Optimising 'positive' findings from judgement bias tests: a consideration of inherent confounding factors associated with test design and biology

Alexandra L Whittaker[1]*, Timothy H Barker[2]

1 School of Animal and Veterinary Sciences, The University of Adelaide, Roseworthy Campus, Roseworthy, South Australia, 5371. E: alexandra.whittaker @adelaide.edu.au

2 Joanna Briggs Institute, The University of Adelaide, South Australia, 5005. E: timothy.barker@adelaide.edu.au

***Corresponding Author**

Abstract

The assessment of positive emotional states in animals has been advanced considerably through the use of judgement bias testing. JBT methods have now been reported in a range of species. Generally, these tests show good validity as ascertained through use of corroborating methods of affective state determination. However, published reports of judgement bias task findings can be counter-intuitive and show high inter-individual variability. It is proposed that these outcomes may arise as a result of inherent inter- and intra-individual differences as a result of biology. This review discusses the potential impact of sex and reproductive cycles, social status, genetics, early life experience and personality on judgement bias test outcomes. We also discuss some aspects of test design that may interact with these factors to further confound test interpretation.

There is some evidence that a range of biological factors affect judgement bias test outcomes, but in many cases this evidence is limited and needs further characterisation to reproduce the findings and confirm directions of effect. It is our proposition that researchers should consider dedicated study on these factors and their impact on judgement biasing. This is needed to confirm effect and investigate mechanisms. Alternately, consideration and reporting of these factors in JBT studies through incorporation in statistical analyses will provide much needed additional data on their impact. These actions will enhance the validity and practical applicability of the JBT for welfare assessment.

Keywords: Judgement Bias, Personality, Social Status, Test Design

1. Introduction

Recently, scientists have tended to utilise the school of animal welfare science, which considers how animals' 'feel', in preference to assessment of biological function or 'natural-like' state (Boissy et al., 2007). Concomitantly, researchers have concentrated their efforts on assessment of positive affective states (Mellor, 2012). Affective states being defined according to their two main dimensions, 1) arousal or magnitude of activation and, 2) valence or direction of effect. Positive welfare is understood to be a complex equilibrium between providing the animal with conditions that encourage positive emotional (affective) valence and an evaluation of the maintenance requirements of that animal (Yeates and Main, 2008). As a result, there is a general desire to design housing and husbandry systems, that not only minimise suffering and pain, but maximise factors likely to induce positive affect (Harding et al., 2004; Matheson et al., 2008; Brydges et al., 2011; Bethell et al., 2012). However, to do this, a reliable method of assessing both arousal and valence of affective state is required. Whilst a variety of methods for assessing arousal are validated and commonly used, measures of valence are less well characterised (Whittaker and Marsh, 2019).

It is generally accepted that the valence of an animal's affective state cannot be measured directly (Mellor, 2012). In spite of this there are known linkages between an animal's affective state and the functional states that generate them. These functional states include four components: behavioral, neurophysiological, cognitive and subjective (Mellor, 2012). The latter is the most controversial with there being controversy over what animals' emotional experiences consist of, and their level of conscious awareness of emotional state (Boissy et al., 2007). The most widely investigated components in relation to animal welfare are neurophysiological and behavioural markers (Mendl et al., 2009; Novak et al., 2015). However, there are some well-described challenges associated with the use of existing measures for welfare assessment. As a representative example, an increase in plasma glucocorticoids may occur, but there is no means of determining the original source of stimulus in the brain. This increased synthesis may have been triggered by a positive event such as reward, or negative event such as fear (Ralph and Tilbrook, 2016). Glucocorticoids, and many other biomarkers, are therefore measures of emotional arousal, able to identify the strength of animal response, but not if positively or negatively valenced. This ambiguity in interpretation has encouraged development of measures of animal welfare that specifically measure the emotional valence of animals (Mendl et al., 2009).

