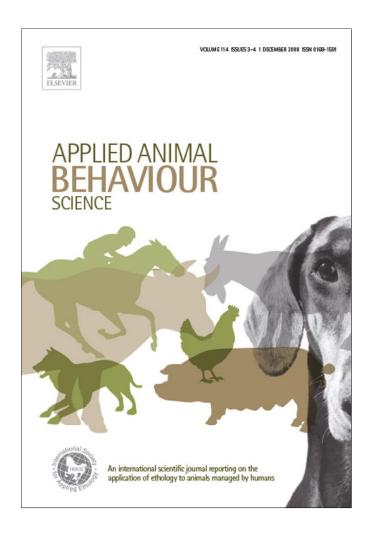
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# On the rewarding nature of appetitive feeding behaviour in pigs (*Sus scrofa*): Do domesticated pigs contrafreeload?

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#### **Abstract**

Contrafreeloading is the phenomenon that animals prefer to "work" for food even though "free" food is available nearby. In this study, we investigated whether pigs express contrafreeloading in a test situation where the searching, finding and consuming of food items resembles a natural foraging situation. For that purpose, we investigated whether pigs prefer an environment with straw and hidden food rewards (chocolate raisins) to an environment with straw, but without hidden food rewards and with food rewards "freely" available in a trough. Preference behaviour was investigated in a Conditioned Place Preference task (CPP). Typically, CPP measures the conditioned preference *in the absence* of reinforcers so that unwanted interference with the reinforcers during testing does not take place. The results show that (a) CPP can be used to establish the preference of pigs for different environments (experiments 1–4); (b) that pigs prefer to forage for food over "freely" available food from a trough (experiment 3) and (c) that anticipating a food reward has reinforcing effects above and beyond the reinforcing effects of acquisition of a food reward alone (experiment 4). The results therefore show that pigs express contrafreeloading when using a natural foraging task and they suggest that the reinforcing effects of anticipation, which occurs during natural foraging in the delays between searching and finding food, may contribute to the observed expression of contrafreeloading in pigs.

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Keywords: Pigs; Foraging; Feeding; Appetitive; Anticipation; Reward; Contrafreeloading; Welfare

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#### 1. Introduction

Under (semi-) natural conditions pigs (*Sus scrofa*) spend a large portion of their daily activity budget (40–70%) on foraging behaviours (Blasetti et al., 1988; Gustafsson et al., 1999; Jensen, 2002). Under intensive husbandry conditions however, the environment provides little or no opportunities to forage and nutrient requirements are fulfilled by the provision of pellets which are often consumed in a limited amount of time. The occurrence of oral stereotypies in pig husbandry systems, often concentrated in periods around feeding, has been associated with these behavioural restrictions (Lawrence and Terlouw, 1993). Evidence therefore suggests that the expression of appetitive feeding behaviour is important for the welfare of pigs in husbandry systems (Mason, 1993; see also Bergeron et al., 2006 for an extensive discussion about the motivational aspects of stereotypic behaviours in pigs and other ungulates).

Appetitive behaviours (like foraging) are searching behaviours motivated by an 'appetite' for a particular stimulus (Wallace, 1979), whereas actions that fulfil a motive and cause appetitive behaviour to end (like food ingestion) are consummatory behaviours. Both appetitive and consummatory components of behaviour may have rewarding properties that can be distinguished (De Jonge, 1986; Inglis et al., 1997). However, it has been difficult to specify the causal mechanisms that may underlie rewarding properties of appetitive feeding behaviour in pigs. Suggestions include the possibility that the performance of foraging behaviour is rewarding in its own right (Hogan, 1967; Gardner and Gardner, 1988; Hughes and Duncan, 1988) or that foraging behaviour, more than the consumption of food pellets alone, increases aspects of "perceived control" over the environment (Singh, 1970; Inglis et al., 1997; Bassett and Buchanan-Smith, 2007).

Contrafreeloading is the observation that animals prefer to "work" (for instance by pressing a lever) to receive food even though identical "free" food can easily be obtained in a nearby dish (Osborne, 1977). It has attracted the attention of applied ethologists because it indicates that the expression of appetitive feeding behaviour is indeed rewarding (Hughes and Duncan, 1988). A functional explanation of contrafreeloading has been given by Inglis and Shepherd (1994), Inglis et al. (1997) and Inglis et al. (2001) who argued that animals work (forage) for food under natural conditions because it is related to the advantage for animals of gathering information in changing environments (information primacy hypothesis). Factors that contribute to the expression of contrafreeloading include such factors as hunger motivation, rearing conditions, the amount of effort required to obtain a reward and the nature of the task (Inglis et al., 1997).

