Anticipation and frequency of feeding affect heart reactions in domestic pigs

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ABSTRACT: Measuring heart reactions has become a widely used method for the assessment of emotions. Heart rate and its variability, which can quite easily be noninvasively recorded, reflect the inputs of the sympathetic and parasympathetic branches of the autonomous nervous system. We tested the hypothesis that frequent anticipation of a positive event results in an increased state of welfare in pigs, expressed as positive arousal in anticipation of announced feeding as well as lowered heart rate and augmented heart rate variability during resting periods. We used a controlled paradigm with 3 groups of young domestic pigs (Sus scrofa domestica). We compared frequent acoustic announcement of feed delivery (group 1: 3 feedings between 0730 h and 1030 h plus 3 feedings between 1200 h and 1530 h) with the same number of feedings as in group 1 but without a temporal relation to the sound (group 2) and with a fixed-schedule feeding (group 3: 2 feedings at 0600 h and 1500 h). Specific cardiac and behavioral reactions indicated short-term (1 min) anticipation in the conditioned group. In this group, heart rate increased (P < 0.001) mainly through vagal withdraw and behavior became more active (P < 0.001). Only the conditioned group displayed changing heart rate characteristics during the sound. Pigs in the frequent unpredictable feed group reacted to feed delivery with increased heart rates (P < 0.001), whereas the heart-rate characteristics of pigs with the fixed schedule were unchanged during the sound and while the other 2 treatment groups were feeding. Clear evidence for long-term anticipation (over the course of hours) was not present in the data. Comparisons between the 3 treatment groups suggested that in housing conditions where pigs cannot obtain feed by their actions but must wait for feed delivery, feeding at 2 fixed times would be preferred. Animals in this treatment group presented lower resting heart rates at the end of the experiment than animals in the other 2 groups (P < 0.01). Therefore, merely announcing a positive stimulus without giving control to its access is apparently not suitable for increasing welfare.

Keywords: behavior, feeding rate, heart rate, heart rate variability, Sus scrofa, animal welfare

INTRODUCTION

Anticipation may influence welfare by allowing animals to prepare for an upcoming event (Badia et al., 1979). Heart reactions have become widely used parameters for the assessment of emotions, such as those related to anticipation, as well as stress, in farm animals (von Borell et al., 2007). This is because the limbic brain system, with its widely distributed hormonal and neuronal efferents, also affects the heart as an allostatic effector organ. Heart rate (HR) and heart rate variability (HRV), which can quite easily be noninvasively measured, reflect the input of the sympathetic and parasympathetic nervous system.

In humans, increased vagal activity (i.e., reduced HR and increased HRV) is associated with sustained attention in nonfrightening situations and with positive perceptions (Matsunaga et al., 2009). Vagal withdrawal, characterized by reduced HRV and increased HR, is associated with fear responses. Sustained low resting HRV has been correlated with a negative mood (Kemp et al., 2010; Stapelberg et al., 2012). On the other hand, high HRV during relaxed states is considered to be a

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sign of a well-balanced mood (Boissy et al., 2007). In the current study, we tested the hypothesis that frequent anticipation of a feeding event would result in an increased state of welfare in pigs, reflected in lowered resting HR and augmented vagal activity at rest, whereas positive arousal would be reflected in sympathetically induced HR increases during positive anticipation. We developed a controlled paradigm that prevents physical social interaction and limits locomotion because locomotor activity increases HR (Brenner et al., 1998). The experiment included the assessment of short-term and long-term anticipation as well as unpredictable and predictable delivery of feed.

MATERIALS AND METHODS

Animals and Housing

All procedures involving animal handling and treatment were approved by the Committee for Animal Use and Care of the Agricultural Department of Mecklenburg-West Pomerania, Germany (AZ LALLF M-V/TS/7221.3–1.1–056/09).

