

Can farm animal welfare be understood without taking into account the issues of emotion and cognition?

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ABSTRACT: Although the concept of welfare makes reference to feelings of individual animals, the exact nature of these feelings and their relationship to emotions and cognitive abilities of the animals under consideration are never detailed. Based on the concepts of stress and coping, an extensive list of indicators of physical health, production, behavior, and physiology has been set up for the purpose of recognizing good from bad welfare. However, these indicators do not allow us to make any inference about mental states. This issue is important because welfare considerations apply to farm animals of different species and, within a given

species, to animals of different ages, which are likely to have varying degrees of emotional and cognitive capacity. In the past, disagreements about exact definitions of emotion and cognition have blurred the matter and hampered research. However, this should no longer be the case; the study of emotions and feelings has emerged as a field of active research in psychology and neuroscience over the last two decades. It is now possible to go over philosophical discussions on the nature of feelings and to set up a research agenda on emotion and cognition in farm animals that should help us to understand their welfare requirements.

Key Words: Cognitive Development, Domestic Animals, Emotions, Neurology, Stress

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Introduction

Statements about the nature of animal welfare make explicit or implicit reference to mental states. As a typical and influential example, Broom (1986) defines the welfare of an animal as “its state as regards its attempts to cope with its environment.” In the report of the European Scientific Veterinary Committee on the welfare of calves (European Commission, 1995), this definition sets the scene and is followed by the statement that “the state of the animal, as referred to in the definition, includes the feelings of the individual animals as its physical state. Suffering is one of the most important aspects of poor welfare and we should investigate the existence of good or bad feelings wherever possible when trying to assess welfare.” However, the problem is that what these mental states termed “feelings” exactly consist of, and how they relate to coping, is never clarified. As pointed out by Dawkins (2001), research on the psychological health of farm animals has mainly concentrated on establishing checklists of biochemical, physiological, and behavioral indicators without taking the necessary steps to relate them to the occurrence

of positive and negative emotional states. There are obvious reasons for that, the main one being the reluctance of ethologists to engage in a thorough study of emotions in animals. There is still the biased prejudice that research on emotion and cognition is unscientific and should be carried out only on human beings, who can express what they feel via verbal reports. The purpose of this theoretical review paper is to show that there are ways out of this conservatory attitude and it is possible to engage in objective studies of emotions in farm animals and how they relate to cognition.

Emotion and Cognition

The most elementary component of an emotional state is its affective dimension. According to Cacioppo and Gardner (1999), affective categorization and responses have been shaped by evolution to allow differentiation between hostile and hospitable stimuli. This differentiation is so critical that organisms have rudimentary reflexes for categorizing and approaching or withdrawing from certain classes of stimuli and for providing metabolic support for these actions. An additional adaptive advantage is conferred to species whose individual members have the capacity to learn based on the unique environmental contingencies to which they are exposed, to represent and predict events in their environment, to manipulate and plan based on

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representations, and to exert some control over their attentional and cognitive resources.

The affective component of an emotional state can be simply assessed by determining whether the animal approaches or avoids the eliciting situation either spontaneously or after appropriate classic or instrumental learning. An object is described as pleasurable, and the animal is assumed to experience pleasure, if this object is approached and eventually consumed or if the animal remains in close contact with it. Conversely, an object is said to be aversive, and an animal exposed to this object is assumed to experience a negative emotion, if this animal escapes it or subsequently makes every effort to avoid it. Preference tests in applied ethology make use of this basic distinction to determine what is good and what is bad for the welfare of an animal. Typically, if a pig that is given the choice among two types of floor stays longer on a given floor type (e.g., a straw-bedded floor) and hardly walks or lies down on the other floor type, (e.g., concrete slats), its state of welfare will be reputed to be good or bad depending on what type of floor it is normally exposed to. More sophisticated methods have been developed to find out how much animals value resources by measuring how high a price, in terms of time and energy, they will pay to access or avoid them (Dawkins, 1983). The rewarding nature of a single resource such as food can be estimated by the use of a progressive ratio schedule that consists of requiring an animal put into an operant conditioning chamber to press a panel once to get the reward, then twice, then four times in a row, and so on, until the reward is no longer worth the effort (the so-called breaking point) (Dantzer, 1976). Several resources can be compared by use of closed-economy set-ups in which animals have permanent access to several resources providing they pay the appropriate cost (e.g., by pushing through weighted doors) (Mason et al., 2001).