Although contrafreeloading appears to contradict least effort learning rules (Osborne, 1977), it has been argued by Inglis et al. (1997) that it does fit with reinforcement theory, provided that the sensory reinforcement obtained from stimuli associated with the earned food is also taken into account. More in particular, it was argued that the degree of sensory reinforcement provided by food under natural conditions is affected by such factors as its novelty, ambiguity and surprisingness and that animals actually work to reduce "environmental uncertainty". Aspects of "environmental uncertainty" in natural foraging tasks or in test situations where the finding and consuming of foods resembles natural foraging, include the variability in quality and in location of the food or variability in the delay between searching and eventually finding the food.

Recently, Young and Lawrence (2003) investigated whether pigs express contrafreeloading in an environment in which pigs had continuous access to operant and identical free food. However, contrary to expectation, they failed to find evidence for contrafreeloading. The authors then suggested that the degree of species domestication may have affected the level of contrafreeloading observed (Young and Lawrence, 2003; Schűtz et al., 2001), thereby

suggesting that the rewarding effects of appetitive feeding behaviour may be less (or absent) in domesticated species than in their wild counterparts. We suggest however, that characteristics of the operant task and test situation used, may also play a role. For instance, it has been noted by Breland and Breland (1961) that the animal's motivation to perform operant tasks may differ from those involving more "natural" tasks and it was noted by Inglis et al. (1997) that more natural tasks tend to facilitate the expression of contrafreeloading. In the present study, we therefore investigated whether pigs express contrafreeloading when using a "natural" foraging task (instead of an operant response). For that purpose we investigated whether pigs prefer an environment with straw and hidden food rewards over a (straw-embedded) environment in which food rewards were not hidden, but "freely" available in a trough.

In the present study, we investigated the pig's preference in a Conditioned Place Preference task (CPP). The advantage of the CPP is that a preference for certain environments can be measured in the absence of the specific reinforcements. In that way unwanted interference with the reinforcers during testing can be avoided. In short, pigs tested in a CPP express a preference for a context (either a black or a white compartment) due to the contiguous association between the context and a stimulus (in our case an environment which allows for different components of appetitive behaviour). CPP has typically been used to investigate the rewarding or aversive properties of drug treatments (for reviews, see Bardo and Bevins, 2000; Tzschentke, 2007), but the use of CPP with natural reinforcers has also been reported (Oldenburger et al., 1992). However, to our knowledge CPP has never been used for investigations in pigs before. In order to verify whether the pig's preference for different foraging environments would be expressed in a CPP procedure, we followed a stepwise approach. Therefore, the pig's preference for a compartment filled with straw and hidden food rewards (which allowed for both appetitive and consummatory aspects of foraging behaviour) was first compared to an empty environment (experiment 1), subsequently to an environment filled with straw without hidden food rewards (experiment 2) and finally to a compartment filled with straw without hidden food rewards but with food rewards "freely" available in a trough (experiment 3).

In the study of Young and Lawrence a Fixed Ratio (FR) reinforcement schedule was compared to a Variable Ratio (VR) schedule, but the expected increase in contrafreeloading on the VR schedule due to increased "environmental uncertainty" was not observed. We also recently investigated whether pigs in an operant task would prefer to work for food on a variable interval (VI) schedule (resembling the relative unpredictability of gaining reinforcers under natural foraging conditions) over a fixed interval (FI) schedule, but failed to find evidence either (De Jonge et al., 2008). We therefore predicted in the present study that not the variability of the delay, but rather the *delay itself* (between searching and finding the food) may contribute to the reinforcing effects of contrafreeloading in a natural foraging task. This assumption was based on the finding that the expression of anticipation behaviour during a delay between CS (conditioned stimulus) and US (unconditioned stimulus) is closely correlated with the release of Dopamine from brain reward centers (Nucleus Accumbens) (Spruijt et al., 2001; Berridge, 2004, 2007), that predictability of both negative and positive stimuli is beneficial for welfare (Wiepkema and Koolhaas, 1993; Bassett and Buchanan-Smith, 2007) and finally that anticipation behaviour (presumably because of its rewarding effects) could be used as a behavioural therapy in a depression model in rats (van der Harst et al., 2005) and could ameliorate the consequences of weaning stress in piglets (Dudink et al., 2006).

