NEUROPHYSIOLOGY AND ASSESSMENT OF WELFARE

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ABSTRACT

Concern for animal welfare is a major consideration in meat production and is based upon the belief that animals can suffer. Welfare may be considered in terms of the subjective experiences of animals; preference testing is often used in this approach. Neurophysiology has provided insight into the biological basis of emotions and into the mechanism of learning and memory, which are important to interpret the results of preference tests. Welfare may also be defined in terms of the biological functioning of the animals; physiological measures of stress such as plasma levels of glucocorticoids, catecholamines, prolactin and endorphins, as well as heart rate and brain levels of neurotransmitters are then used to assess welfare. Individual differences in the stress response are important in welfare issues. Slaughter poses particular problems and neurophysiology has provided objective criteria to assess the effectiveness of electrical stunning. It is concluded that neurophysiology has made important contributions to assess and improve animal welfare.

1. INTRODUCTION

Scientific interest in animal welfare has rapidly grown in recent years. This has been largely due to the fact that meat consumers increasingly demand that animals are reared, transported and slaughtered in a humane way (Appleby and Hughes, 1997).

It could be argued that in many countries -such as Spain and some other southern European countries, for example- animal welfare is not an important issue (Appleby et al., 1992). Although this may well be the case, it should be kept in mind that public pressure for increased protection of animals comes primarily from a largely urbanised population and is therefore inversely related to the proportion of the population engaged in agriculture (Appleby et al., 1992). Since this proportion is rapidly decreasing in southern Europe (AEA, 1983, 1994), it seems likely that animal welfare will become an important issue in these countries in the near future.

Both transport and slaughter of farm animals are important areas from a welfare point of view. During transport and lairage, animals are exposed to a variety of stressors in a relatively short period of time, and this may cause suffering (Grandin, 1993; Warris, 1996). Such stressors include fasting and water deprivation, mixing of unacquainted individuals, handling by humans, exposure to a novel environment, noise and vibration, forced physical exercise and extremes of temperature and humidity (Sainsbury and Sainsbury 1988). Similarly, pre-slaughter handling may cause fear and anxiety, and animals may suffer severe pain if not properly stunned and slaughtered (Blackmore and Delany, 1988).

Welfare problems during transport and slaughter are important not only for ethical reasons, but also because they may cause great economic losses through bruising, stress induced meat quality problems and even death during transport and lairage (Grandin, 1993).

Concern over the welfare of animals is contingent upon the belief that animals may experience pain and suffering (Dawkins, 1990). However these are defined and measured the ability to perceive pain and suffering lies in the central nervous system. Therefore, neurophysiology could greatly contribute to our understanding of animal welfare issues. The aim of this paper is to discuss such a contribution with particular emphasis on welfare problems associated to transport and slaughter.

2. ASSESSING WELFARE

2.1. Definitions of animal welfare

Welfare can be defined in a number of different ways. According to Duncan and Fraser (1997) these can be grouped into three main approaches: a "feeling-based" approach, a "functioning-based" approach and a third set of approaches in which welfare is measured by assessing whether the animal can live according to its inherent "nature". The first two approaches are particularly relevant to this paper and will be discussed in detail.

2.2. "Feeling-based" approach: contributions of neurophysiology

According to the "feeling-based" approach, animal welfare involves the subjective feelings of animals, so that welfare will be reduced by negative subjective states such as pain and fear, and will be improved by positive states. The task for science, therefore, is to study the subjective experiences of animals (Duncan and Fraser, 1997). The main problem with this approach, however, is that subjective experiences cannot be observed directly. This raises a long-standing debate as to whether trying to study them falls within the realm of science. A thorough discussion of the arguments involved in this debate is beyond the scope of this article and the reader is referred to Dawkins (1990) and references therein for further information.

Neurophysiology can contribute to this debate by providing insight into the similarities between human and non-human brains and therefore into the kind of emotions and perceptions that animals are likely to have (Wiepkema and Koolhaas, 1992). Indeed, if the functional feature or the anatomic structures that are responsible in humans for a particular emotional state or subjective feeling are also present in animals, then it seems more likely that animals are able to experience such feelings (Wiepkema and Koolhaas, 1992).

