In 2015, the societal and scientific context promoted reflection on animal consciousness and related key concepts. Following a previous INRA multidisciplinary scientific assessment requested by the French ministries of Agriculture and Research on “Animal pain” (2009), INRA, upon request of the European Food Safety Authority (EFSA, in Parma, Italy), launched a new multidisciplinary scientific assessment aiming to produce a critical updated review of literature on animal consciousness. The mandate recommended focusing on farm animals.

Epistemological and philosophical issues of consciousness

Animal consciousness has been a research topic for philosophers for centuries. The philosophical questioning began as early as Aristotle, continued with Descartes and Rousseau, and today remains an active field of research. Scientists began pondering on the issue much later and some were even very reluctant to consider it as a valid scientific issue. In the 19th century, naturalists such as Lamarck, Darwin and Romanes, and later comparative psychologists and ethologists such as Morgan and Griffin further questioned the mental states of animals. Based on their observations of behaviour, they came to the conclusion that consciousness does occur in animals, especially in vertebrates. Research on biological and psychological issues resulted more recently in several major conceptual innovations which established that consciousness is the outcome of brain processes and that it is a legitimate topic of scientific enquiry.

We, as humans, are engaged in a continuous exchange of information, services, and affectivity with domestic species (farm or experimental animals, or pets). A certain kind of relationship can also at times occur with wild animals. Whatever their role is, we need to understand their mental world to ensure we treat them well, we respect their well-being and we minimize occurrence of pain in their life. Behind the theme of animal cognition lies the ethical issue of our responsibility towards animals, that is, our responsibility for their physical and mental well-being.

What is consciousness in humans?

As most research on consciousness has been, and still is, conducted in humans, animal consciousness cannot be explored without considering recent definitions and knowledge of human consciousness. Human consciousness is typically defined as the subjective or phenomenal experience we have from our surrounding environment, own body and/or own knowledge. We refer to this definition when considering animal consciousness bearing in mind that consciousness in humans is a subjective and private experience communicated to others not only through language but also through non-verbal means (i.e., behaviour). Although verbal language provides adult humans with a communication tool whose level of sophistication is unavailable to any other species, animals – just as humans - rely on other forms of non-verbal communication from which we can, to a certain extent, infer the properties of their consciousness.
The review done on human consciousness followed a two-dimensional analysis focused on level and content. The level of consciousness refers to states of vigilance ranging from being in a coma to being fully awake. The content of consciousness refers to the subjective experience associated with the perception of internal and external sensory information, as well as cognitive processes that do not involve perception, and to metacognitive processes (that are defined as the ability to consciously monitor and control one’s own mental states). It is important to stress that level and content of consciousness are related, as rich contents of consciousness are usually observed during wakefulness, except for dreaming and specific neurological disorders. After defining the levels and contents of consciousness, the contrastive approach was presented as the main empirical method to study them. It relies on a comparison of behavioural and neural responses measured under high vs. low levels or contents of consciousness. Based on this contrastive approach, several behavioural markers of consciousness in humans were reviewed, and potential neural correlates of consciousness described, defined as the neural mechanisms that are both necessary and sufficient to bring about conscious experience.

Two of the main theories of consciousness published so far are presented as a way to make sense of published empirical results; they both consider consciousness as an emerging property resulting from interactions between nervous structures:

i) the global workspace theory, which suggests that consciousness involves the broadcasting of information by parieto-frontal neurons, throughout the brain, to all the other nervous structures and particularly telencephalic cortex (Figure 1).

ii) the integrated information theory which assumes that the essence of consciousness is the capacity of the different nervous structures to integrate information.