The experiments were conducted with young German Landrace pigs bred at the Leibniz Institute for Farm Animal Biology (FBN) in Dummerstorf, Germany. At the age of 28 d, the piglets were weaned and grouped litterwise to avoid social stress caused by mixing. Seven litters were assigned to 3 experimental groups. Thus, 21 piglets were used in total and each experimental group consisted of 7 individuals. Feed and water were available ad libitum, and the pen was equipped with a fully slatted floor. At the age of 40 d (d 0 in Fig. 1), the animals (with weights ranging from 7.7 to 13.0 kg) were transferred to the institute’s experimental laboratory building, the environment of which could be controlled for day/night rhythm, air temperature, and humidity. The experimental room measured 4.0 × 3.4 m, with a temperature of 22 ± 2°C and humidity of 50%. The animals were kept on a 12/12 light-dark cycle (light from 0600 to 1800 h, −1515 h, Monday to Friday; d 0 to 30; Fig. 1) to limit movements. There were a total of 7 experimental animals in each treatment group. Every repetition included 1 animal of each treatment group housed in the same room so that each animal heard the same acoustic sound but with a different relation to the feeding event, depending on the experimental group it belonged to. The different treatments were as follows.

1) Feeding 1/6 of the daily allowance 6 times/day in contingency with a sound signal (announced feeding [AF]). A trace conditioning paradigm was employed in which the feed was delivered after the end...
of the signal (delay between offset of the signal and start of feed delivery = 1 s). A loudspeaker attached to the ceiling emitted an acoustic signal at 3 pseudo-random times in the morning session (0730 to 1030 h) and at 3 times in the afternoon session (1200 to 1500 h). The signal times were generated automatically and on a fixed timetable each morning by the control computer, which also triggered the feed delivery (see below). The start times of the signals were controlled by the software, with a minimum temporal interval of 20 min. The acoustic signal had a duration of 1 min and consisted of a sine tone modulated sinusoidally in frequency (800 to 1300 Hz) and amplitude (+3 dB) with a modulation frequency of 0.25 Hz. The average intensity of the modulated signal at floor level below the loudspeaker was 82 dB. The signal, thus, was very well within the hearing range of pigs (Heffner and Heffner, 1990) and avoided acoustic adaptation by its modulation.

2) Feeding was performed 6 times per day at random times as in 1) but was not preceded by the sound (noncontingent random feeding [RF]).

3) Feeding 1/2 of the daily allowance at 2 fixed times, 0600 and 1500 h (fixed-schedule feeding [FSF]).

In addition to serving as experimental animals for the effects of long-term anticipation, the FSF animals served as controls for the heart reactions and behavior of AF animals, as the sound signal should be completely meaningless for the FSF animals. RF animals were not suitable controls because their random feeding could partly overlap with the feeding of the AF animals, such that their reactions to the sound could be masked by feeding.

Behavioral observations and heartbeat measurements of trained animals were performed at the end of the experiment, at d 24, 25, 28, 29, and 30. Saliva was again collected on d 29 and 30.

A diagram of the complete experimental cycle is provided in Fig. 1.

**Heartbeat Measurements**

The Polar S810i device (Polar Electro Oy, Kempele, Finland) was used for the noninvasive, telemetric measurement of heartbeat activity (R-R intervals). Chest belts with the Polar recording units were applied at 0700 h. The chest belts were removed after the animals had been released from restriction at 1515 h. To optimize the contact, electrode gel (Heiland VET, Hamburg, Germany) was applied. The pigs were allowed to habituate to the measuring equipment during the first 3 d of the experiment. Cardiac data were stored on a computer.

Automatic correction for artifacts was applied before analysis (Polar Precision Performance Software 4.00.023). The procedure used was validated by Marchant-Forde et al. (2004). In addition, subsequent manual editing (visual control) of the corrected data was performed to eliminate remaining artifacts by interpolation. Only segments with error rates of less than 10% were included in the analysis, i.e., approximately 80% of all segments (Camm et al., 1996; Mohr et al., 2002). Time-domain analyses of HRV were conducted using the Kubios HRV 2.0-software (Biomedical signal and Medical Imaging Group, Department of Physics, University of Kuopio, Kuopio, Finland).