It is possible to go one step further and qualify the specific emotional state that is experienced by an animal. Primary emotions refer to a set of six to eight basic emotional reactions (e.g., fear, joy, disgust, sadness, surprise, and anger) that are innate and found in human and non-human animals (Leventhal, 2000). The usual approach for determining experimentally whether an animal can express a given emotion is to expose this animal to an emotional stimulus that is assumed to be at the source of the emotion under consideration and to assess whether it presents the behavioral and physiological changes that are congruent with the emotional nature of the stimulus. A chicken is described as frustrated if it responds to a situation in which it is prevented from performing a motivated behavior by showing signs of behavioral agitation (e.g., wing flapping, aggression toward conspecifics, spot pecking, or pacing). In the same way, a chicken is assumed to be frightened if it responds to a potentially threatening stimulus by behavioral signs of fear that vary according to the distance from the threat and the ability to avoid it. Fear responses in chickens include flight, fighting,

and tonic immobility. All these behavioral responses are usually accompanied by changes in physiology that reflect activation of the hypothalamic-pituitary-adrenal (HPA) axis and the orthosympathetic branch of the autonomic nervous system. These physiological changes do not necessarily differ according to the emotion that is experienced (Dantzer, 1989). Their relation to the subjective component of emotions is quantitative rather than qualitative, in the sense that the magnitude of the physiological arousal modulates the intensity of emotion. An emotion requires both a physiological arousal and the perception of a meaningful, contextual-environmental cognition (Schachter and Singer, 1962). There has been much debate on the relative importance of the visceral and the cognitive processes in the genesis of emotion, and the order in which they take place (i.e., does the visceral arousal precede cognition, or vice-versa?). In the present case, it is not necessary to enter the details of this controversy, and it is sufficient to state that modern theories of emotion agree on the role of the environmental context in determining the specific quality of the emotional response (Leventhal, 2000). This allows us to understand why behavioral and physiological indicators of emotion in animals are mostly used for describing emotionality and its variation according to genotype and previous experience, whereas contextual cues are used to specify which type of emotion is experienced.

Whether emotions are defined on a bidirectional axis (pleasure vs displeasure) or in terms of discrete emotional states, the assumption remains the same. Animals that display behavioral and physiological signs of emotion are assumed to experience the corresponding emotional state. Many scientists choose to stay at this level when it comes to defining emotions. A typical example is Panksepp (1988), who started his career with the description of stimulus-bound behavior in rats, i.e. behavioral responses elicited by electrical stimulation of specific brain sites. Panksepp (1982) claimed that the primary emotions animals are endowed with (expectancy, rage, fear, and panic; joy was added later) arise from the operation of hard-wired neural circuits in the visceral-limbic brain that facilitate diverse and adaptive behavioral and physiological responses to environmental challenges. The mere existence of the appropriate behavioral and physiological signs of emotion allows us to infer that the corresponding emotional state exists in the animal under consideration. Although the Panksepp (1988) description is limited to the mammalian brain, it is certainly possible to find equivalents of such circuits in the reptilian brain that birds are equipped with, especially so because Panksepp also worked with chicks.

The problem with the Panksepp (1988) description of emotional states is that it does not allow us to differentiate fixed response patterns that are hard-wired and do not necessarily require a central nervous system from more plastic, adaptive responses. As aptly pointed out by Staddon (1983), relatively simple built-in re-

sponses such as tropisms enable animals to display a large set of very well-adapted behaviors, including avoiding bad things and approaching good things. Rolls (1999) claims that such adaptive mechanisms that require little or no dependence on past history do not involve any intervening emotional state. Emotions come into play when adaptive behavior depends more and more on the animal's past. Emotions, therefore, require the ability to establish temporal and instrumental contingencies. Learning a temporal contingency refers to the ability to relate the occurrence of one stimulus to another one when both occur in succession, and to make the first one a possible causal factor for (or a predictor of) the second one. Learning an instrumental contingency refers to the ability to assess the consequences of one's response on the environment (e.g., to learn that a given response is followed by a set of specific consequences). In this context, emotions provide the common currency with which animals can balance conflicting demands of avoiding bad things and approaching good things and evaluate the priority to be given to one over the other.

