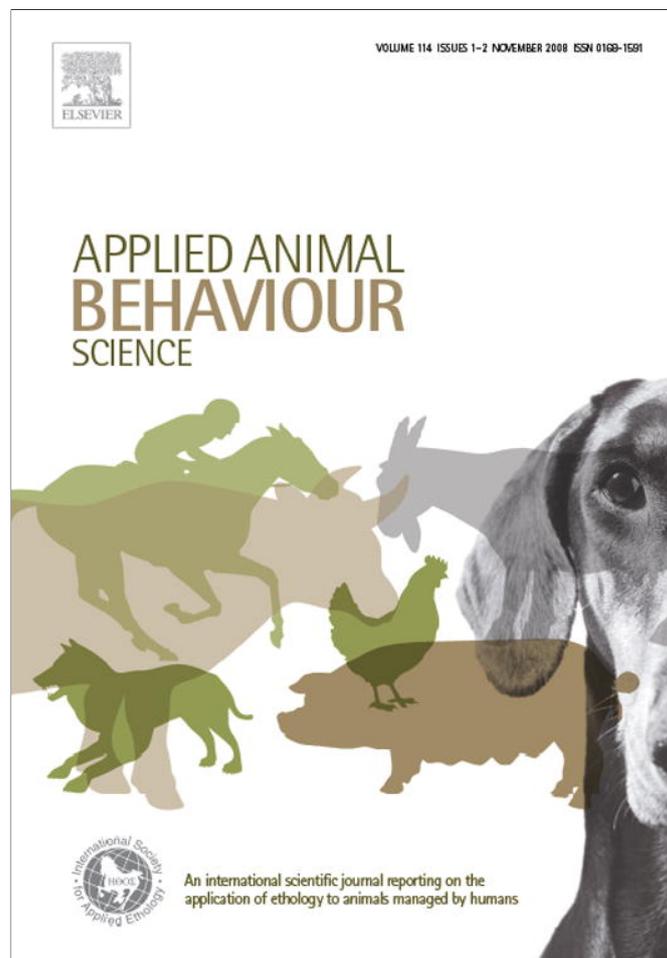


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Are pigs sensitive to variability in food rewards?

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Abstract

Pigs are non-specialist feeders with high capacities to adapt their diets within wide limits to prevailing and unpredictable conditions. Under husbandry conditions however, pigs are usually fed under extremely predictable conditions, i.e. with highly uniform and standardized diets, ad libitum or at standardized times. Although pigs, in this way, obtain their food with the lowest amount of effort and costs, studies in various different species have shown that animals may prefer to work for food, rather than receiving food for free. In addition, recent studies showed that animals may also be sensitive to risk and variance associated with food sources which may be expressed as a preference for unpredictable over predictable schedules when working for food in an operant task (risk-sensitive foraging). Since feeding is an important aspect of the daily animal husbandry routine which is likely to have a high impact on animal welfare, it is important to know whether (domesticated) pigs also prefer to work for unpredictable as opposed to predictable feeding schedules under husbandry conditions. For that purpose, nine gilts (Finish Landrace × York) were trained to respond in a two-choice operant task. In Test 1, pigs could choose between response options associated with either a FI-8 s schedule (predictable delay) or a VI-8 s reinforcement schedule (unpredictable delay). In Test 2 they could choose between choice options associated with the delivery of either a predictable food item (identical at all times) or an unpredictable food item (differing in nature across trials), delivered according to a FI-8 s schedule. Based upon natural foraging strategies of pigs it was expected that that pigs would prefer the unpredictable options in each test. However, the results from our experiment did not support this hypothesis. Factors that may influence the pig's sensitivity to variability in food rewards, are discussed.

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Keywords: Pigs; Learning; Operant conditioning; Variability; Risk-sensitive foraging; Predictability; Unpredictability; Welfare; Foraging; Feeding

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1. Introduction

The availability of food resources is seldom stable for animals in natural environments. Over the course of time particular feeding sites or prey types may change in availability, location, distance or quality. These changes are often unpredictable and may be caused by several factors, like depletion or depression by other foragers, or by seasonal or weather influences (Bateson, 2003). To cope with this problem a foraging animal is forced to explore its environment regularly to gain information about food sources (Inglis et al., 1997, 2001; Talling et al., 2002; Bateson, 2003).