The group of structures hypothetically responsible for the expression and sensation of emotions are often referred to as the limbic system. The term limbic system was popularised in the 1950's by Paul MacLean, who argued that its evolution enabled higher vertebrates to experience emotions (MacLean, 1955). Indeed, the brain circuits underlying the basic emotions appear to be common in their structure between humans and non-humans mammals at least (Panksepp, 1982). It is likely, therefore, that man and higher vertebrates experience emotions in a comparable way (Wiepkema and Koolhaas, 1992).

In contrast to the inter-specific similarity in mechanisms underlying emotion, the differences in cortical mechanisms are enormous (Panksepp, 1982), particularly in the so-called association areas, which are responsible for the highest cognitive functions (King, 1987). In a famous passage published in 1789 in which it was argued that animals ought to be protected by law, Bentham said "... the question is not, can they reason? nor, can they talk? but, can they suffer?" (Bentham, 1789). It seems, therefore, that from a welfare point of view the homology in the brain circuits responsible for emotions are more important than the differences in the brain circuits responsible for the highest cognitive functions, such as abstract reasoning and speech.

Pain perception provides a further example of the anatomical and functional similarities between humans and non-humans. Pain fibres identical to those found in humans exist in mammals (Iggo 1984). Further, the pattern of electrical activity in the somatosensory cortex of several mammalian species to electrical stimulation of the pulp of a tooth is similar to that evoked in human somatosensory cortex (Chudler and Dong 1983). Mammals and birds also have opioid receptors, which are related to central analgesia in humans. Finally, some of the central nervous system structures that are responsible for the affective component of pain -such as the thalamus, for example- are well developed in all mammals. Taken together, these facts strongly suggest that animals -at least mammals and birds- have an experience of acute pain similar to humans (Bateson 1991).

The "feeling-based" approach has often been tackled by studying the preferences of the animal for different environments and the strength of the animal's motivation to obtain or avoid certain environmental features (aversion-learning techniques and preference and motivation tests)(Duncan and Fraser, 1997). The underlying assumption is that the animals will tend to avoid those situations that evoke negative feelings of displeasure and will try to gain access to those that evoke positive feelings (Duncan and Fraser, 1997). Dawkins (1990) and Rushen (1986) provide a review of the current status of preference tests in the assessment of animal welfare. These techniques have been used to measure the amount of distress caused by several procedures associated to handling, transport and slaughter. For example, Rushen (1990) using aversion-learning techniques found that physical restraint is distressing for sheep. Stephens and Perry (1990) similarly showed that young growing pigs find the noise and vibration caused by a transport simulator to be aversive. In their experiment, all the pigs learned to press a switch panel that turned the transport simulator off and by the fourth training session they kept the apparatus switched off for about 75% of the time.

Aversion-learning techniques and preference testing, however, are not without problems and these have been summarised by Rushen (1986) and Fraser and Matthews (1997). A main limitation may occur if the test requires a level or type of cognitive ability that the animal does not possess. This may be the case, for example, when the animal is required to perform an instrumental or operant response (such as pressing a lever, as described in one of the previous experiments) in order to obtain a reward (Fraser and Matthews, 1997). Certain instrumental responses are appropriate for certain types of reward but not for others, and this may vary between species (Garcia et al., 1968; Hinde and Stevenson-Hinde, 1973). Similarly, individual differences and breed differences in learning and memory ability could be mistaken for individual or breed differences in reaction to the treatment (Rushen, 1990).

A further problem may arise when the experimental procedure interferes with memory formation. For example, electroconvulsive therapy (ECT) of humans is similar to electrical stunning of animals (Warrington, 1974), and it is known that humans subjected to ECT develop some degree of amnesia. Sheep allowed to recover from an electrical stun did not develop an aversion to the procedure (Leach et al., 1980); this result, however, could be due to the stimulus not being noxious or to the animals not failing to remember it as noxious. Knowledge of the mechanisms of learning and memory in farm animals is therefore important, and cognitive sciences and neurophysiology can make an important contribution in this respect.