The following parameters in the time domain were quantified: square root of variance of all R-R intervals (SDNN) as a combined measure of sympathetic and parasympathetic (vagal) activity (von Borell et al., 2007), root mean square of successive differences of R-R intervals (RMSSD) as a measure of mainly vagal activity (von Borell et al., 2007), and the RMSSD/SDNN ratio as a global indicator of general changes in vagosympathetic balance.

Heart rates were recorded on the last 5 experimental days (Fig. 1) to determine the heart reactions to 6 instances of feeding in trained (AF) animals, untrained (RF) animals, and the FSF control animals. Time-domain analyses were performed during 3 windows, 6 times/day: 1 min before the sound signal (base), during the 1-min sound signal (sound), and during 1 min of food delivery after the sound signal (feed). Because emotions are transient, these measurements must be taken in relatively short time windows. Accordingly, analyses within 1-min time windows have previously been shown to be appropriate in a number of studies (Despres et al., 2002; Braesicke et al., 2005; Desire et al., 2006; Düpjan et al., 2011; Imfeld-Mueller et al., 2011; Zebunke et al., 2011; Zebunke et al., 2013).

Time-domain analyses were also used to evaluate anticipation in the FSF animals during the afternoon until feeding at 1500 h. The afternoon recordings of the experimental d 25, 28, 29, and 30 were divided into 4 periods around feeding (120 to 90 min, 75 to 45 min, 30 to 0 min, and 0 to 5 min) using recording and analysis windows of 5 min while the animals were either resting (120 to 0 min) or feeding (0 to 5 min).

**Cortisol Analyses**

Saliva samples were collected by allowing the pigs to chew on cotton buds until they were moistened starting at 1030 h (at least 20 min after the last feeding) on d −6, −5, 3, 4, 29, and 30 (Fig. 1). The cotton buds were immediately centrifuged at 3,000 × g for 15 min at 4°C, and the samples were stored at −20°C before the analyses. Salivary cortisol concentrations were measured in duplicate using a commercial enzyme immunoassay (DSL Inc., Sinsheim, Germany) according to the instructions of the manufacturer. The assay was validated for use with porcine saliva. The test sensitivity was 0.35 ng/mL, and the intra-assay and interassay coefficients of variation were 2.0% and 8.7%, respectively.
**Behavioral Observations**

The continuous signals of the observation cameras above each pen were transferred via cable to a control room adjacent to the animal laboratory room. The signals were stored on a video recorder (Samsung SVR-960PRT, Seongnam City, South Korea) and then digitized off-line and analyzed using The Observer XT 10.0 software (Noldus Information Technology, Wageningen, the Netherlands).

To test whether AF animals showed anticipation behavior, they were observed during the sound signal (continuous recording). FSF pigs, for which the sound was meaningless, were observed during the same sound signal to test whether the sound itself caused behavioral reactions. As a control for behavioral reactions to feeding, RF animals were observed during the minute before feeding. The last 5 d of the experiment were analyzed (Fig. 1). The observation parameters were 1) standing or moving 1 or 2 steps in front of the trough (active), 2) sitting in front of the trough (sit), and 3) lying either on the side or belly (rest).

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The same observation parameters were used to examine the long-term effects of the different feeding treatments. Activity and resting behavior were investigated for 30 min during the midday stimulation-free period at the end of the experiment, when the animals were well acquainted with the procedures (d 28, 29, and 30; Fig. 1).

To test whether the behavior of the FSF animals changed in the afternoon, we recorded their behavior during 3 time periods leading up to feeding (120 to 90 min, 75 to 45 min, and 30 to 0 min, where 0 min = start of feeding) at d 24, 25, 28, and 29 (Fig. 1). The observation parameters were as in the RF animals.

All data can be provided on request from the corresponding author.

**Statistical Analysis**

Statistical analyses were conducted using SAS for Windows, Version 9.2 (2009; SAS Inst. Inc., Cary, NC). Descriptive statistics and tests for normality were calculated with the UNIVARIATE procedure of Base SAS software. HR, HRV parameters, salivary cortisol, and behavioral observations were analyzed by repeated measurement ANOVA using the GLIMMIX procedure of SAS/STAT software. Repeated measurements on the same animal were taken into account by the “residual” option of the “random statement” of the GLIMMIX procedure using a compound symmetry structure for the block diagonal residual covariance matrix.

