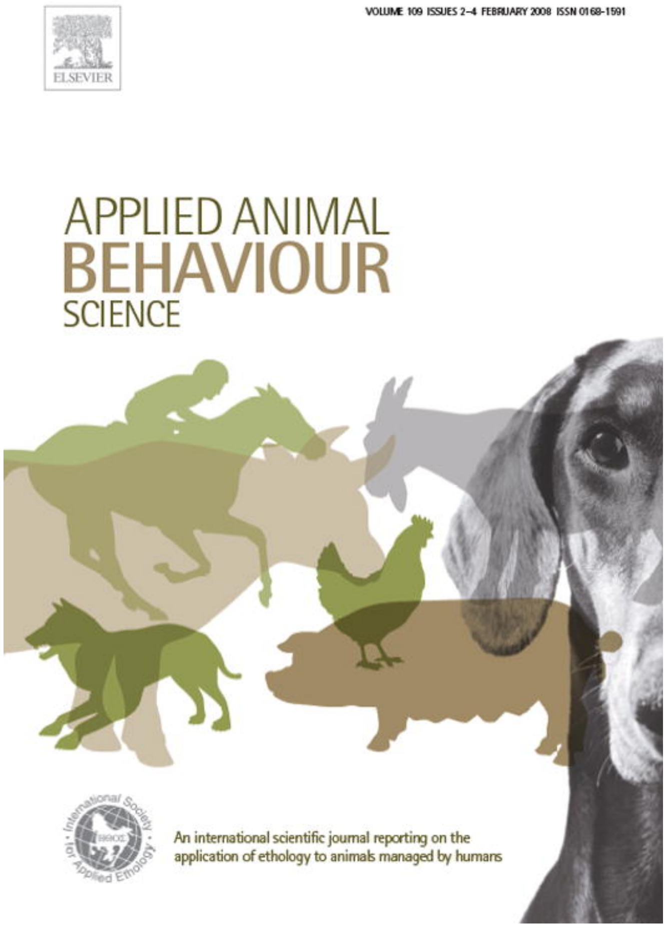
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Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*)

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Abstract

Anxious and depressed humans typically view circumstances more pessimistically than non-depressed individuals. Here, we explore the proposal that such cognitive biases also exist in non-human animals, and could be used as novel measures of animal welfare. Specifically, we test the hypothesis that wild-caught captive European starlings (*Sturnus vulgaris*) are more optimistic in their interpretation of ambiguous stimuli when they are housed in cages designed to promote greater welfare compared with when they are housed in standard laboratory cages. Starlings were trained using a choice procedure to discriminate between two temporal stimuli (2 s versus 10 s duration light stimulus) associated with outcomes of a different value (instant or delayed food). Next, the birds' responses to ambiguous, unreinforced stimuli of intermediate duration ranging from 2 to 10 s were examined under two housing regimes designed to manipulate the birds' welfare: big enriched cages versus standard cages (smaller and unenriched). The birds' probability of classifying an intermediate stimulus as that associated with the instant food outcome was significantly higher in the enriched cage compared with the standard cage. Thus, the birds displayed greater optimism in the face of uncertainty under housing conditions in which other measures indicate better welfare. These findings support the use of cognitive bias-based tasks as a novel, non-invasive technique for assessing affective state in non-human animals.

Keywords: Cognitive bias; Choice; Temporal discrimination; Affective state; Environmental enrichment; Animal welfare; Emotion

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1. Introduction

The ability to measure the emotional or affective state of non-human animals would be of value in many fields of behavioural science. In humans, verbal self-report is usually regarded as the most direct method for determining subjects' feelings, however, animals cannot tell us how they feel, and to assess their emotions we are forced to rely on indirect methods such as measurement of stress hormones or abnormal behaviour patterns. Recently, Mendl and Paul (Mendl and Paul, 2004; Paul et al., 2005) proposed a novel approach to affective state in animals, based on measuring emotionally induced biases in decision making. Their ideas are supported by an intriguing experiment that they interpret as showing 'pessimistic' response biases in rats subjected to conditions found to induce other symptoms of depression (Harding et al., 2004). In this latter paper and throughout the current paper, pessimism is defined operationally as an increased probability of classifying an ambiguous stimulus as predicting a negative outcome. Here, we present a new experiment that addresses a potential confound in this latter study, and extends the approach to a second species and a different manipulation of affective state.

