at all. In abattoirs, the stunning and killing process needs skilled operators with appropriate training and further progress is still needed on this point. Finally, many animal keepers, including farmers, are close to their animals and provide positive emotions through positive contacts (Lensink *et al.*, 2000). Further progress may be made on this point, possibly through programmes purposely and formally aiming to facilitate the occurrence of positive emotions in animals.

5.3.2. Ethical implications of consciousness

Most theories in animal ethics take at least some mental states to be relevant (necessary and/or sufficient) criteria for moral status. Most, notably Singer (1990), focus primarily on **sentience**, referring to the capacity to experience suffering and pleasure. Some also include other morally relevant cognitive capacities such as self-awareness, memory, symbolic language, social understanding, or mindreading. Desires and preferences are also central to a conscious animal's wellbeing. Hence, generally, moral status is taken to depend, at least in great part, on mental life (DeGrazia, 1996). Consciousness occupies a pivotal role in determining the importance of the different aspects of mental life to what matters to animals (Rollin, 1989). Where animal protection is concerned, European policy relies much more on scientific knowledge now than several decennia ago. However, many welfare policies fail to match up-to-date knowledge of animal cognition and even the least demanding theories of animal ethics (cf. e.g. Dawkins 2012; Jones 2013). Furthermore, although there is much scientific agreement on the general definition or description of animal sentience (see glossary), animal welfare policies and regulations fail to propose an operational definition of sentience that would make them more easily enforceable across all contexts. The reasons are probable several-fold. First, clear consensus often takes time to emerge among scientists from converging scientific conclusions. The streamlining from such conclusions into new policies needs additional time. Relative to sentience, the present document illustrates clearly that despite the general agreement on the existence of animal sentience, its richness and heterogeneousness across animal taxa and species make it impossible, at least today, to draw its exact contours and even less to draw up precise rules that delineate what is ethically acceptable and what is not. However, it is also clear that just using the rudimentary knowledge on sentience of today might commit legislators and policymakers to granting animals much more stringent protections than current practices in agriculture and research actually do. There is thus a tension between what sentience plausibly entails and what public policies take it into account. There is a further, related, tension between the ethical implications of sentience and the 'non-ideal', enforceable protections that could be realistically implemented. The latter point should be considered within the agricultural and animal research context and between agriculture practices and human needs. First, tensions exist when a choice is to be made between practices presenting simultaneously advantages and disadvantages. For example, outdoor rearing may give more space and freedom to animals, but less comfort in adverse weather conditions and less protection from parasites. Second, tensions may arise when a choice is to be made between animal protection and human needs. For example, animal research may give rise to important medical care advances; intensive housing of animals causes stress but allows low-cost production of animal products, hence accessible to low-income people. These tensions are also clearly present in debates between animal rights groups and public policy, where at least part of the arguments revolve around justifying existing human feeding regimes, habits, needs or demands.

Sentience is a form of consciousness. Animal consciousness, as Allen and Bekoff (2007) note, has straightforward ethical implications because of the widely, though not universally, accepted "biconditional statement: animals deserve moral consideration if and only if they are sentient (especially possessing the capacity to feel pain)." According to this view, sentience is necessary and sufficient for moral consideration. Sometimes, as the authors note, "*if there is uncertainty about whether other animals really are conscious, the morally safe position is to give them the benefit of the doubt*."

Pain and pleasure are morally relevant **hedonic states** (i.e. pleasant/unpleasant experiences), which, in almost every view of animal welfare, is at least one fundamental aspect of welfare. Pain and pleasure not only signal to the organism what is good or bad for it. Their experiential character is itself pleasant or unpleasant to the organism insofar as it experiences these states subjectively. Pain and pleasure are experienced (i.e. felt) *as* good or bad, not merely as indicators of probable damage or desirability. Hedonic states therefore matter to welfare in two respects: because of what they signal or indicate about the *body*, and because of their *mental* aspect. Appleby (1999) and Fraser (1995; 1999; 2008) describe these two dimensions of welfare and a third, 'species-specific' or 'nature' dimension (i.e. the natural behaviours and environment of one's kind). In this respect, animals being conscious makes their welfare morally distinctive in contrast to what is good or bad for plants and other non-sentient organisms. Questions about welfare are thus closely tied to questions about consciousness, especially suffering and enjoyment. Organisms without subjective experience raise few direct ethical concerns about their individual treatment besides environmental concerns. The capacity to suffer or enjoy, on the other hand, should be taken into account, morally speaking, when deciding how to treat them or considering the impacts of our policies, practices and individual actions on them. This is why their welfare matters in a distinctive way—both with respect to positive and negative attitudes (sensations, feelings, emotions, desires).

