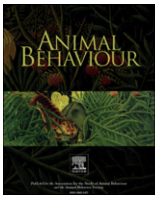
Animal Behaviour 81 (2011) 169–175

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Environmental enrichment induces optimistic cognitive bias in rats

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A R T I C L E I N F O

Article history:
Received 23 March 2010
Initial acceptance 20 May 2010
Final acceptance 20 September 2010
Available online 23 November 2010
MS. number: 10-00203R

Keywords:
affective state
animal welfare
emotion
environmental enrichment
judgement bias
positive cognitive bias
rat
Rattus norvegicus

People's affective or emotional state can alter their cognitive processing, biasing interpretation of ambiguous stimuli. Those in a more positive state interpret such stimuli in a more optimistic manner than those in a negative state. Recently this research has extended to animals, and has shown that manipulations associated with negative affect cause animals to interpret ambiguous stimuli more pessimistically. We investigated whether exposure to environmental enrichment engenders optimistic responses to ambiguous stimuli. Rats, *Rattus norvegicus*, were trained on a novel conditional discrimination task whereby they learned the correct response necessary to obtain a food reward given the stimulus present during approach (rough or smooth sandpaper). One stimulus was associated with a higher-value reward than the other. Once the rats were trained, cognitive bias was probed by exploring their responses to an ambiguous stimulus (intermediate grade of sandpaper); a rat was defined as optimistic if it chose the response appropriate to the stimulus associated with the better reward. Animals transferred from unenriched to enriched cages showed more optimistic responses following the change. A control group maintained in unenriched cages showed pessimistic responses throughout. These results demonstrate for the first time that environmental enrichment can induce an optimistic cognitive bias in rats previously housed in standard caging, possibly indicative of a more positive affective state. These results add support to the suggestion that measuring cognitive biases can give an insight into animal emotional states; this has implications for animal welfare and preclinical testing of potential therapeutics for mood disorders.

It is well established in humans that affective state can influence many aspects of cognition (Williams et al. 1997; Haselton et al. 2009). Affectively induced cognitive biases have been described in relation to the information attended to, how it is interpreted and how it is remembered (Leppanen 2006; Bar-Haim et al. 2007; Coen et al. 2009; Inaba & Ohira 2009). For example, socially anxious people interpret the emotional valence (strength of positivity or negativity) of ambiguous statements (e.g. 'that is an interesting shirt you have on') more negatively than nonanxious individuals (Wells & Matthews 1996; Amir et al. 2005). Therefore, testing an individual's interpretation of ambiguous stimuli can potentially reveal something about their emotional state. In recent years there has been a move towards using techniques involving interpretation of ambiguous stimuli in nonhuman animals (hereafter referred to as animals), in an attempt to assess their affective state (Paul et al. 2005; Mendl et al. 2009).

Certain aspects of animal welfare, such as biological function, are relatively straightforward to measure (e.g. productivity, immune and reproductive function or growth rate; Dwyer & Bornett 2004; Klasing 2007). However, mental or subjective experiences are less tractable, as animals cannot communicate their experiences to us verbally. Current attitudes suggest that modern assessments of animal welfare should be expanded to include measurements of subjective experience, and should focus on positive as well as negative affect (Desire et al. 2002; Boissy et al. 2007; Broom 2007; Dawkins 2008). It has been suggested that cognitive assays could provide an indirect way of measuring subjective experiences, and a variety of such assays have been suggested (Paul et al. 2005; Brydges & Braithwaite 2008). One particularly promising avenue appears to be the cognitive bias approach. Mendl et al. (2009) have enumerated several potential advantages of this approach, including: the ability to make a priori predictions for different species; specific measurement of emotional valence; the strong correlation between cognitive biases and subjectively experienced emotion in humans; and the potential to measure positive, as well as negative, affect. However, the reality of these advantages remains to be demonstrated in animal studies.

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doi:10.1016/j.anbehav.2010.09.030

A number of researchers have investigated whether environmental manipulations chosen to induce negative affect also produce pessimistic cognitive biases in animals' responses to ambiguous stimuli (reviewed in Mendl et al. 2009). In the first of the studies, Harding et al. (2004) trained rats, *Rattus norvegicus*, to press a lever to obtain a food reward in response to one 'training' tone (the positive stimulus) and to refrain from pressing in response to a different 'training' tone (the negative stimulus) to avoid a burst of aversive white noise. After the rats had learned this discrimination, they were exposed to probe tones that were intermediate between the two trained tones. Those animals housed in unstable conditions (hypothesized to promote mildly 'depressive' effects) showed longer response latencies and tended to respond less often to the 'positive event' tone and probe tones close to it. The authors interpreted these findings to suggest that unstable housing induces negative (or 'pessimistic') cognitive bias in rats. Following this pioneering study, a number of experimenters have further investigated how environmental manipulation affects judgement biases in animals. For example, removal of environmental enrichment or exposure to anxiety-inducing conditions increases 'pessimistic' judgements in both rats (Burman et al. 2008a, b, 2009) and European starlings, *Sturnus vulgaris* (Bateson & Matheson 2007; Matheson et al. 2008). Furthermore, both congenitally helpless rats (a genetic model of animal depression) and starlings with locomotor stereotypies (which are often interpreted as indicative of inadequate housing) show more pessimistic judgement biases than normal animals (Enkel et al. 2009; Brilot et al. 2010). Thus there is mounting evidence that cognitive bias could be a useful tool for assessing both state and trait negative affect in animals.