In humans, cognitive changes associated with mood have been demonstrated in numerous tasks involving attention, memory and judgment (Williams et al., 1997). Research into the effects of emotions on judgment has established that anxious or depressed subjects tend to have pessimistic interpretations of ambiguous stimuli (e.g. Eysenck et al., 1987). Furthermore, there is some evidence that such cognitive biases may depend on the subjective, felt component of emotion (e.g. Schwarz and Clore, 1983). Based on these findings Paul et al. (2005) have argued that measures of cognitive bias my offer potential advantages as measures of affective state in animals. First, they may be better for assessing the valence (pleasantness versus unpleasantness) of an emotion. Second, if, as sometimes appears to be the case in humans, cognitive biases arise directly as a result of conscious emotional feelings entering into the processes of judgment and decision making, the demonstration of similar biases in animals could potentially tell us something about how they feel.

In the first attempt to produce a non-verbal analogue of a cognitive bias task Harding et al. (2004) trained rats on a go/no-go task to press a lever to obtain a food reward on hearing a positive tone, but to refrain from pressing the same lever to avoid unpleasant white noise on hearing a negative tone. Once trained on this task rats were allocated to either predictable or unpredictable housing. The unpredictable housing condition was designed to mimic the chronic mild stress manipulation, a commonly used animal model of depression (Willner et al., 1998). Following the housing manipulation the rats were tested with non-reinforced stimuli intermediate between the positive and negative tones. The animals' anticipation of a positive outcome was estimated by the probability with which they lever-pressed in response to the ambiguous tones. Rats in the unpredictable group showed fewer and slower responses than rats in the predictable group, leading to the conclusion that, just as in humans, depressed rats may demonstrate pessimism. This finding is supported by a recent demonstration that European starlings trained on a go/no-go foraging task also show increased pessimism in their judgement of ambiguous visual stimuli when environmental enrichment is removed from their cages (Bateson and Matheson, 2007).

However, a criticism of the interpretation placed on the above studies is that depression tends to be associated with reduced activity and also anhedonia and reduced food consumption (Willner et al., 1998). Thus, it is possible that the reduced tendency to press the lever in the unpredictably-housed rats and to obtain mealworms in the enrichment-deprived starlings could be explained by reduced activity levels or reduced motivation for food, as opposed to a pessimistic bias in judgement of the ambiguous stimuli. In support of Harding et al.'s interpretation, they report that the rats in the two groups did not to differ in independent measures of activity, food consumption and anhedonia, however, it would be cleaner if a task could be devised where these potential confounds were eliminated.

The aims of the current study are twofold. First, we develop a novel operant cognitive bias task based on a choice procedure as opposed to a go/no-go procedure. By requiring our subjects to respond actively to both the positive and negative stimuli we thereby reduce the possible confound between pessimism and a reduced motivation to respond for food in depressed subjects. In our procedure the subjects are always reinforced with food, and we generate the necessary differential value in the reinforcements by altering a potent determinant of reward value, namely the delay to reward (Bateson and Kacelnik, 1996, 1997). Thus, in our task the positive stimulus is associated with immediate reward, and the negative stimulus with delayed reward. Second, we test our novel task in European starlings subjected to a manipulation of the size and level of enrichment of their cages. We chose starlings as our experimental subjects for a number of reasons. Starlings are the most widely-used wild-caught passerine in biological research yet there is currently little agreement on husbandry procedures in this species (Asher and Bateson, 2007). There is a clear need for new, non-invasive methods for welfare assessment, that can be used to justify improvements in starling husbandry. In our study we chose to study the effects of environmental enrichment because there are extensive data on both behavioural and physiological measures suggesting that environmental enrichment is associated with welfare benefits and arguably therefore, more positive affective state in both starlings and other species (reviewed in Young, 2003, and see Asher et al., in preparation for data on starlings). In addition, we already have preliminary data from a go/no-go task that removal of environmental enrichment is associated with increased pessimism in laboratory starlings (Bateson and Matheson, 2007).