The judgement bias paradigm has been proposed to provide a means for ascertainment of animal emotional valence and arousal, in an objective manner (Mendl et al., 2009). The basis of the method being that cognitive processing of a stimulus influences the emotional response that an animal makes, whilst the affective state of an animal will bias this cognitive processing to produce variable emotional responses (Mendl et al., 2009). First proposed by Harding et al. (2004), the judgement bias test involves animals learning to respond with two different behaviours, to two different stimuli. A positive reward is associated with one stimulus. Upon exposure to the stimulus, for example a low frequency tone, the animal learns to display a certain behavior to obtain a reward. A second, different stimulus (e.g. high frequency tone), provokes a second behaviour that will allow the animal to avoid an aversive outcome. When the animal is introduced to a stimulus that is different, but of the same nature as the two learned stimuli (e.g. an intermediate frequency tone), the behavioural response to this stimulus can provide insight into the animal’s relative anticipation of positive or negative outcomes. If the animal exhibits behaviours normally associated with the positive reward, that animal has an enhanced expectation of positive events and may be in a positive emotional state. If the animal displays the behaviours associated with the aversive outcome, there is reduced anticipation of a positive outcome, which implies the animal is in a negative affective state (Figure 1). Some tests include several ambiguous probes to increase the sensitivity of the test; responses to these being considered to represent predicted biases intermediate between the positive and negative extremes, for example the difference between anxiety and depression (see Mendl et al., 2009 for full discussion). Although the terminology is controversial, these behavioural responses are often said to be indicative of an ‘optimistic’ and ‘pessimistic’ judgement bias respectively (Bateson, 2016). For simplicity, this review will use this terminology noting the objections to it.

