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INTRODUCTION

The increasing consumption of animal products over the last decades led into highly intensified animal production systems. The conditions under which animals used for this production are born, raised, kept and slaughtered are under increased public scrutiny (Kanis et al., 2003). In order to meet consumer demands, high production levels require to be maintained whilst the welfare of the animals used is ought to be improved. With the by now commonly accepted recognition that animals are sentient beings who are also able to experience emotions (Špinka, 2012), it is crucial for the successful improvement of animal welfare to develop objective methods to assess emotional states of animals (Dawkins, 2008). Emotions enable survival and therefore animals avoid situations which cause pain or fear and strive towards situations which cause pleasure and contentment. Scientists hesitated for a long time about whether non-human animals were capable of emotions, but nowadays it is accepted that almost certainly all mammals experience emotions in a comparable fashion as humans do (Špinka, 2012). Good welfare is often described as not only the absence of negative affective states but more importantly, the presence of positive affective states (Bradburn, 1969; Seligman and Csikszentmihalyi, 2000) which distinguishes a good quality of life (Morton, 2007). The study of emotions in animals developed an imbalance towards the investigation of negative emotions such as stress and fear (Boissy et al., 2007). The reason for this is probably the fact that negative affective states are expressed more intensively (as they are potentially life-threatening) whilst their positive counterparts are more subtle and harder to study (Boissy et al., 2007).

This introductory chapter aims to review the current state of knowledge on positive emotional states, their occurrence; measurability and relevance for the assessment of animal welfare (see also Table 1). In the following, firstly, positive emotions will be defined. Thereafter, the development of positive emotional states over the course of evolution and their neurobiology within the brain will be addressed. Thirdly, different ways of measuring positive emotional states will be outlined and it will be examined how the previous findings could be of use for the assessment of well-being in animals.

The present doctoral dissertation aims to identify indicators of positive emotional states. Three experiments were conducted to establish a link between behavioural indicators and physiological changes that go along with positive emotional states in pigs. In the last chapter of this thesis, the experimental results will be set into context with the findings from the scientific literature.

Definition of positive emotions

When thinking about positive emotions, the major questions arising are: How are positive emotions defined? What makes an emotion positive? And what sets a positive emotion apart from other pleasant affective states such as sensory pleasure or positive mood? What are positive emotions with regards to animals?

The study of positive emotions has received particular attention as they may serve as indicators for well-being (Diener and Seligman, 2004; Kahneman et al., 2004). A common characterization of positive emotion could very generally be described as the facilitation of approach behaviour (Cacioppo et al., 1993; Davidson, 1993). The experience of a positive emotion encourages an organism to actively interact with its environment. This connection between positive emotion and active engagement with the environment is often called “positivity offset” (Diener and Diener, 1996; Ito and Cacioppo, 1999). This positivity offset prompts individuals to approach novel objects, situations or other individuals (Frederickson and Cohn, 2008). The outline of this definition is rather general and it should be kept in mind that positive emotions also arise from various approach-avoidance situations, so can for example avoiding an unpleasant situation result in the positive emotion of relief (Frederickson and Cohn, 2008).

The common denominator of positive emotion and sensory pleasure is the accompanying pleasant feeling which is experienced subjectively. However, sensory pleasure is commonly characterized as the correction of internal trouble: for example the satiation of hunger and thirst or warming up when cold (Cabanac, 1971). In contrast, positive emotion always requires assessment of the meaning of a given stimulus. For example, food corrects the internal trouble of hunger (sensory pleasure) but can also lead to a feeling of contentment (positive emotion) (Frederickson and Cohn, 2008).

The differentiation between positive emotion and positive mood is given through the fact that a positive emotion is centred on an object, something meaningful to the individual of which it is consciously aware of. Positive emotions are typically also much more short-lived than positive moods. Positive moods in contrast, are objectless, longer lasting and the individual is only peripherally aware of this state (Oatley and Jenkins, 1996; Rosenberg, 1998).