The ANOVA model for FSF-treated animals on d 25, 28, 29, and 30 (5-min measurements) contained the fixed-factors period of time (120 to 90 min, 75 to 45 min, 30 to 0 min, and 0 to 5 min), day (25, 28, 29, and 30), repetition, and the interaction between period of time and day.

For cortisol, the ANOVA model contained the fixed-factors treatment (AF, RF, and FSF) and phase of the experiment (levels: before [average of d −6 and −5], start [average of d 3 and 4], and end [average of d 29 and 30]) and the corresponding interaction.

The ANOVA model for behavioral variables (duration of active, sit, and rest) contained the fixed factors treatment (AF, RF and FSF), observation minutes (before sound and during sound), day (24, 25, 28, 29, and 30) and all two-way interactions between the fixed factors.

To analyze the long-term effects of the different feeding treatments, an ANOVA model with the fixed-factors treatment (AF, RF, and FSF), day (28, 29, and 30), and their interaction was used to test behavior (active, sit, and rest) measured from 1100 h to 1130 h each day.

The behavior of the FSF group was further analyzed using an ANOVA model with the fixed-factors day (24, 25, 28, and 29), periods of time (120 to 90 min, 75 to 45 min, and 30 to 0 min), and their interaction.

Least square means (LSM) and their standard errors (SE) were calculated and pairwise tested for each fixed effect in these models using the Tukey-Kramer procedure for pairwise multiple comparisons. The results were considered to be significantly different if \( P < 0.05 \). In all figures, LSM and SE are depicted.

**RESULTS**

**Heartbeat Measurements**

**Effects of AF and RF on Cardiac Reactions.** There was a significant main effect of recording minutes on the parameters HR (\( F_{4,24.94} = 37.13, P < 0.001 \)), RMSSD (\( F_{4,20.23} = 9.07, P < 0.001 \)), SDNN (\( F_{4,20.70} = 16.33, P < 0.001 \)), and RMSSD/SDNN (\( F_{4,24.81} = 7.21, P < 0.001 \)). HR increased significantly over recording minutes. HR was the highest during feed delivery in both groups (Fig. 2A). Accordingly, the AF animals displayed significantly lower RMSSD of base values compared to feed delivery as well as during the sound signal compared to feed delivery (Fig. 2B). In parallel, SDNN increased significantly between base and sound and decreased between sound and feed in the AF animals (Fig. 2C). Consequently, the RMSSD/SDNN ratio decreased significantly from base to sound in the AF group and from base to feed in the RF group (Fig. 2D). The heart rate characteristics of FSF animals, which served as controls here, were unchanged during the sound and while the other 2 treatment groups were feeding (Fig. 2A–2D).
Heart Activity Before and During FSF. There was a significant main effect of period of time on HR (F<sub>3,143.00</sub> = 64.28, P < 0.001), RMSSD (F<sub>3,143.00</sub> = 8.43, P < 0.001), SDNN (F<sub>3,143.00</sub> = 5.5, P < 0.01), and RMSSD/SDNN ratio (F<sub>3,143.00</sub> = 6.12, P < 0.001).

HR decreased significantly until feeding but then increased to its highest level during feeding (Fig. 3A). The decreasing HR leading up to feeding corresponds to a significantly increased RMSSD (Fig. 3B) and RMSSD/SDNN (Fig. 3D) over all periods of time until feeding. Conversely, the sympathetic influence on heart reactions increased significantly during feeding (Fig. 3A and 3C).

Heart Rate Variability During Midday Rest. Although all groups started with comparable resting heart rates in the stimulation-free period around midday, the resting heart rate in the FSF animals was significantly lower at the end of the experiment compared to AF and RF animals. Compared to the beginning of the experiment, RMSSD showed a significant decrease in all groups along with a decrease of SDNN in both the AF and RF animals. The RMSSD/SDNN ratio decreased from the beginning to the end of the experiment in all groups (Fig. 4).