Sentience does not only consist in the capacity to have hedonic states but also ***conative attitudes*** (i.e. wants, aims, intentions, desires and preferences). In fact, Feinberg (1974) suggests that a "conative life" is necessary for having *interests*, which are components of one's good or welfare. Conative attitudes clearly matter to what is good or bad for an organism if their satisfaction or frustration is *experienced as* good or bad by the organism, as well as if hedonic states themselves are defined in relation to their desirability. Animals with forms of consciousness can have conative attitudes in a sense that matters to their welfare and hence that matters morally (DeGrazia, 1996).

Beyond sentience, an organism's ability to recognize itself can sometimes affect moral status according to some authors (McMahan, 2002; Singer, 2011; Varner, 2012). Beings that are self-aware are sometimes considered to have a higher form of moral status or 'standing' typically associated with, or close to, the status of persons, e.g. on Kant's account of (autonomous) moral agency. The ability to reflect on the contents of one's own mental states seems at least necessary for higher cognitive capacities such as rational understanding, mindreading, or episodic memory. Whether some nonhumans possess such abilities is thus significant to the extent that such considerations are relevant to moral status.

Consciousness comes in various kinds and degrees. Different species (and individuals) are conscious along a continuum of such forms. In what follows, autonoetic consciousness is introduced. Yet it should be clear that, while sentience as just defined is widespread among animals (all vertebrates and probably some invertebrates such as some cephalopods and crustaceans), more sophisticated forms of consciousness have only been documented across a much smaller range of species. So, the ethical conclusions that follow from one form of consciousness do not necessarily apply indiscriminately. Still, because consciousness is a spectrum across and within species, one can expect individuals of different species to share commonalities with respect to the kinds or degrees of consciousness they possess. Infants as well as severely cognitively impaired, comatose, demented or senile people, depending on their conditions, may not all share the typically higher forms of consciousness of 'normal' adult humans. At the same time, individuals of some so-called 'higher' species may possess levels of consciousness that compare to those of non-paradigmatic humans. This refers to the problem of 'marginal cases,' taken by some authors to suggest that, because morally relevant capacities are not evenly distributed along species boundaries, our species-centric attitudes may need to be revised (McMahan, 2002; Singer, 2011). But some have argued that human infants, children and cognitively disabled individuals, unlike most animals, can have the same moral standing as 'normal' adults, i.e. **personhood**, within "person-rearing relationships" (Jaworska and Tannenbaum, 2014).

- ***Autonoetic consciousness*** was defined by the psychologist Tulving (1985) as "*the kind of consciousness that mediates from the personal past through the present to the personal future*" as "providing the characteristic phenomenal flavor of the experience of remembering" and allowing for "mental time travel". Tulving focused on *episodic* memory, i.e. "remembering personally experienced events", as opposed to *semantic* memory, i.e. "symbolically representable knowledge that organisms possess about the world" (p. 2). Autonoetic consciousness (or awareness) is thus the conscious access to information relative to one's own past, present, and future. It is sometimes called the capacity for "mental time travel," or to place events in time (the so-called what, where, when: WWW, as already described in chapter 3).

Varner argues that "*individuals with a robust, conscious sense of their own past and future have special moral significance in comparison to those of the merely sentient.*" (Varner, 2012), this capacity "*can make an individual's life go better or worse than it could otherwise. This is because it is possible to benefit or harm an individual with autonoetic consciousness in ways that it is impossible to benefit* *or harm an individual that lacks autonoetic consciousness*.". The ability to anticipate one's future consciously and remember one's past affects the quality of one's life. The lives of animals with autonoetic consciousness are thus more "morally charged". Because they can have desires that extend further into the future and the past, such animals can be more dramatically affected by aversive experiences—including perhaps the fear of their own death—which they can re-experience or dread. Their lives also have "greater moral significance" because they contain more opportunities for pleasant and unpleasant experiences—more opportunities for welfare. Finally, such animals can consciously plan for the future and thus have desires that can be frustrated or satisfied in a way that is not available to the "merely sentient". In contrast, "implicit anticipation" and "implicit memory," available to merely sentient animals, lack backward- or forward looking content "that the animal can consciously attend to." (Varner, 2012). They can make such an animal's life go better or worse for it, insofar as they are unpleasant psychological states, "*but they do not add as much value or disvalue as consciously re-experiencing a satisfying event or consciously dreading an anticipated event*." (*ibid.*)

Varner (2012) considers three areas of research relevant to the question of autonoetic consciousness: ***episodic memory,*** relevant to backward-looking (past), ***mirror self-recognition,*** relevant to the present, and the use of the ***theory of mind*** and certain kinds of ***planning,*** both relevant to the forward-looking element of autonoetic consciousness (future; see also Chapter 3). Varner reviews a large number of studies suggesting that at least gorillas, dolphins, scrub jays and rats have episodic memory; that some chimpanzees, bonobos, orangutans, gorillas, dolphins and elephants passed the mirror self-recognition test; that both monkeys and apes use at least some aspects of a theory of mind (understanding at least what others can and cannot see), as well as perhaps elephants and dolphins; that scrub jays use theory of mind; that apes and dolphins probably employ higher order representations of their own and others' mental states; finally that both bonobos and orangutans can select and save tools for later use, and scrub jays can selectively cache food in places for future use taking in account the others.