**Figure 1**: schematic representations of interactions between telencephalic neurons in a conscious versus non-conscious human brain according to the “global workspace theory”. (from Dehaene et al., 2006)

Side views of the human brain (frontal section on the left, occipital on the right)

- **NON-CONSCIOUS STATE**
  - Neuronal structures in telencephalic cortex involved in the emergence of conscious state (associated with increasing activities)
  - Other intra-cortical connections

- **CONSCIOUS STATE**
  - Top-down connections originating from parieto-frontal neurons
Consciousness in animals

Some levels of consciousness in animals have already been acknowledged, notably by considering sleep/awakeness as a modulator of the level of consciousness. There are however strong scientific arguments in favour of extending such statement to the contents of consciousness, including perceptual, emotional, cognitive, and metacognitive capacities. There are at least three issues that make this task a challenging one:

i) The absence of narrative language in animals can be overcome by developing appropriate behavioural tests and comparative analysis of brain responses;

ii) The term ‘animals’ includes a large diversity of species, vertebrate and invertebrate, living in different environments. In that context, one might anticipate that consciousness may take different forms among species;

iii) Most of the reported studies have not been originally designed to analyse consciousness in animals. Nevertheless, they can be discussed in relation to it.

The properties of animal consciousness

They have been analysed along five main domains:

**Emotions** are defined as modulators of cognitive capacities involving changes in attention, judgement learning, or memory. The empirical proof that emotional responses occur in animals does not imply that they are systematically associated with consciousness. However, many animals, including fish, are capable of the same evaluation processes as those thought to trigger conscious emotions in humans. For instance, studies on expectations of reward in sheep and pig clearly show that animals not only respond to the intrinsic value of a reward but also according to their previous experience with the reward. Moreover, some animals such as cow and sheep, do experience and share with others a wide range of emotions that might be consciously experienced.

**Metacognition** is defined as “cognition about cognition”. That is the ability to monitor and control one’s own cognitive processes. It is thought to be a crucial component of self-awareness.

Two kinds of paradigms are widely used in animals to study metacognition: those that evaluate metacognitive monitoring (the ability to judge one’s own state of knowledge: the animal could in pushing buttons express a positive or negative answer, or that it does not know the answer, as tested with primates, poultry or corvidae, see box 1) and those that are designed to measure metacognitive control (the ability to seek information when lack of knowledge has been detected: ask for more information before answering). Those experiments are suggesting that some animal performances meet the criteria for metacognitive responses that appear homologous to conscious responses in humans in functionally similar conditions. This was for instance observed in pigeons and hens.

**Box 1**

**Example of an experimental procedure to test animal metacognition**

In this experience, an object (here a star) is first submitted to an animal. The latter obtains a reward when, during the test phase, it finds, within a wider list of items, the one already been presented beforehand. The animal may choose not to go through the test and obtain a lower reward by conducting a simple action such as pressing a button.

<table>
<thead>
<tr>
<th>Submission of an object</th>
<th>Delay</th>
<th>Search for the object</th>
<th>Reward</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1" alt="Star" /></td>
<td><img src="image2" alt="Arrow" /></td>
<td><img src="image3" alt="Search" /></td>
<td><img src="image4" alt="Apple" /></td>
</tr>
</tbody>
</table>

The authors observed that some animals (birds, primates) systematically and properly engage in the task when it is an easy one. But when the task is made more difficult (by increasing the delay between the submission and the test phases or by increasing the number of tested items), they tend to decline more the task and opt for the action which is assured to yield the less important reward.

Such results show that some non humans animals have metacognitive skills and are able to assess the level of their knowledge. It seems that they know whether or not they know.
Processing of past and future. Episodic memory is defined in humans as memory of autobiographical events. It has been demonstrated by assessing whether various animal species, especially primates, corvids and rodents, can characterize what, where and when, or in which context, they experience specific events. The characteristics of episodic-like memory studied in animals have many similarities to episodic memory in humans, in both behavioural and neurobiological aspects. Moreover, recent studies of primates, corvidae and weasels indicate that they can plan future actions independently of their current motivational state and their innate tendency to express certain behaviours, such as migratory behaviour (box 2).