Cortisol Analysis

The experimental treatments did not significantly affect salivary cortisol levels (F<sub>3,18.21</sub> = 0.775, P = 0.523). However, there was a significant effect of the phase of the experiment, such that cortisol concentrations significantly decreased in all treatment groups from before the start of the experiment (d −5 and −6; 3.21 ± 0.21 ng/ml) and shortly after the start of the experiment (d 3 and 4; 3.72 ± 0.21 ng/ml) to the end of the experiment (d 29 and 30; 1.71 ± 0.21 ng/ml; P < 0.001).

Behavioral Observations

Anticipation Behavior. The results of behavioral observations during the sound (AF and FSF groups) or during the minute before feeding (RF group) showed a significant main effect of treatment on the behaviors active (F<sub>2,569.00</sub> = 80.95, P < 0.001), sit (F<sub>2,569.00</sub> = 96.21, P < 0.001), and rest (F<sub>2,569.00</sub> = 165.41, P < 0.001). During anticipation, the AF group displayed significantly less resting and more active and sitting behavior than the RF and FSF groups (Fig. 5).

Observation (1100 to 1130 h) of the animals during the resting period (1030 to 1200 h) revealed no significant main effect of the treatment. All treatment groups showed the same percentage of lying behavior (AF: 84.14 ± 3.35%, RF: 85.95 ± 3.38%, FSF: 84.24 ± 3.35%, differences nonsignificant).

Behavior of FSF Animals Before Feeding. There was a significant main effect of period of time on the
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Behaviors active ($F_{2,31.00} = 8.54, P < 0.01$) and rest ($F_{2,31.00} = 3.46, P < 0.05$) for FSF animals. In the period immediately before feeding (30 to 0 min), these animals showed significantly less resting and more active behavior than in the first period (120 to 90 min; Fig. 6).

**DISCUSSION**

Heart reactions are thought to reflect the brain’s affective activity. This is because the heart is directly innervated by the sympathetic and parasympathetic branches of the autonomous nervous system. Although there is good evidence that sympathovagal activity monitored in heart reactions reflects emotional states in animals (for a review, see von Borell et al. [2007]), other physiological factors such as physical activity or breathing may also have an influence (Billing, 2013). To minimize the influence of these latter factors in our interpretation of putative emotional states, we have investigated HR and HRV changes under well-controlled conditions such as single housing and movement restriction in domestic pigs. Using a controlled feeding paradigm, we compared frequent short-term anticipation of feed delivery with long-term anticipation of feeding and with frequent unpredictable feed delivery. We showed that mental anticipation resulted in specific cardiac and behavioral reactions.

Our investigations were based on previous theoretical considerations (Spruijt et al., 2001; Bassett and Buchanan-Smith, 2007; Boissy et al., 2007; Manteuffel et al., 2009a; Manteuffel et al., 2009b) and experiments with pigs (Ernst et al., 2005; Ernst et al., 2006; Puppe et al., 2007; Zebunke et al., 2011). We tested the hypothesis that frequent short-term anticipation of feed delivery would result in positive changes in porcine welfare.

Stress, disease, behavioral abnormalities, temperament, and emotional status have an impact on welfare and are reflected in changes in sympathovagal balance (de Jong et al., 1998; Mohr et al., 2002; Geverink et al., 2003; Kuwahara et al., 2004; von Borell et al., 2007). An increase in vagal activity is considered as one indicator of welfare, as it indicates a relaxed state (Boissy et al., 2007). Accordingly, Lee et al. (2005) demonstrated higher HRV and lower HR in humans during positive emotions. We therefore expected that resting HR would be lower and HRV higher in animals anticipating feeding compared to the other 2 treatments tested. In previous experiments with pigs that were called individually to the feeding place, vagal HRV was elevated while pigs anticipated feeding and during feeding (Zebunke et al., 2011; Zebunke et al., 2013). Anticipation of feed was elicited by Pavlovian-like conditioning where a sound was played 1 min before
feed was dispensed (trace conditioning). The effect of successful conditioning was reflected in specific heart reactions and behavioral responses during the signal sound. Only in the conditioned (i.e., the anticipating) group, HR as well as the complex autonomic SDNN increased, and behavior became significantly more active. These changes were not observed in response to the sound in the unconditioned RF group showing that the sound was not a signal per se to the animals but needed previous coupling to the unconditioned feeding stimulus to become meaningful.