doi:10.20944/preprints202005.0452.v1

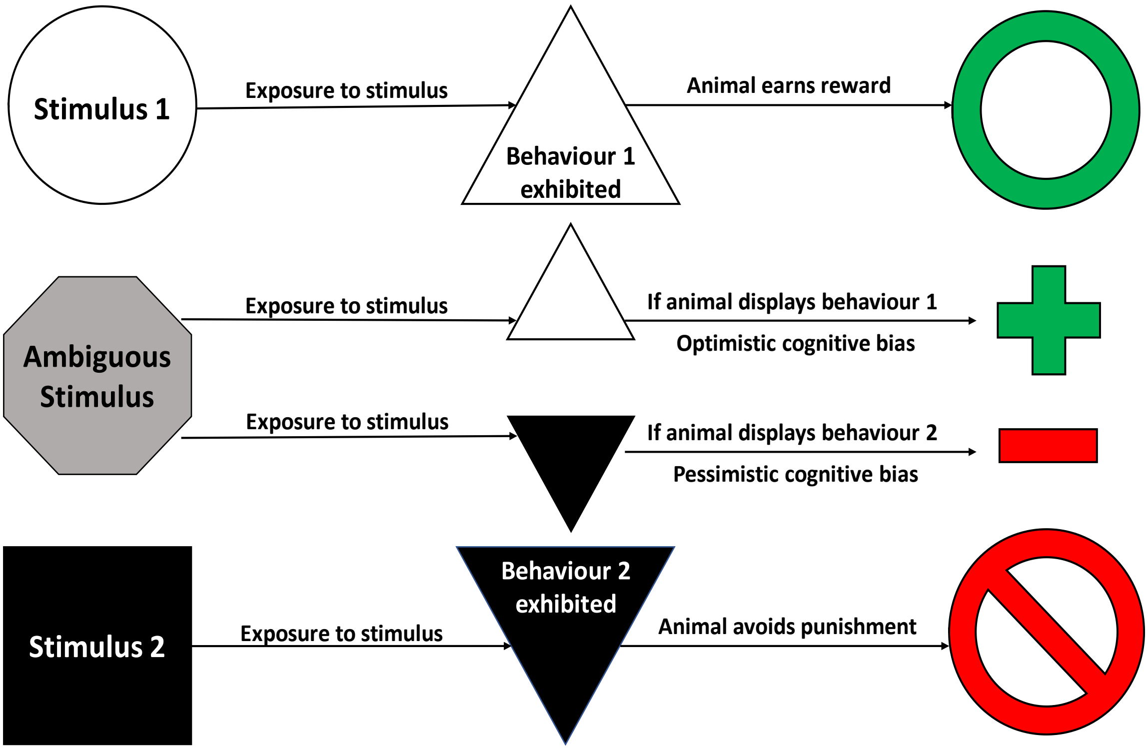

Figure 1 – Flowchart of the judgment bias paradigm learning procedure

Positive reward is always associated with stimulus 1. Exposure to stimulus 1 results in expression of behaviour 1 to obtain the reward. The negative reward is always associated with stimulus 2. Exposure to stimulus 2 results in expression of behaviour 2 to avoid punishment. A stimulus directly intermediate between the two previously learned stimulus introduced. Depending on the behaviours expressed to the ambiguity, a cognitive bias can be discerned.

The practical application of these tests for animal welfare assessment is that it is assumed that an intervention, for example housing change or treatment of illness, will alter animal affect, which can be determined by task performance. This provides information on the impact of the change of welfare, and can be used for ongoing monitoring of welfare state. As already discussed the task has advantages over traditional assessment methods since it can establish valence of emotional response. Additionally, it has been suggested that the task is better suited to measuring long-term mood, rather than shorter-term emotion (Bethell, 2015). Since welfare generally refers to a lasting state made up of an individual's cumulative experiences, and their relative weighting over time (Mellor and Beausoleil, 2015), the outputs of the judgment bias task therefore align neatly with our current welfare definition.

There are two current impediments to widespread implementation of these tasks in animal enterprises for practical welfare assessment. The first is that significant training of animals in the task is required before it can be used to gauge affective state. This issue is not insurmountable, with some progress already made towards automating a judgment bias task in rats, using their natural inquisitive behaviour to drive self-direction of the task (Jones et al., 2018). The second issue arises due to the relative novelty of the test. At the current time, potential confounders of the test results are not well documented or characterised. These confounders may result from test design (reviewed extensively by Mendl et al., 2009, Bethell, 2015), but also as a result of inherent biological variation between animals, or due to the imposition of social structures. This review uncovers the literature on the impact of these factors on judgement bias task (JBT) interpretation, posing questions for further research. We consider the influence of sex and reproductive cycles, social status, genetics, and personality on judgement bias test outcomes. We then discuss specific facets of test design that may influence JBT outcomes and provide suggestions for mitigating these impacts. Throughout, we refer to state and trait effects. Traits being defined as behaviours or emotions that are resistant to change and enduring, whereas states are usually temporary and influenced by the immediate situation (Steyer et al., 2015).

2. Judgement Bias Task (JBT) Types

Published JBTs vary in design in accordance with the learning capability of the animal, ethological relevance of the behaviours required to the species in question, and the parameters of interest (Mendl et al., 2009; Bethell, 2015). These tests are commonly categorised as being go/no-go, or active choice tests and are described briefly below (see Bethell (2015) for review).

A go/no-go test involves presenting two stimuli to an animal, with one stimulus encouraging the animal to perform an action, such as pressing a lever (*go response*). Alternatively, the animal learns to *not* perform an action in response to the second stimulus (*no-go response*). When the unlearned, intermediate stimulus is introduced, performance of the go response equates with an ‘optimistic’ response or enhanced anticipation of positive events, and vice versa for performance of the no-go response. This procedure type has been utilised in multiple studies to identify a judgement bias in animals (Harding et al., 2004; Asher et al., 2009; Doyle et al., 2010a; Anderson et al., 2012; Bethell et al., 2012; Douglas et al., 2012; Destrez et al., 2013; Neave et al., 2013; Daros et al., 2014; Destrez et al., 2014; Starling et al., 2014; Verbeek et al., 2014b).