The main problem with all of that which precedes is that it describes the way an emotional system in the brain is operating and the minimum mental operations it requires, but it says nothing about the subjective aspects of emotions, or feelings. As pointed out by Le Doux (1996), "a subjective emotional experience, like the feeling of being afraid, results when we become consciously aware that an emotion system of the brain, like the defense system, is active." To have a defense system that gives rise to appropriate behavioral and physiological responses in the face of a threatening situation is not sufficient to feel afraid; we need to have the key elements of consciousness that allow us to be aware of the activity of this defense system. Duncan and Petherick (1991) stand on the same ground when they claim that the extent to which animals are aware of their internal state while performing behavior known to be indicative of so-called states of suffering, such as fear, frustration, and pain, will determine how much they are actually suffering. Of course, emotions have evolved as brain states and bodily responses, and not necessarily as subjective feelings conveyed linguistically; otherwise, Darwin (1872) would not have been able to study their phylogeny. However, these basic elements are not sufficient to make up a full emotion. Some elements of consciousness are still necessary. For LeDoux, there is nothing special in the conscious operations that allow us to be aware of our emotional states. The mental representation of a flower and the mental representation of a threat make use of the same building blocks. What is specific is the way the sensory input is processed to give rise to a mental representation. Emotional stimuli are given a special treatment in the sense that most of them escape the sensory cortical analyzer to be deciphered at the subcortical level, via a shortcut, a neural pathway directly connecting the sensory thalamus to the amygdala.

Damasio (1998) has added to this description the somatic marker hypothesis, which allows us to relate visceral responses to feelings. Those brain areas in which emotions are represented in the form of motor programs need to be able to process visceral information and to re-actualize this processing according to the way emotions are expressed both behaviorally and physiologically. In the brain, the mechanisms of emotions are part of a survival kit, just above the basic motivations. Feelings come into action to allow anticipation of what can happen or prediction of what is going on during the course of an emotional situation that emotional responses are already dealing with. Consciousness of an emotion is a form of a meta-knowledge because it corresponds to the knowledge of one's ability to experience emotions (Damasio, 1998).

In more general terms, the issue of the relationship between emotion and cognition has already received a lot of attention in psychology. Contrasting theories have been put forward, some proposing that there cannot be any emotion without some form of cognition, others pointing out that emotion and cognition are distinct processes. Without getting into the details of the controversy that is mainly based on empirical work carried out in human subjects, it is important to know what is at stake here because it has significant implications for the conceptualization of emotions in animals. A few scientists, such as Zajonc (1980), claim that emotions, actually confounded with preferences, are more primitive than cognition, represented by mental operations such as object recognition, and therefore can occur in the absence of any cognitive operation. The vast majority of psychologists, however, agree that an emotion involves some form of cognition about an emotional situation. For Lazarus (1984), an emotional state requires a primary appraisal of the emotional stimulus. This primary appraisal is responsible for the setting and execution of action plans, and it is followed by a secondary appraisal of the consequences of action. Contemporary psychologists have tried to describe more precisely the exact dimensions of the eliciting situation that are evaluated and give rise to an emotion. Although their description usually tells us nothing or very little about the contribution of physiological activation to this appraisal process, the dimensions that have been identified are certainly useful for trying to describe in very objective terms the types of emotion that are accessible to different animals and the way they can differ according to age and species. A very good example of this type of contribution is that provided by Scherer (1997), with his theory of the emotion-antecedent appraisal process. In contrast to most of his colleagues working on appraisal, he chose not to rely on verbal reports to assess the way appraisal is carried out; instead, he concentrated on the objective antecedents or eliciting conditions for emotional reactions. The major criteria he listed for an emotional object are its novelty, intrinsic pleasantness, goal significance, coping potential, and relevance to external and internal standards.

Table 1. Appraisal patterns (listed in rows) for some primary emotions (listed in columns)^a

Item	Disgust	Sadness	Fear	Rage	Happiness
Novelty					
Suddenness	Open	Low	High	High	Low
Familiarity	Low	Low	Low	Low	Open
Predictability	Low	Open	Low	Low	Medium
Pleasantness	Very low	Open	Low	Open	High
Goal significance					
Outcome probability	Very high	Very high	High	Very high	Very high
Urgency	Medium	Low	Very high	High	Very low
Coping potential	Open	Very low	Open	High	Open

^aAdapted from Scherer 1988. Note that goal significance includes only outcome probability and urgency, and coping potential refers only to controllability. The status of a given antecedent varies between low and high. Low familiarity, for instance, corresponds to novelty; high urgency refers to the obligation of doing something very quickly in order to deal with the situation. The status is said to be open when its level is not relevant; for instance, disgust can be induced by sudden as well as by slowly developing taste stimuli.