2. Materials and methods

2.1. Experimental subjects

Subjects were eight adult, wild-caught European starlings (*Sturnus vulgaris*); four males and four females housed indoors in air conditioned rooms maintained at approximately 17 °C with a 14:10 light:dark cycle. The birds were caught from the wild as fledglings 5 years prior to this study. They had previously served as subjects in various non-invasive foraging experiments, and were well habituated to human handling. Prior to this study the birds were group-housed in a room (255 cm high × 268 cm wide × 350 cm long) enriched with natural branches, water baths and bark chippings on the floor. Birds were fed Purina Wild Game Starter supplemented with, mealworms (*Tenebrio* larvae), fruit and *ad libitum* drinking water. At the start of this study birds were moved to individual wire cages 44.5 cm high × 75 cm wide × 45 cm deep equipped with water bottles, dowelling perches and paper lining the floor. For the experimental manipulation phase of the experiment birds were transferred to new cages (see below).

This research adhered to the Association for the Study of Animal Behaviour's guidelines for use of animals in research, and all experimental protocols were subject to internal ethical review. The starlings were caught under licence from English Nature.

Free-feeding masses for each bird were established for 1 week prior to the start of operant training. The birds were weighed daily before experimental sessions and fed a ration after the experimental session that was adjusted to maintain their masses such that females had a condition index (CI = mass in g/tarsus length in mm) close to 1.96 g/mm and males a CI close to 2.14 g/mm. These CIs had been previously calculated to correspond to the average condition of a bird food deprived to 90% of its free-feeding mass (Bateson and Rowe, unpublished data). If a bird's CI was below 1.96 for females and 2.14 for males at the morning weighing the bird was given *ad libitum* food and not run in the experiment that day. At 90% free-feeding mass starlings retain some visible pectoral fat stores indicating that they are not dangerously thin (unpublished data). Birds were familiarised with the operant boxes and trained to retrieve pellets from the hopper prior to being trained to peck at illuminated keys for food using a standard auto-shaping procedure (e.g. Bateson and Kacelnik, 1995).

2.2. Apparatus

For the experimental sessions the birds were transferred to custom-built operant boxes (Bateson, 2002). Each box was equipped with a horizontal array of three pecking keys (4 cm diameter) mounted in the vertical plane that could be trans-illuminated with red, green or amber light of equal intensity. Birds were reinforced with custom-made 45-mg starling pellets (P.J. Noyes, Lancaster, New Hampshire, USA) delivered by an external dispenser to a central food hopper. A water bottle was situated on the opposite wall of the box and was available throughout the experiment. Each box was continuously lit by a white house light and was housed inside a sound-attenuating chamber fitted with fans to provide continuous ventilation and masking white noise. The boxes were connected to an Acorn Archimedes PC equipped with the Arachnid experimental control language and associated interfacing hardware (CeNeS, Cambridge, UK) that controlled the presentation of stimuli and reward contingencies and collected the data.

2.3. Cognitive bias task

The full cognitive bias task is summarised in Fig. 1. Training on the task proceeded in two stages. First, the birds learned to discriminate two time intervals (2 and 10 s) that would subsequently become the positive and negative stimuli analogous to the tones in Harding et al. (2004). A trial started with the centre key flashing amber (on for 0.7 s, off for 0.3 s). The bird had to peck once at the flashing key to initiate the trial. Following the first peck the centre key stopped flashing and was illuminated continuously for one of the two possible stimulus intervals (2 or 10 s) before extinguishing. As soon as the centre key extinguished, the two side keys started flashing (on for 0.7 s, off for 0.3 s), one red and the other green, to indicate that the bird could make a choice. The bird had to make a single peck to one of the keys to indicate its choice. For each