There are well-documented concerns associated with the go/no-go methodology. Depression and anxiety have been associated with a decrease in activity level and a decrease in overall food consumption (Willner et al., 1998; Mendl et al., 2009). Therefore, a reduction in the number of "no go" responses could be attributed to this reduced activity, or reduced motivation for food, as opposed to a negative judgment bias (Matheson et al., 2008). In recognition of this concern, judgment bias tasks have been developed where the animal is required to respond actively to both the positive and negative stimuli (Matheson et al., 2008);so-called 'active choice' tests.

The active choice test differs from the go/no-go in that an active response is required to the presented stimuli, *and* the response required is the same in nature and therefore should be unaffected by motivation (Bethell (2015)). An active response is defined as being a deliberate, quantifiable action by the animal (Burman et al., 2008). Active responses that have been documented include foraging behaviours (Brydges et al., 2011; Chaby et al., 2013; Barker et al., 2016), removal of lids from a rewarded receptacle (Brilot et al., 2010; Pomerantz et al., 2012; Keen et al., 2014; Gordon and Rogers, 2015) or simply attempting to consume the reward item that would normally be present during a training trial (Boleij et al., 2012; Seehuus et al., 2013; Titulaer et al., 2013; Kis et al., 2015). A key facet of this test design is that the same type of behaviour is required in response to both conditioned stimuli.

There are variations of active choice tests whereby they may use positive reinforcement, typically with presentation of a preferred and less preferred reward (see e.g. Brydges et al., 2011, Pomerantz et al., 2012; Murphy et al., 2015), or where negative reinforcement is used. In the latter, animals must still respond actively to both stimuli, in contrast to the go/no-go test, but a response to stimulus 2 (or the 'negative') prevents the onset of the aversive reinforcement see e.g. (Rygula et al., 2012; Papciak et al., 2013; Rygula et al., 2014a; Rygula et al., 2014b).

The use of negative reinforcement for test design in studies assessing animal welfare is inappropriate since the task can then be an additional source of stress to the animals, modifying affective state and rendering animal welfare determination as a result of the intervention or husbandry change problematic (Brydges et al., 2011). The learning capabilities of animals subjected to intensive stressful regimes may also be reduced (Vögeli et al., 2014). Therefore, a positive versus less-positive, or neutral reward paradigm is suggested to optimise judgement bias task interpretation and reliability of results.

3. Animal Characteristics

3.1 Sex Differences

It is well established from human studies that there are trait differences in affective state between males and females. Negative affectivity, or the tendency to experience negative affect, is generally greater in women (Watson et al., 1988). Evidence of women brooding on distressing life events, leading to stress generation (Nolen-Hoeksema and Jackson, 2001; Hammen, 2005) implies that there is a cognitive risk factor (Gray and McNaughton, 2007). This may in part explain the increased tendency for women to suffer from anxiety and depression (Altemus, 2006; Gray and McNaughton, 2007).

Most published investigations into the JBT, in a range of species, have only investigated one sex. Consequently, there is limited evidence of the existence, or nature of, any sex differences in response. A subset of studies have used both sexes in experimental design (Roelofs et al., 2019, Briefer and McElligott, 2013; Gordon and Rogers, 2015; Murphy et al., 2015; Asher et al., 2016; Barker et al., 2016; Brown et al., 2016; Carreras et al., 2016; Takeshita and Sato, 2016; Barker et al., 2017a; Roelofs et al., 2017). Unfortunately, the picture obtained as to differences is unclear. No difference in JBT response was seen between sexes in dogs, pigs and marmosets (Müller et al., 2012; Gordon and Rogers, 2015; Asher et al., 2016; Carreras et al., 2016; Roelofs et al., 2017; Roelofs et al., 2019). Other studies have found differences in responses but with differing direction of effect (Briefer and McElligott, 2013; Barker et al., 2016; Brown et al., 2016; Takeshita and Sato, 2016; Barker et al., 2017a).