With the help of these criteria, he was able to distinguish most primary and secondary emotions, and even to find emotional states for which there is still no verbal emotion label (Table 1).

A Strategy for Studying Emotion and Cognition in Farm Animals

Because applied ethology deals with a wide range of species, some standardization is obviously in order to describe the range of emotional states that are accessible to farm animals. It is necessary to overcome the previously described limitations of the behavioral approaches that have been used so far for studying emotional responses in animals. In order to incorporate in this task an appropriate evaluation of cognitive abilities of farm animals, the reference framework has to rely as far as possible on observable elements rather than on linguistic labels. The appraisal model elaborated by Scherer (1997) can be proposed for this purpose. It is relatively easy to plan similar emotional situations for different animal species based on the elementary appraisal dimensions that are delineated in the Scherer (1997) theory (novelty, pleasantness, coping potential, etc.) and to investigate the details of the appraisal process rather than debating the extent to which it is cognitive or not. Based on Leventhal's theorizing, emotions can be seen as developing from relatively simple, reflex-like forms (wired in innate sensory-motor processes) into complex cognitive-emotional processes that result from the participation of at least two distinct levels of memory and information processing, a schematic and a conceptual level (Leventhal and Scherer, 1987) (Figure 1).

Imagine an emotional state with the following antecedents: suddenness, low familiarity, low predictability, very low intrinsic pleasantness, high goal significance, and low coping potential; in all likelihood, this emotional state corresponds to frustration. This emotional state is characterized by behavioral agitation and in-

creased pituitary-adrenal activity, as already described in pigs that have been trained to work for a food reward by pushing a panel with their snouts in an operant conditioning cage, and which, on the test day, are put into the cage with the feeder turned off (Dantzer et al., 1980). These behavioral and physiological reactions form a basic vocabulary of primitive emotions that is suggestive, and only suggestive, of the presence of an emotional state and its associated emotional experience.

Although behavioral agitation and physiological arousal are the most visible components of the pig's automatically elicited emotional state of frustration, they are short-lived and not necessarily accompanied by a feeling of frustration. Such a feeling is most likely to arise if the pig is able to elaborate on what has happened to it and how it has reacted to it. This is where the schematic level of processing comes in. The minimum requirement here is the ability to form what cognitivists call schemata (i.e., neural representations of the situation and the organism's response to this situation). If a pig that is repeatedly exposed to a stimulus that signals the cessation of delivery of food learns to respond to it by emitting a response that terminates the signal so that it can now be rewarded, then there is some reason to believe that it is able to feel frustrated. Note that schemata operate automatically and are not easily controlled by conscious reasoning or voluntary effort. The fact that mammalian farm animals can learn temporal and instrumental contingencies is a good index of their ability to form schemata. A pig that has learned to avoid impending electric shocks by jumping from one side of a two-compartment cage to the other will respond to a fear signal (i.e., a tone previously associated with electric shock) by increasing its response rate (Dantzer and Mormède, 1976) (Figure 2). Conversely, it will react to a safety signal (i.e., a tone signaling the absence of electric shock) by decreasing its response rate. In other words, pigs make use of their past experience to predict what is likely to happen in the situation they are exposed to.