Pigs (*Sus scrofa*) are omnivorous animals and are highly motivated to explore their environment. Under natural conditions, pigs do fill a substantial part of their time with exploratory and foraging behaviours like rooting, chewing and smelling (Gustafsson et al., 1999; Jensen, 2002), thereby feeding on resources that are variable both in content and spatial distribution. They are non-specialist feeders that are readily able to adapt their diets within wide limits to the prevailing conditions (Jensen, 2002; Held et al., 2004). Moreover, pigs sometimes predate on prey and a characteristic of prey is the relative unpredictability of their presence (van Rooijen, 1991). Hence, as noted by van Rooijen (1991), pigs are, to some degree, adapted to this unpredictability.

Recent studies have shown that animals are sensitive to risk and variance associated with different food sources (Roche et al., 1997; Bateson, 2002). These experiments have shown that when offered a choice between a predictable and unpredictable food source, with the same long-term rate of gain, animals will often behave either risk-prone, or risk-averse (risk-sensitive foraging theory) (Bateson and Kacelnik, 1995; Bateson, 2002). Under certain circumstances animals will prefer the unpredictable option even when the rate of reinforcement on the predictable option is higher (Bateson and Kacelnik, 1997). Unpredictable options may therefore be preferred over options for getting food with the lowest amount of costs, which would rather be predicted by optimal foraging theory (Stephens and Krebs, 1986).

Risk-sensitive foraging has been described in various taxonomic groups including insects, birds, fish and mammals (Kacelnik and Bateson, 1996). Whether animals behave risk-prone or rather risk-averse appears to depend on several factors. First, the type of variance that is associated with the feeding options appears to influence the direction of the preference. Different experiments have shown that when unpredictability is generated in the *amount* of food, animals behave more often risk-averse, whereas unpredictability that is generated in *delays* to food facilitates animals to behave risk-prone (Bateson and Kacelnik, 1995; Kacelnik and Bateson, 1997; Bateson, 2002). Secondly, the energetic status of the animal appears important. The energy-budget rule refers to the phenomenon that (especially small) animals (birds, insects), with a high metabolic rate, with a negative energy budget, which depend on the successful acquisition of a meal to survive, will generally behave risk-prone, rather than risk-averse (Bateson, 2002). Finally, the preferences of animals may depend upon the number of feeding options that are available to choose from (Bateson, 2002).

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 delivered in a highly predictable manner and often consumed in a limited amount of time. The development of oral stereotypies in pig husbandry systems, often concentrated in periods around

feeding, have been associated with these feeding procedures (Lawrence and Terlouw, 1993) and it has been concluded that the pig's behavioural need to forage will decrease only if the animal performs and experiences the consequences of both appetitive and consummatory components of feeding (Mason, 1993).

Because it is often not possible under commercial husbandry conditions to provide pigs with substrate that allows for the full expression of natural foraging behaviours, it is important to find out how different components of the foraging behaviour contribute to the pig's welfare. In addition to hypotheses that execution of the behaviour itself is intrinsically rewarding (Hughes and Duncan, 1988; Gardner and Gardner, 1988) and/or the evidence that animals prefer to “work” for food instead of getting it for free (contrafreeloading) (Inglis et al., 1997, 2001), it has been speculated that aspects of unpredictability or “surprisingness” (in terms of location of the food, type of food etc.) may contribute to the reinforcing effects of natural foraging behaviour (Wiepkema and Koolhaas, 1993; Inglis et al., 1997). One aspect of such unpredictability or “surprisingness” may include the variability in delay between searching and finding a food item under natural conditions (Inglis et al., 1997; Bateson, 2003). Another aspect of such unpredictability may include differences in nature of the food item (Day et al., 1998). Rewarding effects of unpredictability in delay to reinforcement would be in line with (a) risk-sensitive foraging theory (which predicts that animals are sensitive to variability in delay (Bateson, 2003)) (b) learning theory (which shows that variable interval reinforcement schedules have greater reinforcing power than fixed interval reinforcement schedules (Lieberman, 1993)), and (c) with recent animal welfare enrichment literature postulating that welfare would be enhanced by a predictable environment which *includes* variability in delays between the predicting stimuli (CS) and the reinforcers (US) (Bassett and Buchanan-Smith, 2007). Thus, Bassett and Buchanan-Smith (2007) in a review about the value of predictability of reinforcers for animal welfare argued that a distinction should be made between “signalled predictability” (it would be important for welfare that stimuli predict in a reliable way whether or not food is available) and “temporal predictability” (welfare would be enhanced when variability between the predicting stimulus (CS) and delivery of reward (US) would be enhanced).