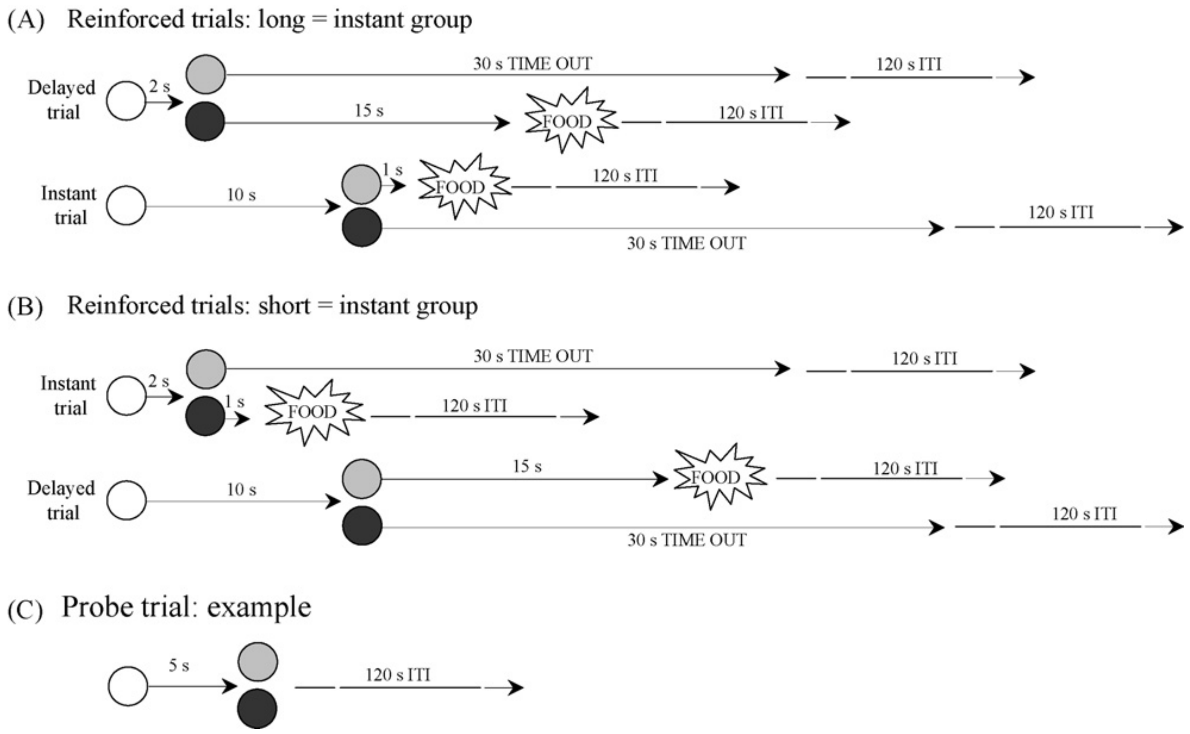

Fig. 1. Details of the operant task. (A) Long = instant group. (B) Short = instant group. The allocation of colours to the two options in the choice phase was counterbalanced within each group. (C) Example of a probe trial.

bird, one colour was designated as the correct response if the initial interval was 2 s and the other colour if it was 10 s; assignment of colours to intervals was counterbalanced across birds, and for each bird colour associations remained the same throughout the experiment. A correct response resulted in the chosen key stopping flashing and remaining lit for 2 s, after which time the first peck to the key resulted in immediate reinforcement with one pellet. An incorrect response resulted in both of the keys extinguishing and a 'time-out' of 30 s, during which pecking at the keys had no effect. All trials ended with an inter-trial interval (ITI) of 120 s. For each bird the daily session comprised a maximum of 54 trials, 27 with the 2-s stimulus and 27 with the 10-s stimulus in a pseudorandom sequence. Sessions ended after 2.5 h if the bird had not yet completed all the trials. Training continued until the birds chose the correct response on a significant number of trials (binomial test, $p \leq 0.05$, i.e. 65% correct given 54 trials) for 3 consecutive days; one bird never met this criterion and was dropped from the experiment at this point.

In the second stage of training, two changes to the basic discrimination task were introduced. First, the delay to reward following a correct response was changed to create differentially valued outcomes analogous to the food and white noise in Harding et al. (2004). For each bird, correctly discriminating one stimulus (either 2 or 10 s) was followed by a 1-s delay to reward (the instant outcome), and the other by a 15-s delay to reward (the delayed outcome). Three of the birds had the 2-s stimulus associated with the 1-s delay (the 'short = instant' group), and the other four had the 10-s stimulus associated with 1-s delay (the 'long = instant' group). Second, the probability of reinforcement was reduced from 1.00 to 0.33 by the introduction of unreinforced probe trials in which the initial stimulus had a duration of 2, 3, 4, 5, 6, 7, 8, 9 or 10 s. On a probe trial, the centre key was illuminated for the designated interval the expiration of which was followed by the choice of red and green as described above. The first response made by the bird resulted in both keys extinguishing and the start of the ITI. Each session comprised 18 reinforced trials (nine 2-s and nine 10-s trials) and 36 probe trials (four of each probe value) arranged in a pseudorandom order, different in each session. Sessions ended after 2.5 h if the bird had not yet completed all the trials. Training continued until the birds had a significant discrimination (binomial test, $p \leq 0.05$, i.e. 77% correct given 18 reinforced trials) for a minimum of 3 consecutive days. One bird died during this stage of training; the bird's weight record ruled out starvation as a possible cause; a post-mortem was conducted but failed to confirm the cause. After reaching criterion, the remaining birds had a minimum of eight further days of training to establish stable baseline performance prior to starting the cage manipulation.