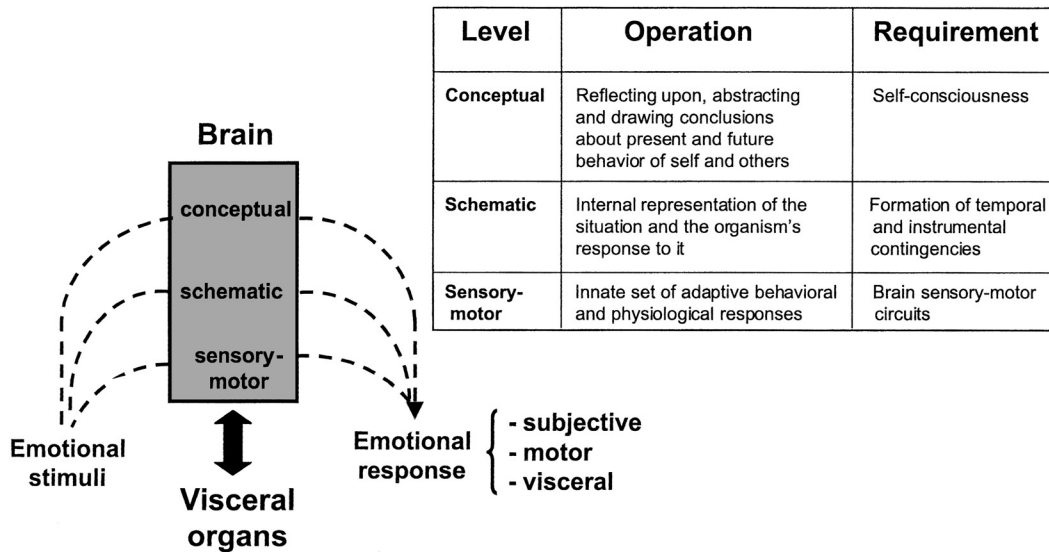


Figure 1. Multilevels of emotion processing (adapted from Leventhal and Scherer, 1987).

The synchrony between behavioral and physiological responses that is characteristic of an emotional response takes place not only at the sensory-motor level, but also at the schematic level that involves situational and response expectations. The ability to control the emotional situation by a suitable behavioral response

results in physiological de-activation (Dantzer, 1989, 1993). Conversely, the inability to control the situation is a strong inducer of physiological arousal. The way animals respond to the frustrating situation is determined by their expectation of the food reward, which itself influences their blood levels of cortisol. This syn-

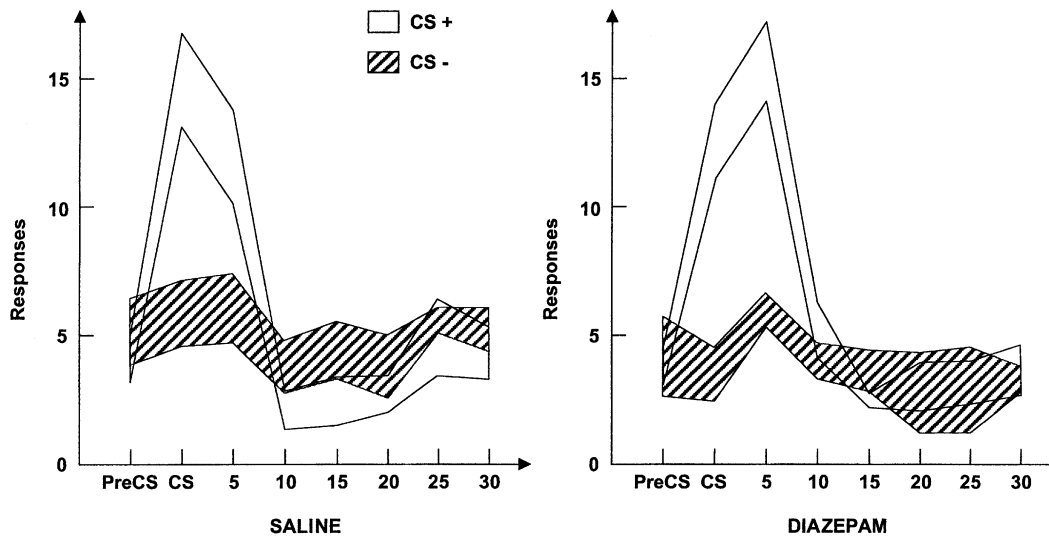


Figure 2. Behavioral responses of pigs with a continuous avoidance history to a fear signal (CS+) and to a safety signal (CS-). Pigs were trained to avoid painful electric shocks by crossing a barrier in a two-compartment cage according to a continuous avoidance procedure (shock-shock interval = 10 s, response-shock interval = 30 s). After stabilization of performance, they were presented with a 5-s tone always (CS+) or never (CS-) followed by shock, 10 times for each tone, in four conditioning sessions. On the next day following the last discriminative fear conditioning session, they were tested in the two-compartment cage in extinction conditions (i.e., without any shock), and CS+ and CS- were presented in random order nine times each. Half the pigs were pretreated with saline (n = 4) or with 1 mg/kg diazepam (n = 4) 30 min before the session. Each graph shows the mean number of responses (mean ± SEM) in 5-s successive intervals just before the CS (-5 s), during it (0 s), and after (5 to 30 s). Note that presentation of the fear signal increased response rate whereas that of the safety signal had the reverse effect. Diazepam injected at an anxiolytic dose had no effect. Adapted from Dantzer and Mormède, 1976).