Social behaviour. Many animals live in groups of variable composition and size. Their group structure depends on social cognitive abilities. Individuals, particularly among sheep and cattle, need to perceive and recognise each other to build a reliable and protracted relationship. Several examples of social behaviour were analysed. They address issues related to the theory of mind, which is the ability to infer the knowledge, intentions and emotions of other animals and underlying behaviours such as deception or empathy. Due to a wide variety of experimental protocols and species studied, there is an agreement that many animals, are not only automatically reacting to the behaviour of conspecifics, but also use their past social experience and ongoing relationships to adjust their behaviour to reach immediate goals. This capacity requires mastery of sophisticated means of perception, integration, planning, and communication, all of which are probably linked to consciousness.

Human-animal relationships: With the recent intensification of studies on domestication and animal welfare, human-animal relations have become a topic of scientific enquiry. Several studies developed in animals such as primates, dogs or sheep suggest that they are able to mobilize cognitive and emotional abilities when interacting with humans to build a mental and functional representation of their human partners. Studies involving human-animal relations highlight the potential role of an animal’s subjective experience of humans. Moreover, these studies show that distinct human individuals are differentially perceived by animals. The outcome is adapted, predictable and consistent emotional and behavioural responses ranging from avoidance to bonding. This indicates that conscious, rather than strictly pre-determined and automatic processes, may emerge in the development of human-animal relationships.

Box 2

Episodic memory in pig?
from Kouwenberg et al., 2009

This experiment is based on the fact that pigs prefer to explore unfamiliar objects depending on location and context. Objects A and B are presented to pigs as in the sequence below:

1st exposure phase: grey floor, object A on left side, object B on right side

2nd exposure phase: white floor, object B on left side, object A on right side

Test phase (4 trials): white floor, object A on both right and left sides

Pigs were exposed to objects A and B as well as white and grey floor backgrounds the same number of times. Nevertheless, during the test phase, object A located on the left side is less familiar due to its left side location against a white floor background. It is this one that pigs preferentially explored.

This experiment shows that pigs possess episodic memory skills. This is borne out by their capacity to memorize the “what”, “where” and “when and in what situation” components essential to episodic memory.
Towards a neurobiological approach of animal consciousness

Following the review of empirical evidence regarding consciousness along the five domains described before, current studies explore the neural correlates of consciousness in animals. A given dimension of consciousness is unlikely to be related to a single brain structure or neural network, as illustrated by research on humans. There are few comparative studies providing a direct mapping of behavioural performances of animals on specific neural substrates. In mammals, recent evidence indicates that telencephalic cortical areas sharing rich connections with other parts of the brain may be involved in consciousness. In birds and fish, such cortical areas are not present but functionally-related structures like the telencephalic pallium or the mesencephalic tectum may enable the animal to experience conscious content. The role of mid-brain nuclei, which are present in all vertebrates, should also be stressed. In any case caution is required when excluding the presence of consciousness in species that do not have the same brain structures as mammals, because different neural architectures may mediate comparable processes.

Review on the functional elements and the contents of animal consciousness

Several aspects of animal behavioural and cognitive capacities allow us to sustain the idea of the occurrence of consciousness in animals and to sketch its content. Overall, this leads us to conclude that these cognitive processes indicate the existence of different forms of consciousness with variable degrees of complexity. As for humans, animal consciousness might be best described as the emerging product of interactions between different functional layers constituted by perceptual, attentional, mnestic, emotional and evaluative 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 interact to ultimately produce interpretations and intentionality which are externalized through the expression of conscious actions. 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 external factors considered, consciousness may fluctuate from:

i) low contents: involving fewer brain structures and lower levels of complexity as well as limited associative learning capacities,

ii) to high contents: involving numerous brain structures and complex integrative processes, more decision making processes, numerous functional layers, highly flexible associative learning. This make conscious action and learning possible.

