Animal Behaviour 81 (2011) 481–489

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Autonomic reactions indicating positive affect during acoustic reward learning in domestic pigs

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ARTICLE INFO

Article history:
Received 23 April 2010
Initial acceptance 14 July 2010
Final acceptance 16 November 2010
Available online 24 December 2010
MS. number: 10-00283R

Keywords:
animal welfare
autonomic nervous system
cognition
emotion
environmental enrichment
heart rate variability
operant conditioning
Sus scrofa

Cognitive processes, such as stimulus appraisal, are important in generating emotional states and successful coping with cognitive challenges is thought to induce positive emotions. We investigated learning behaviour and autonomic reactions, including heart rate (HR) and its variability (standard deviation (SDNN) and root mean square of successive differences (RMSSD) of a time series of interbeat intervals). Twenty-four domestic pigs, *Sus scrofa*, housed in six groups of four, were confronted with a cognitive challenge integrated into their familiar housing environment. Pigs were rewarded with food after they mastered the discrimination of an individual acoustic signal followed by an operant task. All pigs quickly learned the tasks, while baseline SDNN and RMSSD increased significantly throughout the experiment. In reaction to the signals, pigs showed a sudden increase in HR, SDNN and RMSSD, and a decrease in the RMSSD/SDNN ratio. Immediately after this reaction, the HR and SDNN decreased, and the RMSSD/SDNN ratio increased. During feeding, the HR and the RMSSD/SDNN ratio stayed elevated. The pigs showed no cardiac reaction to the sound signals for other pigs or their feeding pen mates. We concluded that the level of cognitive challenge was adequate and that the observed changes in the autonomic tone, which are related to different dimensions of the affective response (e.g. arousal and valence), indicated arousal and positive affective appraisal by the pigs. These findings provide valuable insight into the assessment of positive emotions in animals and support the use of an adequate cognitive enrichment to improve animal welfare.

In recent years, much attention has been paid to animal cognition, emotion and appraisal (Mendl & Paul 2004; Paul et al. 2005; Boissy et al. 2007a). An emotion is defined as an intense, short-lived affective response to a stimulus or an event accompanied by physiological and behavioural reactions and subjective experiences (Désiré et al. 2002). It is accepted that animals perceive and evaluate their environment in an emotional way (Wiepkema & Koolhaas 1992). Shaped by evolution, emotions serve as natural reinforcers or internal feedback to guide behaviour and to ensure survival and successful reproduction (Dawkins 2000). Thus, animals learn to avoid situations or stimuli that elicit negative emotions and to seek situations or stimuli that induce positive emotions (Désiré et al. 2002).

The appearance of emotion is a hierarchical, neurophysiological process in the brain. Sensory input from a situation or stimulus is evaluated and leads to specific neurophysiological changes that are called 'core affect' (Russell & Barrett 1999; Posner et al. 2005; Carretié et al. 2009). Often emotion and affect are used inconsistently or as synonyms, which leads to misunderstanding. Posner et al. (2005) defined affect as a fast neurophysiological reaction to an event to prepare the body for action in a given circumstance. This process occurs subcortically and is therefore unconscious. Further processing of affect recruits other brain systems involved, for example, in autonomic regulation, motor execution and cognitive operations, such as attention, learning, memory and action planning. Some of these brain systems are neocortical and can cause a conscious experience or a subjective feeling, that is, an emotion in the narrower sense (Russell 2003).

Most scientific research on emotion and affect has focused on responses to negative stimuli (LeDoux 1995; Carretié et al. 2009), which are faster, stronger and more reliable than reactions to positive stimuli (this phenomenon is known as negativity bias, Taylor 1991). However, investigation of positive affect and emotion has become more important (Burgdorf & Panksepp 2006; Berridge & Kringelbach 2008; Matsunaga et al. 2009) in addressing questions of consciousness and animal welfare (Dawkins 2000; Paul et al. 2005; Boissy et al. 2007b; Fraser 2009). The welfare of an individual can be defined as its state as it regards its attempts to cope with its environment (Broom 1988) and its emotional-based assessment of the result (Puppe 1996). In other words, welfare is a subjective state that depends on whether an animal perceives a given stimulus or situation as aversive or pleasurable (Dawkins 1998).

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doi:10.1016/j.anbehav.2010.11.023

The allostasis concept, which means stability through change, predicts that both hyperstimulation and hypostimulation have adverse effects on animal welfare (Korte et al. 2007). Thus, moderate stimulation and well-balanced emotional experiences facilitate good welfare (Spruijt et al. 2001). It is known that cognitive processes, for example the appraisal of stimuli, events and situations, play an important role in the generation of emotional states (Toates 2004; Paul et al. 2005). Using the cognitive approach, Manteuffel et al. (2009a, b) suggested that adequate challenge of the cognitive abilities of farm animals (known as cognitive enrichment, see Milgram 2003) could be achieved through positively motivated instrumental behaviour. Moreover, Meehan & Mench (2007) concluded that successful coping with adequate cognitive challenges can induce positive emotion and that the implementation of cognitive challenges into animal housing is a promising approach to induce long-lasting positive effects on animal welfare.