The ethical implications of awareness of time in animals had been previously recognized. Peter Singer, in particular, distinguished *persons* on that basis (1979 and 1993 editions of Singer 2011), although he has more recently (2011) updated his view to include more animals (including farmed animals such as pigs, cows, chickens and fish) in the range of those that can have future-directed preferences. Mendl and Paul (2008) note that, as recognized by the 1965 UK Brambell Committee report, the extent to which animals live in the present has a major impact on their capacity for suffering. In the light of recent evidence on the capacity of some animals for mental time travel, they outline some implications for welfare: "*animals lacking mental time travel would miss the beneficial consequences of using previous experience to plan and organise future behaviour, but also the detrimental consequences of being able to ruminate on the recalled past and worry about the imagined future. Emotional responses, including future-directed anxiety would be temporally bound by the presence of relevant stimuli or cues and, therefore, potentially be short-lived. However past experiences could, through the actions of non-episodic memory systems attributable to other brain structures, still impact on emotional state via (implicit) learning of associations between cues and emotional events. Cumulative effects of past experience on stress response mechanisms and baseline stress or mood states would also be expected to occur*." They conclude, "*Mental time travel may thus bring both welfare benefits and problems.*"

Welfare may also include an *integrity* component, perhaps in relation to the third, 'natural' dimension already mentioned. Rendtorff and Kemp (2000) have suggested that some fundamental principles of biomedical ethics in particular vulnerability and integrity could be applied to animals, but probably not informed consent and dignity of persons. Informed consent involves sophisticated forms of cognition and may therefore only concern certain individuals, including among humans, depending on their mental and physical abilities. Dignity has, in this context, a Kantian sense that appears to require rational autonomy. But vulnerability (susceptibility to harm) and integrity (coherence of one's organism) are aspects of a life that plausibly all conscious animals share. Since these animals have intrinsic value and hence their welfare matters morally, their integrity is morally significant. Notably, animals that possess autonoetic consciousness might have an increased interest in the preservation of the integrity of their bodily and mental life given their capacity for mental time travel. Self-aware animals in this sense can remember their past and learn from it in anticipation of their own future, thus constructing at least basic patterns of proto-personal identity.

If integrity matters, these animals require a distinct form of respectful treatment. Yet, because nonverbal animals most probably lack a “biographical sense of self” and the ability to tell stories about themselves and others, their integrity may not matter as much them as it does to typical humans (Varner, 2012). Their life is not shaped like a narrative in a way that supports a robust temporal coherence of their self-identity. But if these forms of consciousness are distributed along a spectrum, one can expect the moral significance to be a matter of degree rather than kind. It might be that DeGrazia’s (2009) notion of bodily self-awareness supports some awareness of one’s integrity without a robust cognitive sense of time and oneself. So, even animals that cannot give informed consent may still have an interest in having their integrity respected over time as part of their welfare. Domesticated species and research animals in particular that depend on human care for their flourishing are highly vulnerable and susceptible to violations of their integrity, through, for instance, various mutilations, experiments, and the shaping of their social and reproductive lives. If integrity matters to them, especially by virtue of their being self-aware, these are important welfare considerations.

Finally, the consideration of consciousness across species raises questions of shared vulnerability and suffering, especially between dependent animals and their human caretakers (e.g. among companion, service or farm animals). In relation to *empathy*, it is likely that the suffering of either party to a relationship can adversely affect the other. Insofar as one can be aware (perceptually or cognitively) of another’s suffering, relationships can thus give rise to additional ethical questions. If, in addition, empathy is channelled by *mindreading* (e.g. perception of another individual’s perceptions, emotions or intentions), an animal can become aware, if only perceptually, of another animal’s conscious pain, fear or distress. This shows, again, that the different levels and forms of consciousness give rise to different ethical considerations. Based on the evidence gathered in the previous chapters, it appears that a wide range of animals, with various abilities, raise important moral issues regarding their breeding, handling, confinement, reproduction, and killing. Over the past decennia, European policy has increasingly taken into account the existence of animal sentience leading to substantial improvements of regulations concerned with the use of animals in farming, research, for work and companionship and in various captive settings. A deeper understanding of animal sentience and consciousness can hopefully contribute to new and revised regulations in the future, as regards issues such as pain management, transportation, confinement, breeding, and slaughter, among others. Science is naturally shy when it comes to producing firm conclusions, particularly when it concerns immeasurable matters to which animal sentience pertains. However, partly due to new techniques, research and reflection on human consciousness and, as a consequence, animal consciousness show exciting advancements from which new promising ideas and concepts are emerging. The purpose of the present document is to produce a general overview of current developments and help further constructing the bridge between science and policy and to contribute to new insights and progress both in science and policy making.