Female goats (Briefer and McElligott, 2013) and rats (Barker et al., 2016) responded with greater number of optimistic biases after experiencing a stressful treatment compared to males.

However, there is the possibility that these findings may not represent a sex difference in affective state in the imposed housing scenarios, but represent differences in response to stressor removal i.e. in the Barker et al 2016 study a rebound optimism was experienced by females when taken out of the metabolic cages for the purposes of testing. This rebound response, where a pessimistic bias was predicted yet not seen, has been reported elsewhere (Doyle et al. 2010a, Doyle et al., 2010a; Sanger et al., 2011; Briefer and McElligott, 2013; Düpjan et al., 2013; Keen et al., 2014; Verbeek et al., 2014a; Hernandez et al., 2015; Barker et al., 2016) but not in the context of sex differences.

Conversely, female lister-hooded rats had decreased response latencies in comparison to males. On the face of it this suggests a decreased expectation of positive events in the former (Brown et al., 2016). However, females were slowest to approach an unrewarded location compared to the rewarded or ambiguous, implying positive affect. There is the possibility that in the context of this particular study design, the apparent sex differences actually reflected differences in learning, with the implication being that males extinguish previous learned associations quicker than females (Brown et al., 2016, Dalla and Shors, 2009). Differences have also been observed in non-mammalian cognitive bias studies with female Japanese pygmy squid (Idiosepius paradoxus) being more likely than males to make pessimistic decisions after non-reward for behaviours that would normally go rewarded (Takeshita and Sato, 2016).

There is some evidence from the Barker et al., 2017a study that variability in between sex JBT comparisons may have actually arisen because of greater intra-individual variability in the female rats. The most likely cause of this is the cyclic release of hormones as part of the oestrus cycle. The psychiatric literature supports this with evidence that some rare disorders appear in synchrony with ovarian cycle phases, for example premenstrual dysphoric disorder (Einstein et al., 2013). Further more compelling evidence for the link is that the increased prevalence of mood disorders in women only commences at puberty, and subsides after menopause (Kessler et al., 1993).

To our knowledge, only one study has examined the influence of oestrus stage on JBT responses in animals. Rats in the dioestrus phase showed reduced optimistic biasing compared to other phases (Barker et al., 2018). Previous rodent studies using traditional behavioural tests of anxiety similarly demonstrated that dioestrus was associated with anxiety-like behaviours (Marcondes et al., 2001; Devall et al., 2009; Brunton and Russell, 2010). Interestingly, pro-oestrus was not associated with increased optimism as might be expected given that rats generally show greater sociability and exploration at this time to increase the chance of securing a mate (Frye et al., 2000). There may be considerations other than a change in affective state which contributed to this finding. The increased progesterone of dioestrus may reduce spatial memory (Sutcliffe et al., 2007). This has implications for JBTs that utilise spatial reference locations with no other associative cues.

Whilst there is no consensus as to the nature of inherent sex differences in response to the JBT, due to the complex nature of the task, with the need for prior conditioning, retained memory of the associations and even a possible role for risk taking, sex differences are likely. Further investigation of this will improve the reliability of JBTs in animal welfare assessment and assist in tailoring husbandry conditions based on sex if required. Whilst the effects of sex cannot be controlled for, including sex as a predictor variable in data analysis should be performed, and consideration of reproductive cycle effects should be considered when using animals as their own controls.

3.2 Early Life Experience

There is extensive evidence of an association between adversity in early life, peri- and postnatally, and risk of later neuropsychiatric disease (Heim et al., 2008; Kessler et al., 2010; Pechtel and Pizzagalli, 2011). This link has been supported by findings from animal research, largely using rodent models, and has elucidated various contributing mechanisms. During early life the brain shows considerable plasticity and it is postulated that adversity enhances or inhibits maturation of brain regions responsible for emotional function, and the hormonal responses to stress, such as the cortico-limbic system (Schore, 2000; Meaney, 2001). Anxiety behaviour (Avital and Richter-Levin, 2005), fear conditioning (Toledo-Rodriguez and Sandi, 2007), neurogenesis (Barha et al., 2011), learning and memory (Chaby et al., 2015), and HPA axis regulation may be modified as a result (Barha et al., 2011). In rodents, a number of conditions are used in modelling early life stress including various forms of maternal separation, limited bedding or nesting leading to poor maternal care, variable short-term stressors and an unenriched environment (Brydges et al., 2012, Schmidt et al., 2010; Murthy and Gould, 2018)