2.4. Cage manipulation

Following the training described above, we compared the performance of the birds on the final version of the task in two treatments: standard and enriched cages. In both treatments, birds were housed three to a cage. In the standard treatment the cage was the same as the cage described above with the exception that access to a water bath was now unpredictable, with only a 50% chance of a bath on a given day. Cleaning times were also unpredictable, and sometimes occurred when the birds were in the cage. In the enriched treatment the cage was bigger (82 cm × 141 cm × 85.5 cm), but of the same shape. Other differences included continuous access to water baths, perches made from natural branches of differing thicknesses, and bark chippings on the floor to provide a substrate for the birds to forage in. The daily ration of mealworms was distributed in the bark as opposed to being placed in the bowls with the other food. The enriched cage was always cleaned when the birds were in the operant boxes to minimise disturbance. Each of the six birds experienced both cage types in a repeated measures design with order of treatment counterbalanced across birds. Each cage treatment lasted for a total of 14 days: 4 days to allow the birds to settle, followed by 10 days with sessions in the operant boxes.

2.5. Analysis

We recorded the option chosen by the bird in all the probe trials during the cage manipulation phase of the experiment. Data for each of the nine probe stimulus values from the 10 sessions in each cage type treatment were pooled resulting in a maximum of 40 trials per probe value per treatment for each bird. These data were used to plot the probability of choosing the option associated with the instant reward as a function of the value of the probe stimulus for each bird in each of the two cage treatments.

The above data were fitted with a cumulative normal curve using the Probit analysis option in SPSS version 10.0, and the resulting functions used to derive four parameters that could be used to compare performance in the two treatments: the bias, which is the probe value corresponding to the 0.5 probability of choosing the instant reward; the sensitivity to the probe stimulus length, which is the slope of the function between 0.25 and 0.75 probabilities; the probability of choosing the option associated with the instant reward at the probe value associated with the delayed reward; and finally, the probability of choosing the option associated with the instant reward at the probe value associated with the instant reward. These parameters were compared in the two treatments using repeated measures General Linear Models with factors cage type (within subjects) and task group (between subjects). All data were inverse-transformed to homogenise the variance.

3. Results

3.1. Task acquisition

The birds took 26.67 ± 2.777 (mean ± 1S.E.) sessions to reach criterion on the discrimination of 2 s versus 10 s. On the last 3 days of this stage of training the performance of the birds that would become the long = instant group in the next stage was 77.4 ± 3.9% correct (mean ± 1S.E.) and the performance of the birds that would become the short = instant group was 76.3 ± 4.5% correct. The birds took a further 15.83 ± 3.260 sessions to reach criterion on the full task. We were concerned that the birds might prefer the option associated with more immediate reward irrespective of whether this was the reinforced response, however, there was no evidence that this happened. In the reinforced trials of the final eight sessions of training, performance in trials in which the correct response was the option associated with instant reward was 80.0 ± 5.99% correct (mean ± 1S.E.) compared with 81.0 ± 3.62% correct in trials in which the correct response was the option associated with delayed reward. However, in the same data, performance was 84.0 ± 2.36% correct (mean ± 1S.E.) for the long = instant group and 68.0 ± 1.54% correct for the short = instant group. Thus, the introduction of differential delays to reward appears to be associated with a difference in performance according to whether the 2-s stimulus was associated with a 1- or 15-s delay to reward.

3.2. Cage manipulation

A total of six birds were successfully trained on the full cognitive bias task and tested in the two cage treatments. Of these six birds, four completed the maximum of 360 probe trials (i.e. 40 at each of 9 probe stimulus values) in both the standard and enriched treatments. One bird completed the full 360 probes in the enriched treatment but only 351 in the standard treatment due to equipment failure. Another bird regularly failed to finish 54 trials within the 2.5-h limit, and completed only 197 probe trials in the enriched treatment and 338 in the standard treatment. Means of the observed data and fitted functions for the six birds in the two treatments are shown in Fig. 2.