5.4. Conclusion

Chapter 5 presents information on the conscious or unconscious processing of internal and external information by the brain across species and the ethical implications of these capacities in terms of animal use by humans.

Organisms with brains have different needs at different times and deploy varying behavioural strategies to fulfil them. Decision-making has to integrate both needs and opportunities. It involves selection of action, selection of targets and motivational ranking. Attentional processes are involved in the selection of those stimuli considered a priority. Processes related to consciousness help integrate the information into a larger picture, allowing relevant information to be summarised, making it accessible for higher level cognitive treatment.

Theories of conscious processing of information agree on the central role of subcortical neural processes. Specifically, the thalamus has an essential role. It is placed centrally in the brain and receives input from the reticular formation in the brain stem, involved in the sleep-wake cycle and arousal. It projects to and receives projections from the cortex. The thalamus is an essential relay station for visual, auditory and somatosensory information. It plays a role in attention and in attentional shifts within (e.g. within vision) and across modalities (for example between vision and audition) and participates in the gating of sensory and motor information to the cortex.

Cortical input allows more complete and complex processing than subcortical neural structures. Particularly, the thalamo-cortical circuit would allow for the highest-order conscious processing. However, we lack knowledge on the exact contribution of the cortex in lower-order conscious processing. It is not yet clear from work on humans whether the mere presence of subcortical structures allows forms of conscious processing and to what extent higher order conscious processing such as abstract thinking or introspection need the presence of an intact cortex.

Although human and non-human mammalian brains show differences, characteristics of their peripheral and central nervous systems, essential for complex processing of information, show many similarities. Although bird and fish brains are even more different from human brains, they contain homologs for at least part of the mammalian brain areas essential for complex information processing.

Like humans, animals experience positive and negative emotions that add further to the complexity of the integrated image that the brain processes. Emotions are adaptive; they drive motivations, and thus orient motivated behaviour. Pain is a complex phenomenon; it includes a physical sensation and a potentially strong negative affective state. Animals, including birds and fish, are equipped to detect and react to noxious stimuli. The brain structures involved in the complex affective processing of pain signals are those involved in the processing of other forms of complex information processing. Non-primate mammals possess many of the brain structures needed for the conscious perception of the aversive component of pain. Avian and fish brains have homologs for at least part of these structures, which makes it highly likely that birds and fish have to a certain degree a conscious experience of the negative affective component of pain. Thus, vertebrates are equipped with nervous systems that are able to process consciously complex information, comprising positive and negative emotions, including those caused by noxious stimuli. Although invertebrates appear to have less complex nervous systems than many vertebrates, some invertebrate species have complex information processing capacities, including observational and conceptual learning suggestive of at least some level of consciousness or subjective experience.

This existing knowledge leads us to consider ethical questions about the way humans use animals. Most philosophical theories in animal ethics consider that sentience is a relevant criterion for defining the moral status of animals. Pain and pleasure are hedonic states that on the one hand convey a moral status to the beholder and on the other hand are generally considered fundamental aspects of animal welfare. Hedonic states matter to welfare in two respects: because of what they signal or indicate about the body, and because of their mental aspect. Sentience goes further in that it includes the capacity to have conative attitudes such as wants, aims, intentions, desires and preferences. These are believed to be necessary for having interests, which are components of one’s welfare.

Consciousness occupies a pivotal role in determining the importance of the different aspects of mental life to what matters to animals. Sentience is conscious and widespread among animals, but more sophisticated forms of consciousness have only been documented across a much smaller range of species. Thus, an organism’s ability to recognize itself is sometimes considered to indicate a higher form of moral status. Autonoetic consciousness is defined as “*the kind of consciousness that mediates from the personal past through the present to the personal future*,” “*providing the characteristic phenomenal flavour of the experience of remembering*”. It is a pillar of the episodic memory as described in chapter 3. As animals with autonoetic consciousness can have desires that extend further into the future and the past they can be more dramatically affected by aversive experiences. Consequently, there is a greater moral charge on their lives. For example, animals lacking mental time travel would miss the beneficial consequences of using previous experience to plan future behaviour, but also the detrimental consequences of recalling past negative experience or apprehending the future.