Heart reactions in pigs to short-term-anticipated or nonanticipated feeding were transient. Whereas HR increased after feed delivery in the unpredictably fed group (RF), this increase started during the anticipation phase in the anticipating group (AF). In parallel, SDNN increased and RMSSD/SDNN ratio decreased during anticipation. These results indicate a short-term activation of the sympathetic nervous system (Despres et al., 2002; Langbein et al., 2009; Zebunke et al., 2013). Sympathetic activation in anticipation of incentive foods has been found in common marmosets and has been interpreted as an indicator of positive emotional arousal (Braesicke et al., 2005). In a fear-conditioning paradigm in rats, sympathetic activation accompanied fear reactions (Inagaki et al., 2004). Thus, sympathetic characteristics alone are not sufficient to identify the perception of a stimulus as positive or negative and further physiological and behavioral parameters have to be taken into account (von Borell et al., 2007). The changes of sympathetic activity found in our experiment may indicate arousal caused by anticipation during the sound signal, which was also supported by increasing behavioral activity during anticipation. For example, the increase of HR in pigs during feeding is well known in adult and young animals (Schouten et al., 1991; Scalzo, 1992). Long-term confinement in stalls even increased sympathetic responses to important stimuli such as feeding in pigs (Marchant et al., 1997).

Do pigs display long-term anticipation? To address this question, the FSF group was fed at a fixed time in the afternoon (in addition to an initial feeding in the morning). Afterward, the animals were released from confinement. In principle, these pigs could then anticipate 2 consecutive positive events. In the 2 h before feeding, the pigs reduced their resting behavior by approximately 15%. During the same time, active behavior increased by approximately 4.8-fold. However, even in the 30 min before feeding, resting behavior exceeded

Figure 4. Heartbeat characteristics in the stimulation-free resting periods around midday. (A) Heart rate (HR), (B) RMSSD, (C) SDNN, and (D) RMSSD/SDNN ratio at the beginning (white columns) and the end of the experiment (black columns). Asterisks indicate significant differences between the beginning and the end of the experiment: **P < 0.01; ***P < 0.001.
active behavior and sitting by more than threefold. During the resting periods, HR decreased over time, parallel to an increase in HRV (RMSSD), which might indicate a deeper state of relaxation during resting closer to the time of feeding.

Taken together, the results of the FSF animals appear to some degree paradoxical. On the one hand, the HR parameters do not point to anticipation but rather to increasingly deep relaxation during resting periods with progressing time in the afternoon. The observed decrease in HR was very likely a circadian effect that, in pigs, results in a steep descent of HR, in parallel to an increasing vagal influence in the afternoon (Kuwahara et al., 1999). On the other hand, the increasing amount of active behavior may indicate anticipation. However, increasing activity could likewise be explained by increasing hunger, particularly because the animals were starved since the early morning. In conclusion, evidence for long-term anticipation in pigs was not clear in the data from the fixed-schedule feeding compared to the clear evidence for short-term anticipation in the AF group, where resting behavior decreased by approximately 50% and was roughly equal in duration with activity and sitting and where HR and SDNN were both elevated. A similar result was found by Imfeld-Mueller et al. (2011), who used a 10-s delay trace-conditioning experiment in pigs to reveal similarly increased HR and SDNN in the anticipation phase, independent of the valence of the anticipated stimulus.