Therefore, experiment 4 was designed to investigate whether delay, as an aspect of "environmental uncertainty" of a natural foraging environment, may contribute to the expression of contrafreeloading in pigs. During the association trials of experiment 4, both compartments A

and B were covered with straw. In A however, a CS (flash-light) was immediately followed by the delivery of food (US) in a food trough, while in compartment B, a delay was introduced between presentation of the CS and food delivery (US). It was predicted that pigs would prefer the CS-DELAY-US compartment if delay would be an aspect of environmental uncertainty that contributes to the reinforcing value of appetitive feeding behaviour.

#### 2. General methods

#### 2.1. Animals, housing and management

In the present study, 63 female piglets from 14 different crossbred litters (Large White × Landrace) participated in 4 different experiments. Within each experiment, litters were born within 24 h. The number of female piglets per litter ranged from 3 to 8. Litters from first parity sows were not selected and three piglets were excluded from experimentation because they did not meet the criteria during the handling phase (see Section 2.2). Experiments took place in the experimental pig farm "de Tolakker" (Utrecht, The Netherlands).

Piglets were reared according to standard conventional pig husbandry procedures in The Netherlands. Thus, sows and litters were housed in commercial farrowing pens (1.75 m  $\times$  2.4 m) with half-slatted, half-solid floors and no bedding. Within the farrowing pens, sows were confined in crates to prevent crushing of the piglets A heating lamp and floor heating were used when necessary. Standard procedures, like ear tagging, tail clipping, castration of the males and iron injections were done in the first week after the piglets were born. One-week-old piglets were provided with starter pellets mixed with milk powder solution, followed by grower pellets. Water was always available ad libitum. The light regime was 9/15 h with the lights turned on at 7:00 h and turned off at 16:00 h. The temperature of the room was controlled (at  $\pm 24$  °C).

Piglets were weaned at approximately 31 days of age ( $\pm$  2 days). After weaning litters were moved to a 'weaner unit' where either two or three litters were mixed in new groups of about 20 animals. Experimental litters were always regrouped together. The sides of the new pen (3.8 m  $\times$  2.2 m with partly slatted floors) allowed weaned piglets to have limited visual, auditory and tactile contact with the piglets in neighbouring pens. Each pen in the weaner unit had a 3 hole self-feeder. The temperature was maintained at  $\pm$ 26 °C.

Experimental animals were subjected to a handling procedure preweaning, while testing took place after weaning. During that time, experimental piglets were individually identifiable by large numbers which were painted on their backs and repainted weekly.

#### 2.2. Handling procedure

At the age of 10 days ( $\pm 2$  days) experimental animals were subjected to a 21-day handling period. During handling, the experimenter was sitting in the farrowing pen. Handling took place according to a predetermined protocol including 5 steps. Individual piglets entered the next step in the protocol when they stopped showing signs of fear (vocalization, pacing and turning away from the handler) and when they voluntarily approached the handler or accepted being approached by the handler without showing signs of fear. The five steps of the protocol were as follows: (1) speaking (friendly voice); (2) gently stroking all parts of the piglet's body: successively the shoulders, back, hindquarters and head; (3) lifting the hindquarter of the piglet; (4) lifting both hind and forequarter at least 30 cm from the ground for a total 5 s; and (5) lifting the piglet out of the farrowing pen and placing it into a neighbouring hallway (1 m  $\times$  5 m)

enriched with food (seeds) and straw. Piglets were left in the enriched part of the hallway during 20 s (first trial) up to 3 min (last trial) before they were replaced in their litter.

During the handling period, experimental piglets were also habituated to feed rewards. For that purpose, feed rewards were given from the third day of the handling procedure and onwards. At first the feed reward consisted of mixed seeds (chicken feed). When piglets had learned to eat the seeds, they additionally received up to 10 chocolate raisins a day from the experimenter.

From the total of 63 piglets, three piglets were excluded from experimentation during the handling phase: one did not eat any raisins and two did not pass the required steps of the handling protocol within the 21-day period.