A further consideration is that physiological measures can help with the interpretation of behavioural tests such as those described here and more integrated studies that combine both approaches are needed (Rushen, 1990). Physiological measures used in animal welfare studies are described in the next section.

2.3. "Functioning-based" approach: contributions of neurophysiology

Many scientists agree that although an animal's experiences of suffering are the defining traits of its welfare, such experiences are difficult to assess, whereas measures based on biological functioning and on the animals' ability to cope with the environment provide relevant information. Researchers following this approach have been greatly influenced by the concept of stress (Duncan and Fraser, 1997). In 1929 Cannon described stress as the sympatho-adrenomedullary (SA) system's attempt to regulate homeostasis when threatened by a variety of aversive stimuli. Later on, Selye (1936) conducted some of his classic studies on the response of the hypothalamic-pituitary-adrenal (HPA) axis to noxious stimuli; Selye suggested that the organism reacted in a nonspecific manner to a wide variety of aversive stimuli, and this stress reaction was termed "General Adaptation Syndrome". More recently, Mason (1971) suggested that the psychological component of the aversive stimuli is the main determinant of the stress response. For example, animals that could control and/or predict the occurrence of an electric shock showed less pronounced stress responses than counterparts with no control or warning signals (Weiss, 1970, 1971). Most researchers agree that the animal's appraisal of the situation is a major determinant of the stress response (Terlouw et al., 1997).

Current research on stress biology has addressed the role of the brain (Chrousos et al., 1988). Several areas of the brain are involved in the organisation of responses to aversive or threatening stimuli, and these areas interact extensively. Neurones in the hypothalamus, for example, are sensitive to internal physicochemical stimuli and to external physical and psychosocial stimuli (Laborit, 1991). To a great extent the stress response is mediated by the hormone CRF -corticotropin releasing factor-, that is secreted mainly by the paraventricular nucleus of the hypothalamus (Dunn and Berridge, 1990). CRF has an anxiogenic action and its administration is aversive to the animal (Dunn and Berridge, 1990). This gives support to the use of stress parameters as indicators of welfare problems and provides a link between the "feeling-based approach" and the "functioning-based approach". Indeed, both approaches often give similar results (Duncan and Fraser, 1997). Plasma levels glucocorticoids, catecholamines, prolactin and endorphins as well as heart rate are among the most frequently used parameters to study short-term welfare problems as those encountered during transport and lairage (Broom and Johnson, 1993). Levels of neurotransmitters in the brain -although less frequently used- are also of interest (Broom and Johnson, 1993).

Plasma levels of glucocorticoids. Secretion of glucocorticoids by the adrenal cortex is the final step in a cascade of events beginning in the brain. After a stimulus is perceived by the brain, CRH is released from the hypothalamus and stimulates the anterior pituitary gland to release adrenocorticotropic hormone (ACTH), which in turn stimulates the adrenal gland to release glucocorticoids (Sapolsky, 1992). In aversive situations, plasma concentration of glucocorticoids increases within a few minutes. Uncertainty and anxiety are among the most potent stimuli for HPA activation, whereas reward and sense of control result in suppression of HPA activity (de Kloet et al., 1991).

Although plasma levels of glucocorticoids have been widely used as measures of welfare (eg Dantzer et al., 1983; Dantzer and Mormede 1983; Moberg, 1985), interpretation of results is not without problems (Mason and Mendl, 1993; Rushen, 1986, 1991) and in some cases different research groups have failed to agree on how a particular environmental challenge affect plasma glucocorticoid levels (Rushen, 1991). There are several possible explanations for this lack of agreement. First, glucocorticoid release is episodic and sometimes highly irregular, and this makes the sampling protocols critical. For example, Engler et al. (1989) showed that only by sampling at 2-min interval can some high-frequency low-amplitude pulses of cortisol release be detected. Fundamental physiological studies should help to clarify the pattern of glucocorticoid release in each species as well as the factors that may affect it. Further, it is not known yet if the metabolic and immune consequences of altered glucocorticoid secretion depend upon mean daily levels or upon the frequency, duration and amplitude of the secretory episodes (Rushen, 1991).