Vulnerability and physical integrity are intrinsic values that have moral significance for welfare of probably all conscious animals. In particular, animals possessing autonoetic consciousness and a capacity for mental time travel might have an increased interest for these aspects potentially constructing at least basic patterns of a proto-personal identity. Yet, because animals most probably lack a narrative or "biographical sense of self", the temporal coherence of their self-identity may be less robust than in humans. But different forms of consciousness are best considered as being distributed along a spectrum, so that the moral significance is a matter of degree rather than kind.

The different levels and forms of consciousness give rise to different ethical considerations. Still, because consciousness is a spectrum across and within species, one can expect individuals of different species to share commonalities in the kinds or degrees of consciousness they possess.

A wide range of animals, with various abilities, are bred, handled, confined, reproduced, and killed by humans. Taking animal consciousness into consideration questions a number of common practices involving animals in farming and research, for work and companionship and in various captive settings.

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OVERAL CONCLUSION

Consciousness allows a widespread sharing of information within the brain; the more widespread it is the larger the content of consciousness. This widespread processing may include cognitive processing and memory, as well as autobiographical consciousness, going beyond the here and now. Different forms of consciousness in humans and animals have been described by philosophers, psychologists, and biologists, including “access consciousness”, “phenomenal consciousness” and “self-consciousness”. These concepts are complex and diverse at the mechanistic level, as well as in terms of nature of responses. Answering the question “is there consciousness in animals?” with a simple yes or no is thus inappropriate. There are many levels and contents of consciousness in animals as well as in humans. Recognizing this can only acknowledge the heterogeneity of conscious processing in animal species.

Human consciousness is by definition subjective and private, and mostly studied through verbal, non-verbal or instrumental reports. However, language is not present in animals, but consciousness can still be assessed in them through behavioural and cognitive measures, as it is in preverbal humans. Like humans, animals display different behaviours as a function of levels of consciousness: during deep sleep, anesthesia, coma and seizures, all species including humans are not able to process information and are unconscious, or have very low levels of consciousness. By contrast, behavioural and neurobiological data lead to the conclusion that animals can express some forms of higher level of consciousness. This supports an assumption held for the last 300 years by many authors with various philosophical and scientifical backgrounds. But so far, the whole range of the forms and manifestations of consciousness described in human adults is not fully demonstrated in adult animals from all species.

The corpus of studies about consciousness in animals reviewed in this report covers a wide phylogenetic spectrum, but most studies were run on laboratory animals or wild species and very few on livestock species. Livestock species, such as poultry, pigs, and sheep, exhibit cognitive behaviours that seem to imply levels and contents of consciousness that until recently were considered exclusive to humans and to some primates. That is even more the case for fish and invertebrates that until recently were not even considered as sentient. This change in understanding was attained through conceptual and methodological breakthroughs made possible through modern approaches on animal consciousness.

Many techniques have been used to investigate consciousness-related phenomena and allow us to reach the following conclusions:

1. At the behavioural level, studies ranged from ethological observation and experimentation on animals in their familiar environment to very specific set-ups deriving from psychological paradigms. Studying the content of consciousness, that is the richness of conscious experience in animals appears even more challenging than in humans due to the lack of verbal reports. However training animals to obtain subjective reports is possible for many species. We report here consciousness-related behavioural constructs obtained in different cognitive contexts, ranging from emotionality, sociality and animal-human relationships to memory and metacognitive abilities. From this cumulative behavioural evidence, we conclude that some forms of consciousness may be attributed to non-human species.

2. Neurobiological investigations relying on modern technological developments defined certain neural correlates of consciousness. Most studies in vertebrates conclude that the cortex (or its functional equivalent in non-mammalian species), and its neural connections with the thalamus, underlay consciousness. Specifically, non-primate mammals possess many of the brain structures needed for the conscious perception of the aversive component of pain. Avian and fish brains have homologs for at least part of these structures, which makes it highly likely that birds and fish can consciously experience the negative component of pain at least to a certain degree. More generally vertebrates are equipped with nervous systems that are able to

process the complex information that leads up to positive and negative emotions including those caused by noxious stimuli.

Overall, we recommend caution before excluding consciousness in invertebrates which are structured differently in neural terms, as they may have evolved from different brain architectures to fulfil homologous consciousness-related processes.

From a functional perspective, these different forms of consciousness are considered to favour the capacity of animals to cope with unpredictably changing environments. However, such “adaptationist” interpretations, and the cognitive capacities they imply, should be considered cautiously until more in-depth investigations become available. Nonetheless, it is reasonable to assume that higher levels of consciousness result from natural selection to ensure better adaptive flexibility and robustness of individual organisms and of their social network.