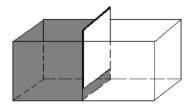
# 2.3. Conditioned Place Preference apparatus (CPP)

The Conditioned Place Preference apparatus (see Fig. 1) consisted of a wooden box  $(80 \text{ cm} \times 144 \text{ cm} \times 244 \text{ cm})$ , divided in two compartments of identical size  $(80 \times 144 \times 122)$ . The two compartments either did (during conditioning trials) or did not (during pre-tests and during test trials) contain a partition  $(80 \text{ cm} \times 144 \text{ cm})$  that prevented the animal from moving from one compartment to the other. The walls and floor of one compartment was painted black, the other compartment was painted white. The upper side of the CPP was open. To allow measurement of the time spent in different locations of the CPP, each compartment was also divided in three hypothetical zones (zone a–c) of the same size each covering one-third of a compartment (see Fig. 1).

# 2.4. CPP procedure

For each animal, the CPP-procedure included (a) one pre-test, (b) 10 conditioning trials (except for experiment 4 which included 14 conditioning trials) and (c) one test trial. The CPP-procedure lasted 7–9 days in total and started on the 4th day post-weaning. Duration of the pre-tests (1 min) and conditioning- and test trials (3 min) were based on experience gained in a preliminary experiment (results not presented). Pre-tests always confirmed that piglets do not show an unconditioned preference for either the black or the white compartment. We therefore used an unbiased procedure (Tzschentke, 2007) in which allocation of treatments to either the black respectively the white compartment was assigned semi-randomly within each experiment. More in particular, within each experiment, half of the animals (randomly chosen) were assigned to a specific treatment in the white compartment, whereas the other half received that specific treatment in the black compartment. Also the testing order of the animals was randomised within each experimental day. Within trials the CPP was thoroughly cleaned.

During pre-tests, the partition was removed, allowing subjects free access to both compartments of the apparatus. A single piglet was then taken from his home pen and gently



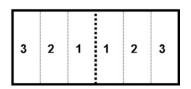


Fig. 1. Schematic representation of the conditioned place-preference apparatus CPP (left). The three different zones within each location are indicated at the right. The food trough was always placed in zone 3 (experiments 3 and 4).

placed in the middle of the CPP apparatus for a 1 min trial. The apparatus was completely empty and located 2 m from the home pen of the piglets. The experimenter was out of sight and standing behind the home pen of the piglets. Duration and frequency of visits to both compartments were measured through video analysis. Subjects were designated to be in one compartment when the two front legs were in that compartment.

During conditioning trials the partition was placed within the CPP, thereby preventing the animals from moving from one compartment to the other. During 10 3-min conditioning trials, piglets were either placed in the black  $(5\times)$  or in the white  $(5\times)$  compartment. During conditioning trials, each compartment contained a different enrichment such as straw and/or food rewards (see description of the separate experiments). For each piglet one compartment was always associated with the same type of enrichment. Two conditioning trials were conducted each day (one for each compartment), separated by at least 2 h. The order of testing (first black then white and vice versa) was alternated over subsequent days. When straw was used as bedding, straw was always first gently shaken on a sieve in order to remove remaining grains.

The day after the final conditioning trial, piglets were subjected to test trials. This procedure was exactly the same as the procedure described under "pre-test" (i.e. the partition was removed, piglets had access to both compartments and the CPP was completely empty), except that the trial duration was 3 min (similar to the conditioning trials). Again, duration and frequency of visits to both compartments and the duration on different locations within compartments were collated from video recordings.

#### 2.5. Experiments

Four different experiments were conducted. In each experiment, two different environments were associated with the two different compartments of the CPP. The different environments allowed for different appetitive and consummatory aspects of foraging behaviour. A schematic overview of the experiments is presented in Table 1.

#### 2.5.1. Experiment 1: Straw + Hidden Food reward versus Empty

In the first experiment, piglets (n = 14, 4 litters) were exposed during conditioning trials to one compartment which was always covered with straw with 15 chocolate raisins hidden in the straw (15 raisins per trial). Chocolate raisins were always evenly distributed over the compartment according to a predetermined pattern that varied on each subsequent trial. The alternative compartment was completely empty. During the final test trial both compartments were completely empty. The average number of raisins eaten in the " $Straw + Hidden\ Food\ Reward$ "—trials increased from 2.8 (first trial) to 3.9 (last trial) and the number of raisins eaten per trial varied between 0 and 15. One piglet did not eat a raisin on any trial.

## 2.5.2. Experiment 2: Straw + Hidden Food Reward versus Straw

In the second experiment, piglets (n = 12, 3 litters) were exposed during conditioning trials to two compartments that were both covered with straw. In addition, and exactly according to experiment 1, compartment 1 also contained 15 chocolate raisins hidden in the straw. The alternative compartment however, only contained straw but no hidden food rewards. During the final test trial both compartments were completely empty. The average number of raisins eaten in the " $Straw + Hidden\ Food\ Reward$ "—trials increased from 5.4 (first trial) to 8.0 (last trial) and the number of raisins eaten per trial varied between 0 and 15. There was no piglet that never ate raisins.