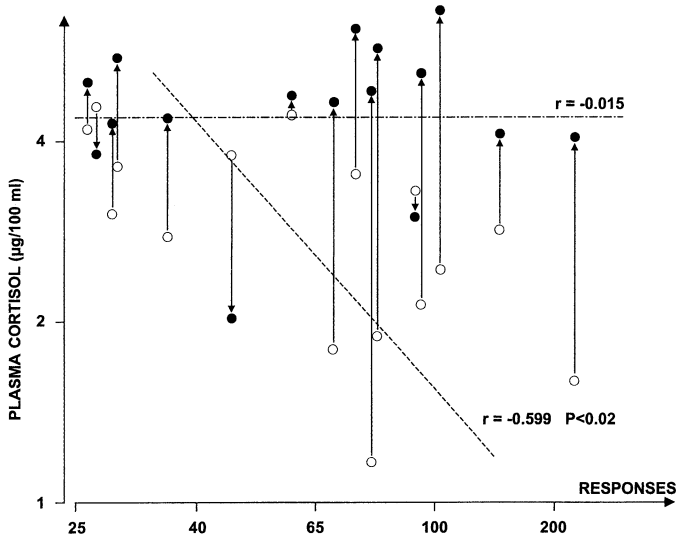


Figure 3. Relationship between plasma cortisol levels and behavioral response to frustration in pigs. Pigs that had learned to get a food reward by pressing a panel with their snouts were put into the operant conditioning cage on the day of test with the food dispenser turned off. Open circles show for each pig the initial plasma cortisol levels, measured just before the start of the session, and closed circles the plasma cortisol levels measured 30 min after completion of the frustration session. Note that the number of responses emitted during the session was correlated negatively to initial (dotted line) but not to final (interrupted line) plasma cortisol levels. Adapted from Dantzer et al. (1980).

chrony between physiological activation and behavior can be seen from the positive correlation between blood cortisol levels at the start of the frustration session and the number of times pigs continue presenting the previously rewarded response (Dantzer et al., 1980) (Figure 3).

Because of this synchronization process, changes in circulating hormones can be used *a posteriori* to assess whether the behavioral response to the situation is truly indicative of an emotional state. This possibility has been very elegantly made use of by Mason et al. (2001) to show that the way mink value different resources in a closed-economy set-up does not necessarily imply that the lack of preferred resources is detrimental to welfare. In their experiment, urinary cortisol levels increased only when mink were prevented from getting access to a water pool, but not when they were unable to visit an alternative nest site or an empty cage, two resources with lower incentive value than the water pool. Elevations in urinary cortisol of mink denied access to the water pool were of the same magnitude as those observed in mink deprived of food. Activation of the autonomic nervous and neuroendocrine systems serves to fuel the motor components of the emotional response. However, it is not its sole role. By their action on the brain, hormones influence the way animals cope

with the situation (e.g., high cortisol levels are associated with a higher probability of engaging in passive coping, whereas high catecholamine levels are associated with a higher probability of engaging in active coping; Dantzer and Mormède, 1983). They also allow brain memory systems to differentially process for further use sensory aspects of the emotional situation and outcomes of emotional behavior (Mormède and Dantzer, 1978).

A full account of emotional reactions in farm animals requires at least the assessment of the extent to which the necessary synchronization between behavioral and physiological responses takes place. This type of research is unfortunately still relatively rare. In the case of chickens, for example, frustration has been defined at the behavioral (Duncan, 1970) but not at the physiological level, so that it is not yet known whether the operating characteristics of the emotional system at the sensory motor level are the same in mammals and in birds.

In Leventhal's theory, the third level of processing is the conceptual (Leventhal and Scherer, 1987). At this level, it becomes possible to reflect upon, abstract, and draw conclusions about the environment and one's emotional responses to it. This is analogous to the meta-knowledge discussed before (Damasio, 1998), and it can be safely assumed that it needs a minimum form of abstraction and self-consciousness to be achieved. Therefore, the probability that this level is accessible to farm animals is unlikely.

