Animal welfare: neuro-cognitive approaches

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ABSTRACT

Many people maintain a naive belief that non-human animals consciously experience pain and suffering in similar ways to humans. Others tend to assume a more sceptical or agnostic attitude. Drawing on recent advances in research on animal cognition and neuroscience, the science of animal welfare is now beginning to address these issues empirically. We describe recent advances that may contribute to the main questions of animal welfare, namely whether animals are conscious and how we can assess good and bad welfare in animals. Evidence from psychology is described which demonstrate that many complex actions in humans can be carried out quite unconsciously and that human patients with certain sorts of brain damage can behave and manipulate objects properly while at the same time o consciously denying experience of them. The relevance of these findings with respect to the issue of animal consciousness is discussed. Evidence from animal cognition is described concerning the possibility that animals monitor the state of their own memories, show episodic-like knowledge and exhibit self-medication. Evidence from neuroscience concerning brain lateralization in non-human animals and its relevance to animal welfare is described. It is argued that in animals raised for economic purposes (milk and meat production) differences in cognitive abilities and brain lateralization can affect adaptive behavioural, physiological and immune responses to environmental stressors.

Key words: Neurosciences, Animal cognition, Brain lateralization, Welfare, Animal production.

RIASSUNTO

BENESSERE ANIMALE: L'APPROCCIO NEURO-COGNITIVO

Molte persone hanno la convinzione ingenua che gli animali provino le stesse esperienze cognitive del dolore e della sofferenza che proviamo noi esseri umani. Altre tendono invece ad assumere una posizione più scettica e agnostica. Sulla scorta degli studi più recenti di neuroscienze e cognizione animale, la ricerca che si occupa di benessere animale sta iniziando ad affrontare empiricamente tali problematiche. Nel presente lavoro vengono descritte alcune delle più recenti acquisizioni che possono contribuire ad una migliore comprensione delle principali questioni che riguardano il benessere animale, in particolare se gli animali siano coscienti e come possiamo valutare uno stato di benessere animale. La ricerca in neurop-

sicologia ha dimostrato che molte delle più complesse azioni umane possono essere effettuate del tutto inconsciamente e che pazienti umani con alcuni tipi di danni cerebrali possono rispondere correttamente a certi stimoli pur negando di avere alcuna esperienza cosciente di tali stimoli. Viene discussa l'importanza di questi rilievi in relazione al tema della coscienza animale. Vengono riportate inoltre evidenze sulla capacità degli animali di monitorare lo stato della loro memoria, di possedere memorie di specifici eventi ed episodi e di mettere in atto comportamenti di automedicazione. Vengono discusse altresì le evidenze a favore dell'esistenza di fenomeni di lateralizzazione cerebrale negli animali non umani e la loro possibile rilevanza sul benessere animale. Si ipotizza che negli animali allevati per scopi economici (produzione di latte e carne) le differenze nelle capacità cognitive e nei pattern di lateralizzazione cerebrale possano influenzare le risposte comportamentali, fisiologiche e immunitarie ai fattori stressanti.

Parole chiave: *Neuroscienze, Cognizione animale, Lateralizzazione cerebrale, Benessere, Produzione animale.*

Introduction

People who are not specialists in cognitive science and neuroscience take for granted that other animals consciously experience pain, suffering or other negative or positive emotions in ways that are identical to human beings. Yet, from a scientific point of view, understanding consciousness, either in humans or as it pertains to other animals, is a difficult problem, probably the most difficult in biology (Koch, 2004). No doubt species other than humans, even those reputed as being cognitively humble, show cognitive capacities (Vallortigara, 2006c). This is well-documented and little disputed (Hauser, 2000). However, as to conscious experience, we must admit that we have no idea as to how nerve cell activity gives rise to conscious thoughts and emotions. Nonetheless, current approaches in cognitive sciences and in neurosciences may significantly contribute to a science of animal welfare. The present Chapter comprises two parts. In the first part, a short overview of recent research in neuro-cognitive sciences that may have relevance to animal welfare is provided. The review is by no means exhaustive and it is highly selective. For instance, contribution from the so-called cognitive ethology (Griffin, 1992; Allen and Bekoff, 1997), that tends to deduce phenomenal consciousness from

evidence of higher cognitive abilities in animals, would be not considered. We favoured instead evidence that directly arises from research and methods developed within human cognitive psychology and neuropsychology and that appears to be transferable to animal research. In the second part, we addressed a specific topic, namely brain lateralization, which is the main research interest of the authors. We briefly considered the relationships between lateralization and some animal mental phenomena and its possible use for a science of animal welfare.