Plasma levels of glucocorticoids -as well as other stress parameters such as plasma levels of prolactin and heart rate- may also change in response to non-aversive events. For example, corticosteroid levels have been shown to increase during coitus in some male rats (Szechtman et al., 1974) and also while nursing (Walker et al., 1992). Furthermore, it has been suggested that the extent that corticosteroid levels raise may be more related to tha extent that the animals learn about the situation than to the degree of aversion to the treatment (Rushen, 1986). Clearly, more research is needed on the relationship between aversiveness and physiological parameters of stress such as corticosteroid levels. This suggests that behavioural tests -such as preference testing- could help with the interpretation of experiments involving the use of physiological measures (Rushen, 1990).

It is important to consider that the nature of the aversive stimulus may influence the animal's reaction to it. For example, whereas anxiety is generally believed to cause an increase in levels of glucocorticoids (Mason 1971), whereas pain does not reliably result in such an increase (Rushen 1986; Bateson, 1991). Thus, an important contribution of neuroendocrinology would be to further clarify the particular type of response that is elicited by a given challenge. It is also important to consider that species may differ from each other in their responses to some situations, while resembling each other in others (Mason and Mendl, 1993). Clearly, more work is needed on this area in farm animals.

Another problem is that the action of taking a blood sample often causes a considerable increase in plasma levels of glucocorticoids and can therefore mask the effect of the treatment under study. However, in most species the delay before glucocorticoids are released is at least 2 minutes, so the effects of a particular treatment can be measured if a blood sample is collected within 2 minutes of the beginning of the blood sampling procedure (Broom and Johnson, 1993). Further, in some situations glucoocorticoid levels can be measured in saliva (Cooper et al., 1989) and this makes the sampling procedure easier, particularly when several samples have to be obtained from the same animal during a relatively short period of time.

Finally, it is widely assumed that chronic stress results in a hyper-reactivity of the adrenal cortex, so that the animal's response to an acute stressor - such as transport, for example - would be greater if the animal had been repeatedly exposed to other stressors while on the farm (Broom, 1988). This would have obvious implications about how to reduce welfare problems during transport and slaughter. However, the evidence supporting this assumptions is far from conclusive, and there are papers reporting an increase in adrenal responsiveness following chronic stress (eg Sakellaris and Vernikos-Danellis 1975), papers that reported a decrease (eg Rees et al 1985) and papers that reported no change (eg Cure 1989). Further research is also needed on this topic.

Despite all these difficulties, plasma levels of glucocorticoids are useful to assess welfare problems and they have provided important insights into the effects of transport and slaughter upon the animals, often in combination with other measures. For example, Broom et al. (1996) studied the hormonal effects of a 15 hour road journey in sheep and showed that the major changes in plasma levels of cortisol and prolactin occurred in the first 3 hours of transport while, during the remaining 12 hours, the stimulatory effect of transport was present but small. This would suggest that welfare may be particularly poor when animals are loaded and shortly afterwards.

Another example relates to the fact that the existing legislation in some countries prohibits slaughter of red meat animals within sight of others. Although this prohibition is intended to protect the welfare of animals, it can result in too long an interval between stunning and sticking (Anil et al., 1996, 1997). Experiments done with sheep (Anil et al., 1996) and pigs (Anil et al., 1997) have failed however to show any effect of witnessing the slaughter act on plasma levels of cortisol and other measures indicative of stress. This would suggest that the assumption that the slaughter of animals within sight of others can be distressing to the witnessing animals may be groundless.