Table 1 Schematic overview of the 4 different Conditioned Place Preference (CPP) experiments

Experiment		Exp 1	Exp 2	Exp 3	Exp 4
Treatment associated with compartment A		Straw + Hidden Food	Straw + Hidden Food	Straw + Hidden Food	Straw + Announced Food in Trough + Delay
vs		vs	vs	vs	vs
Treatment associated with compartment B		Empty	Straw	Straw + Food in Trough	Straw + Announced Food in Trough
Appetitive aspects	Environment allows for performance of behavioural patterns associated with foraging	A	A + B	A + B	A + B
	Environment requires natural foraging behaviour in order to achieve Food Reward	A	A	A	none
	Acquisition of food reward is associated with anticipation to Food Reward during delay.	A	A	A	A
Consummatory aspects	Environment associated with Consumption of Food Reward	A	A	A + B	A + B

For each experiment, the environments associated with the two different compartments A and B of the CPP are presented in the second row. Shaded cells indicate which associated appetitive or consummatory components of foraging behaviour were possible for in one environment, but not in the alternative environment.

# 2.5.3. Experiment 3: Straw + Hidden Food Reward versus Straw + Food Reward in Trough

In the third experiment, twenty-one piglets (n = 21, 4 litters) were exposed during conditioning trials to compartments that were both covered with straw. In one compartment chocolate raisins were hidden within the straw exactly according to the procedures described in experiments 1 and 2. In the alternative compartment however, straw was present, but chocolate raisins were presented in a trough, placed in zone 3. The number of raisins presented in the trough was adjusted for each trial to the number of chocolate raisins that were eaten in the previous "Straw + Hidden Food"—trial. Because the piglets could earn chocolate raisins on both conditioning trials, the total number of chocolate raisins that were hidden in the "Straw + Hidden Food"—trials was limited to 10 in this experiment. The total number of raisins eaten on a day (i.e. sum of two daily trials) varied between 1 and 20. The average number of raisins eaten in the "Straw + Hidden Food Reward"—trials increased from 2.0 (first trial) to 4.0 (last trial) and the average number of raisins eaten in the "Food Reward in Trough"—trials increased from 1.8 (first trial) to 5.7 (last trial). There was no piglet that never ate raisins.

# 2.5.4. Experiment 4: Straw + Announced Food Reward in Trough versus Straw + Announced Food Reward in Trough + Delay

In the fourth experiment, thirteen piglets (n = 13, 2 litters) were exposed during conditioning trials to compartments that were both covered with straw. In both compartments, a feed trough was placed in zone 3 and white light flashes could be delivered from a 60 W white light bulb mounted 50 cm above the feed trough. In both environments, two light flashes (CS) were delivered immediately after the piglet had been placed in the compartment during a conditioning trial in order to announce the delivery of 3–5 chocolate raisins (US). However, in one compartment the food reward was delivered immediately after the CS, while in the alternative compartment, the delivery of the food reward (US) was delayed with 8 s (first trial) up to 14 s (last trial). Previous studies had shown that such a delay between the conditioned stimulus and unconditioned stimulus allowed for the occurrence of anticipatory behaviour (see Dudink et al., 2006).

In contrast to the previous experiments,  $2 \times 7$  (14) conditioning trials were run in experiment 4 (instead of 10) and conditioning trials were limited to 1 min which was just enough for the piglets to consume their food rewards. Finally, the number of chocolate raisins given per trial was limited to 3 during trials 1 and 2 and increased to 5 in trials 5–7 in order to ensure that all piglets ate all raisins offered. All chocolate raisins were eaten on each association trial.

#### 2.6. Statistics

Data were statistically analysed using SPSS (Version 15+). Preference (PREF) of piglets for compartment A over B during pre-tests and test trials was calculated as the % of time spent in compartment A relative to the total time spent in either compartment A or B. PREF of 50% therefore indicates that piglets do not prefer one over the other compartment. PREF was analysed using Analysis of Variance (ANOVA) and lower and upper bound 95% confidence intervals of the parameter estimates were calculated in order to test if PREF was significantly different from 50%. Frequency of visits was analysed by Generalized Models (GEE), correlations between the number of consumed rewards and PREF were calculated by Spearman Rank procedure (for details see below).