With regards to positive emotions in animals, four categories can be defined: (i) consummatory satisfaction (e.g. contentment after eating), (ii) pleasant sensory activity (e.g. affiliation between social partners or parent and offspring, homeostatic thermal conditions such as lying in the sun or in the nest), (iii) positive expectation (e.g. anticipatory joy; Boissy et al., 2007) and (iv) emotional action activities (e.g. play or explorative behaviour; Panksepp, 2004).

Evolutionary development of positive emotions and their neurobiology in the brain

In the process of evolution, natural selection is a key mechanism. Natural selection is characterized by differences in survival and reproduction of individuals due to differences in their phenotypes (Williams, 1966). Along the process of natural selection, traits which serve an important biological function are shaped. The ability to experience various emotional states was favoured by natural selection because emotions increased an organism’s ability to cope with adaptive challenges. Adaptive challenges are threats or opportunities in specific situations (occurring repeatedly over evolutionary time) for which each emotional state represents a mode of reaction both physiologically and behaviourally (Nesse, 1990). Animals therefore have evolved emotional processes to help them avoid situations which can potentially cause harm (avoid punishment) and approach situations potentially incorporating pleasure (seeking reward; Rolls, 2000; Cardinal, et al., 2002). While punishers are potentially life threatening (such as a predator attack or thermal damage), rewards are ensuring survival (i.e. food, water, shelter). Rewards and punishments are in essence the basis of emotional states (Barrett et al., 2007; Nesse and Ellsworth, 2009) and striving to the acquisition of rewards and avoiding fitness threatening punishers lies at the heart of survival (Rolls, 2005; Burgdorf and Panksepp, 2006).

It is important for an individual to be able to classify whether an external stimulus represents a reward or a punishment. Mendl and Paul (2004) describe this classification process of the stimulus as ‘appraisal’. Stimuli which are classified as being pleasant, at least moderately predictable and not sudden may evoke positive emotions. It seems therefore, that specific appraisal patterns elicit corresponding emotions (Scherer, 1999). It therefore increases fitness to build sensory systems which are able to sense for example nutrient need and perform behaviours which work towards obtaining nutritious rewards when hungry.

Emotional states can be considered as interfaces between sensory inputs and action systems which create corresponding outputs (Rolls, 2000). Positive emotions are mediated through certain neural structures, the so-called reward circuits such as the mesolimbic-dopaminergic (ML-DA) axis. Once an individual encounters a potential reward (e.g. shelter, food, conspecifics), the reward circuit is activated. Within this system, neuro-modulatory substances involved in positive emotions are dopamine, opioids and oxytocin. The neurotransmitter dopamine is transmitted from the ventral tegmental area (VTA) of the brain to the nucleus accumbens (NAcc), located in the ventral striatum. Opioids (such as e.g. endorphin) released from the pituitary gland, act on the ML-DA axis either by stimulating dopaminergic VTA neurons or by increasing the concentration of dopamine in the NAcc (Mirenowicz et al., 1996: studied in monkeys; Van der Harst et al., 2003: studied in rats). The hormone oxytocin, also released from the pituitary, acts on the NAcc where it increases the release of dopamine especially in the context of social bonding (Champagne et al., 2004: studied in rats). According to the review of Berridge (1996), the positive emotional valence "wanting", regarding motivation, is mediated by the transmitter system of dopamine; whereas the emotional valence "liking", regarding pleasure, is rather mediated by the transmitter system of opioids. The transmission of dopamine therefore determines the degree of motivation for reward (differentiation between highly rewarding and less rewarding) whilst the concentration of opioids rather determine what is wanted (e.g. elicitation of feeding (animal models reviewed by Levine, 2006), social interaction or play (Vanderschuren et al., 1995: studied in rats)).