The issue of the phylogenetic origin of consciousness is linked to that of its function. Amongst many authors, Morgan and Griffin repeatedly claimed that, to exist, animal consciousness does not need to be the same as that of humans. The global workspace theory is compatible with consciousness being a fundamental feature of living organisms with corresponding ancient roots. However functional studies of the components of the global workspace such as episodic memory and emotions raise conceptual and methodological difficulties in tracing these processes across species. Neuroanatomical studies also give an incomplete picture because they are limited to organisms that are related to humans and it is still possible that different forms of consciousness have arisen independently on many occasions during the evolution of vertebrates and invertebrates like cephalopods and arthropods.

The literature that we have examined leads us to consider ethical questions about the way humans think and behave towards animals. Most philosophical theories in animal ethics consider that sentience is a relevant criterion for the moral status of animals. Pain and pleasure are hedonic states that, on the one hand, convey a moral status to the beholder and, on the other hand, are generally considered fundamental aspects of animal welfare. Hedonic states are important in welfare in two ways: first, because of what they signal or indicate about the body, and second, because of the way they affect mental processes. In addition, sentience determines response at the conative level, such as wanting, goal-directedness, intentionality, and preferences.

We conclude that there is a wide range of animals which have a wide range of conscious abilities and this raises moral issues about the way they are bred, handled, confined and killed. If the richness of consciousness in animals remains to be fully described, the morally safe position is to take that ability in account. Taking animal consciousness into consideration questions many common practices involving animals in farming, research, workforce, companionship, and confinement.

GLOSSARY

Those definitions have been found in texts from several authors, referenced in a specific list.

Definition	Author-Year	Definitions
Access consciousness	Block 1995	Mental representations cognitively available for use in rational control of action or speech.
Affect	Paul 2005	Commonly used by emotion researchers, some regard affect as essentially involving the psychological qualities of pleasantness or unpleasantness. Others use the term to refer to behavioural and physiological responses (and in conscious beings, feelings) that can vary both in terms of valence (pleasantness/ unpleasantness) and also intensity (arousing or activating qualities).
Autonoetic consciousness	Tulving 1985	The kind of consciousness that mediates from the personal past through the present to the personal future. Providing the characteristic phenomenal flavor of the experience of remembering and allowing for mental time travel.
Animal consciousness	Chandroo *et al.* 2004 Brown 2015	Broad concept that includes sentience, intelligence and self-awareness. Consciousness might be broadly described as an awareness of internal and external stimuli, having a sense of self and some understanding of ones place in the world
	Damasio 2010	No one can prove satisfactorily that nonhuman, nonlanguaged beings have consciousness, core or otherwise, although it is reasonable to triangulate the substantial evidence we have available and conclude that it is highly likely that they do. The triangulation would run like this: (1) if a species has behaviors that are best explained by a brain with mind processes rather than by a brain with mere dispositions for action (such as reflexes); and (2) if the species has a brain with all the components that are described in the chapters ahead as necessary to make conscious minds in humans; (3) then, dear reader, the species is conscious.
Animal insight	Shettleworth 2009	The concept of animal insight have relied on a definition proposed by Thorpe over half a century ago as ‘‘*the sudden production of a new adaptive response not arrived at by trial (and error) behaviour*.’’.
Animal self	Damasio 2010	Most species whose brains generate a self do so at core level. Humans have both core self and autobiographical self. A number of mammals are likely to have both as well, namely wolves, our ape cousins, marine mammals and elephants, cats, and, of course, that off-the scale species called the domestic dog.
Anticipatory behaviour	Peters 2012	Anticipatory behaviour has been described as a typical arousal with goal-directed activity that occurs during the appetitive phase when the actual reward is not present yet.
Attention	Buschman and Miller 2007	Volitional shifts of attention are thought to depend on “top-down” signals derived from knowledge about the current task (e.g., finding your lost keys), whereas the automatic “bottom-up” capture of attention is driven by properties inherent in stimuli— that is, by salience (e.g., a flashing fire alarm)
Bodily self-awareness	DeGrazia 2009	“An awareness of one’s own body as importantly different from the rest of the environment – as directly connected with certain feelings and subject to one’s direct control.”
Cognition	Okon-Singer 2015	Cognition is a fuzzy category that conventionally includes processes involved in knowing or ‘thinking,’ including attention, imagination, language, learning, memory, and perception.
Conative attitude	Feinberg (1974)	Having interests: wants, aims, intentions, desires and preferences, It matters to what is good or bad for an organism; if their satisfaction or frustration is experienced as good or bad by the organism.
Conscious mind	Damasio 2010	Conscious minds begin when self comes to mind, when brains add a self process to the mind mix, modestly at first but quite robustly later. The self is built in distinct steps grounded on the protoself. The first step is the generation of primordial feelings, the elementary feelings of existence that spring