Cognitive processes, consciousness and welfare in non-human animals

The discussion about the status of mental experience in other species is further complicated by some recent advances in cognitive psychology. Evidence suggests that in human beings a variety of quite complex actions and activities can be routinely carried out unconsciously (Blackmore, 2003). Furthermore, neuropsychological research has revealed a dissociation between behavioural activity and conscious experience: neurological patients with blindsight can successfully reach for an object that they deny to be consciously aware of (Weiskrantz, 2003). Thus, they are simultaneously blind (with respect to their conscious experience) and

sighted (with respect to their overt reaching behaviour). The crucial point here is that if a certain complex behaviour (in humans) can be carried out either in a conscious or in an unconscious way, then the traditional argument that animals must be conscious because they exhibit behaviours similar to those exhibited by human beings appears to be questionable.

Interestingly, however, evidence has been collected demonstrating that animals too can show the blindsight phenomenon. Cowey and Stoerig (1995) successfully trained monkeys, following unilateral removal of area V1, to detect visual stimuli in their "blind" hemifield. The same monkeys were then required to classify trials in the blind hemifield as a blank (no object present) or a stimulus (object present) trial. Monkeys classified objects (that they have been proved able to detect) as "unseen". Given this apparent demonstration of vision without awareness in monkeys with no striate cortex, one may perhaps argue that monkeys' usual (unimpaired) vision is, in fact, a conscious one.

Further evidence from comparative cognitive neuroscience that attempted to address empirically the issue of mental experiences in other species is associated with the demonstration of episodic-like memories and meta-memory in animals.

In contrast to semantic memory, which contains general knowledge, episodic memory provides access to personally experienced events. In humans it is associated with the phenomenological experience of "remembering" as opposed to "knowing", or what Tulving (1985, 2005) calls autonoetic or self-knowing aspects of consciousness (e.g., recollecting where and when one learned that Rome is the capital of Italy, is different from merely knowing that fact).

In some beautiful work carried out by Nicola Clayton and her collaborators it was found that scrub jays (*Aphelocoma coerulescens*) can select food locations not only according to the type of food, but also according to how long it has been stored. For example, they will recover recently cached worms in preference to nuts, since fresh worms are more palatable, but if the worms have been cached for too long they will retrieve the nuts, since the worms will have decayed and become unpalatable (Clayton *et al.*, 2003). Scrub jays seem to know "what" has been cached, "where" it was cached, and "when" it was cached. However, some investigators maintain that a what-where-when ("www") criterion does not need to imply true episodic memory, since there is a lack of evidence about autonoetic consciousness (Tulving, 2005) – indeed, it is unclear how such evidence can be gathered in non-linguistic creatures (Clayton *et al.*, 2003; Emery and Clayton, 2004). Nonetheless, evidence for mental travel in the past, using the "www" criterion has been documented recently even in rats (Babb and Crystal, 2005). Moreover, there is also some evidence of animals' mental travelling in the future, i.e. planning ahead. Mulcahy and Call (2006) trained bonobos and orangutans to obtain food from an apparatus using a tool. Access to the apparatus was then blocked and the animals were presented with a selection of two suitable and six unsuitable tools which they could take into a waiting room. An hour later they were allowed back into the testing room and given access to the apparatus. The apes appeared able to carry a suitable tool into the waiting room and returned with it to obtain food an hour later. When tested with an overnight delay between tool selection and return, they still returned with a suitable tool in more cases than would be expected by chance (and see also Raby *et al.*, 2007 for recent evidence in birds).

A particularly interesting approach has focused on the possibility that animals can monitor the state of their memories, i.e. that they know, for instance, whether they remember something or not. Hampton (2001) reported intriguing evidence that monkeys performed better when allowed to choose whether to take a test, or an easier, but less rewarding, option than when the experimenter decided for them. These results suggest that monkeys know how much they remember.