Given that the literature on both rodents and humans suggests that early life stress increases trait anxiety, it would be assumed that JBT responses would reflect animals' decreased expectation of positive events. However, study findings are conflicting. In the study by Bateson et al., 2015 this proposition was supported with starlings that had come from bigger broods, with larger nest competitors, indicating pessimistic responses in a go/no go task. A later starling study, albeit with a slightly modified protocol, found opposing results such that birds reared under the least stress were faster in probe response (Gott et al., 2019).

In rats, two studies also provide conflicting data. In the Brydges et al. 2012 study juvenile stress was induced by a variety of short-term stressors including swim stress, restraint stress and footshocks. Rats, in an active choice task, made optimistic responses in spite of showing increased anxiety in the traditional Elevated Plus Maze task. The authors reconciled this unexpected finding by considering that these animals were underweight, presumably as a result of stress-induced metabolic processes, and that this may have led them to be risk prone because of the high value nature of the reward. A later rat study using a similar JBT paradigm produced the predicted response (Chaby et al. 2013). Similarly, controversy exists in pigs. No effect of low birth weight on judgement bias was seen in Roelofs et al., 2019. Low birth weight is associated with impaired cognitive and emotional development in humans. However, these animals did take longer to learn the task hinting at cognitive impairment (Roelofs et al., 2019), in contradiction to a previous study where low birth weight pigs learned the task faster (Murphy et al., 2015).

Given the perceived importance of early life experience to later-life welfare and the development of resilience, this area clearly needs further investigation. The JBT may not be the best tool for assessment in this area. Issues arise since the JBT requires elements of learning and memory with are often impaired by early life experiences, rendering the readout not representative of affective state. Impacts on response inhibition and food motivation may also arise confounding test interpretation.

3.3 Social Status

Most animal species have social structures that may be incredibly complex. Some animals are highly social and live in groups throughout life, whilst others may only group periodically (Parreira and Chikhi, 2015). In many group-living animals, dominance hierarchies emerge as a means for coexistence of animals in the face of constant threat and limited resources (Jones and Monfils, 2018). However, established hierarchies may be destabilised by dispersal, age-related changes or reproductive status (Broom et al., 2009). Animal emotional state is likely to contribute to establishment of social hierarchies through effects on aggressiveness, as well as change as a result of re-ranking. Furthermore, a range of studies have demonstrated links between social status and cognition with dominance typically being associated with faster discriminative learning and improved spatial cognition (Wascher et al., 2018). Taken together, these findings would suggest that JBT outcomes would be influenced by social rank in both stable and unstable hierarchies.

There is some support for this proposition in a range of species. In a spatial JBT in sows, dominant animals were more likely to exhibit positive judgement bias than subordinate sows (Horback and Parsons, 2019). Similarly, dominance status was associated with increased positive responses in capuchin monkeys (Schino et al., 2016), rats (Barker et al., 2017b, Barker et al., 2018) and starlings from large broods (Bateson et al., 2015). Other indications of an effect of social relationships on JBT response were found in a study of dolphins where dolphins that swam together, a socially affiliative behaviour, made more optimistic choices (Clegg et al., 2017). More pessimistic calves, that showed some fearful behaviour, were more selective in their social relationships, forming preferential relationships (Lecorps et al., 2019a). In accordance with the literature on effects of social status on learning, (Barker et al., 2020) also demonstrated that dominant rats learnt JBT associations to reach the standardised criteria faster than their subordinate counterparts. However, rats did go on to learn the required associations. Training times may need to be extended to account for this, rather than simply excluding animals as non-learners. Only one study that investigated social status of animals found no difference in JBT response as a result. This study involved laying hens performing a spatial judgment bias task. The author did pose that a possible explanation for the null finding was that lower ranking birds, free from usual competition, seized the opportunity to gain the food reward in the JBT (Lindström, 2010).