Plasma levels of catecholamines. The principal products of the SA axis to emergency situations are the catecholamines epinephrine (adrenaline) and norepinephrine (noradrenaline). Whereas epinephrine often reflects psychological stress, norepinephrine is more closely correlated with the physical activity of the animal (Henry and Stephens, 1977; Scheurink et al., 1989). The release of these catecholamines from the adrenal medulla occurs within 1 or 2 seconds of the perception of the initiating stimulus and their metabolism is very rapid (McCarty, 1983). Therefore, the use of plasma epinephrine and norepinephrine as a measure of welfare in conditions lasting for a short period of time is of value, but only when samples can be taken very rapidly after the treatment (Broom and Johnson, 1993). A further problem is that catecholamine concentrations may increase in pleasant as well as aversive situations (Manser, 1992). Stunning can also cause a dramatic rise in plasma levels of epinephrine and norepinephrine (Pearsson et al., 1977) and therefore they are of little value to assess welfare during slaughter.

Plasma levels of prolactin. Plasma levels of prolacting have been shown to be affected by environmental challenge in a variety of species and are thought to be a good indicator of the anxiety level. In rats, for example, even small disturbances can elicit plasma prolactin increases (eg Gärtner et al., 1980) and -at least in some cases- prolactin levels are proportional to the magnitude of the treatment (eg Kant et al., 1986). Although plasma prolactin levels can provide useful information on the welfare of farm animals (eg Broom at al., 1986) it should be kept in mind that not all stressors have the same effect. For example, Parrott (1990) working with sheep found that restraint caused elevation of plasma prolactin, but isolation, which results in cortisol increase, had no effect on prolactin levels. This shows the need to further study what are the best indicators of stress for each situation.

A further problem is that the magnitude of the prolactin response depends upon the basal levels, which depend in turn on the sex of the individual and, in females, on the stage in the oestrus cycle (Riegle and Meites, 1976).

Plasma levels of beta-endorphin. Aversive stimuli increase the concentration of endorphins in the brain and blood. Release of beta-endorphin -which is measurable in the plasma (Manser, 1992)- is stimulated by CRH and often occurs simultaneously with ACTH release (Hadley, 1992). Plasma levels of beta-endorphin increase in farm animals in response to transport, handling and slaughter (Fordham et al., 1989) and recovery from stun is associated with an increase in beta endorphin concentrations (Anil et al., 1990). Beta-endorphin and other opioids seem to be involved in pain perception, acquisition of avoidance behaviours and behavioural and emotional responses to aversive stimuli (Clark et al., 1997). Although all these actions have obvious welfare implications, the physiological role of endogenous opioids is not fully understood (Clark et al., 1997).

Neurotransmitters. Responses to novel or aversive stimuli involve dopaminergic and noradrenergic pathways in the brain (Smelik, 1987). After exposure to such situations, these neurotransmitters may be depleted in parts of the brain or there may be an increase in some of their metabolites. Changes in neurotransmitter levels in the central nervous system can only be measured in situations in which the animals will be killed or under very particular set of experimental conditions -ie using brain cannulae-, and this has restricted their use in animal welfare studies. Further, levels of some neurotransmitters in the brain vary according to the particular nature of the aversive stimulus, so the value of such measurements is dubious (Broom and Johnson, 1993).

Some studies have looked at changes in the plasma or urine levels of the major noradrenaline metabolite, 3-methoxy-4-hydroxyphenyl-ethylene-glycol (MHPG) (Rubin et al., 1970). At least in some species, however, MHPG levels are affected by diet and therefore results should be interpreted cautiously (Sedlock et al., 1985).

The neurotransmitter serotonin is also of interest in animal welfare studies, although for a different reason. Increasing the dietary concentration of tryptophan relative to other large, neutral amino acids elicits an increase in brain serotonin synthesis and has a sedative effect in several species (Leathwood, 1987; Laycock and Ball, 1990). Further, aggression -particularly social aggression- decreases when serotonin function is enhanced (Kalat, 1992). This is particularly important since mixing of unacquainted animals is a common practice in transport and lairage and leads to an increase in agonistic activity in several species, such as pigs (McBride et al 1964). Fighting may cause injuries and is also known to be a potent activator of the pituitary-adrenal axis (Arnone and Dantzer, 1980; Blecha et al., 1985). Further, mixing shortly before slaughter can lead to reduced quality of carcass and meat (Guise and Penny, 1989). Adeola and Ball (1992) showed that supplemental dietary tryptophan may offer a practical means of reducing the stress response and the incidence of PSE meat caused by mixing unacquainted pigs. Although most attempts at solving welfare problems have been directed at ameliorating the environment provided to the animals, modifying the animal's response to the actual environment without reliance on prescription drugs would also be of interest. This is particularly relevant because procedures such as transport will always pose an environmental challenge to the animal, even if carried out in optimal conditions.