Despite evidence from humans that positive affect is associated with greater optimism (e.g. Nygren et al. 1996; Waters 2008), animal studies have so far failed to demonstrate clear optimistic judgement biases in response to manipulations designed to induce positive affect (Bateson & Matheson 2007). The aim of this study was therefore to explore whether cognitive bias can be used to measure positive affect in rats experiencing a sudden improvement in environmental conditions for the first time in their lives.

In this study we developed a novel cognitive bias test for rodents logically identical to two of the tasks previously used with starlings (Matheson et al. 2008; Brilot et al. 2010). Unlike the original Harding et al. (2004) go/no-go task described above, our rats were required to respond to both the positive and the negative cues by making an active choice response. We have argued that this design reduces the likelihood of confounds caused by changes in activity or motivation to feed inherent in a go/no-go task (Matheson et al. 2008; see also Enkel et al. 2009 for similar arguments). In the rat version of our task the positive stimulus (either fine- or coarse-grade sandpaper) was associated with a high-value reward (chocolate) and the negative stimulus (the opposite grade of sandpaper to the positive stimulus) with a lower-value reward (cereal). Rats will forage for both of these rewards, but are assumed to have a strong preference for chocolate over cereal. We chose not to use a punishment (white noise or electric shock) as in previous rat studies for two reasons: first, it has been hypothesized that tasks using positive and neutral reinforcers might be best at detecting positive affect or 'happiness' (Mendl et al. 2009); and second, we were concerned that repeated experience of punishers during daily cognitive bias testing might itself affect the state of the animals adversely. As enrichment has been used in previous animal tests of cognitive bias, and is widely thought to improve animal welfare (Garner 2005; Swaisgood & Shepherdson 2005), we tested the responses of rats to ambiguous probe cues before and after the addition of environmental enrichment, with the hypothesis that provision of enrichment would induce optimistic shift in cognitive bias. Rats were chosen for the study as they are among the most commonly used animals in biological research. Therefore, the successful development of the cognitive bias protocol in this species has profound implications both for the assessment of welfare and as a potential new research tool in the preclinical testing of mood-altering therapeutics.

METHODS

Subjects and Housing

We used 12 male Sprague Dawley rats (bred from an in-house colony and raised by their own mothers at the University of Edinburgh), approximately 6 months old at the start of testing. Post-weaning but before experiments began (i.e. weaning to 6 months), rats were housed in two groups of six in standard cages (61 x 43.5 cm and 21.5 cm high, Techniplast) lined with wood shavings (Lillico) but containing no environmental enrichment on a 12:12 h light:dark cycle and fed standard rat chow (RM1, Special Diet Services, Lillico, Surrey, U.K.) and water ad libitum. Temperature and humidity were maintained between 19 and 21 °C and 45 and 60%, respectively. Rats were identified using rings of permanent marker around the tail. Rats were killed using a schedule one method (cervical dislocation) at the end of the experiment.

Apparatus

In a room separate to the housing area we set up a simple maze consisting of a clear Perspex start box (61 x 43.5 cm and 21.5 cm high) connected to a clear Perspex goal box (61 x 43.5 cm and 21.5 cm high) via a large piece of white Perspex drainpipe (diameter 10 cm, length 80 cm). The goal box contained two foraging bowls (diameter 9 cm, height 5 cm) one black, one white, and the entire maze was set on a bench side (1 m high) under regular room lighting (Fig. 1).

Habituation

To habituate rats to the food rewards and maze apparatus, we handled each rat for 10 min daily and fed it food items to be used as rewards in the task (white chocolate drops and Honey Nut Cheerios) for 5 days (phase A). For the next 5 days, we also placed rats into the maze apparatus for 5 min per day (phase B). During this phase, the foraging bowls were filled with scented sand. One foraging bowl was filled with coriander-scented sand (1% by weight coriander), and the other with cinnamon-scented sand (1% by weight cinnamon). For each rat, each reward was specifically paired with a particular bowl colour and scent, and a particular bowl colour was either on the left or the right of the goal box, and this arrangement remained consistent for each individual throughout the experiment (e.g. chocolate reward always in black cinnamon bowl on left, Cheerio reward always in white coriander bowl on right), but was randomized between individuals. These pairings were counterbalanced between treatment groups (enriched versus unenriched). The inside of the tunnel linking the start and goal boxes was completely lined with Silicon Carbide Waterproof sandpaper (3M, U.K.; P600 grade; this was different to the sandpaper used in later phases) to habituate rats to the presence of sandpaper in the tunnel. This complete lining facilitated maximal contact between the rat (feet and whiskers) and the surface of the sandpaper.

Training

During phase C, each rat underwent four training trials per day in the maze apparatus for a period of 5 days, two between 0900