#### 3. Results

Analysis of the distribution of the values of PREF, revealed that PREF of both pre-tests and test trials fitted a normal distribution (One-Sample Kolmogorov–Smirnov Test; pre-test: Z = 0.639, p > 0.81; test trial: Z = 0.683, p > 0.739). Tests for Homogeneity of Variance however, revealed significantly larger deviations in the pre-tests (Standard Deviation (S.D.): 24.39) than in the test trials (S.D.: 15.33) (Levene's test for homogeneity of variance; F = 12.55, p < 0.001). Within pre-tests and test trials, preconditions for homogeneity of variance between experimental observations were met (F = 0.774, p > 0.5 respectively F = 1.47, p > 0.23). It was therefore decided to analyse pre-tests and test trials in two separate ANOVAs.

Analysis of PREF during pre-tests confirmed that differences between experiments were absent during pre-tests and that piglets did not have an unconditioned preference for either of the compartments. Thus, Univariate Analysis of Variance (ANOVA) including the independent factor experiment (4 levels) and the random factor LITTER showed that lower and upper bound 95% confidence intervals for parameter estimates ranged between 30.17% an 65.5% for all experiments (mean  $\pm$  S.E.M.: experiment 1 (49.63%  $\pm$  8.08); experiment 2 (49.25%  $\pm$  8.06); experiment 3 (41.92%  $\pm$  4.76); experiment 4 (51.89%  $\pm$  6.08). No significant effect for the factor EXP (F(3,56 = 0.693, p > 0.56) was found.

PREF on test trials (see Fig. 2) was also analysed by ANOVA including the independent factor EXP (4 levels) and the random factor LITTER in the model. In contrast to the pre-tests, analysis of the lower and upper bound 95% confidence intervals of the parameter estimates subsequently indicated that PREF was significantly different from the 50% level in all four experiments. Thus, analysis of the parameter estimates shows that piglets from experiment 1 significantly prefer the compartment previously associated with *Straw* + *Hidden Food Rewards* over *Empty* (experiment 1:95% confidence interval for PREF: 61.0–76.68%). Results from experiment 2 show that piglets significantly prefer the compartment previously associated with *Straw* + *Hidden Food Reward* over *Straw* (experiment 2: 95% confidence interval for PREF: 64.3–81.3%). Results from

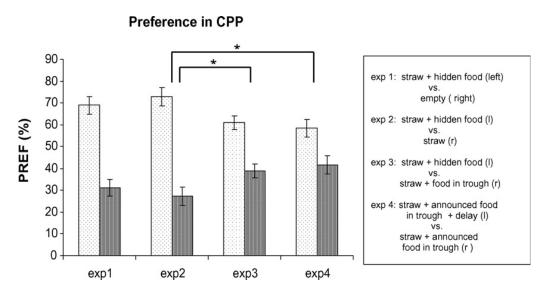


Fig. 2. Preference (PREF) for compartments of the CPP that were associated with different treatments (see legends at the right for treatments). PREF is calculated as % time spent in compartment A relative to total time spent in compartment A + B. The 50%-level indicates that animals do not have a preference. In all four experimental groups PREF was significantly different from 50% (p < 0.05).

experiment 3 show that piglets significantly prefer Straw + Hidden Food Rewards over Straw with Food in Trough (experiment 3: 95% confidence interval for PREF: 54.65–67.46%). Finally, results from experiment 4 show that piglets significantly prefer Straw + Announced Food + Delay over Straw + Announced Food (experiment 4: 95% confidence interval for PREF: 50.2–66.49%). In addition, the analysis showed a significant effect of EXP (F(3, 56) = 2.838, p < 0.05). Subsequent post hoc contrasts showed that PREF of experiment 2 was significantly different from experiment 3 and from experiment 4 (both p < 0.05).

The frequency of shifts from one compartment to the other was analysed with a Generalized Linear Model (Generalized Estimated Equations) with Poisson distribution and associated LOG link function. Independent and random factors included in the model were the same as for PREF. No significant effects of EXP were found (p = 0.204)(data not presented here).

The number of consumed chocolate raisins per association trial differed considerably among individuals (median (minimum–maximum): experiment 1: 1.8 (0.2–15); experiment 2: 6.7 (1.4–13); experiment 3: 6.2 (0.2–10); experiment 4: 4.7 (constant)). For each experiment separately (except for experiment 4), a spearman rank correlation coefficient was calculated between the total number of chocolate raisins eaten in the association trials versus PREF in the test trials. No significant correlations were found (experiment 1: rho = 0.24, p = 0.40; experiment 2: rho = 0.524, p < 0.080; experiment 3: rho = 0.22, p < 0.33). Correlations for experiment 4 were not calculated because the number of consumed raisins was experimentally kept constant.