Analysis of the four parameters described in Section 2.5 reveals the following findings (Fig. 3). The bias was not significantly different in the two cage type treatments ($F_{1,4} = 3.219$, $p = 0.147$, Fig. 3A), however, the birds in the long = instant group were significantly more optimistic (i.e. had a function shifted towards the left) of the birds in the short = instant group ($F_{1,4} = 13.70$, $p = 0.021$, Fig. 3A). Sensitivity was marginally higher in the standard treatment

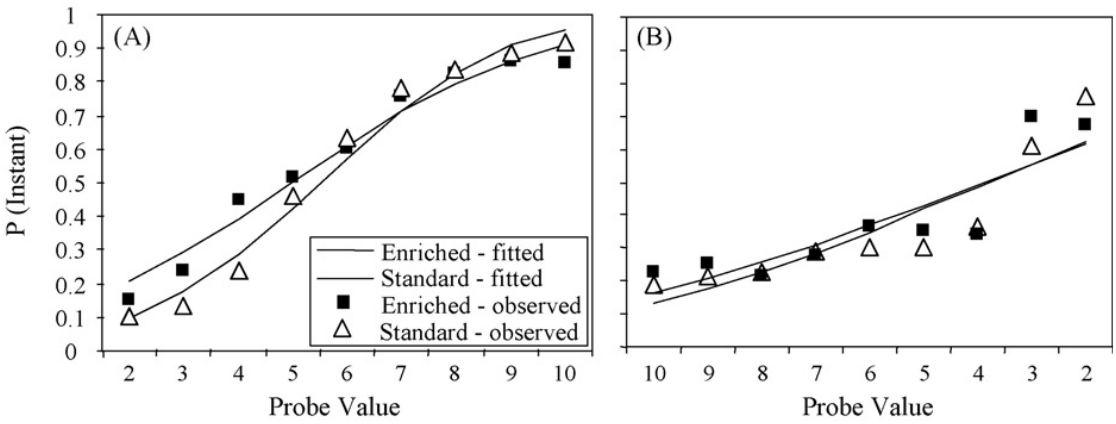

Fig. 2. Performance following experimental manipulations: mean proportion of probe trials of each value on which a bird chose the option associated with instant reward in enriched and standard treatments. Lines show the means of the fitted functions derived for each bird. (A) Long = instant group. (B) Short = instant group.

than the enriched treatment ($F_{1,\ 4} = 7.413$, $p = 0.053$, Fig. 3B), and significantly higher in the long = instant group than in the short = instant group ($F_{1,\ 4} = 14.963$, $p = 0.013$, Fig. 3B). At the probe stimulus value associated with delayed reward the birds were significantly more optimistic in the enriched treatment than in the standard treatment ($F_{1,\ 4} = 8.943$, $p = 0.040$, Fig. 3C), and