Basic sensations like pain and suffering are also under scrutiny. The discovery of nocioceptors in fish (Sneddon *et al.*, 2003) has led some scientists to argue that they also feel pain and can suffer. In fact, a direct way of deciding whether animals are conscious would be to compare human and animal brain functions. Unfortunately, up to now no clear correlates of conscious experience have been identified in humans (but see for a possible recent advance; Lau and Passingham, 2006). It is interesting nevertheless to mention in this context the evidence, obtained from farm animals, for self-medication. For instance, broiler chickens with leg diseases can spontaneously learn to take food (using colour as a cue) containing an anti-inflammatory drug that, in humans, relieves pain; chickens in good health showed no such a behaviour (Danbury *et al.*, 2000). Again, whether this should be accompanied by a conscious experience is hard to say. Learning about the food (choosing food that contains "healing" components) has been long known in the literature. Rats with deficient diet in vitamins would also prefer food containing the missing substances. However in any case this does not suggest consciousness. Nonetheless, the cognitive mechanisms underlying these abilities are certainly of much interest in the science of animal welfare.

Neuro-cognitive approaches: the case of brain and behavioural lateralization

Three very important characteristics of our species, language, right-handedness and tool use, have been traditionally associated with a single and (allegedly) unique characteristic of the human brain, namely brain lateralization. Lateralization of the brain (or brain asymmetry) refers to the different functional specialization of the left and right side of the brain. For instance, in most (right-handed) individuals of our species the brain mechanisms for language production are located in the left hemisphere. Lateralization of the brain can manifest itself in behavioural asymmetries (or lateralities), such as asymmetric use of the hands, turning asymmetries, visual hemifield asymmetries and so on. According to some authors, consciousness should be regarded as a uniquely human characteristic precisely because of the special properties of the left hemisphere of the human brain (Gazzaniga, 1995).

Anatomical and functional differences between the left and right side of the nervous system have been implicated in several aspects of brain function and dysfunction in humans, including developmental disorders with a genetic basis, such as schizophrenia (Petty, 1999), depression (Pujol *et al.*, 2002), autism (Herbert *et al.*, 2002) and dyslexia (Robichon *et al.*, 2000). Despite this potentially striking medical relevance, we have a limited understanding of the origin of morphological asymmetries in the brain and of their importance in lateralized cognitive processes. This is in part due to a lack of adequate model systems: as mentioned above, for a long time lateralization of brain function has been considered unique to the human neocortex. However, research in the last years has clearly shown that lateralization is widespread among vertebrates, and it

is not at all unique to the human brain (see for recent reviews Vallortigara, 2000, 2006a, 2006b; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). Although most of the research has been carried out using laboratory animal models, there is now increasing interest in lateralization in farm animals (e.g. horses: McGreevy and Rogers, 2005; sheep: Morgante *et al.*, 2007) and pets (dogs: Wells, 2003; Quaranta *et al.*, 2004).

Of particular interest for animal welfare is the possible association between lateralization and the immune response, which was first argued for by Geschwind and Galaburda (1985). These authors argued for an association between left-handedness (or atypical lateralization) and a variety of immune disorders. Although the original hypothesis, that people showed different levels of the male hormone testosterone during fetal development and that testosterone affected both brain development and the development of the immune system, has proved to be somewhat controversial (McManus, 2002), the availability of animal models has allowed a fresh approach to the issue of whether the left and right sides of the brain play different roles in the modulation of immune responses (reviews in Neveu, 1988, 1996, 2002). For instance, right cortical lesions produced a depression of mitogen-induced lymphocyte proliferation and enhanced antibody production in mice, whereas similar lesions of the left cortex did not affect immune responses (Barnéoud *et al.*, 1987). Moreover, left cortical lesions depressed T-cell functions, whereas right cortical lesions either enhanced T-cell function or had no effects (Neveu, 1988). Individual differences in turning bias have also been associated with differences in immune responses: rats that circled preferentially to the left showed higher levels of lymphocytes than rats that circled to the right (Neveu, 1988).

Several studies have used the preferential use of one limb as a behavioural measure of brain lateralization with the mouse as a model. Mice that preferentially used their left paw to reach into a tube to obtain food showed higher mitogen-induced T-lymphocyte proliferation than mice that preferentially used their right paw (Neveu *et al.*, 1991). Ablation of the left cortex abolished this difference in T-cell function between left- and right-pawed mice, whereas ablation of the right cortex had no affect (Neveu *et al.*, 1991).