In our experiment, all groups were subjected to the same restrictive conditions. Cortisol data, as well as resting HR in the control animals (FSF), indicated that the pigs in our experiment were not chronically stressed by the treatment and single housing. This confirms earlier results in long-term confined pigs of the same age and breed (Jaskulke and Manteuffel, 2011). The only detectable effect of movement restriction was a decrease of the RMSSD/SDNN ratio during the midday rest over the experimental period. This is in good agreement with a study on horses which showed that movement restriction increased sympathetic activity during resting periods (Vitale et al., 2013). Therefore, it cannot be concluded from our results that these animals do not suffer chronically from poor housing. If this was the case, however, markers such as behavioral reactions or cortisol may not reflect this suffering. The slight decrease of salivary cortisol concentrations in all groups over the experimental period suggests an adaptation to the new housing and treatment. However, salivary cortisol did not exceed basal levels at any of the tested sampling times. For comparison, it has been shown that pigs that were relocated and newly grouped at 60 d of age had 4 to 6 times higher salivary cortisol concentrations (Otten et al., 2010).

Comparisons between the treatment groups suggest that in housing conditions where pigs cannot acquire feed by proper actions but must wait for feed delivery, anticipated or not, feeding at 2 fixed times would be preferred. Animals in this treatment group displayed more relaxed behavior and HR characteristics. In these confined, passive pigs, a regular and predictable feeling of complete satiety may be most important. This is apparently more readily achieved by 2 feedings, with half of the daily allowance at each feeding, than by 6 feedings with relatively small portions each time. In the latter case, in fact, the animals showed increased arousal during anticipation of feed but were apparently not completely relaxed during stimulus-free periods. This was indicated by their resting heart rates. While it showed an age-related decrease in FSF pigs, it stayed high in AF and RF pigs.
In active pigs, the situation might be somewhat different. Pigs can learn to adapt to environments where feed is available in small portions. If the conditions are such that the animals can predict the delivery of feed when they perform situational appropriate behavior that may be innate (i.e., rooting [de Jonge et al., 2008] or acquired by operant learning [Ernst et al., 2005]), this behavior is rewarding by itself as it activates the mesolimbic brain axis (Manteuffel et al., 2009a). Under these conditions, the positive welfare aspect has been demonstrated in preference tests (de Jonge et al., 2008) and by collateral behavioral (Puppe et al., 2007) and physiological indicators (Ernst et al., 2006; Zebunke et al., 2011; Zebunke et al., 2013). In the experimental setting of de Jonge et al. (2008), pigs preferred searching for palatable food hidden in straw over freely accessible feed of the same type after they had learned that they could find this food by rooting. In the study of Ernst et al. (2005), pigs learned to approach and enter an electronic feeder after a specific sound was played by that feeder (call feeding). In this setting, the animals learned that they could feed without being disturbed by other group members (that were trained to other sounds) and could predict when feed would be available. The animals were called up to 30 times/day and received a small portion of feed with each proper action. As a result, they displayed increased immune cell proliferation, better wound healing and by collateral behavioral (Puppe et al., 2007) and physiological (Ernst et al., 2005), this increase above baseline shortly after the calling sound had started (Zebunke et al., 2013). In sows in a call feeding regime, however, few (1 or 2) call feedings per day were optimum (Kirchner et al., 2012).

The main difference between anticipation in the classical conditioning approach, as was used in our study, and the various aforementioned approaches, where operant behavior was included, is the presence of control. A situation in which an animal is able to control its access to an appetitive stimulus is fundamentally different from one in which it must wait for the stimulus to come, where it may not matter whether the arrival is announced. Hence, gaining and keeping control lead to increased welfare, which is chiefly attributable to the anticipation of the consequences of one’s actions (Sambrook and Buchanan-Smith, 1997; Manteuffel et al., 2009a; Manteuffel et al., 2009b).

CONCLUSIONS

This comprehensive study on domestic pigs combined physiological parameters, such as cardiac activity and cortisol, with behavioral observations in an anticipation paradigm. Our data clearly show that pigs are able to anticipate positive stimuli such as feed on a short-term basis. However, we could not support our initial hypothesis that frequent anticipation of a small portion of feed is a preferable type of feeding in pigs if the animals are otherwise passively waiting to be fed. Hence, merely announcing a positive stimulus is apparently not a suitable substitute for active control of access to a positive resource.

LITERATURE CITED


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