Application of the hierarchical model of emotion to farm animals allows us to determine more precisely the type of emotional experience that is accessible to them. The case of sows in maternity stalls illustrates this issue very well. The nervousness and stereotypes pregnant sows develop just before parturition are often interpreted as indices of the frustration these animals are experiencing. It is said that sows feel frustrated because they cannot engage in the nest-building behavior they would normally present in the wild. However, based on the multilevel theory of emotion, frustration can develop only if sows are able to form schemata, in the present case a mental representation of what they are missing (e.g., adequate material for nest building). The path is open here for a logical trap. By definition, frustration can only occur in individuals that are missing something they have experienced earlier. Sows that are confined in gestation stalls are obviously likely to miss several features they have already experienced, such as the ability to move around and to interact with conspecifics. This can be a source of frustration, and the level of frustration confined sows experience is a function of the relative importance of the items they are missing. In order to assess this relative importance, the same type of procedure as that used by Mason et al. (2001) for mink can be put to work. However, once more, the positive results obtained with such a procedure will not demonstrate the existence of a frustration in a situation other than the one that has been set up

for the experiment. The mink that were studied in the Mason et al. experiment had no previous experience with the swimming pool. In order to learn to push open a door so as to get access to the swimming pool, they obviously had to develop some representation of what a swimming pool is and what it means to their welfare. The fact that subsequent blockade of access to the swimming pool door caused behavioral agitation and increased urinary cortisol levels was clearly indicative of a state of frustration. However, these findings do not imply at all that mink that are raised as fur animals and have never seen a swimming pool are frustrated when there is no swimming pool in their cage. Such a conclusion is condemned to be logically flawed as long as mink have not been shown independently to be able to form mental images of something they have never experienced.

The appropriate vocabulary here is therefore that of motivation, or need, not that of emotion. To come back to sows in maternity stalls, they are likely to be in the same state, in relation to the hormonally induced changes in their internal milieu, as are hungry animals in relation to their energy status. Hunger is a motivation, not an emotion. The fulfillment of a need takes place at the level of sensory-motor processing. It obviously has an affective dimension that is generally positive, but such an affective state is independent of the ability to form schemata. Being hungry is certainly aversive in most situations and will therefore be actively avoided. However, being hungry is a necessary but not a sufficient condition for frustration because frustration does not occur just because of the lack of food but because of the lack of expected food.

This type of reasoning must not be pushed too far, however; otherwise it leads to another trap, that of dogmatism. Engrained in the multi-level theory of emotion developed by Leventhal (Leventhal and Scherer, 1987) is the possibility that when an emotion takes place in a system that has the capacity of forming memories, the brain in that case, it will leave memory traces that, under certain conditions, can be reactivated by only part of the conditions that initially triggered the emotion. In other words, processing of information at one level of the multilevel process that is at the source of emotion, even when this level is the most elementary one, may trigger the full-blown emotion. As a typical example, agoraphobic patients can develop a panic attack when exposed to a place in which they feel trapped. However, the same pathological emotion will also develop when they are exposed to alkalosis, whether produced by hyperventilation or by sodium lactate infusion (Maddock, 2001). The explanation here is that under the effect of these treatments, panic patients experience visceral sensations that are reminiscent of those associated with the panic episode. It can be imagined that a similar process takes place in animals that have been repeatedly exposed to strong or repeated emotional experience, especially in unpredictable and uncontrollable conditions. In the case of sows in maternity stalls,

the triggering factor would be the restlessness and enhanced arousal associated with the beginning of parturition, and the resulting emotional state would be that of the frustration already experienced during confinement in gestation stalls. There are several direct and indirect ways of testing this possibility. An obvious approach is to verify that the postulated emotional state develops less easily in those animals that are exposed to the situation but have had limited opportunity to previously experience the same emotional state than in those animals that have already had ample opportunity to experience it. However, such an experiment is not necessarily easy to set up. An indirect approach would be to search for evidence of the plastic changes in the brain that underlie the expression of such a phenomenon. At the neurobiological level, the process that allows a full emotion to develop in response to a weak stimulus that normally has no effect on its own is known as sensitization. When the initial stressor is sufficiently intense, the neural circuitry that mediates the corresponding emotion may undergo a long-term increase in sensitivity (Antelman et al., 2000). The cellular and molecular basis of this sensitization process has been elucidated in several neurochemical systems *in vivo* (Bremner et al., 1996; Post and Weiss, 1997), and even in simpler animal models such as the gill-withdrawal reflex of *aplysia* (Cohen et al., 1997). In neurobiological terms, however, what is relevant for emotion is not the nature of the biochemical process *per se* but where exactly it takes place in the brain.