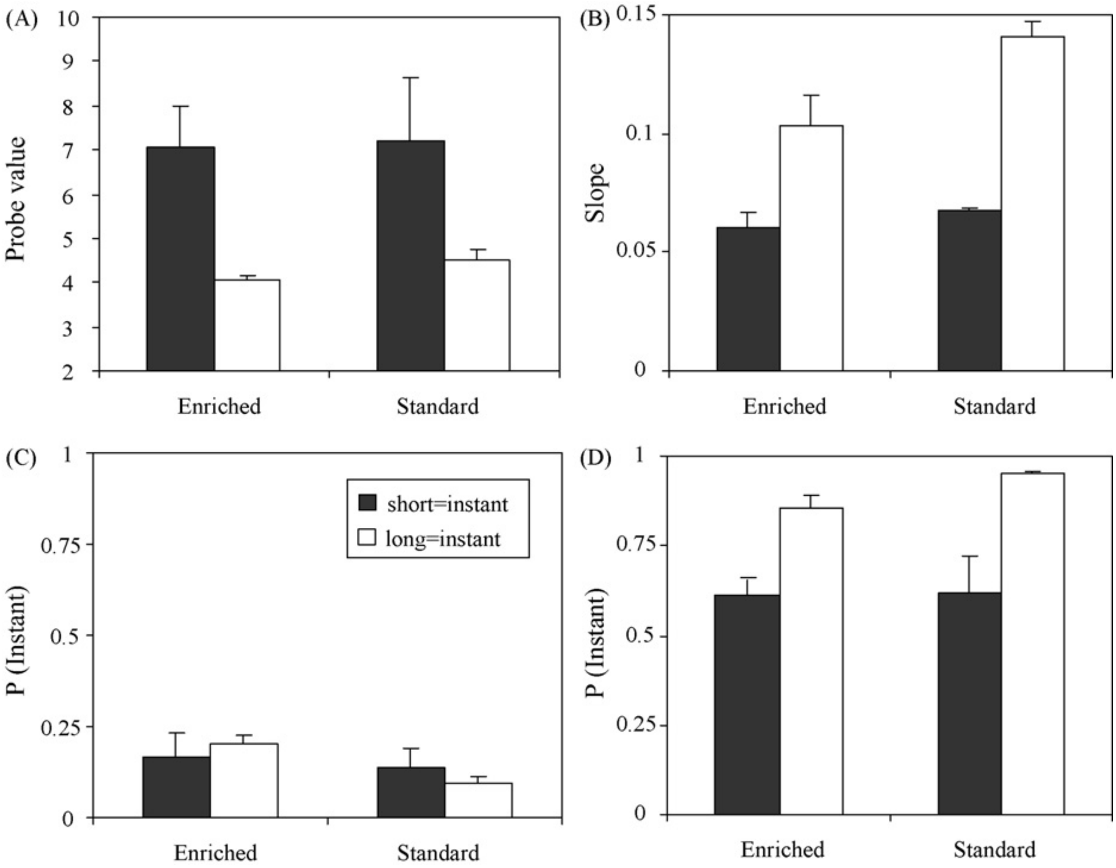

Fig. 3. Mean (±1S.E.) values of the four parameters derived from the fitted functions as described in the text. (A) Probe value corresponding to the 0.5 probability of choosing the option associated with instant reward (i.e. the bias). (B) Slope of the fitted function (i.e. the sensitivity). (C) Probability of choosing the option associated with the instant reward at the probe value associated with the delayed reward. (D) Probability of choosing the option associated with the instant reward at the probe value associated with the instant reward.

there was no significant effect of group ($F_{1,\,4} = 0.001$, $p = 0.978$, Fig. 3C). At the probe stimulus value associated with instant reward there was no significant effect of cage treatment ($F_{1,\,4} = 1.490$, $p = 0.289$, Fig. 3D), but birds were significantly more optimistic in the long = instant group ($F_{1,\,4} = 32.198$, $p = 0.050$, Fig. 3D).

Given that the birds were significantly less sensitive to the value of the probe stimulus in the short = instant group, we reanalysed the four parameters for just the long = instant group. For this group, bias was significantly more optimistic in the enriched cage treatment than the standard cage treatment (paired *t*-test, 3 d.f., $t = 3.643$, $p = 0.036$). Sensitivity was significantly higher in the standard treatment than in the enriched treatment (paired *t*-test, 3 d.f., $t = 3.440$, $p = 0.041$).

4. Discussion

The primary aims of this study were first, to develop a task based on a choice procedure that could be used to measure optimistic and pessimistic biases in animals' judgments of ambiguous stimuli, and second to use this task as a novel means of assessing affective state in non-human subjects. We trained starlings on a temporal discrimination whereby to obtain reinforcement with food they had to choose the correct one of two different coloured keys following a 2- or 10-s light stimulus, and the two correct responses were associated with rewards of different value (instant or delayed food). We tested the birds' responses to unreinforced light stimuli between 2 and 10 s duration, with the idea that we could measure changes in pessimism by examining how the birds classified these ambiguous stimuli. Increases in optimism would be revealed by an increased probability of classifying an ambiguous stimulus as being the one associated with instant reward, whereas increases in pessimism would be revealed by an increased probability of classifying an ambiguous stimulus as being the one associated with delayed reward. Using this approach, we showed that starlings housed in larger, enriched cages showed significantly increased optimism than when housed in smaller, standard cages. We have therefore successfully replicated the basic effect first described by Harding et al. (2004), that animals housed in conditions associated with better welfare show more optimistic judgments of ambiguous stimuli. Our data also support evidence from starlings trained on a go/no-go cognitive bias task that removal of environmental enrichment is associated with increased pessimism (Bateson and Matheson, 2007). By simultaneously manipulating several aspects of the cage design our aim was to maximise the difference in the welfare of the birds housed in the different cage types. Further experiments will be needed to establish which of our various manipulations (cage size, enrichment or cleaning regimen) was responsible for the shift in optimism recorded.