Heart rate. Heart rate can be a useful measure of the response of an animal to environmental challenge (Broom and Johnson, 1993). The mechanisms whereby emotional responses modify heart rate have been reviewed elsewhere (Duan et al., 1997). Two major difficulties should be kept in mind, however, when using heart rate in animal welfare studies (Broom and Johnson, 1993). First, changes due to physical activity should be distinguished from changes caused by emotional responses. This problem can be overcome by measuring the basal levels of heart rate of animals engaged in different levels of physical activity and taking account of the level of activity during the experiments (eg Baldock and Sibly, 1990). Second, the system used to monitor heart rate must not itself cause too much disturbance to the animal; telemetric methods and monitors carried by the animal have proved to be useful (Broom and Johnson, 1993). For example, our own research has shown that when sheep are transported by road, the movements of the vehicle caused by poor driving or bad road conditions caused an increase in heart rate that can not be explained solely in terms of increased physical activity of the animals. This result would suggest that sheep find this situation aversive. Further, transport conditions leading to an increase in heart rate also caused an increase in the incidence of DFD meat (Ruiz-de-la-Torre et al. in prep.)

Individual differences. Individual differences in temperament are often invoked to explain why many differences in the stress response are seen when individuals of the same species, age and sex are exposed to the same situation (Mendl and Harcourt, 1988). Temperament has been defined as the individual's basic stance towards environmental change and challenge (Mason 1984, cited in Lawrence et al., 1991). The use of the word "temperament" implicitly assumes that there is some degree of consistency in which a given individual responds to situations; evidence for this is accumulating from a variety of studies on laboratory and farm animals (Bohus et al., 1987; Lyons and Price, 1986, Lawrence et al., 1991; see Manteca and Deag, 1993 for a review). Although the characteristics that are responsible for such differences are at present poorly known (Lawrence et al., 1991), it is clear that individual differences in temperament are related to characteristics of the central nervous system (Bohus et al., 1987, Hessing et al., 1994, Terlow et al., 1992).

Work with laboratory rodents has shown that early stimulation greatly affects the animal's response to environmental challenge later on in life, and this effect seems to be mainly due to changes in the activity of the HPA axis (Gandelman, 1992). Work with poultry has also shown that environmental enrichment may decrease general, non-specific fearfulness (Jones, 1982; Jones and Waddington, 1992). Similarly, pigs that have experienced some type of environmental enrichment, through contact with objects in their pen, can be moved with novel surroundings more easily (Pedersen, 1992). Differences in temperament may also have a genetic origin (van Oortmerssen and Bakker, 1981), and selection for decreased fearfulness indicates that change in the right direction is possible in some species but is far from solving practical welfare problems at present (eg Mills and Faure, 1991; Mills et al., 1994). The study of individual differences in temperament with particular reference to the environmental and genetic factors that are responsible for them is a promising area of research, not only to improve our ability to assess welfare by reducing the variability of the experimental results but also to ameliorate welfare problems by rearing animals that react less to the environmental challenges commonly encountered during rearing, transport and slaughter.

3. SPECIFIC WELFARE PROBLEMS RELATED TO SLAUGHTER: CONTRIBUTIONS OF NEUROPHYSIOLOGY

A key issue of farm animal welfare is to ensure that animals do not suffer needlessly during slaughter. Preslaughter stunning is used to ensure that the animal is unconscious and suffers no pain or anxiety from slaughter procedures. Electrical head-only stunning, ie the passing of an electric current through the head of an animal, is routinely used in meat processing as a means of preslaughter stunning. It is important, therefore, to ensure the humanness of the procedure (Cook et al., 1992).