Psychostimulants such as amphetamine or cocaine elicit positive emotions in humans because the drugs activate dopamine in the ventral striatum (Drevets et al., 2001; Volkow and Swanson, 2004). Drug injections into the ventral striatum elicit vocalizations in rats which are associated with positive emotion (Burgdorf et al., 2001). The ventral striatum has also been found to be involved especially in positive emotional states such as anticipation of a reward (Knutson et al., 2001a and b: studied in humans).

Studies on the electrical stimulation of the NAcc showed that positive emotions (smiling, laughter, euphoria) could thereby be induced in humans (Heath, 1972; Okun et al., 2004). Also in non-human primates, stimulation of the NAcc elicited vocalizations which are observed to be associated with unexpectedly finding highly palatable food or being reunited with a conspecific (Jürgens, 1976). In guinea-pigs it was found, that electrical stimulation of these brain regions elicited vocalizations associated to sexual excitement and social attachment (Kyhou and Gemba, 1998).

These action systems are predominately under the control of the limbic- and further sub-neocortical systems in the brain (MacLean, 1990: reviewed in humans; Panksepp, 1998: reviewed in human and animal models). In the study of Damasio et al. (2000) human individuals were asked to think of various emotional states which they have deeply experienced themselves (e.g. happiness, sadness, anger). The tested individuals were given water infused with radioactive substances and thereafter PET images of their brains were taken. The results clearly showed increasing arousal in the sub-neocortical areas of the brain once the individuals re-lived the different emotional states and at the same time a reduction in blood flow in the neo-cortex was found. Therefore, during the experience of emotional states, a reduction of information processing in neocortical brain areas can be assumed (Liotti and Panksepp, 2004: studied in humans).

There exists only little evidence for the involvement of neocortical regions in the generation of emotional experiences. However, these regions are essential for the cognitive memories associated to various emotional states. In other words, emotional states are communicated via specific neuro-dynamic circuits to higher brain areas (orbitofrontal and medial frontal regions) so that a cognitive evaluation of the specific emotional state can take place (Alcaro et al., 2007: reviewed in human and animal models). In order to investigate neocortical involvement in play behaviour, Panksepp et al. (1994) surgically removed the neocortex of juvenile rats and observed the animal's subsequent behaviour. The authors concluded from their results that the motivation to play must be sub-cortically organized because surgically treated animals still frequently displayed play behaviour. The stimulation of sub-neocortical regions of the brain leads to much stronger emotional responses than the stimulation of neocortical regions. The sub-neocortical regions of the brain might therefore hold the emotional action systems designed to appraise objects or situations and provide behavioural reaction codes according to their survival value (Burgdorf and Panksepp, 2006: reviewed in animal and human models). However, the precise mechanisms through which behavioural patterns are established under the influence of dopamine remain unclear (Alcaro et al., 2007: reviewed in human and animal models).

Emotional responses, however, entail a cognitive component as an adaptive value (Mendl et al., 2010; Broom, 2014) as they occur tightly connected to learning and evaluation of environmental stimuli (Broom, 2014). An example for emotional involvement in cognition is the phenomenon of cognitive bias. An individual's interpretation of an ambiguous situation is influenced by its underlying emotional state. Individuals in a negative emotional state interpret the ambiguous stimulus as negative and react to it as if a negative outcome will occur and vice versa (Mendl et al., 2009; Broom, 2014). Emotional state is also affecting learning behaviour. In an experiment of Carey and Fry (1993), pigs were trained to show an operant response when injected with an anxiolytic drug and a different operant response when injected with saline. When the pigs were then confronted with other anxiety-inducing stimuli (transportation, novel object, novel pen or an unfamiliar conspecific), they showed the same operant response as if injected with the anxiolytic drug. Thus, the operant response they chose to display indicated their emotional state of anxiety.