		spontaneously from the protoself. Next is the core self. The core self is about action—specifically, about a relationship between the organism and the object. The core self unfolds in a sequence of images that describe an object engaging the protoself and modifying that protoself, including its primordial feelings. Finally, there is the autobiographical self. This self is defined in terms of biographical knowledge pertaining to the past as well as the anticipated future. The multiple images whose ensemble defines a biography generate pulses of core self whose aggregate constitutes an autobiographical self. The protoself with its primordial feelings, and the core self, constitute a “material me.” The autobiographical self, whose higher reaches embrace all aspects of one’s social persona, constitute a “social me” and a “spiritual me.”
Consciousness	Damasio 2010	Consciousness is a state of mind in which there is knowledge of one’s own existence and of the existence of surroundings. Consciousness is a state of mind—if there is no mind there is no consciousness; consciousness is a particular state of mind, enriched by a sense of the particular organism in which a mind is operating; and the state of mind includes knowledge to the effect that the said existence is situated, that there are objects and events surrounding it. Consciousness is a state of mind with a self process added to it.
	Lamme 2010.	We should understand consciousness as the integration of information.
	Nicol 1995	Consciousness may have evolved to enable animals to attribute mental states to others.
	Piggins 1998	Consciousness is the ‘‘ *. . . state of being that enables the perceiver to perceive, or the observer to observe*’’
	Metzinger 2009	In essence, consciousness is the *space of attentional agency*: Conscious information is exactly that set of information currently active in our brains to which we can deliberately direct our high-level attention.
	Dennett 1991	So the conscious mind is not just the place where the witnessed colors and smells are, and not just the thinking thing. It is where the appreciating happens. It is the ultimate arbiter of why anything matters
	Stuart Sutherland 1989	The having of perceptions, thoughts, and feelings: awareness. The term is impossible to define except in terms that are unintelligible without a grasp of what consciousness means. Consciousness is a fascinating but elusive phenomenon; it is impossible to specify what it is, what it does, or why it evolved. Nothing worth reading has been written about it.
	Damasio 2009	The commonplace dictionary definitions of consciousness tend to fare better since they often state that consciousness is the ability to be aware of self and surroundings. These definitions are circular – given that awareness is often seen as a synonym of consciousness itself, or at least as a significant part of it.
	Damasio 2009	We propose that consciousness begins to occur *when the brain generates a non-verbal account of how the organism’s representation is affected by the organism’s processing of an object, and when this process enhances the image of the causative object, thus placing it saliently in a spatial and temporal context*
	Graziano 2013	A scheme is detailed in Chapter 1
Emotions/feeling of emotions	Okon-Singer 2015	Emotion is a fuzzy, contentious category that conventionally includes valenced processes (e.g., action tendencies, attention, overt behavior, subjective feelings, and alterations in peripheral physiology) that are triggered by specific external or internal stimuli (e.g., actual or remembered threat for fear); often taken to include states of anger, disgust, fear, happiness, and sadness.
	Paul 2005	Emotions refer to processes which are likely to have evolved from basic mechanisms that gave animals the ability to avoid harm/punishment and seek valuable resources/reward… in humans at least, they include a conscious subjective component—the feeling of the emotion.
	Damasio 2010	Emotions are complex, largely automated programs of actions concocted by evolution. The actions are complemented by a cognitive program that includes certain ideas and modes of cognition, but the world of emotions is largely one of actions carried out in our bodies, from facial expressions and postures to changes in viscera and internal milieu
	Damasio 2010	Feelings of emotion are composite perceptions of what happens in our body and mind when we are emoting. As far as the body is concerned, feelings are images of actions rather than actions themselves; the world of feelings is one