A clear limitation of our current knowledge comes from the low number of species so far investigated, among which very few farm animals. The species considered, however, cover a broad spectrum from invertebrates to vertebrates, it seems therefore reasonable to cautiously generalize our conclusions beyond the study cases.

Function and evolutionary process of consciousness

Such heterogeneity of conscious processes in animals is not surprising when one considers the variety of challenges which can be encountered in life and the accordingly considerable diversity of solutions evolved to adapt to contrasting physical, biotic and social environments. The question, in that context, is whether the cognitive abilities engendering consciousness are the result of evolutionary processes. They could also be the result of convergence in evolution which has occurred in species not related phylogenetically, thus having different neuronal structures, but facing equal environmental constrains.

The constant need to adjust to the environment might have exerted a selective pressure for consciousness to emerge, provided relevant brain architecture developments occur. Then the link between behavioural correlates of consciousness with specific neural structures across phyla seems difficult to assess.

Although a clear demonstration of an evolutionary role for consciousness is still lacking, one possibility is that consciousness may have evolved because it provides a competitive advantage, allowing flexible answers to the various challenges the animal should face. The precision of the mental representations of the environment is crucial for the animal to be able to choose the appropriate behaviour to a given situation.

After reviewing current evidence on the role of consciousness in adaptive processes, the issue of its evolutionary emergence across different animal phyla was raised. Conceived as a global workspace to cope with the complexities of life, consciousness may be seen as a fundamental feature of animals which appeared and evolved independently in different phyla and multiple times.

Conscious perception of sensory signals relative to pain

The recognition of a conscious processing of sensory information relative to pain by animals and humans, raises questions regarding the consequences of the perception and the processing of pain by animals.

Recent knowledge on perception should be taken into account from an ethical point of view when considering the use of animals by humans.
Among sensory information arising from the body, pain has a particularly high potential to interrupt attention or modify behaviour. Pain represents a nociceptive sensation associated with a negative affective sensation. Most animal species, including birds and fish, are equipped to detect and react to noxious stimuli. Mammalian animals share with humans most of the brain structures involved in the conscious perception of pain including its negative affective component. Avian and fish brains have homologs of mammalian brain structures that are likely to enable them to experience pain consciously. While invertebrates obviously react to noxious stimuli as well, presence of subjective negative affective experience related to pain is still debated in invertebrates which are much less studied. Thus, current knowledge suggests that at least vertebrates are equipped with nervous systems that support conscious processes of complex information, including negative emotions caused by noxious stimuli.

**Ethical issues**

This current knowledge has to be taken into account when considering ethical issues related to humans use of animals, or relationships. Most philosophical theories in animal ethics consider that sentience, referring to the capacity to experience suffering and pleasure, constitutes a relevant criteria when considering the moral status of animals. Beyond sentience, which is the minimal level of consciousness, our understanding of consciousness occupies a pivotal role in defining what matters to animals and the different aspects of their mental life. While sentience may be widespread among animals, more elaborate contents of consciousness have only been documented across a small range of species, among primates, corvidae, rodents and ruminants. Such higher contents need in particular autobiographic memory, or episodic memory. Because animals with autobiographic memory, as observed in primates, corvidae and rodents, can have desires and goals that extend into the past and the future, they can be negatively affected by aversive experience. The different levels and contents of consciousness documented in animals should give rise to commensurate ethical considerations, especially regarding domestic animals used in farming, research, work, sports or companionship.

**Conclusion**

Animals of diverse species display a diversity of various abilities in terms of consciousness.

This multidisciplinary scientific assessment does not equate the contents of consciousness described in humans with those occurring in animals. However, the overall picture provided by this collection of behavioural, cognitive and neurobiological studies supports the notion that, high content of consciousness does occur in some of the species studied so far.

**Future research**

Because research in the field of animal consciousness was until now focused on a small number of species of mammals and birds, it would be desirable to fill these gaps by widening the field of investigation to a larger range of species, in particular vertebrates, including fish.