Measurement of positive emotions

For the study of positive emotions, different approaches have been applied including physiological and behavioural parameters. In physiological studies, one major focus is on the neurobiological functions. With the help of modern brain imaging, changes within the brain accompanying positive emotional states can be mapped. One technique which is frequently used in this context is functional magnetic resonance imaging (fMRI). Here, changes in brain activity are detected through measuring changes in blood flow (Huettel et al., 2009). fMRI brain imaging is suitable for detecting the cognitive processes associated to an emotional state as they are generated very rapidly in response to sensual inputs, e.g. memory of an event which triggered an emotional state in the past. However, the actual emotional state of an organism emerges less rapidly and is therefore suggested to map core affective states in the brain with an imaging technique such a positron emission tomography scanning (PET scan; Burgdorf and Panksepp, 2006). This imaging technique is based upon radioactive tracers with which the test subjects are injected. The tracer substance emits gamma rays which are detected by the tomograph. The concentration of the tracer substance indicates the amount of metabolic activity within the specific brain regions (Bailey et al., 2005). Increases in activity of specific brain regions could therefore indicate involvement of said region in the generation and experience of various emotional states.

As mentioned above, the limbic system, located in sub-neocortical areas of the brain, is largely involved in generating emotions. A main efferent pathway of the limbic system is the autonomic nervous system (ANS) consisting of sympathetic and parasympathetic control mechanisms which reflect the physiological state of an organism, e.g. stress or homeostasis (Boissy et al., 2007). This physiological state is generally reflected by heart rate and heart rate variability (HVR) as the heart is both under the control of the sympathetic and parasympathetic branch of the ANS. Through direct innervation of the heart through sympathetic and parasympathetic fibres, emotions therefore have a large effect on cardiac activity (Saul, 1990). The pulses of heart beat are generated by the sinoartrial node (SN), who acts as primary pacemaker. Through depolarisation of cells in the SN, electrical stimulation then activates the heart muscles. The SN is innervated by sympathetic and parasympathetic nerve fibres which, depending on which fibres dominate, influence the heart rate and HRV in distinct ways (Von Borell et al., 2007). Sympathetic control of heart activity is associated with an increase of heart beats and decrease of heart rate variability, commonly associated with stress responses and negative emotional states whereas parasympathetic control of cardiac activity is associated with lower heart rate and higher HRV, commonly associated with relaxation and positive emotional states (Rainville et al., 2006; Von Borrell et al., 2007). HRV therefore provides a potential indication on the emotional state experienced by an organism. However, a rise in HR can not only be the result of a dominant sympathetic activation, but also that of a decrease in vagal activation or from changes in both nervous systems (Von Borell et al., 2007). Also, HR can be influenced by neurotransmitters such as Acetylcholin (decreasing HR) or adrenalin and cortisol (increasing HR). In a study by McCraty et al. (1995), human test persons were asked to mentally recall and visualize past positive experiences. Electrocardiographic measurements were then taken and it was found that test persons' HRV increased in response to the positive emotional state. The authors also report a lowering of blood pressure when patients experience a positive emotional state (McCraty et al., 1995). Fox (1989) described a close relation between HVR and their reactivity to positive or negative events in human infants. Children with high HRV were more approachful and more inclined to engage with their mothers and strangers at play (Fox, 1989). HR and HRV are therefore insightful indicators for measuring emotional changes physiologically. Measurement of HR and HRV is mostly carried out non-invasively and handling of the required equipment is fairly straight forward.

A further physiological indicator for positive emotion was found in studies assessing saliva samples of human test subjects. Test subjects experiencing a positive emotional state showed increases in the saliva concentration of 20-200 kD proteins whereas subjects experiencing negative emotions had a decrease of said proteins (Grigoriev et al., 2003). Interestingly, 20-200kD proteins are associated with α-amylase and increases of these proteins are related to relaxation-induced parasympathetic secretion of saliva through the parotid and submaxillary gland as found by Morse et al., 1989. In this study, human adult patients' anxiety levels were investigated based on a questionnaire and saliva samples taken before and after a dental procedure. With half of the test persons, relaxation techniques (meditation and hypnosis) were practiced in combination with receiving a sedative prior to the dental procedure. The other half of the patients were only given a sedative without practising relaxation techniques. All persons of the test group that received both the relaxation technique and the sedative reported reduced anxiety levels. Whereas in the test group that only received the sedative (and not the relaxation technique), reduced anxiety was only found in one third of the group (Morse et al., 1989). According to Boissy et al. (2007) the relation between salivary amylase and emotional states remains unclear but further insights into such measures in animals could be a useful tool to monitor their emotional states.