Finally, analysis of the time spent in zone 3 of a compartment (TZ3), relative to the total time spent in that compartment, was calculated for the different experiments (see Fig. 3). This was analysed in order to investigate whether pigs expressed a special preference for the zones of experiments 3 and 4 where food troughs were placed. Univariate analysis of variance including the independent factor EXP (4 levels) and the random factor LITTER, indicated that TZ3 upper and lower bound 95% confidence intervals only differed from the predicted 33.3% (one-third of the time) in experiment 1 (upper bound and lower bound 95% confidence interval for Straw + Hidden Food Compartment: 10.7-28.4; for empty compartment: 10.7-28.4; for empty compartment: 10.7-28.4; for empty compartment and revealed no significant effects (p > 0.1).

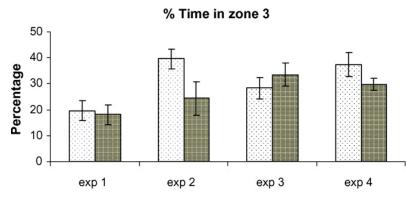


Fig. 3. Percentage of time spent in zone 3 of a compartment of the CPP relative to total time spent in that compartment during test trials. The food trough was placed in zone 3 during association trials (experiment 3: left bar; experiment 4: both bars). Only in experiment 3 the times spent in zone 3 differed significantly from the predicted level of 33.3% (one-third of the compartment). Within experiments, time spent in zone 3 never differed between compartments. See legends of Fig. 2 for explanation of treatments.

#### 4. Discussion

In the present study, it was shown that pigs express contrafreeloading in a test situation where the finding and consuming of food resembles natural foraging (experiment 3). In addition, the results show that anticipating a food reward has reinforcing effects above and beyond the reinforcing effects of acquisition of a food reward alone (experiment 4). Finally, it was shown for the first time that a Conditioned Place Preference task can be used to establish the pig's preference for a context associated with specific rewards (experiments 1–4). Typically, CPP measures the pig's preference *in the absence of* reinforcers which prevents unwanted interference with the reinforcers during testing. The CPP may therefore provide significant advantages over more traditional preference tests.

Young and Lawrence (2003) studied contrafreeloading in pigs, but did not find any effects of contrafreeloading. They suggested that the degree of species domestication may affect the level of contrafreeloading expressed (Young and Lawrence, 2003, but see also Schűtz et al., 2001) but our results suggest that experimental conditions play a more prominent role. For instance, we used a more natural foraging task (searching food in straw), while Young and Lawrence (2003) used an operant task (pressing a lever) to investigate contrafreeloading. In addition, we used a CPP to measure preference behaviour thereby avoiding unwanted interference with the reinforcers during testing.

That a natural foraging task tends to increase the level of expression of contrafreeloading, has been noted before by Inglis et al. (1997). Two underlying mechanisms may be proposed. Either the performance of foraging behaviour (i.e. the execution of motor patterns) is rewarding in its own right (Hogan, 1967; Gardner and Gardner, 1988; Hughes and Duncan, 1988) or the degree of sensory reinforcement provided by food under natural conditions (which is affected by such factors as its novelty, ambiguity and surprisingness; Inglis et al., 1997) is much larger than that achieved by reinforcement schedules in an operant task. Each of these two mechanisms will be discussed below.

The idea that the performance of natural foraging behaviour (i.e. execution of motor patterns) is reinforcing in its own right, was originally explained in terms of innate behaviour patterns connected or unconnected with appetitive or consummatory acts (Hogan, 1967; Gardner and Gardner, 1988; Hughes and Duncan, 1988). In line with the review by Inglis et al. (1997), our results give little evidence in support of this hypothesis. In experiment 3, pigs could perform foraging activities (execution of motor patterns associated with foraging) in both environments, the only difference being that foraging behaviour in the preferred environment was contingent upon finding rewards. In addition, when performance of foraging behaviour would have been rewarding in its own right, the preference for an environment with Straw + Hidden Food Rewards over an empty environment (experiment 1) should have been greater than the preference of Straw + Hidden Food Rewards over straw only (experiment 2). This was not the case.