Lateralization of limb usage at the population level has been reported in other non-human species (reviews in Rogers, 2002), including pet animals. For instance, recent evidence has shown that dogs show paw preferences at the population level, though different in direction between males and females: the former favouring left paw use, the latter right paw use (Wells, 2003). This seems to be consistent with the previous evidence of Tan (1987) who reported a slight preference for right paw use in a sample of dogs in which females were the larger group. A link between cerebral lateralization and immune system in this species was first demonstrated by Quaranta *et al.* (2004) looking at paw preference in a task consisting of the removal of a piece of adhesive paper from the snout. Population lateralization was observed in opposite directions in the two sexes: male dogs preferentially used their left paw, female dogs their right paw. Nevertheless, no association was detected between sex and paw preference with respect to immune responses. In both sexes, left-pawed dogs had a higher percentage of lymphocytes than either right-pawed or ambidextrous dogs, whereas granulocyte percentage was lower in left-pawed than in right-pawed or ambidextrous dogs. Moreover, the total number of lymphocyte cells was higher in dogs that preferentially used

their left paw than in dogs that either preferentially used their right paw or in ambidextrous dogs, whereas the number of gamma-globulins was lower in left-pawed than in right-pawed or in ambidextrous dogs.

In subsequent work by the same group the production of specific antibodies (IgG), IL-10 and IFN-γ was evaluated in dogs in relation to behavioural lateralization as assessed by paw preference (Quaranta *et al.*, 2006). Left-pawed, right-pawed and ambidextrous dogs of mixed breed were selected on the basis of their performance in a task consisting of the removal of a piece of adhesive paper from the snout. All dogs were immunized with rabies vaccine. IgG anti-rabies antibody response was evaluated by IFI (indirect immunoflorescence). Serum IFNγ and IL-10 levels were measured by ELISA in animals showing significant individual left-, right- or no-paw preferences in the behavioural test. The results showed that the direction of behavioural lateralization influenced the immune response in dogs. The titers of anti-rabies antibodies were lower in left-pawed dogs than in either right-pawed or ambidextrous dogs. Similarly, the IFNγ serum levels were lower in left-pawed dogs than in right-pawed and ambidextrous dogs. IL-10, on the contrary, seemed to be an immune parameter which was not affected by lateralization. These findings suggest that immunomodulation can be correlated with brain laterality in canine species by the regulation of the production of antibody and some cytokines such as IFNγ, which are molecules involved in the immune-neurohumoral crosstalk.

Recent results obtained in sheep point to a relationship between behavioural lateralization and several physiological measures associated with stress responses. Sheep are strongly lateralized at the neurobiological (Broad *et al.*, 2002; Peirce and Kendrick, 2002) and behavioural (Peirce *et al.*, 2000) levels with regard to face recognition of conspecifics, showing a dominance of their right hemisphere. For instance, da Costa *et al.* (2004) reported that when sheep experience social isolation, the sight of pictures of the faces of familiar sheep significantly reduces behavioural (activity and protest vocalizations), autonomic (heart rate) and endocrine (cortisol and adrenaline) indices of stress compared to those of faces of goats or to inverted triangles. Moreover, the sight of familiar-face pictures also increases mRNA expression of activity-dependent genes (c-fos and zif/268) specifically in the right hemisphere, which is specialized for processing faces (temporal and medial frontal cortices and basolateral amygdala) and for emotional control (orbitofrontal and cingulate cortex), while reducing their expression in regions associated with stress responses (hypothalamic paraventricular nucleus) and fear (central and lateral amygdala).

Recently, we documented lateralization at the population level in a variety of motor behaviours associated with turning around an obstacle ('detouring') in order to rejoin conspecifics (Versace *et al.*, 2007). Lateralization at the individual level was also observed in certain behaviours (for instance the direction of rumination with most individual showing striking preferences but with a 50:50 distribution of left- and right-preferent individuals in the population). The effects of lamb separation and manual milking, which are stressors usually associated with the productive cycle of a dairy sheep farm, were investigated by comparing short-term (24h) adaptive responses in strongly versus weakly-lateralized dairy ewes (Morgante *et al.*, 2007). Functional lateralization was scored using a series of behavioural tests (direction of free turning, direction of obstacle turning, preferential leg use in front of an obstacle) followed by

a daily period of hormonal, biochemical and clinical assays on two groups of 6 strongly lateralized (SL) and two groups of 6 weakly lateralized (WL) ewes, divided for lamb presence or separation. Differences were observed for several parameters of energetic metabolism (cholesterol, insulin and glucose) as well as ACTH as a function of the degree of lateralization score and stressor application.