Emotional limbic activity in the brain was also found to influence immunological processes with immunoglobulin A (IgA) playing a crucial role in the immune function (Haas and Schauenstein, 1997). There are studies correlating immune activation with anxious or depressive behaviours in humans (Dantzer, 2001; Dunn et al., 2005). Salivary IgA concentration was found to be modulated by experiencing positive emotions (McCraty et al., 1996; Watanuki and Kim, 2005). A study of Stone et al.

(1987) investigated positive versus negative mood of male students. Test persons were asked to fill out questionnaires describing their mood as well as taking salivary samples three times weekly. The authors found, that the saliva IgA levels were depressed on days of high negative mood and elevated on days with high positive mood. Further, daily stress increased negative mood and decreased positive mood along with a reduction of IgA. The authors concluded that stress increases the likelihood of encountered viruses gaining entry into the body (Stone et al., 1987). Salivary composition could therefore potentially be used as a monitoring tool for emotional states. However, immune parameters such as IgA are under the influence of multidimensional factors and can easily be biased by unapparent infections in the body and therefore the interpretation of changes in their concentration can be ambiguous (Boissy et al., 2007).

For the measurement and assessment of positive emotion, the insight into physiological and neurobiological pathways provides very important understanding of the underlying mechanisms. However, physiological changes are merely action patterns dictating an individual how best to behave in a specific situation. Behavioural changes can therefore also be used as a reliable measure to assess emotionality in animals. Unconditioned, spontaneous behaviour of an individual towards a situation or object can be regarded as action patterns which reflect the individuals' accompanying emotional state. Generally, approach or avoidance can be cues to the valence an object or situation might have for the individual (Paul et al., 2005). In the case of a positive underlying emotional state and thus a positive appraisal of a situation or object, animals' behaviour might be of exploratory, playful or consumptive nature (Špinka et al., 2001; Paul et al., 2005). In contrast to spontaneously occurring behaviour, behaviour tests can also be used to assess animal emotion. In a recent study of Reimert et al. (2013), it was found that various behaviours tended to occur significantly more often when the test animals (pigs) were given a positive treatment (two acquainted pigs were given access to a large area filled with peat, straw and chocolate raisins), thus probably facilitating positive emotion compared to the negative treatment (isolation from conspecific in small barren pen). It was found that the test animals showed significantly more play behaviour, more tail wagging and emitted more barking vocalizations when given the positive treatment. In contrast, when exposed to the negative treatment, the test animals exhibited more standing alert behaviour, made more escape attempts, urinated more, held their ears in a more backwards position and emitted more high pitched vocalizations (Reimert et al., 2013).

Relevance of positive emotions for the assessment of animal welfare

The understanding of animal emotion is crucial because the mere existence of these emotional states is the underlying factor of growing concerns of both public and scientific interest in animal welfare. In a recent review on the study of emotions in pigs, Murphy et al., (2014) state that experiences of positive emotion contribute to good welfare of an animal. However, in modern pig production systems the basic needs of pigs regarding cognitive challenge and the ability to express species-specific behaviour are not met. As a consequence, pigs kept in such production systems are predominately experiencing negative emotional states and their welfare is therefore reduced (Murphy et al., 2014). It is important to be able to assess under which circumstances animals experience positive emotional states (Boissy et al., 2007), and facilitate these circumstances in order to improve the animals' quality of life.