		of perceptions executed in brain maps.
	Damasio 2009	The term emotion usually conjures up the primary emotions (e.g., fear, anger, sadness, happiness, disgust) or the social emotions (e.g., embarrassment, guilt, compassion), but the phenotypes of emotion also include background emotions, which occur in continual form when the organism is not engaged in either primary or social emotions.
Episodic like memory	Freitas Barbosa 2009	Human episodic memory refers to the capability of recollecting what, when and where a specific event occurred. It also involves mental time travelling and requires “autonoetic” consciousness.
	Crystal 2009	Episodic memory may be defined in at least two ways. Defined from the perspective of content, episodic memory stores representations of unique, personal past events. Defined from the perspective of experience, episodic memory has been described as re-experiencing a unique personal past event.
	Hampton 2004	the recollection of specific events in one’s past, accompanied by the experience of having been there personally.
	Templer 2013	episodic memory enables use of contextual information about distinct episodes from one’s personal past to guide behavior.
Integrated information theory	Mudrik 2014	A cognitive definition of integration is the generation of a nonperceptual, abstract representation by associating distinct signals into a new one Integrated information theory (IIT): identifies consciousness with information integration, so that the level of consciousness of a system is equivalent to its ability to integrate information over and above the information that is integrated by the union of its parts.
Introspective awareness	DeGrazia 2009	“Awareness of (some of) one’s own mental states such as feelings, desires, and beliefs”. The “mental reflexivity” of such awareness might require “the conceptual rocket of language”, but it is also plausible that “insofar as bodily self-awareness rests partly on having various sensations, and noting their connection with one’s body, bodily self-awareness may implicate a basic sort of introspective awareness.”
Mental time travel	Raby 2009	Describes the ability to project yourself into your personal past and remember or re-experience specific events or to project yourself into your personal future and imagine or pre-experience possible events.
Metacognition	Couchman 2010	Humans’metacognitive behaviors indicate important mental capacities, including hierarchical layers of cognitive control, self-awareness, and declarative consciousness.
	Middlebrooks 2011	Our operational definition of metacognition is that a monkey displays metacognition if its bets track its decisions.
	Morgan 2010	Metacognition refers to the ability to reflect on one’s thoughts
	Musholt 2012	Metacognition is defined as the ability to represent one’s own intentional and epistemic states (or as ‘thinking about one’s own thinking’), thus allowing, among other things, for the monitoring and control of one’s cognitive behavior.
	Proust 2014	Self-evaluation capacity: Epistemic self-evaluation allows remembering problem solving.
Mind	Gallup 1975	Mind is the ability to monitor your mental states and the corresponding capacity to use your experience to infer the experience of others.
Phenomenal consciousness	Nagel 1979, Chalmers 1996, Block 1995	Qualitative, subjective, or phenomenological aspects of conscious experience, sometimes identified with *qualia* (experiences such as colors, tastes, noises and other sensations with their own distinctive characters).
Phenomenal integration	Mudrik 2014	A phenomenological definition of integration is the combining of different features (e.g., parts of an object that are detected independently of each other into a unified percept (the binding problem)
Object permanence	Nawroth 2012	Object permanence refers to the notion that objects are perceived by subjects as separate entities that continue to exist even when they are out of the observer’s sight.
Secondary emotion	Morris 2008	Secondary emotions are the emotional reactions we have to other emotions. For example, a person may feel ashamed as a result of becoming anxious or sad.
Self-agency	Couchman 2015	Ability to recognize that some actions are generated by the self. Demonstrating

		metacognition indicates that the subject has some ability to monitor its mental states and, therefore, possibly some concept of self.
	Couchman 2012	The sense that some actions are self-generated.
Self-awareness	Couchman 2012	the sense that one is an individual separate from the environment
	Rajala 2010	Capacity to comprehend that one exists as an individual separate from thoughts, other individuals, and the environment.
Self-consciousness (or *self-awareness*)	DeGrazia 2009 Varner 2012	Capture an organism's capacity for second-order representation of its own mental states. Because of its higher order character, this capacity is often tied to the possession of Theory of Mind. The notion of self-consciousness usually encompasses several distinct abilities, including self-recognition, episodic memory, metacognition, and mindreading (implicit, for instance, in deception, imitation and complex social understanding).
Sentience	Dawkins, 1998 Appleby and Sandøe 2002 ; Brown 2015	According to an ethical context : ability to experience pleasure and pain (i.e. subjective, perceptual experiences)
	Mellor and Diesch 2006	Sentient living creatures are "*capable of experiencing positive and negative affective states*.", "*A sentient animal is one that has the ability to obtain and interpret stimuli from its internal and external environment and has at least a basic ability for memory, judgment and emotions*."
	Duncan 2006	"Sentience, a major contributor to evolutionary fitness in a complex environment, implies 'feelings that matter"
	DeGrazia 2009 Varner 2012	Corresponds to subjective experience, able to experience pain and pleasure as well as other affective and conative states
Social self-awareness	DeGrazia 2009	"awareness of oneself as part of a social unit with differing expectations attaching to different positions", "is present in highly social creatures" and "presupposes bodily self-awareness insofar as deliberate social navigation is possible only in creatures aware of their own agency."
Theory of mind	DeVeer 1999	Theory of mind can be defined as an organism's insight into its own mental state (self-awareness) and into those of other individuals (e.g. their beliefs, desires, feelings and intentions) and to act accordingly.
	D'Arcy and Povinelli, 2002	The abilities to understand false belief*, attention, the perceptual sources of knowledge, the communicative intention underlying the gestural acts of pointing and looking, visual perspective-taking, and even the distinction between accidental and intentional actions. **the ability to reason about other people's mental states. e.g a person puts an object into a box then leaves the room. Another person comes in and removes the object from the place where it was and puts it into another box. Understand fasle beliefs= understanding the difference between their knowledge and the wrong belief of the original person*
Triadic awareness	Perry 2004	Animal A understands some aspect of the quality of relationship between animals B and C

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