Most of the choice experiments in relation to risk sensitivity are based upon experiments with rodents, birds and social insects (Lea, 1979; Lieberman, 1993; Kacelnik and Bateson, 1996). It is not well established, however, whether or not a similar sensitivity to (un)predictability is also present in (omnivorous) production animals like the domestic pig and whether it is expressed under standard husbandry conditions. This might be interesting because feeding of animals is a regular and important aspect of husbandry practice, which is likely to have a high impact on animal welfare. If preference tests reveal that pigs behave risk-prone when given the choice between unpredictable as opposed to predictable schedules of reinforcement, these results might provide caretakers with useful tools to offer food in a more welfare friendly way.

The aim of the current study was to investigate whether pigs prefer unpredictable as opposed to predictable reinforcement schedules in an operant task that was especially designed for pigs. In separate tests, this unpredictability was introduced in terms of *delays* to food and in terms of the *nature* of food rewards that could be earned. This was tested by means of a preference test for which gilts were trained to respond in a two-choice operant task.

Based on natural foraging behaviours of pigs, and based on the several different lines of evidence mentioned before, it was predicted that pigs would express a preference for the unpredictable options in our test situations.

2. Material and methods

2.1. Animal, housing and care

Nine gilts (Finish Landrace \times York), weaned at 4 weeks of age, were housed in groups of 4–5 in pens of 2.4 m \times 1.4 m according to standard housing conditions at the experimental pig farm 'de Tolakker', in Utrecht. The experiment started when the animals were 8 weeks old. In order to accommodate to increasing body size during the experiment, the gilts were moved to a larger pen (2.4 m \times 2.1 m) within the same unit at 17 weeks of age and at 20 weeks of age, they were again moved to a third pen of 3.6 m \times 2.1 m. All pens had concrete semi-slatted floors with access to a water nipple. In the first pen the gilts had ad libitum access to a conventional grower feed from 'de Heus Brokking Koudijs' (EW 1.12%, 17.7% crude protein), which was switched at 12 weeks of age to a conventional sow feed from the same company (EW 1.08%, 14.9% crude protein). This feed was also provided throughout the rest of the experiment. After their transfer to the second pen (week 17) the gilts received a restricted diet which was fed twice a day (at 7.30 a.m. and 4.00 p.m.).

Feeding troughs were always closed overnight during the nights preceding experimental testing to ensure that the feeding motivation of the gilts was maintained throughout the whole experimental testing period. Pilot experiments had indicated that overnight fasting was sufficient to motivate pigs to participate in the operant task.

2.2. Testing apparatus and experimental arena

Pens in which the experimental animals were housed opened in a concrete walkway (2.9 m \times 1.1 m). The testing apparatus was located in this walkway and consisted of a multiplex board (1.10 m \times 1.11 m) with two operant levers on both sides and a food trough in the middle. The gilts had to press the levers to receive a food reward. Using a short funnel at the back of the apparatus, food rewards were manually delivered in the trough by the experimenter. The experimenter was invisible behind the apparatus. Using two half PVC-tubes, one or both of the operant levers could be covered in case one or both levers were scheduled to be unavailable during the experiment (see below).

Animals were trained and tested individually and the experimental area was cleaned after each test. The gilts were deprived from sight from their pen mates during testing, but not from sound and smell.

2.3. Habituation to the test environment

Gilts were first habituated to the experimenter, the testing area, and the apparatus for four consecutive days. On the first habituation day, the gilts were allowed to walk and explore the experimental area with the whole group together. This was done for three periods of 10 min with intervals of at least 90 min between each period. On the three following days, gilts were individually released into the walking area for three times a day for 10 min, also with an interval between periods of at least 90 min.

2.4. Training and testing sessions

The gilts were trained and tested 1–4 times a day, depending on the time available, the animal's motivation to respond in the operant task (see below) and the stage of the experiment. Training and testing times were between 10.00 a.m. and 4.00 p.m. A testing or training session started when a gilt was brought into the experimental area and the experimenter was at the back of the apparatus. A session ended when (a) the maximum amount of food rewards was earned or (b) the gilt did not want to cooperate any further. Non-cooperation was defined as: (a) the delay between two lever presses exceeded 90 s or (b) when one or several of the following behaviours were performed on more than five occasions: walking away from the apparatus, jumping or climbing on it, lying down and chewing or pushing parts of the apparatus other than the operant levers.

Three gilts were excluded from the final tests due to more than six non-cooperative sessions in the first five testing days (two in Test 1 and one in Test 2). Data from non-cooperative sessions were excluded from the analysis. In total, less than 4% of the sessions during test procedures was excluded for this reason.

2.5. Outline of the procedure

The test procedure used in this experiment is based upon the procedure previously described by Bateson and Kacelnik (1997). In short, the gilts went through three consecutive training phases (*Training Phase I, II and III*) and subsequently through Test 1 (*choice between unpredictable and predictable delays*) and Test 2 (*choice between unpredictability as opposed to predictability in nature of rewards*). Test 1 was also followed by a Transfer Procedure for two gilts. Test 1 and the Transfer Procedure each consisted of 25 trials with inter-trial intervals of approximately 24 h, Test 2 consisted of 20 trials.

2.5.1. Training

The gilts learned to earn food rewards by lever-pressing during the three consecutive training phases. Food rewards provided to the gilts were M&M's[®] Crispy. First, in Phase I, the animals learned that food was delivered into a trough (magazine training). Criterion to complete this phase was that the interval between delivery and eating of the reward was less than 4 s. Both operants were covered during this phase. In Phase II, the gilts had to learn that they could obtain food rewards by pressing each of the operant levers. The learning criterion was that the interval between pressing and eating of the obtained reward was less than 4 s for six consecutive times. Finally, in Phase III, the gilts were trained to manipulate each of the two levers in order to obtain food rewards on a fixed interval of 8 s (FI-8 s schedule). The criterion to complete this phase was that the interval between pressing and eating the obtained reward was less than 4 s for six consecutive times. During Phase II and III, only one of the two operant levers was available. The side of the apparatus at which the gilts had to start (left or right lever) on a session was randomly chosen. After earning the first six rewards, the first lever was covered and the alternative lever became available. Hence, the maximum amount of rewards for each session was 12.

2.5.2. Test 1: choice between unpredictable and predictable delays

At the start of this test the gilts were ± 13 weeks of age. For each animal throughout this test, either the left or the right lever was assigned to the predictable option and the alternative lever with the unpredictable option. This assignment was balanced across gilts. Sessions started on even numbered days on the right side of the apparatus and on odd numbered days on the left side. The gilts were tested in a random order.

Test sessions started with a forced trial at one side with only the 'unpredictable' lever available, being followed by a forced trial at the alternative predictable side (or vice versa). Both these forced trials consisted of a single chain of six delayed reinforcements of one food reward. In each forced trial the first press against the available lever caused the delay to start and the first press after the end of the delay caused the delivery of the reward.

The predictable option consisted of six delays to reinforcement on a FI-8 s schedule (fixed interval 8 s). The unpredictable option consisted of six delays to reinforcement on a VI-8 s schedule (variable interval of 8 s on average). Each delay of the VI-8 s schedule was either short (4 s) or long (12 s) (order randomly determined). A choice trial was initiated after both forced trials. Both levers were available during this trial and for 25 s the gilts could freely respond on both levers. At the end of this 25-s period, the gilts received two food rewards irrespective of performance.

2.5.3. Transfer Procedure

After Test 1, two gilts (1303 and 1306) were subjected to a Transfer Procedure. Gilts were selected for the Transfer Procedure when their average rate of responding during the last 10 trials was $>70\%$ on either the predictable or the unpredictable option. This Transfer Procedure was run in order to control for the possibility that a preference for a specific option was location – related rather than a preference based on the preferred reward schedule. The Transfer Procedure was exactly the same as the testing procedures but this

time both sides were predictable. On the previously preferred side delays were still eight seconds (FI-8 s), but the rate of reinforcement on the previously non-preferred side were doubled (FI-4 s).

2.5.4. Test 2: choice between unpredictability and predictability in nature of rewards

At the beginning of Test 2 the gilts were ± 19 weeks of age. The procedure was identical to Test 1, except for the fact that both response options were linked to a (FI-8 s) reinforcement schedule. This time however, the *nature* of the rewards differed between both response options: for the predictable option each reward consisted of a standard reward of one M&M's[®] Crispy. For the unpredictable option, the reward could be one out of the following items (randomly chosen): (1) a piece of apple (2) a piece of carrot, (3) an almond, (4) a hazelnut, (5) a walnut, (6) a peanut, (7) a raisins, (8) sugared cornflakes or (9) an M&M's[®] Crispy. One week preceding Test 2, the gilts had been tested whether they were eager to eat all different food items, which was the case.

2.6. Variables and statistical analysis

The main dependent measure used in the statistical analysis was the number of lever presses on each of the two levers. These numbers were converted to a preference score of the form: PREF (total number of lever presses on the “unpredictable” lever/total number of lever presses on both levers). During training and testing sessions, the following parameters were also recorded (data not presented): (a) duration of each session, (b) number of rewards delivered, (c) interval between reward delivery and subsequent LP and (d) amount and type of rewards eaten. PREF was analysed by logistic regression, using a Generalized Linear Mixed Model (GLIMMIX procedure of SAS software). The logit function was used, and for each procedure intercept (PREF at start of each procedure) and slope (change in PREF as number of trails increased) were estimated. A natural logarithm transformation was used for the number of trails. Influence of each gilt on intercept and slope were added to the model as random effect, so as to account for the repeated measures for each gilt.

In order to determine individual preferences, predicted PREF and their 95% confidence intervals at the end of each test were calculated for each gilt. If the upper limit of the confidence interval was smaller than 0.5 then the gilt had a preference for the predictable reward. In case the confidence interval included 0.5 the gilt had no preference. If the lower limit of the confidence interval was larger than 0.5, then the gilt had a preference for the unpredictable reward

Other parameters were analysed with ANOVA (SAS).

2.7. Approval by the Ethical Committee

The experiment was approved by the local Ethical Committee for Experimental Animal Testing of the University of Utrecht.

3. Results

3.1. Training phases

The average number of sessions needed for completion of Training Phase I was 11 with a mean duration of 60 min. The gilts on average needed five sessions with a mean duration of 26 min to finish Phase II.

Training Phase III took on average 18 sessions with a mean duration of 132 min. The number of lever presses per reward was calculated for increasing delays and for each of the two levers. Statistical analysis of the results by an ANOVA with the factors SIDE (two levels) and DELAY (seven levels) revealed that there was a main effect of the delay on the number of lever presses ($F_{6,3} = 23.01$; $P < 0.05$), indicating that the gilts increased number of lever presses during

increasing delays. However, there was no effect of side (left or right) ($F_{1,8} = 2.068$; $P = 0.188$). A post-hoc contrast over FI-8 s separately confirmed that gilts did not show location oriented preferences in lever-press behaviour at the end of the training phase ($t = -1.520$; d.f. = 6; $P = 0.179$).

On average, the whole training procedure took 30 days. At the end of training Phase III, the gilt's mean response rate was 0.96/s.

3.2. Lever press behaviour during forced trials in Tests 1 and 2

During the forced trial part of Test 1, the animals readily came to adapt their behaviour to the reinforcement contingencies associated with each lever. This can be seen in Fig. 1 (left panel), which shows the mean number of lever presses that was made for each reward under each of the three delays. An analysis of variance (ANOVA) with Delay as single within-subjects factor revealed a significant effect ($F(2,5) = 29.49$, $P < 0.05$), reflecting that gilts made more unrewarded presses when the delay was longer (for post-hoc contrasts, see Fig. 1). However, there was no overall difference between the mean number of lever presses on the predictable and unpredictable option ($t(6) = 1.97$, $P > 0.05$).

During the forced trials of Test 2 (in which the nature of the rewards was varied), the animals made more responses on the lever that always yielded the same food item than on the lever resulting in the delivery of different types of food (Fig. 1, right panel). A t -test using the corresponding data revealed that the difference was reliable ($t(5) = 2.58$, $P < 0.05$), suggesting a stronger motivation to respond for the predictable food.

3.3. Preference for predictable and unpredictable options (PREF)

Results on PREF were analysed by a Generalized Linear Mixed Model. For that purpose the data of the response variable PREF were fitted with binomial error and logit function, using the GLIMMIX procedure of SAS Software. Intercepts and slopes were used as within-subjects factors. For Test 1, Transfer Procedure and Test 2 (three levels). Results indicate that intercepts

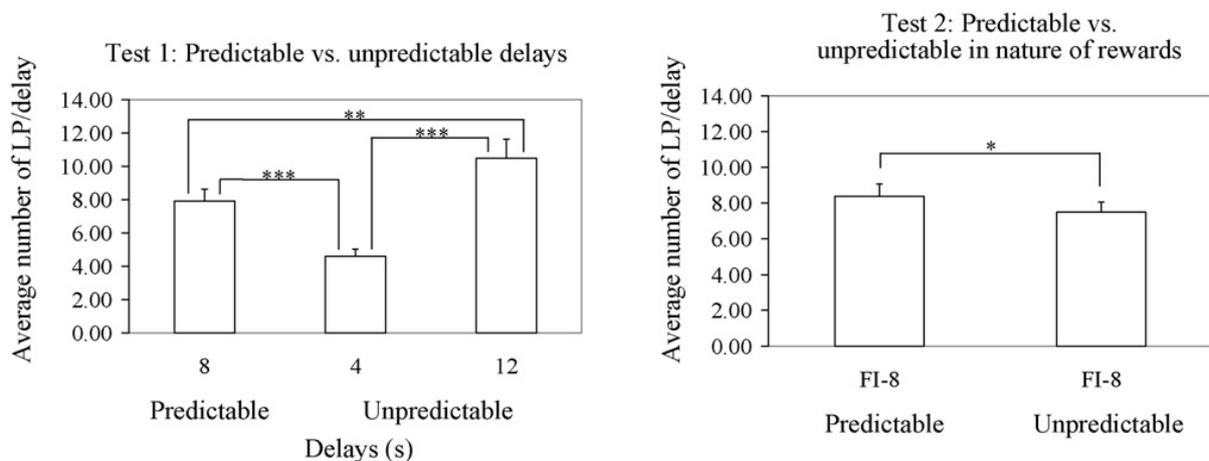


Fig. 1. Left: mean number of lever presses (LP) (\pm S.E.M.) made during each interval (8 s respectively 4 s and 12 s) under two different reward schedules (FI-8 s, VI-8 s). FI 8 s corresponded to the predictable response option, whereas VI 8 s was associated with the unpredictable response option. Right: mean number of lever presses (LP) (\pm S.E.M.) made per delay on the lever that was associated with the delivery of one type of food ('Predictable') and the lever associated with the delivery of different food items ('Unpredictable'). Food items were always delivered according to a FI-8 s schedule.

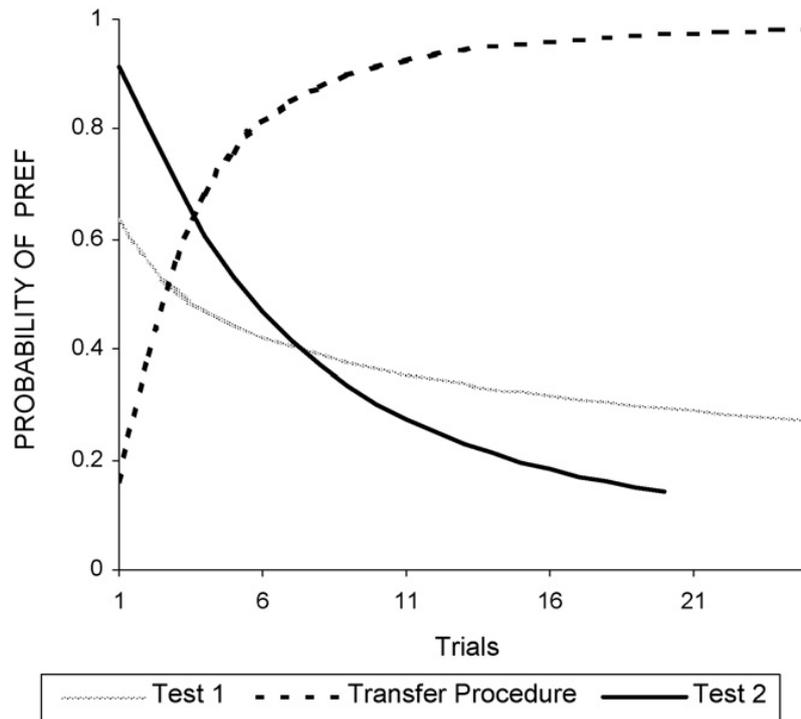


Fig. 2. Probabilities of PREF for the three different test procedures. Test 1: unpredictability versus predictability in delays to reward; Test 2: unpredictability versus predictability in nature of rewards. Higher values indicate a preference for the unpredictable option (Test 1 and 2) resp for the previously non-preferred side (Transfer Procedure).

(PREF at start of each procedure) do not differ among procedures ($F(3,6) = 3.31$, $P = 0.0990$). Results do indicate that slopes (change in PREF as number of trials increased) were different among procedures ($F(3,6) = 4.94$, $P < 0.05$). Subsequent analyses of the separate intercepts show that PREF was not different from 0.5 for Test 1 and the Transfer Procedure, but that PREF was greater than 0.5 for Test 2 (Estimate = 2.38, Standard Error = 0.90, PREF = 0.92, $t(6) = 2.64$, $P < 0.05$). Subsequent analyses of the separate slopes show that PREF did not change with number of trials for Test 1, changed marginally during the Transfer Procedure (Estimate = 1.739, Standard Error = 0.849), $t(6) = 2.05$, $P = 0.0864$), and that PREF did change with number of trials for Test 2 (Estimate = -1.40 , Standard Error = 0.55, $t(6) = -2.55$, $P < 0.05$). Predicted PREF at the end of each procedure, however, was not significantly different from 1/2. Changes in PREF-probabilities over Trials are presented in Fig. 2.

When the response variable PREF was analysed for the gilts separately, the preference criterion was based on the 95% confidence interval of the predicted PREF at the end of each procedure. This resulted in: Test 1: five out of seven animals with a preference for the predictable option, and two did not show a preference; Transfer Procedure: two out of two animals with a preference for the previously non-preferred option; Test 2; one out of six animals with a preference for the unpredictable option, four out of six with a preference for the predictable option and one did not show a preference. Results for individual preferences are presented in Table 1.

The analyses on PREF show that, contrary to our hypothesis, gilts do not prefer a reward schedule which is unpredictable in terms of delay to reward (Test 1). In addition, and also contrary to our hypothesis, they changed their initial preference from a reward schedule with unpredictability in nature of rewards towards a reward schedule with predictability in nature of reward (Test 2).

Table 1
Preference for different options in Test 1, the Transfer Procedure and Test 2

Pig	Unpredictable side	PREF	95% confidence interval		Preference
			Estimate	Lower	
Test 1: unpredictable versus predictable delays					
1299	Left	0.43	0.36	0.49	Predictable
1302	Left	0.36	0.29	0.43	Predictable
1303	Left	0.22	0.17	0.28	Predictable
1304	Left	0.48	0.41	0.54	No preference
1305	Right	0.47	0.40	0.53	No preference
1306	Right	0.02	0.01	0.04	Predictable
1324	Right	0.40	0.31	0.49	Predictable
Transfer Procedure					
1303	Left	0.98	0.96	0.99	Shift to previously non-preferred side
1306	Right	0.85	0.81	0.89	Shift to previously non-preferred side
Test 2: unpredictable versus predictable nature of rewards					
1299	Left	0.44	0.36	0.52	No preference
1302	Right	0.15	0.10	0.20	Predictable
1303	Left	0.08	0.05	0.13	Predictable
1304	Right	0.97	0.95	0.99	Unpredictable
1305	Left	0.00	0.00	0.00	Predictable
1306	Right	0.05	0.03	0.08	Predictable

The criterion for a preference for predictability was that the estimated PREF (GLIMMIX) had an upper limit of the confidence interval smaller than 0.5. Alternatively, the criterion for a preference for unpredictability was that the estimated PREF had a lower limit of the confidence interval larger than 0.5.

4. Discussion

In this experiment the preferences of pigs for unpredictability versus predictability were investigated in relation to delays to food reward and in terms of the nature of food rewards. Based upon their natural foraging behaviour, predictions from risk-sensitive foraging theory (Bateson, 2002) and suggestions that aspects of unpredictability or “surprisingness” during natural foraging may be rewarding (Wiepkema and Koolhaas, 1993; Inglis et al., 1997), it was hypothesized that pigs would prefer the unpredictable options. However, the present results did not support this hypothesis: contrary to our hypothesis, our data show that gilts do not prefer a reward schedule which is unpredictable in terms of delay to reward (Test 1). In addition, a preference for the unpredictable option was also not found in Test 2, in which predictability and unpredictability in the nature of the food items was varied.

It is important to note that preferences made by the animals were not based upon location related choices. First of all, it was shown at the end of the third training phase, that there was not a significant difference between the number of lever presses on the left or right side of the apparatus. In addition, it was shown in Test 1 that there were no significant differences between number of lever presses on both sides of the apparatus. Finally, it was shown during the Transfer Procedure, which was subjected to gilts with a marked preference at the end of Test 1, that gilts readily switched to the previously non-preferred side when the reinforcement rate on the previously non-preferred side was increased. All together, these results indicate that only the nature of the reinforcement schedule influenced choice behaviour of the gilts in our experiment.

Absence of a preference for the unpredictable delay in Test 1 was unexpected. Variable schedules of reinforcement have repeatedly been shown to have more reinforcing power than fixed schedules of reinforcement do. Thus, schedules with unpredictable interval durations typically produce higher and more constant rates of responding compared to fixed schedules (Rice, 1988; Lieberman, 1993). Moreover, unpredictable options were preferred over predictable options in a choice situation in several species (Kacelnik and Bateson, 1996; McSweeney et al., 2003).

In Test 2, we investigated whether gilts prefer to respond on an operant associated with unpredictability in *nature* of reinforcement. Prior to the experiment, it was verified that gilts were eager to eat all food items. In this experiment, gilts initially preferred the unpredictable option. However, they readily switched their preference in the direction of the predictable option with the M&M's[®] over the unpredictable option with various different food rewards. Moreover, the mean number of lever presses per delay was higher for the predictable than the unpredictable option.

However, it remains unclear whether the preference for the predictable option reflects a preference for predictability in food as such, or simply reflects a better palatability or energy content of the M&M's[®] crispies compared to the presented mix of food rewards.

The results of the present study are not in line with prevailing evidence showing that animals tend to behave risk-prone in response to variability in delay (reviewed in Kacelnik and Bateson, 1996). However, almost none of the relevant investigations (except some studies in rats) concern studies in domestic mammals. According to Andersson et al. (2001) and Jensen (2006) it is likely that domesticated animals that are provided with food and protection, and are selected for specific traits, may have other optimal behavioural strategies compared to their wild ancestors that have to deal with unpredictable situations where food is scarce and predation pressures are high. Indeed, an experiment of Gustafsson et al. (1999) showed that domestic pigs use different foraging strategies compared to their wild counterparts during food search. In one recent study investigating contrafreeloading in pigs, Young and Lawrence (2003) failed to find evidence for contrafreeloading in pigs and also failed to find evidence in that study for increased responding on an unpredictable option (variable ratio schedule as opposed to a fixed ratio schedule).

Other recent studies in our department using dogs and goats (de Jonge et al., 2004, 2005) revealed large individual differences in the direction of preferences for (un)predictable options (in delays to reinforcement): about 1/3 of the dogs and goats preferred the predictable option, 1/3 preferred the unpredictable option, and 1/3 were indifferent. Marked individual differences could also be observed in the present investigation: thus, in Test 2, pig 1304 strongly preferred to work for different food items, while pigs 1302, 1303, 1305 and 1306 strongly preferred the M&Ms and 1299 did not show a preference at all. At this time however, we do not know which factors may underly individual differences in preferences for predictable as opposed to unpredictable options.

Under the present test conditions, our results tend to support the idea that unpredictability is not important for gilts. However, it should be stressed that our results do not warrant a generalized conclusion in this respect. A number of qualifications to this conclusion should be mentioned. First, our test situation provides a highly artificial situation that may not correspond at all to the gilt's need for unpredictability associated with foraging behaviour in more natural situations (see also Lea, 1979). Second, it is possible that our gilts, which were reared in standard, barren production environments, have to "learn" to appreciate the rewarding properties associated with unpredictability. In this regard it is of some importance to mention that studies in rats have shown that being reared in environments without opportunities to play may attenuate the sensitivity to both social and non-social rewards in general (van den Berg et al., 1999). Third, since our pigs were food-deprived overnight before testing, a shift towards a preference for predictable as

opposed to unpredictable rewards may be expected according to the “energy-budget-rule” (Bateson, 2002). Finally, pigs may prefer a predictable option in a choice situation in which direct rewards can be earned, while unpredictable options may contribute more to an overall improvement of welfare on the long run (see also Fraser et al., 1997). The present results therefore illustrate that risk-sensitive foraging does not necessarily provide an adequate picture of the proximate control of preferences for unpredictability (Bateson and Kacelnik, 1997) and they illustrate that the animal’s supposed preference for a certain degree of unpredictability (Inglis et al., 1997; Wiepkema and Koolhaas, 1993) needs more extensive investigation before it can more precisely be determined what (un)predictability is actually desired.

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