Another reason why pigs may be more sensitive to the expression of contrafreeloading with a natural foraging task than with an operant task, is because the degree of sensory reinforcement provided by food under natural foraging conditions might be affected more by such factors as its novelty, ambiguity and surprisingness than in an operant task. Aspects of environmental uncertainty present in the Straw + Hidden Food condition are (a) the location of Food rewards (which was varied in each association trial), (b) the delay between searching of food and finding it and (c) the variability of that delay. Young and Lawrence (2003) introduced aspects of "environmental surprisingness" through a VR reinforcement schedule, but that schedule did not result in the expected increase in contrafreeloading. In a recent study, De Jonge et al. (2008)

investigated whether pigs prefer to respond on a VI reinforcement schedule rather than on a FI reinforcement schedule, but also these data failed to support the idea that variability in delay to reinforcement contributes significantly to the reinforcing effects of natural foraging activities in pigs. Thus, combining the results from Young and Lawrence (2003) and our previous experiment (De Jonge et al., 2008), with those from experiment 4, seems to indicate that not the variability in delay, but rather the delay itself between a predicting stimulus (CS) and the delivery of a reinforcer (US) may contribute to the reinforcing effects of foraging behaviour of pigs. It has previously been shown that such a delay elicits anticipation behaviour (Spruijt et al., 2001; Dudink et al., 2006; van den Bos et al., 2003; van der Harst et al., 2003) and that anticipating reward delivery is accompanied by Dopamine release from brain reward centers (Spruijt et al., 2001; Berridge, 2007). In addition, Berridge (2004, 2007) who introduced the two reward concepts of hedonic "liking" and "wanting" (incentive salience attribution during reward prediction) in relation to reward systems in the brain, argued that "wanting" is a separate component of normal reward and that "wanting" and "liking" should act together for a full hedonic experience (Berridge, 2004). The results from this study in pigs therefore confirm previous suggestions from neurobiological correlates of anticipation behaviour in rats and mice that anticipating a reward may be reinforcing above and beyond the reinforcing properties of the reward itself. Thus, it may be concluded from experiment 4 that anticipation is one of the aspects of "environmental uncertainty" by which response dependent foraging behaviour gains its reinforcing value relative to "freely" available food in a trough.

We studied appetitive aspects of foraging behaviour in a CPP task (Bardo and Bevins, 2000; Tzschentke, 2007). CPP reflects a preference for a context due to the contiguous association between the context and a stimulus, in our case an environment that allows for specific components of appetitive feeding behaviour. CPP has been extensively used (over 1000 new studies since 1998!) to study the rewarding and aversive properties of drug treatment mainly in rats and mice. In such tests, the aversive or rewarding aspects of drug treatment are investigated by associating a specific drug treatment with either a black or a white compartment. The main advantage of CPP is that a preference for specific environments can be investigated *in the absence* of the reinforcing effects of that environment. With respect to the study of appetitive aspects of feeding behaviour, this seems important because (a) satiation effects during testing are excluded and (b) the tendency of animals to shift between available food resources, independent of the nature of these food resources, is avoided.

To our knowledge, CPP has not been used in pigs before and optimal procedures to study CPP in pigs were therefore established in a pilot experiment (data not presented here). In this respect it is important to note that short periods of isolation in pigs, unlike in rats, tend to elicit aversive behavioural and physiological reactions (Herskin and Jensen, 2000). Extensive handling procedures were therefore introduced before weaning in order to habituate pigs to stress-free handling and short periods of isolation. In addition, we choose in our tests for much shorter durations of association and test trials (3 min) than is usual in rats (15–20 min). Nevertheless, observation of the animals during association trials (personal observations) suggested that a 3-min exposure to an empty environment (one treatment in experiment 1), in contrast to 3-min exposure to straw-embedded environments, still included aversive components in some animals. It is therefore suggested that foraging behaviour in straw, even when rewards are not found, still fulfil exploratory motivations, which are important to the animal (Inglis et al., 2001).

In summary, our investigation on appetitive components of feeding behaviour indicate that domestic pigs, contrary to previous suggestions by Young and Lawrence (2003), do contrafreeload. In addition, the present results suggest that anticipating a reward during a

delay, rather than the variability of that delay, contributes to the "environmental uncertainty" that seems to be implicated in the reinforcing effects of contrafreeloading. And finally, it was shown that CPP may be a promising procedure in pigs to establish the pig's preference for rewards without unwanted interferences with reinforcers during testing.

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