In our experiment, the effects of the cage manipulation differed according to the stimulus being judged, and were greater for the stimuli towards the negative end of the spectrum. Specifically, the birds in the standard cage were more pessimistic in their judgment of the negative stimulus than the birds in the enriched cage, but were also more likely to classify this stimulus correctly. This compares to what is known in the human literature as ‘‘depressive realism’’, the finding that whereas positive illusions are the norm in healthy people, depressed patients are generally more accurate (and therefore pessimistic) in their judgment of the probability of positive outcomes for themselves (Alloy and Ahrens, 1987; Taylor and Brown, 1988). Harding et al. (2004) also report differential effects of their housing manipulation for the judgment of positive and negative stimuli, but in contrast to our findings, they found that rats in the unpredictable cages were more pessimistic but less accurate in their judgment of the stimuli towards the positive end of the spectrum. Despite this apparent difference, it is possible to reconcile our findings by realising that in both experiments the animals in the poorer environments are biasing their responses in such a way as to reduce their probability of receiving the worst of the three possible outcomes (no food in our experiment and white noise in Harding et al.'s). In our experiment, the starlings in the standard cages minimise their probability of receiving no food at all by correctly classifying the negative stimulus, whereas in Harding et al.'s (2004) experiment, the rats in the unpredictable conditions minimise their probability of receiving white noise by refraining from pressing the lever. Thus, the results from both experiments support the idea that animals in poorer environments are more averse to the risk of a bad outcome. Such a strategy would be adaptive if a poor environment reduces the state of an animal sufficiently that an outcome that could be safely tolerated in a good environment is now detrimental to its fitness.

In addition to supporting the findings reported by Harding et al. (2004), our study also extends these in three important respects. First, by using a choice procedure as opposed to a go/no-go procedure we reduce the problem that changes in affective state may be accompanied by changes in activity levels and in motivation to eat. In Harding et al.'s task, if the chronic mild stress manipulation resulted in reduced motivation to press a lever for reward this could have produced the decreased probability of lever pressing that they observed in the rats subjected to that condition. Thus, a result interpreted as increased pessimism may actually have reflected reduced appetite or motivation to respond. In our task, because the birds had to peck a key to obtain food in response to all stimuli, this criticism does not apply. Second, in Harding et al.'s task there was a good outcome (food) and an aversive outcome (white noise), whereas we used two good outcomes that differed in value (instant versus delayed food). We have therefore extended Harding et al.'s findings by demonstrating that it is not necessary to have an aversive outcome in order to detect changes in cognitive bias. Finally, by using environmental enrichment as a means of manipulating the state of our birds as opposed to the chronic mild stress we have extended the finding of cognitive bias to a manipulation known to be correlated with a number of established measures of animal welfare including abnormal behaviour patterns and physiological markers of stress (Young, 2003). Data from our own laboratory show that starlings housed in the same enriched cages used in the current experiment show fewer repetitive behaviour patterns and lower corticosterone levels (Asher et al., in preparation).

An unanticipated outcome of our experiment was the result that the performance of the birds was different depending on whether the 2-s time stimulus was associated with delayed or instant reward. In the group in which the short stimulus was associated with instant reward the performance of the birds on the temporal discrimination was much less good (Fig. 2), suggesting that the temporal stimuli somehow interact with the delay to reinforcement following the choice to affect performance on the discrimination. It should be noted that prior to the introduction of the differential delays to reinforcement the performance of the birds in the two groups was identical, therefore the performance difference does indeed seem to be attributable to the subsequent change in the delays to reinforcement. It is possible that the group difference may be attributable to an interaction between the duration of the initial stimulus and the delay to reward following choice on the value of the food rewards. Previous studies have demonstrated both that the amount of work done prior to a choice (Kacelnik and Marsh, 2002) and the delay to reward following a choice (Bateson and Kacelnik, 1995, 1996, 1997) affect starlings' preferences. However, ours is the first study to vary both of these schedule parameters simultaneously, and it remains to be established how they will combine to affect reward value. In view of this potential complication with our task, we suggest that future studies revert to using judgments of non-temporal stimuli such as tones or colours.

5. Conclusions

We have presented data that replicates and extends preliminary findings suggesting that better welfare is associated with an optimistic response bias in tasks involving the classification of ambiguous stimuli. Our data support the general suggestion of Paul et al. (2005) that cognitive bias may be a useful measure of affective state in non-human animals.

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