Recently, our research group developed an experimental set-up for domestic pigs, *Sus scrofa*, using an individual acoustic reward-learning paradigm (Ernst et al. 2005). This system enables the study of whether and how cognitive challenges affect the behavioural and physiological reactions of pigs in their familiar housing environment, for example group-housing conditions. The previous results have shown that this cognitive enrichment acts as a biologically relevant stimulus that has a positive impact on behaviour (more active behaviour and less anomalous behaviour, i.e. belly nosing, in the home pen, as well as reduced signs of fear and excitement in behavioural tests, Puppe et al. 2007). This cognitive enrichment also plays a beneficial role in physical welfare (e.g. better wound healing by enhanced immune responses, see Ernst et al. 2006) and causes modifications in the reward-sensitive brain opioid receptors that indicate frequently occurring positive affects (Kalbe & Puppe 2010). All of these findings may also suggest neural and autonomic activation caused by affective and emotional processes as a result of acoustic reward learning in domestic pigs.

However, to corroborate more directly this assumption, further meaningful measures are needed. The present study was designed to examine the question of how appraisal processes and ongoing cognitive coping influence the activity of the autonomic nervous system. Owing to the complex impact of both branches of the autonomic nervous system (i.e. the sympathetic and parasympathetic or vagal branch) on sinoatrial node activity, analysing heart beat dynamics (i.e. heart rate (HR) and heart rate variability (HRV)) is regarded as a suitable approach to determine the activity of the autonomic nervous system in the study of affect and emotion (Beauchaine 2001; Porges 2003; Boissy et al. 2007b; von Borell et al. 2007; Reefmann et al. 2009; Stiedl et al. 2009).

METHODS

Animals, Housing and Husbandry

The study was conducted at the experimental pig unit of the Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany. In each of six replicates, four castrated male pigs of the German Landrace breed from different litters were used ($N = 24$). All pigs were born and raised at the experimental pig unit of the FBN. At the age of 28 days, the piglets were weaned and grouped together in a stall (2.00×1.50 m) with a fully slatted floor to form a stable social group. Feeding occurred ad libitum at a trough with five feeding places.

At the beginning of the 10th week of life (average weight 27 kg), the piglets were provided with an individual ear responder and were transferred to an experimental stall measuring 3.00×4.25 m (partially slatted floor, 3.00×2.08 m concrete/3.00 m $\times$ 2.17 plastic slat). For bedding, the pigs were provided with some straw and hemp pellets daily. Feeding occurred at two call-feeding stations (CFS, for a detailed description, see Ernst et al. 2005). The CFS consisted of a wooden chamber (63×40 cm and 103 cm high) with an entrance with a flexible width and a stainless steel feeding trough in the back. A red plastic button (diameter 6 cm) was located on the upper right side of the trough (approximately 15 cm above ground). The button could be easily manipulated by the pigs standing in front of the trough in the later experimental phases. When the button was not required, it was covered. The antenna of the transponder system ('Allflex', Texas Trading, Windach, Germany, range 60 cm) was placed at the entrance of the chamber. A food reservoir and two loudspeakers were located in the upper part of the CFS. Both CFSs were automatically controlled by a computer system, which coordinated and registered all actions of the individual pigs at the CFSs. An individual acoustic signal (basic triad compositions with loudness of 58 dB) lasting 10 s was assigned to each pig.

The daily food supply of the pigs was assessed according to the feeding recommendations commonly used for commercial pig production (Lindermayer et al. 1994). The food consisted of standard food pellets (Trede und von Pein, Itzehoe, Germany) with a metabolic value of 13.0 MJ/kg (16.0% crude protein, 4.7% crude fibre, 4.4% crude fat and 1.10% lysine). The CFSs offered a weekly increasing amount of food from 1.00 kg/day per animal at the beginning (10-week-old pigs) to 2.08 kg/day per animal at the end of the experiment (16-week-old pigs). Animals always had access to water ad libitum at nipple drinkers.

The cognitive challenge provided by the CFSs during the experiment was intended as a special type of environmental enrichment (cognitive enrichment) and was the subject of this research. To prevent interactive effects, no other environmental enrichment was offered.

The experiment lasted for 7 weeks, up to the end of the 16th week of life (average weight 57 kg). After the experiment, the pigs went back to the standard production management of the FBN and were fattened until slaughter weight. One piglet was excluded from the experiment owing to a rectal prolapse ($N = 23$).

The study was approved by the Scientific Committee of the FBN, and the experimental set-up was generally licensed by the ethics committee of the federal state of Mecklenburg-Western Pomerania, Germany.

Experimental Setting

The conditioning paradigm was modified from that of Ernst et al. (2005) and consisted of three consecutive phases (Fig. 1). Phase 1, the association phase, lasted 1 week and represented a classical conditioning paradigm. Each pig could enter the two CFSs for 24 h a day. At any time, only one of the CFSs was rewarding (this setting was used to prevent preferences for one CFS over the other and was changed randomly every hour). When the pig passed the entrance with the antenna, it was individually registered via its ear responder. Immediately, the individual acoustic signal was played by the loudspeakers and, after 2 s, a portion of food (ca. 35 g) was dispensed. In this phase, the pigs were fed ad libitum, that is, the total amount of food per pig and day was not restricted by the computer system.

Phase 2, the discrimination phase, lasted for 2 weeks and represented an operant conditioning paradigm. Now, each pig was individually called by one of the CFSs to visit it and to get a portion of food as a reward. The number of calls varied between 28 and 33 per day per animal. Calling occurred between 0800 and 2000 hours (with 1 h of rest every 2 h, e.g. 1000–1100 and 1300–1400 hours) with no more than five calling events/animal per hour. The time of calling, the order of the pigs and the CFS were randomly set by the computer system. The CFS repeated the call five times within 3 min as long as the correct pig was identified by the computer system via