The previously delineated description of emotional states has been carried out hardware-free (i.e., without paying any attention to the neural basis of emotion). This attitude was certainly very popular until two decades ago. However, it has been superseded now by the recent developments of research on emotion and cognition in neuroscience. The reductionist power of neuroscience has made clear that mental states are ultimately activities of the nervous system and are not formed at the cellular level, as was wrongly claimed by early neurobiologists, but rather at a certain level of organization of this system, that of the connectivity between different brain structures. There is already evidence that the basic elements of an emotional behavior are organized in the brain stem. This is the case, for instance, for the oro-motor patterns of taste-induced disgust and pleasure that can even occur in anencephalic newborns (Grill and Norgren, 1978). However, the effect of experience enlarges the range of stimuli that are able to trigger these basic responses, and this process takes place in the visceral limbic brain (Yamamoto et al., 1994). It is even possible to assess which neural structure is involved in processing environmental cues associated with specific emotional states. In the case of a conditioned taste aversion that requires the learning of an association between a novel taste stimulus (the conditioned stimulus, or **CS**) and visceral malaise (the unconditioned stimulus, or **US**), the CS-US association seems to take place in the parabrachial

nucleus, whereas the gustatory cortex modifies the strength of this association depending on the novelty of the taste stimulus, and the amygdala is indispensable for the expression of conditioned taste aversion (Yamamoto et al., 1994). In the case of conditioned fear, the amygdala seems to be necessary for forming representation of discrete emotional stimuli, whereas the hippocampus plays a key role when it is necessary to form a representation of the context in which the emotional response has taken place (LeDoux, 1996).

Needless to say, this type of research is still in its infancy in farm animals, with the noticeable exception of the neural basis of the mental representation of social stimuli in the ovine brain (Kendrick, 1991; Kendrick et al., 1997). There is no reason why the study of farm animal welfare should stay away from the move toward the construction of an emotional brain and ignore the way the neuronal architecture of the brain of farm animals enables them to represent the world. This is not just for academic purposes, as exemplified by results from research on pain in animals. The study of pain has benefited very much from the development of new techniques for measuring pain-related behaviors that allow an individual to care for the damaged part of its body and promote recovery (Bolles and Fanselow, 1982). These pain-related behaviors can be easily observed in animals that are inflicted with chronic pain, in the form of arthritis induced by injection of adjuvant or paw inflammation elicited by local injection of formalin. From this perspective, chickens seem to display species-specific pain-related behaviors that serve a protective function similar to those observed in rats. However, whereas removal of the telencephalon eliminates pain-related behaviors in rats, it fails to do so in chickens that have been given an intra-articular injection of sodium urate crystals (Gentle, 1997). Although decerebration is a very crude procedure that needs to be complemented by more precise determination of the neural structures that are activated by nociceptive stimuli, using for instance the expression of early activation genes that are characteristic of neural activation, these findings, if they are confirmed, might imply that pain-related behaviors are organized in the brain stem in chickens whereas they are organized at higher levels of brain functioning in rats. Brain stem structures only allow sensory-motor processing, so it is unlikely that chickens form schemata of the pain they display behaviorally, and their mental experience of pain is therefore probably not the same as that of mammals.

Implications

Research on farm animal welfare has become very conventional. The quest for indicators of welfare is the norm and sets the pace for elaboration and revision of recommendations and regulations. In the near future, progress in deciphering the genome of farm animal species is likely to result in the replacement of behavioral indicators by molecular markers of cellular damage and

death. However, what all these indicators mean in terms of well-being will remain elusive as long as there is little or no research on the basic components of well-being: perceptions, representations, and feelings. It is certainly time for agricultural research to address this question directly, especially because suitable strategies are now available as a result of recent advances in psychology and neuroscience.

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