The experience of positive emotions can be facilitated by the provision of rewards which the animal finds desirable. Spruijt et al. (2001) suggested using anticipation behaviour for the study of emotional states. During Pavlovian conditioning, behaviours between the presentation of the cue predicting the reward and the actual presentation of the reward can be suitable indicators. Spruijt et al. (2001) concluded that the anticipation of a positive event or stimulus can induce a positive emotional state in the animal. Dudink et al. (2006) examined the effects of anticipation in piglets at weaning. They observed that the anticipation of enrichments resulted in major behavioural changes of the piglets, even more so, the anticipation resulted in more profound effects than the presentation of the enrichment alone. In anticipation of access to enrichment the piglets showed more play behaviour and less aggressive behaviour after weaning. Resulting from these behavioural changes, the piglets also had a decreased amount of bodily injuries after weaning (Dudink et al., 2006).

Another factor contributing to the well-being of animals in captivity is their ability to control and cope with the environment they live in. Deliberate actions the animal can take upon facing a challenge within its environment which enable a positive outcome facilitate controllability and therefore positive emotion (Boissy et al., 2007). In this context, cognitive enrichment could offer an interesting approach. Puppe et al. (2007) designed a food rewarded learning system in which pigs were conditioned to associate an individual call type emitted from the feeding station to the arrival of a food reward. All animals learned to discriminate calls which announced food rewards and were also willing to work for food by pressing a button. Further, the conditioned pigs showed less fearful and anxious behaviour in an open-field test compared to a conventionally fed control group. The authors concluded that the cognitive enrichment could have induced frequent positive emotional states (Puppe et al., 2007).

There are numerous attempts to add stimuli to otherwise barren living environments in order to reduce indicators of poor welfare (e.g. chains or wooden bars for chewing), however these strategies rather try to reduce indicators of poor welfare instead of increasing indicators of good welfare (e.g. play). Studies which enabled young animals to have more space showed that the surplus of space facilitated an increase in play behaviour both in calves (Jensen et al., 2000) and in pigs (Blackshaw et al., 1997).

Aim and outline of the thesis

Improvement of animal welfare lies at the heart of animal welfare science, especially regarding the large numbers of livestock animals intensively bred and kept for the supply of animal products for rising human consumption. As intensive livestock production is unlikely to reduce with ever increasing world population in the near future, studies on animal welfare are crucial for the improvement and solution to animal welfare problems for livestock animals. Animal welfare problems such as abnormal behaviour or deficient health are mere red flags of underlying difficulties which go along with “housing” animals and thereby reducing the scope of their natural behaviour. Deeper understanding of the way livestock animals appraise their surroundings in intensive husbandry systems may enable us to determine what causes negative experiences but also what causes positive experiences. Especially the experience of positive emotional states may increase animal welfare greatly and may also weigh against unavoidable husbandry practices that cause negative experiences in animals. If an animal has the opportunity to frequently experience positive emotional states, it leads a life that is of value to the individual itself (McMillan, 2005).

The main aim of the present thesis was to investigate physiological and behavioural indicators of positive emotion in pigs. Research into emotions of animals is a growing interest from the late 20th century onward. The assessment of pain and suffering has been a focus in the endeavour to improve animal welfare and various methods have been developed to that effect by animal welfare scientists (Boissy et al., 2007). Despite the fact that assessment of negative emotional states is of high importance, as they are potentially life-threatening, investigation into the assessment of positive experiences is not as distinctly developed and often characterized by disagreements. Still, the experience of positive emotional states is as crucial to good animal welfare as the avoidance, or manageability, of negative emotions. Therefore, it is a central issue to be able to identify the circumstances under which animals experience positive emotion (Boissy, et al., 2007). The interplay of three components making up an emotion (behaviour, physiology and consciousness) is highly complex. It remains unclear how positive emotions are expressed behaviourally, also taking into account