To improve our understanding of the mechanisms of their mental functioning, experimental protocols will strive to distinguish between those behavioural and physiological answers of animals, that stem from conscious behaviour from those associated with acquired automatisms (which can be complex).

Experiments uncovering analyse on the one hand, the contents of consciousness, and on the other hand, the levels of consciousness, are needed. It would also be useful to study why, and to what extent, certain cognitive capacities, that allow the presence of elaborate contents of consciousness, are found among phylogenetically unrelated species and/or among species with very different neuronal structures?

As regards farm animals, a better understanding of their mental world, the way they represent themselves and their world and how they relate to their environment would enrich our thinking on how to improve their well-being and the way they are handled.

It would therefore be useful to explore high cognitive skills involved in self-consciousness, consciousness of an individual’s own knowledge and of other individuals’ knowledge (theory of mind), including an individual’s capacity for empathy, metacognition, consciousness of time (the ability to distinguish present past and future), as well as attention, memorization and motivation. Such research should also include studies of the so-called positive feelings.

The study of the development of the forms of consciousness at a young age is particularly important for farm animals, which have generally a brief life. It would be advisable to develop the understanding of the impact of the events being set up from the first days to first weeks of life.

The nature of the relationships of animals with the humans who raise them should also be studied in domesticated species.

Some research could be inspired by studies on humans, both at the level of the concepts and of methods of investigation. In particular, technologies studying neurobiological mechanisms, such as functional imaging, could be adapted to animals when it is technically possible.

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1. Relative to the perception of stimulations generating pain
Scientific assessment method

The analysis of the available scientific and philosophical academic knowledge was based mainly on published literature, after an extensive bibliographic search partly retrieved from the Web of Science™ Core Collection (WOS) database. The report ends with a total of 659 references, 75% of which from international scientific journals, and 33% of which were published after 2010; it also references 60 books, including philosophy books.

Assessment organisation

This multidisciplinary scientific assessment was produced upon request of AHAW unit of the European Food and Safety Authority (EFSA) (contract number EFSA/INRA/2015/01). INRA’s Delegation for Scientific Expertise, Foresight and Advanced Studies (DEPE), a division of INRA in Paris headquarters, coordinated the work of seventeen French experts from different scientific fields (biologists, cognitivists and philosophers) and of various affiliations. The report followed INRA’s guidelines.

Scientific coordination was provided by Pierre LE NEINDRE, INRA Director of research, together with Muriel DUNIER (DEPE project leader, INRA Paris), the bibliographic search was done by Emilie BERNARD (INRA Rennes) and the budget management by Kim GIRARD (DEPE, INRA).

The other experts are listed in alphabetic order: Alain BOISSY (INRA Theix), Xavier BOIVIN (INRA Theix), Ludovic CALANDREAU (INRA Nouzilly), Nicolas DELON (New York University), Bertrand DEPUTTE* (Emeritus Veterinary School Maisons-Alfort), Sonia DESMOULIN-CANSELIER (CNRS Nantes), Nathan FAIVRE* (CNRS Paris), Martin GIURFA (CNRS Toulouse), Jean-Luc GUICHER (Beauvais University), Léa LANSADE (INRA-IFCE Nouzilly), Raphaël LARRÈRE (INRA Paris), Pierre MORMÈDE* (INRA Toulouse), Patrick PRUNET* (INRA Rennes), Benoist SCHAAL (CNRS Dijon), Jacques SERVIERE (INRA Paris), Claudia TERLOUW* (INRA Theix).

*: chapter coordinators

Members of the review committee: Robert DANTZER (University of Texas, MD, Anderson Cancer Center, Houston, USA), Linda KEELING (University of Uppsala, Sweden), David LINDSAY (University of Perth, Australia) and Virginie MICHEL (ANSES, Ploufragan, France).

For further details:
