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ORIGINAL PAPER

Decision-making under risk and ambiguity in low-birth-weight pigs

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Abstract Low birth weight (LBW) in humans is a risk factor for later cognitive, behavioural and emotional problems. In pigs, LBW is associated with higher mortality, but little is known about consequences for surviving piglets. Alteration in hypothalamic–pituitary–adrenal axis function in LBW pigs suggests altered emotionality, but no behavioural indicators have been studied. Decision-making under uncertain conditions, e.g., risk or ambiguity, is susceptible to emotional influences and may provide a means of assessing long-term effects of LBW in piglets. We tested LBW ($N = 8$) and normal-birth-weight (NBW; $N = 8$) male pigs in two decision-making tasks. For decision-making under risk, we developed a simple two-choice probabilistic task, the Pig Gambling Task (PGT), where an 'advantageous' option offered small but frequent rewards and a 'disadvantageous' option offered large but infrequent rewards. The advantageous option offered greater overall gain. For decision-making under ambiguity, we used a Judgement Bias Task (JBT) where pigs were trained to make an active response to 'positive' and 'negative' tone cues (signalling large and small rewards, respectively). Responses to ambiguous tone cues were rated as more or less optimistic. LBW pigs chose the advantageous option more often in later blocks of the PGT, and were scored as less optimistic in the JBT, than NBW pigs. Our findings demonstrate that LBW pigs have developed different behavioural strategies with respect to decision-making. We propose that this is guided by changes in emotionality in LBW piglets, and we provide behavioural evidence of increased negative affect in LBW piglets.

Keywords Pig · Decision-making · Judgement bias · Risk · Birth weight · Animal welfare

Introduction

In humans, children who are considered small for gestational age at birth are at greater risk of cognitive impairments in later life, such as impairments in learning and attention (O'Keeffe et al. 2003), academic performance (Strauss 2000) and executive function (Anderson and Doyle 2004). Low birth weight (LBW) is also a risk factor for later behavioural and emotional problems (Hayes and Sharif 2009) such as trait anxiety (Lahti et al. 2010), attention-deficit hyperactivity disorder (Mick et al. 2002) and depression (Raikkonen et al. 2008).

In pigs, *Sus scrofa*, as a consequence of the selection pressure for larger litter sizes, there has been an increase in the birth of LBW piglets (Quiniou et al. 2002). LBW in pigs has mostly been studied with regard to production outcomes; LBW pigs have higher mortality rates (Milligan et al. 2002; Quiniou et al. 2002). However, little is known about the behavioural, emotional and cognitive development of LBW piglets. Gieling et al. (2011) have

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demonstrated that LBW piglets showed delayed reversal learning in a spatial holeboard task, a finding that was not, however, confirmed in a subsequent study (Gieling 2013). LBW has been shown to affect how the hypothalamic–pituitary–adrenal (HPA) axis functions in pigs, possibly leading to long-term augmented stress reactivity (Rutherford et al. 2013). Repeated negative experiences can induce more negative long-term mood states (Mendl et al. 2010a), which can influence decision-making when outcomes are uncertain (Mendl et al. 2009). However, Rutherford et al. (2013) suggest that behavioural measures of altered emotionality are necessary before drawing conclusions about the welfare consequences of alterations in HPA axis activity in LBW in pigs.

Many theoretical models of personality differences in animals propose that inter-individual variation arises from differences in state (state differences may refer to morphology, physiology, neurobiology or environment), which lead to adaptive behavioural responses (Dingemanse and Wolf 2010). LBW pigs differ in morphology, physical size and physiology (see above), compared to their siblings which, according to these models, ought to lead to consistent differences in behaviour. For example, McElreath and Strimling (2006) suggest that when environmental cues about the risk of predation are 'noisy' or unclear, smaller individuals, who may be more at risk, ought to be more cautious about foraging, while larger individuals, who may be less at risk, may be less cautious. While LBW piglets on farms may not be at risk of predation, they are in constant competition with their larger siblings (Milligan et al. 2002) and thus may develop different behavioural strategies in order to adapt.

Animals constantly have to make decisions throughout their daily life, and to make adaptive decisions, the costs and benefits of each option should be evaluated (Sugrue et al. 2005). Both internal factors (e.g., current need, past experience, emotion) and external factors (e.g., environmental conditions, time constraints) can influence this evaluation process. Normally, decisions are made under uncertain conditions (Kacelnik and Bateson 1997), which can be divided into decisions involving risk (where the probability of each outcome is known) and decisions involving ambiguity (where the outcome is unknown) (Bechara et al. 2005; Krain et al. 2006). There is evidence supporting the notion that the two processes, decision-making under ambiguity (judgement) and decision-making under risk, involve different neural substrates (Krain et al. 2006).

Decision-making is not just about making rational choices. Recent research has distinguished between 'cold' decision-making involving cognitive reasoning and 'hot' decision-making that is influenced by affective processes (Peters et al. 2006). Decisions made under uncertain conditions may be more susceptible to emotional influences. In human research, anxiety is associated with mood-congruent biases in decision-making and judgement (Hartley and Phelps 2012; Blanchette and Richards 2010); higher anxiety increases risk aversion and pessimistic judgements of ambiguous stimuli. However, positive mood may also increase risk aversion, whereas the valence of an emotional state (positive/negative) has a more congruent effect on judgement of ambiguity (Mendl et al. 2009; Blanchette and Richards 2010).

In animal studies, the effect of risk on decision-making has been more widely studied than the effect of ambiguity. In typical decision-making tasks, animals choose between two options with the same overall gain, a consistent 'safe' option or a 'risky' option, where risk is manipulated by varying the amount of reward, the time delay until reward or the probability of a reward occurring. Risk-prone individuals prefer the risky option, while risk-averse individuals prefer the safe option (Mazur 1988), although the means by which the risk is manipulated can influence these preferences (Kacelnik and Bateson 1996). More recently, rodent models of the Iowa Gambling Task (Bechara et al. 1994) have looked at decision-making where the overall gain of the 'safe' option (predicting small but frequent rewards) is greater than that of the risky option (predicting large but infrequent rewards) (van den Bos et al. 2006; Homberg et al. 2008; Koot et al. 2010). Interestingly, when the safe option offers greater overall gain, anxiety has been found to lead to more risk-prone behaviour, in both human and rodent models of the IGT (Miu et al. 2008; De Visser et al. 2010, 2011), while positive mood results in earlier choices for the safe option (de Vries et al. 2008). Some studies report that low birth weight in human infants is associated with lower risk-taking behaviours in later life (Hack et al. 2002, 2004; Schmidt et al. 2008); however, in these studies it is difficult to separate out effects of prematurity from birth weight.

Due to the more congruent findings on the effect of emotion on decision-making involving ambiguity, judgement bias has been proposed as a means to study emotional valence in animals (Paul et al. 2005; Mendl et al. 2009; Harding et al. 2004). Typical studies involve training subjects to discriminate a 'positive' cue (predicting a positive or favourable outcome) from a 'negative' cue (predicting a negative or less favourable outcome). Next, unfamiliar 'ambiguous' cues are presented and responses to these cues are rated as 'optimistic' if they resemble responses to the positive cue, i.e. indicative of expectation of favourable outcome, or 'pessimistic' if they resemble responses to the negative cue, i.e. indicative of expectation of less favourable outcome. Within this framework, optimistic and pessimistic responses are used as a proxy indicator of positive and negative emotional states, respectively. A number of studies in a variety of species have demonstrated that presumed positive situations lead to more optimistic judgements of ambiguous stimuli, e.g., enrichment (Brydges et al. 2011; Douglas et al. 2012), while others have shown that presumed negative situations lead to more pessimistic judgements, e.g., pain (Neave et al. 2013) and separation anxiety (Mendl et al. 2010b).

To study whether LBW piglets have developed different behavioural strategies, and whether these strategies are indicative of altered emotionality, the current experiment aimed to compare decision-making under risk and ambiguity in LBW piglets to normal-birth-weight (NBW) sibling controls in two tasks. To look at decision-making under risk, we developed a simple two-choice probabilistic decision-making task, the Pig Gambling Task (PGT), where the 'safe' option offered slightly greater overall gain. To look at decision-making under ambiguity, we tested the same pigs in an active-choice Judgement Bias Task (JBT) similar to that we have previously used with adult pigs (Murphy et al. 2013b), where responses to ambiguous tone cues were rated as more or less optimistic. We expect that LBW pigs should show more risk aversion than NBW pigs and that if LBW pigs demonstrate altered emotionality compared with NBW pigs, they should show a more pessimistic bias towards ambiguity.

Methods

Ethical note

The study was reviewed and approved by the local ethics committee of Utrecht University, The Netherlands, and was conducted in accordance with the recommendations of the EU directive 86/609/EEC. All effort was taken to minimize the number of animals used and their suffering.

Subjects and housing

We used 16 male piglets (cross-breeds Duroc × Yorkshire and Duroc × Danish Landrace) bred at the farm of the Faculty of Veterinary Medicine of Utrecht University. We selected eight male LBW piglets and eight male NBW piglets according to the criteria of Gieling et al. (2011), as follows. All pigs from nine sows were weighed within 12 h of birth. Pigs weighing at least 1 SD less than the litter mean were considered LBW. NBW pigs were those closest to the litter mean when all pigs classified as LBW were excluded. Only 7 of these litters contained suitable LBW piglets, so we selected one of each LBW and NBW piglets from 6 litters and two of each LBW and NBW from 1 litter.

Pigs remained in their litter groups and were weaned at 4 weeks. Some non-experimental siblings were cross-fostered shortly after birth to make litter numbers more even, standard procedure at the breeding unit. At 5 weeks of age, subjects were moved into the research facility and housed in two straw-bedded pens (5 × 3 m). Each pen contained four LBW piglets and four NBW piglets. Sibling piglets were housed in separate pens (except in the case of the four piglets from one sow in which case one LBW and one NBW piglet were housed in each pen). Each pen contained a nest area and was provided with toys for enrichment. Water was available ad libitum, and animals were not food restricted. Instead, they received 25 % of their normal allowance in the morning before testing and the remaining 75 % in the afternoon, after all pigs had been tested. Pigs were weighed regularly to monitor weight gain.

Apparatus

The same apparatus was used for both the PGT and JBT (Fig. 1a). A start box (1.2 m^2) was connected via an antechamber (1.2 m^2) to the test arena (3.6 m × 2.4 m). In the test arena were two goal boxes, each of which contained a food bowl covered by a large, hard-plastic ball. The ball could be raised off the bowl but not knocked off. Guillotine doors were operated remotely by the experimenter controlled access to the test arena and goal boxes. In both the PGT and the JBT, the swing-doors between the antechamber and test arena were kept fully open. In the PGT, the goal boxes were used purely as response points, while in the JBT, the goal boxes were both response points

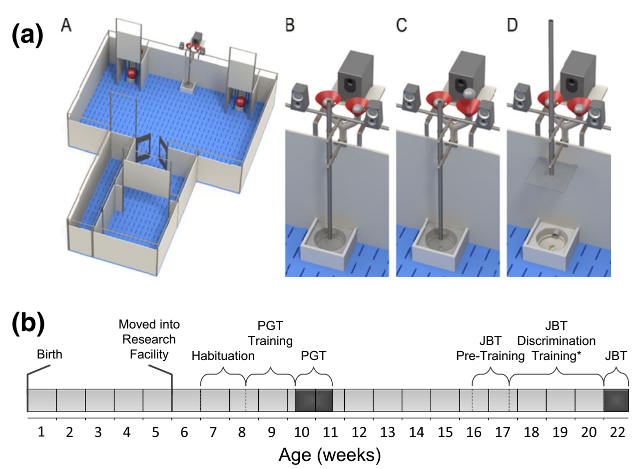

Fig. 1 **a** Design of experimental apparatus used for both the PGT and the JBT, highlighting the food delivery system used in the PGT to render rewards accessible or inaccessible, **b** Experimental timeline. *Asterisk* while the number of sessions necessary to learn the tone discrimination in the JBT varied between individuals, here we present mean number of sessions required by all pigs

and reward points. Rewards used in both experiments were chocolate M&M's® (Mars Nederland b.v., Veghel, The Netherlands).

In the PGT, a food delivery system allowing for delivery of large or small rewards, which could be rendered accessible or inaccessible, was located on the back of the test arena, equidistant from each goal box (see Fig. 1a). Rewards were placed in two funnels connected to a Y-shaped delivery pipe attached at the back of the apparatus, which fed into a food bowl in the test arena. The experimenter controlled the release of rewards from either funnel into the food bowl. The food bowl was covered by a transparent perforated Perspex lid that could only be raised or lowered by the experimenter. With this system, a number of cues indicated to the pig that rewards were present in the food bowl—the sound of the M&M's dropping down the reward delivery tube into the central food bowl provided auditory cues, while the lid allowed both olfactory and visual cues.

In the JBT, the central food bowl was not used and was permanently covered with the lid. Instead, rewards were placed directly in each goal box. Tone cues, generated using the open source software audacity (http://audacity.sourceforge.net/), were used to signal which goal box was rewarded. The training tone cues used were a 200 and a 1,000 Hz pure tone (Waveform: Sine; Amplitude: 1), while the ambiguous tone cues were 299.07, 447.21 and 668.74 Hz pure tone (Waveform: Sine; Amplitude: 1). The tone cues were played using an MP3 player (Archos 18 Vision, 4 GB, Archos GmbH, Grevenbroich, Germany) via speakers (Logitech z-313, Logitech Europe S.A., Morges, Switzerland) attached at the back of the testing arena (Fig. 1a). For an overview of the experimental timeline, see Fig. 1b.

Habituation

After arrival in the research facility, pigs were left to settle undisturbed for 1 week. Over the following 3 days, pigs were habituated to the presence of the experimenter and to the rewards. Next, over 5 days, pigs were habituated to the testing apparatus, initially in large groups of eight piglets (four sessions), then in smaller groups of four animals (four sessions), of two animals (eight sessions) and finally individually (four sessions). Each session lasted approximately 3 min during which the pigs were allowed to explore the apparatus. Rewards were placed in front of each goal box and periodically dropped into the central food bowl so that pigs learned to associate the sound of food delivery with the availability of rewards in the central food bowl. Pigs were deemed ready for training after this procedure as all rewards were consumed during habituation sessions.

Pig Gambling Task training

Pigs were shaped to perform an active response in each goal box in order to receive rewards in the central food bowl. They were trained to move the ball in either goal box to obtain rewards in the central food bowl. To keep the response simple, any lift/push of the ball with enough force to cause the ball to move was considered a 'choice' and resulted in the delivery of reward. In early sessions, some rewards were placed underneath the ball in order to reinforce interactions with the ball. The shaping process was performed over 12 sessions (3 days). Pigs were first trained to approach the goal boxes in order to receive reward in the central food bowl. As sessions progressed, pigs were increasingly only rewarded after touching and then pushing/lifting the balls in either goal box. Each session consisted of ten rewarded actions. All pigs underwent the same training procedure after which they were consistently nudging the ball in each goal box order to obtain rewards in the central food bowl.

Over two further sessions of ten trials each (1 day), pigs were trained to return to the start box after each choice, once rewards had been consumed, before commencing the next trial. At this point, the lid was placed on the central food bowl and, while rewards were delivered immediately after a choice was made, the lid of the food bowl was only raised by the experimenter when the pig was within 20 cm and facing towards the bowl.

Next pigs were taught that both goal boxes would yield a reward in two sessions of 20 'forced' trials (2 days), where only one goal box was available per trial. Left and right goal boxes were available in a pseudorandom order with a maximum of two consecutive presentations of the same goal box. Two rewards were delivered in each trial. Since in a pilot study we encountered the problem that pigs did not appear to sample from both options, we gave all pigs a third session of 20 trials where choices in advantageous and disadvantageous goal boxes were rewarded with two and four rewards, respectively. Advantageous and disadvantageous goal boxes were counterbalanced across LBW and NBW pigs.

Pig Gambling Task

Over six blocks of 20 trials each (one block per day, total: 120 trials), pigs could choose freely between left and right goal boxes. While a choice in either goal box resulted in the delivery of reward into the central food bowl, the quantity and accessibility of reward were governed by a predetermined schedule. A choice for the advantageous goal box yielded small quantities of reward (two chocolate M&M's), but had a high probability that the rewards would be made accessible (eight 'wins' in every ten trials), i.e. a potential total of 16 rewards per 10 trials. A choice for the disadvantageous goal box yielded higher quantities of reward (four chocolate M&M's), but there was a low probability of the rewards being made accessible (three 'wins' in every ten trials), i.e. a potential total of 12 rewards per 10 trials. These reward and probability contingencies were previously used in a rodent model of decision-making (Koot et al. 2010).

In win trials, rewards were delivered into the food bowl immediately after a choice was made. When the pig was in position in front of the central food bowl, the lid was raised giving access to the rewards within. In loss trials, rewards were also delivered after a choice was made, but the lid remained closed, rendering the reward inaccessible. In both win and loss trials, pigs were allowed to return to the start box for the next trial 25 s after making a choice. The order of wins and losses differed daily, but the probability of wins and losses remained the same within each series of ten trials. The number of choices for the advantageous goal box was recorded per pig for each of the six blocks of 20 trials.

Judgement Bias Task: pre-training

After a 5-week break where pigs were left undisturbed, training for the JBT began. As the pigs were already familiar with the apparatus, we were able to start with training for the JPT without any habituation sessions. Pigs were trained, similar to the method used by Murphy et al. (2013b), to associate one training tone with the availability of a large reward (four chocolate M&M's) in one goal box, while the second training tone predicted the availability of only a small reward (one chocolate M&M's) in the other goal box. In this way, one training tone and its associated goal box were labelled 'positive', while the second training tone and associated goal box were labelled 'negative'. Only one goal box was rewarded per trial, and the meaning (positive/negative) of training tones (200/1,000 Hz) and goal boxes (right/left) was counterbalanced across animals. Furthermore, advantageous and disadvantageous goal boxes from the PGT were counterbalanced as positive and negative goal boxes for the JBT for both LBW and NBW pigs. Each pig received one training session per day, and the order of positive and negative trials differed daily in a pseudorandom order with no more than two consecutive presentations of the same tone cue.

We commenced training with four sessions of 'forced' trials (5 positive; 5 negative) where only the correct goal box was available, as predicted by the tone cue, and the associated quantity of reward was available in the goal box. Pigs were brought into the start box, and after a couple of seconds, a tone cue was played. After 1 s of tone cue, the guillotine door between start box and antechamber was raised and the pigs were freely able to enter the antechamber and test arena for 60 s. The tone cue was stopped once a correct response was performed, i.e. a pig had gained access to the rewards present in the goal box. Following this, pigs received three sessions of 'open-choice' trials. Each session consisted of 13 trials: three forced trials (1 positive; 2 negative), as before, and ten 'open-choice' trials (5 positive; 5 negative) in which both goal boxes were available, but only the correct one, as predicted by the tone cue, was rewarded. In open-choice trials, pigs were allowed to choose from both goal boxes until they found the reward so that they could learn that there was always a reward available.

Judgement Bias Task: discrimination training

In the final stage of training, pigs were trained until they demonstrated that they had learned to discriminate the positive and negative training tone cues. Each session consisted of 13 trials; three forced trials (1 positive; 2 negative), as before, and ten free trials (5 positive; 5 negative), where only a correct choice (a choice for the goal box predicted by the tone cue within 30 s) was rewarded. If a correct choice was made, both goal boxes remained open, and once the reward was consumed, the pig was returned to the start box. Incorrect choices or response omissions (failure to respond within 30 s) resulted in both goal boxes being closed and the pig remained in the test arena for a 90 s time-out penalty before commencing the next trial. To qualify for testing, pigs had to respond correctly in 80 % of negative and 80 % of positive free trials in three consecutive sessions.

Judgement Bias Task

Once a pig had reached the learning criterion, it was tested in the JBT over four sessions, one session per day. Test sessions consisted of 16 trials: three forced and ten free trials, as before, along with three ambiguous trials (Trials 6, 11 and 16). In an ambiguous trial, one of the three ambiguous tone cues (termed: 'AmbigNeg', 'AmbigMid', 'AmbigPos' depending upon their relationship to the negative and positive training tone cues) was played instead of a training tone cue for 30 s, and both goal boxes contained their associated quantity of rewards (i.e. one M&M in the negative goal box and four M&M's in the positive goal box). We have previously demonstrated that pigs learn very quickly when ambiguous cues are unrewarded and have suggested that this learning can be slowed down by providing the rewards expected by the pig (for discussion see Murphy et al. 2013b). Each ambiguous cue was presented four times (once per test session). The AmbigMid cue was always presented first each session, while the other two ambiguous cues were presented in a counterbalanced order. The order of trials in test sessions were balanced such that pigs had equal numbers of presentation of positive and negative tone cues before presentations of each ambiguous tone cue.

Saliva sampling

For each pig, in the mornings before test sessions one and two of the JBT, salivary cortisol samples were taken. Pigs were allowed to chew on cotton swabs (Heinz Herenz, Hamburg, Germany, Cotton Swabs 150x4 mm WA 2PL) for 60 s until the swabs were wet through. Two samples were taken per pig and placed in centrifuge tubes (Salivette, Sarstedt, Germany) that were then labelled and refrigerated before transportation to the laboratory. Tubes were then centrifuged at 3,000*g* for 5 min, and the saliva was pipetted into Eppendorf tubes and stored at −20 °C until cortisol could be measured. Cortisol concentrations were measured using a Coat-a-Count radioimmunoassay, according to the manufacturer's procedure (Coat-a-Count cortisol TKCO, Diagnostic products cooperation, Apeldoorn, the Netherlands).

Data recording and analysis

Analyses were carried out using R version 3.0.2, using the package lme4 (Bates et al. 2012). From this library, the functions lmer and glmer were used for the model fitting, the function boot for the bootstrap intervals and the function MuMIn for information-theoretic model selection (AIC). Correlational analyses were carried out using SAS 9.4 (SAS Institute, Cary, NC).

Birth weight

To monitor weight development, we compared weights at birth, following performance of the PGT, and following performance of the JBT between LBW and NBW piglets. A linear model for the weight with random litter and pigs-within-litter effects was used. Weight-Group (NBW, LBW), Time-Point (Birth, Post-PGT, Post-JBT) and the interaction between weight-group and time-point were included as fixed effects in the model.

Pig Gambling Task

The number of choices for the advantageous option was calculated per pig for each block of 20 trials. 'Advantageous Choice' was analysed using a logistic regression model with random litter effects and random pig-within-litter effects. Birth-weight category (LBW/NBW), Block (1–6) and the interaction between birth-weight category and block were included as fixed effects in the model. To see which of these fixed effects were important, different models with different fixed effects were fitted and compared using akaike's information criterion (AIC), based on information theory whereby the model with the lowest AIC value represents the best approximation, i.e. the model in which the least information is lost (Symonds and Moussalli 2011; Burnham and Anderson 2002). For all fixed effects that were important according to the AIC, confidence intervals were calculated using the parametric bootstrap with 1,000 bootstrap samples.

To get an overall measure of decision-making under risk ('Adv. Choice Preference'), orthogonal trend components of the changes over blocks were calculated per animal.

Judgement Bias Task

Judgement bias

Analyses were carried out using R version 3.0.2. The percentage of choices for the positive goal box ('Optimistic Choice') was calculated for each cue type (Negative, AmbigNeg, AmbigMid, AmbigPos, Positive) in test sessions. Optimistic Choice was analysed using a logistic regression model with random litter effects and random pig-within-litter effects. Birth-weight category (LBW/NBW), cue type (Negative, AmbigNeg, AmbigMid, AmbigPos, Positive) and the interaction between birth-weight category and cue type were included as fixed effects in the model. To see which fixed effects were important, different models with different fixed effects were fitted and compared with AIC. For all fixed effects that were important according to the AIC, confidence intervals were calculated using the parametric bootstrap with 1,000 bootstrap samples.

As an overall measure of judgement bias, the mean area under the curve ('Mean AUC') was also calculated per pig as

$$\text{Mean}\left[\left(\frac{\text{Neg} + \text{AmbigNeg}}{2} + \frac{\text{AmbigNeg} + \text{AmbigMid}}{2} + \frac{\text{AmbigMid} + \text{AmbigPos}}{2} + \frac{\text{AmbigPos} \ + \text{Pos}}{2}\right)\right]$$

Latency

In test sessions, the mean latency (s) to respond to each cue type in free trials was calculated per pig. A linear mixed effects model was used on the $\log_{10}$ transformed latency values with random litter effects and random pig-within-litter effects. Birth-weight category (LBW/NBW), cue type (Negative, AmbigNeg, AmbigMid, AmbigPos, Positive) and the interaction between birth-weight category and cue type were included as fixed effects in the model. To see which fixed effects were important, different models with different fixed effects were fitted and compared with AIC. For all fixed effects that were important according to the AIC, confidence intervals were calculated using the parametric bootstrap with 1,000 bootstrap samples.

Cortisol

Cortisol measurements from the mornings before test session, one and two were combined to get a 'Mean Cortisol' value for each pig. To check for differences between LBW and NBW pigs, we used a linear model on the Log Mean Cortisol, with random litter effects and fixed birth-weight effect. Mean Cortisol was added to the Optimistic Choice model to see whether cortisol levels were an important predictor of Optimistic Choice.

To test for any relationship between cortisol and overall performance in the JBT, Mean Cortisol was compared with Mean AUC using Spearman's correlations conducted separately for LBW and NBW pigs.

Decision-making under risk and under ambiguity

To check whether performance in the JBT predicted performance in the PGT, Mean AUC from the JBT was added to the PGT model. Furthermore, to test for any relationship between overall performance on the PGT and the JBT, Adv. Choice Preference (PGT) was compared to Mean AUC (JBT) using separate Spearman's correlations for LBW and NBW pigs.

Results

All descriptive statistics are presented as mean + SEM.

Birth weight

LBW piglets weighed 1.17 ± 0.08 kg at birth, while NBW piglets weighed 1.64 ± 0.08 kg. At the end of the PGT, LBW pigs weighed 34.00 ± 2.35 kg, while NBW pigs were 40.88 ± 2.07 kg. After completion of the JBT, LBW pigs weighed 109.63 ± 5.70 kg, while NBW pigs were 122.63 ± 2.96 kg (see Fig. 2). The full model with both main effects and the interaction had an AIC of 344.76. The linear model with only the main effects, i.e. without the interaction, had a higher AIC of 348.10, indicating that the interaction is important as the model including the interaction had the lowest AIC. Although the 95 % bootstrap intervals would suggest that that the groups did not differ in birth weight (lower: −6.88, upper: 5.77), it is likely that the difference we specifically selected subjects for is not picked up by this model due the small differences between the groups relative to the differences at later time points. LBW pigs remained lighter than NBW pigs when weighed after performance of both the PGT (lower: −13.07, upper: −0.40) and the JBT (lower: −19.65, upper: −6.89).

Pig Gambling Task

All pigs made the required 20 choices per block of trials. Figure 3 shows the percentages of Advantageous Choice as a function of birth weight and trial blocks. The full model, the model with both main effects and the interaction, had an AIC of 714.70. The logistic regression model with only

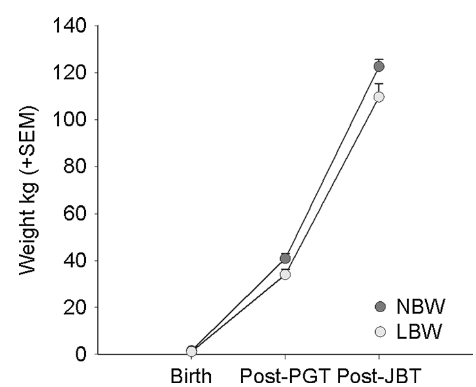

Fig. 2 Weight development of LBW and NBW pigs

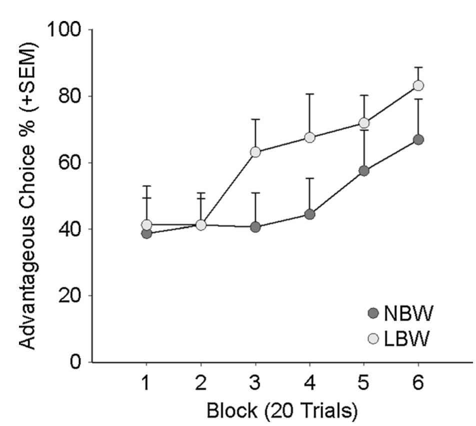

Fig. 3 Percentage of Advantageous Choice per block of 20 trials for LBW and NBW pigs in the PGT

Table 1 The 95 % parametric bootstrap intervals for the difference in Advantageous Choice between LBW and NBW piglets

Block	Lower (5 %)	Upper (95 %)
1	−0.558	1.143
2	−0.763	1.066
3	0.330[a]	2.205[a]
4	0.338[a]	2.196[a]
5	−0.082	1.759
6	0.134[a]	2.020[a]

[a] Blocks where LBW pigs had a higher Advantageous Choice than NBW pigs

the main effects, i.e. without the interaction, had a higher AIC (721.70), indicating that the interaction is important as the model including the interaction had the lowest AIC. Looking at the 95 % parametric bootstrap intervals (Table 1) shows that LBW pigs made more Advantageous Choices than NBW pigs in Blocks 3, 4 and 6.

The variation in the proportion of Adv. Choice Preference across blocks was nearly exclusively covered by the linear trend component, which explained approximately 97 % of this variation and thus could be taken as an adequate description of the development of Advantageous Choices across blocks.

Judgement bias

Learning

Both LBW and NBW pigs learned the conditional discrimination task at a similar rate (LBW: 16.00 ± 1.43 sessions; NBW: 16.00 ± 0.60 sessions).

Judgement bias

All pigs responded in every trial in test sessions (i.e. no omissions occurred). The mean number of Optimistic Choices in response to each cue type is presented in Fig. 4a. The full model, the model with both main effects and the interaction, had an AIC of 192.75. The model with only the main effects, i.e. without the interaction, had a lower AIC of 190.46, indicating that the interaction is not needed in the model. Both the model without cue type and the model without birth-weight category had higher AICs, indicating that both factors are important in the model (AIC without cue type: 788.92; AIC without birth-weight category: 194.84). Thus, LBW pigs made fewer Optimistic Choices than NBW pigs, and both LBW and NBW pigs made increasing numbers of Optimistic Choices as the cue type neared the positive cue (Fig. 4a). The difference in Optimistic Choice between LBW and NBW pigs occurred in response to the ambiguous tone cues, while responses to the training tone cues remained similar for LBW and NBW pigs (Fig. 4a).

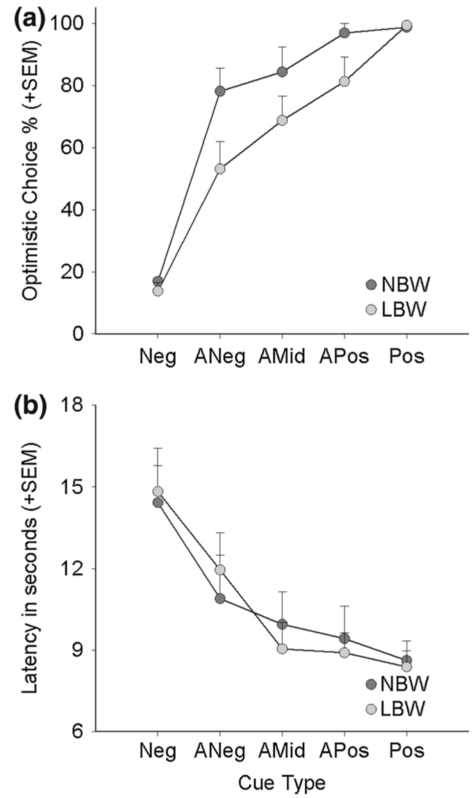

Fig. 4 **a** Mean Optimistic Choice (%), and **b** mean latency to respond per cue type for LBW and NBW pigs in the JBT

Latency

The mean latency to respond (s) to each cue type is presented in Fig. 4b. The full model, the model with both main effects and the interaction, had an AIC of −168.89. When the interaction was removed from the model, the AIC was higher (−95.53), indicating that the interaction is important in the model. Thus, the difference in latency to respond to each cue type between LBW and NBW pigs depends on the cue type. From Fig. 4b, it can be seen that both LBW and NBW pigs respond faster to cues as they near the positive cue.

Cortisol

There were no differences between LBW and NBW pigs in Mean Cortisol. The AIC was approximately the same when birth weight was included in the model (9.89) to when it was removed (9.40). Furthermore, Mean Cortisol was not found to predict Optimistic Choice as again, the AIC was approximately the same whether it was included (196.35) or removed from the model (194.75).

There was no relationship between Mean Cortisol and overall performance in the JBT (Mean AUC) for either LBW ($r_s = -0.55$, $P = 0.16$) or NBW pigs ($r_s = 0.33$, $P = 0.41$) (Fig. 5a).

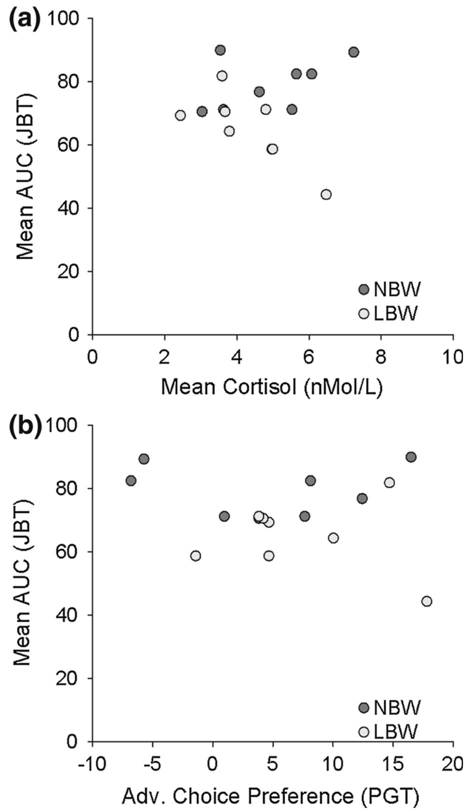

Fig. 5 **a** Relationship between Mean Cortisol and Mean AUC in the JBT, and **b** between advantageous choice preference from the PGT and mean AUC in the JBT. Correlation analyses revealed no relationships

Decision-making under risk and under ambiguity

Mean AUC from the JBT was not found to predict Advantageous Choice in the PGT. The AIC was approximately the same whether Mean AUC was included (714.70) or removed from the model (715.78). Furthermore, there was no significant relationship between overall performance in the PGT (Adv. Choice Preference) and performance in the JBT (Mean AUC) for either LBW ($r_s = -0.14$, $P = 0.74$) or NBW pigs ($r_s = 0.16$, $P = 0.71$) (Fig. 5b).

Discussion

We found that LBW piglets appear to have developed different strategies than their NBW siblings when making decisions under risk and ambiguity. In a PGT used to look at decision-making under risk, pigs were allowed to freely choose between a low-risk, low-reward option but which overall yielded more rewards (advantageous), and a high-risk, high-reward option which overall provided fewer rewards (disadvantageous). While both groups appear to show an increase in choices for the advantageous option over blocks of trials (Fig. 3), we found that LBW pigs chose more often for the advantageous option in later blocks of trials than their NBW siblings.

Looking at decision-making under ambiguity using a JBT, we found that both LBW and NBW pigs learned the task at a similar rate, did not differ in salivary cortisol pretesting, had similar latency responses to the different cues and performed equally well in response to the training tone cues. All pigs responded significantly faster to positive cues than negative cues, confirming that all animals had a preference for the larger reward as we have previously shown (Murphy et al. 2013a, b). However, when presented with unfamiliar, ambiguous, cues, LBW pigs were more likely to choose the negative goal box, i.e. demonstrated a more pessimistic bias than their NBW siblings. Interestingly, there was no relationship between individual pig's responses in the two tasks, suggesting that the two tasks are indeed measuring different facets of decision-making under uncertainty—risk and ambiguity.

Our results lend support to the theory that different personalities can arise from initial differences in state, in this case, physical size, leading to the development of different behavioural strategies (Dingemanse and Wolf 2010). As predicted, our LBW pigs demonstrated a greater preference for the advantageous option compared with NBW pigs. This preference for the advantageous option in LBW pigs may reflect a better rational ('cold') decision-making or be a product of more affective ('hot') decision-making processes. LBW pigs may have been better at weighing the associated probabilities of each option in order to maximise their gain compared with NBW pigs, or they may be more averse to risk as has been shown in studies of LBW in humans (Hack et al. 2002, 2004; Schmidt et al. 2008).

An important distinction between LBW in humans and LBW in pigs in the current study is the level of post-natal care provided in human infants. We defined LBW in piglets according to the criterion used by Gieling et al. (2011; Gieling 2013), and the mean weight of LBW piglets in the present experiment also corresponds with the definition of LBW used by other authors (Gondret et al. 2006; Attig et al. 2008; Baxter et al. 2008). However, in farming practice, piglets weighing less than 1 kg at birth are said to have a poor chance of survival (BPEX 2010), and more strict cut-off points for defining LBW have been used (Quiniou et al. 2002), which may reflect better the definitions used in human studies. Often the very LBW piglets do not survive without the level of postnatal care provided for human infants. Thus, the LBW piglets selected in the present study may represent only a subsection of 'viable' LBW pigs that have developed a successful behavioural strategy to compete against their NBW siblings.

Looking at decision-making under ambiguity in the JBT, we found that, as predicted, the LBW piglets showed a more ‘pessimistic’ bias, i.e. were more likely to choose the goal box offering the lower reward in response to ambiguous tone cues. While it is possible that differences in feeding motivation between LBW and NBW pigs contributed to this difference, some behaviours that may indicate different levels of motivation (rate of learning, speed of responding) did not differ between LBW and NBW pigs. In humans, judgements about the likelihood of future events are influenced by mood (Blanchette and Richards 2010), and these mood-congruent biases in judgement have been proposed as a means of studying emotional valence in animals (Mendl et al. 2009). Within this framework, our findings suggest that LBW may also contribute to negative affect in pigs. Complementary to the evidence of alterations in HPA axis activity in LBW pigs (reviewed by Rutherford et al. 2013), the present study provides potential behavioural indicators of altered emotionality in LBW pigs.

Few studies of decision-making have previously been performed in pigs. In social decision-making settings, Held et al. (2000) showed that uninformed dominant (larger) pigs will choose to follow a pig which they know is informed in order to find food rewards more quickly, while subordinate (smaller) pigs may alter their foraging decisions based on whether they are foraging with a scrounging or a non-scrounging (larger) pig (Held et al. 2010). Thus, in social decision-making situations, smaller pigs may compete by altering their behaviour in the presence of a more dominant (larger) pig. Our findings suggest that LBW may alter decision-making in pigs in non-social situations too, perhaps through emotional biases in the decision-making processes. The fact that individual behaviour on our two tests was not related suggests that these alterations occur across different types of decision-making.

While we did not find differences in salivary cortisol, previous studies have found that cortisol differences occur in response to a challenge in LBW and NBW pigs (Poore and Fowden 2003). Since the mean weight of our LBW piglets falls well below that used by Poore and Fowden (2003), it may be that had we taken cortisol after performance of the test, we might have found a difference corresponding to the difference in behaviour of the LBW and NBW piglets.

We have demonstrated that LBW pigs develop different strategies when making decisions under uncertain conditions than NBW pigs. We do not identify the mechanisms by which these differences in behaviour come about, and our LBW piglets may not entirely reflect LBW in humans. In terms of welfare, however, understanding the cognitive and emotional functioning of these viable LBW pigs is of high interest for the very reason that they survive and have to compete with stronger siblings. The altered decision-making patterns may reflect an adaptive strategy used by LBW piglets in response to constant competition with larger pigs. We propose that this altered decision-making is guided by changes in emotionality in LBW piglets, and we have provided behavioural evidence of increased negative affect in LBW piglets.

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Conflict of interest The authors declare that they have no conflict of interest.

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