These results suggest that behavioural lateralization parameters should be taken into consideration as a crucial variable in the understanding of stress responses and their modulation in relation to animal welfare.

Perspectives in the use of lateralization and other neuro-cognitive measures to assess animal welfare

We believe that linking animal science and veterinary medicine with modern animal cognitive neuroscience could provide insights and unexpected novel approaches to improve both animal welfare and the techniques for animal production. A few examples may illustrate our point.

The issue of animal emotion is strictly related to the possibility of measuring behavioural responses in ways that could be usefully related to brain processes associated with certain emotional states. A fitting example is provided by the recent finding that the direction of tail wagging in dogs may be associated with hemispheric activation during viewing of different emotive stimuli (Quaranta, Siniscalchi and Vallortigara, 2007). Amplitudes of tail wagging to the left and to the right side were measured in dogs looking at different stimuli. When faced by their owner, dogs exhibited a striking right-sided bias in the amplitude of tail wagging. A similar striking bias was observed when dogs were shown an unfamiliar human be-

ing, though in this case followed by an overall decrease in the amplitude of tail wagging. When faced with a cat, dogs showed much reduced tail wagging movements, but there was still a slight bias favouring the right side. In contrast, when tested alone or in the presence of an unfamiliar, dominant, conspecific, dogs showed a left-sided bias of tail wagging. It is noteworthy that the direction of the bias did not simply reflect the strength of wagging behaviour: a significant bias in the same direction (to the right) was observed with high (owner), medium (unknown human being) and very low (cat) amplitudes of tail wagging. This pattern of results is in agreement with the hypothesis that asymmetry in the control of functions is related to emotion. Davidson (2004) suggested that the anterior regions of the left and right hemispheres are specialized for approach and withdrawal processes, respectively. This hypothesis was developed in the context of human neuropsychology, but approach and withdrawal are fundamental motivational dimensions which may be found at any level of phylogeny (Schneirla, 1959). In the experiments with dogs, stimuli that could be expected to elicit approach tendencies (such as seeing a dog's owner) were associated with higher amplitude of tail wagging movements to the right side (left brain activation) and stimuli that could be expected to elicit withdrawal tendencies (such as seeing a dominant unfamiliar dog) were associated with a higher amplitude of tail wagging movements to the left side (right brain activation: in dogs the rubrospinal tract, which is the predominant volitional pathway from the brain to the spinal cord, decussates just caudal to the red nucleus and descends in the controlateral lateral funiculus; fibres of the rubrospinal tract terminate on interneurons at all levels of the spinal cord; see Buxton and Goodman, 1967).

Such prominent behavioural asymmetries could be profitably used in dogs' welfare and veterinary behavioural medicine as a simple, non-invasive method to estimate quantitatively positive and negative emotions elicited by a variety of stimuli.

Conclusions

As for farm animals, in particular animals used for meat and milk production, research on behavioural and brain laterality can prove useful in at least two ways. Firstly, it could be used to optimize automated productive processes with respect to the behavioural characteristics of the animals. An example concerns robotized milking machines, the use of which tends nowadays to be more widespread. To check whether animals show side biases as to the left/right direction of milking, for instance associated with antipredator responses or social responses mediated by one or other visual hemifield/hemisphere, may prove instrumental in avoiding both bad working of the automatic set ups as well as repeated traumas and stress of the animals, both of which ultimately affect the quality of milk production. Similarly, the positioning of the feedingr-trough and water containers as well as the runways leading the animals to different parts of the farm environment could be planned by taking into account right-left biases in behaviour and individual differences in such biases.

Secondly, the presence of individual variability in behavioural lateralization -which is at least in part explained by genetic variation (see Vallortigara and Rogers, 2005) - would make it possible to artificially select individuals with different degrees (or different direction) of side biases in relation to the peculiar needs of any particular type of breeding scheme and of the associated productive processes, in order to increase animal welfare.

Finally, the existence of a link between the pattern of behavioural lateralization and the individual variability in the responses associated with the immune system and disease resistance could be profitably used to select animals that are more likely to fit the specific rearing conditions requested by animal production.

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