There are two quantifiable measures of the efficacy of head-only electrical stunning. First, recordings of both the electroencephalogram (EEG) and the electrocorticogram (ECoG) show that a successful head-only electrical stun induces a state of seizure-like activity that is suggestive of a loss of consciousness. Second, if an animal is allowed to recover from the seizure-like state, a period of apparent analgesia is observed. This analgesic effect would act as an adjuvant to the seizure state in assuring animal welfare (Cook et al., 1995). Some studies, however, have failed to prove the existence of this period of analgesia (Lambooy, 1981).

Electrical head-only stunning induces a release of several neurotransmitters in the brain. Several studies in which these neurotransmitters have been measured coupled with pharmacological manipulation experiments suggest that the seizure-like state induced by electrical stun is dependent upon the release of the amino acid neurotransmitters glutamate and aspartate (Cook et al., 1992). The analgesia that follows the seizure-like state would be caused -at least in part- by the release of a third amino acid neurotransmitter, gamma amino-4-butyric acid (GABA) (Cook et al., 1992).

The insight into the stunning process that has resulted from neurophysiological studies is important for two reasons. First, the epileptic-like seizure and the analgesia allow other parameters used in electrical stunning to be assessed objectively and also allow the humanness of a stunning system -either in practice or proposed for introduction- to be assessed (Cook, 1992). For example, Cook et al. (1995) used electroencephalographic recordings and measures of neurotransmitter release to assess the effect of electrical head-only stun duration on welfare. They concluded that an electrical stun of 1.0 A and 0.2 s produces unconsciousness and analgesia to subsequent slaughter procedures, although maximum welfare benefits appear at durations between 2.0 and 20.0 s.

Second, an understanding of the physiological mechanisms underlying the effects of electrical stunning may help to clarify the effect of several conditions on the effectiveness of stunning. For example, animal stress before slaughter, which could change amino acid neurotransmitter release, could modify post stun reflexes and unconsciousness (Cook et al., 1992). Other studies (Cook et al., 1996) have shown that combining head-only stunning with throat cutting has a synergistic effect on glutamate and aspartate release and could therefore increase the time period until consciousness is regained.

Further research, however, is needed in several areas, and these have been reviewed by Blackmore and Delany (1988). A major point that deserves particular attention is whether stunning actually renders the animal insensible. Although this is usually believed to be the case, recent experimental findings cast some doubts upon this assumption.

4. SUMMARY AND CONCLUSIONS

Animal welfare research is often problem-oriented; although this type of research is important, the need for work at a more fundamental level should not be overlooked. Neurophysiology has contributed in several ways to our understanding of animal welfare issues, particularly at this fundamental level, and it is expected that it will contribute even more in the future. Some of the main contributions of neurophysiology are as follows:

1. Concern over the welfare of animals is contingent upon the belief that animals are able to experience emotions of pleasure and displeasure. Whether the study of such emotions falls within the realm of science is a matter of debate. Nevertheless, neurophysiology has provided insights into the similarities between the brain of humans and non-human animals, and has therefore helped to clarify what kind of feelings animals are likely to have. It has been suggested that the application of imaging technologies to study brain functioning may have the potential for further understanding basic processes of cognition, feeling and motivation in nonhuman animals (Clark et al., 1997).

2. Preference testing has made important contributions to animal welfare issues. Neurophysiology can help this type of research by providing further knowledge of the mechanisms of learning and memory in farm animals.

3. The biology of the stress response is central to animal welfare. Current research on stress largely focuses on the brain's role in coordinating the response to environmental challenge. Many important questions, however, remain. The implications of the nonspecificity of the stress response and the role of several mediators of stress - such as endorphins, for example - are but two of these questions.

4. Individual differences in response to environmental challenge are most relevant to animal welfare. Neurophysiology should help to understand the brain mechanisms underlying such differences as well as the environmental and genetic factors that are responsible for them.

5. Neurophysiology can contribute not only to welfare assessment but also to solving welfare problems. Modifying neurotransmitter levels -and thus the stress response- by introducing dietary changes is one example of this type of contribution.

6. Slaughter poses specific welfare problems. Neurophysiology has provided objective ways to assess the efectiveness of stunning and the factors that may modify it.

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