Whilst, the impact of social status on the JBT has received limited study there is enough evidence to suggest it should at least be a consideration in JBT experimental design. A challenge in determining causation is however inherent. A submissive state may lead to negative affective state and reduced expectation of positive events, or trait effects such as negative affectivity may influence formation of social relationships (Lecorps et al., 2019a). Whilst, social status as a potential confounder cannot be removed from JBT experimental design in group-housed animals, we recommend investigation of, and account of the effect, by determining social status through established methods and including it as a covariate in results analysis.

3.4. Genetics, Personality and Laterality

3.4.1.Breed

It is quite likely that differences in JBT responses may be seen between breeds or strains of animals based on differences in trait effects (particularly in rodents), and learning ability. A number of studies have investigated this in rodent models with known depressive phenotypes (see Enkel et al., 2010; Richter et al., 2012; Kloke et al., 2014). However, of more value for applied animal welfare are whether differences exist as a result of standard breeding rather than in mutant/transgenic strains. This has indeed been shown. Differences in discrimination ability, influencing task learning, were found between the BALB/cJ and 129P3 strains (Boleij et al., 2012). Similarly, Göttingen minipigs learnt the discrimination task faster than conventional pigs (Murphy et al., 2015). However, presence of the halothane, or porcine stress gene, which is present in many commercial pig lines did not affect JBT results (Carreras et al. 2016).

Given the limited study, it is impossible to say whether breed affects JBT performance. Whilst a dearth of literature suggests there may be differences, it has also been suggested that differences may be rare, but due to publication bias studies reporting no differences remain unreported (Bushby et al., 2018). Further considerations are that current evidence on breed differences relates to learning of the test, rather than actual differences in affective state. This should be considered in experimental design by providing longer for training, rather than excluding animals who do not meet test training criteria. A second consideration is that breed may not be the correct factor to be considering. Different breeds commonly have different temperaments (Bushby et al., 2018), and even within a breed inter-individual differences are apparent as a result of personality traits. These factors may alter affective state or the likelihood of engaging with a task.

3.4.2.Personality

A fascinating, emerging area of research is that of animal personality, and how this shapes behavioural responses. Epigenetics, the microbiome and early learning may bring about inter-individual variations in behaviour. The resulting consistent, between individual, differences in behaviour comprises ‘personality’(Sih et al., 2015). Human studies have shown measurable associations between personality traits and emotion with neuroticism tending to cause negative effect, and extraversion leading to heightened positive states (Gross et al., 1998). In spite of the human link, effects of personality traits on the JBT is relatively uncharted territory.

In a recent canine study the assumed link was supported (Barnard et al., 2018). Dogs that scored higher on sociability, excitability and non-social fear in standardised personality assessment protocols showed reduced latency to probes than those with traits for separation-related anxiety and dog-directed fear. However, some associations between personality types and the JBT that were predicted did not eventuate, for example an effect of curiosity and playfulness. In red jungle fowl chicks, personality was assessed through traditional behavioural tests, including the novel object/arena and tonic immobility tests. The chicks then performed an active choice JBT with the finding that less nervous chicks were more optimistic than their nervous counterparts (Jansson, 2015).

However, the relationship between personality and the JBT may not be simple. Asher et al., 2016 demonstrated in pigs that mood and personaility traits intereracted to influence judgement biasing. Pig personality was measured using the coping styles apporach where pigs were classified as being proactive or reactive. JBT outcomes differed based on personality classification and mood state (inferred from housing treatment), with reactive pigs in a less enriched environment being more pessimistic than those in the enriched environment. Proactive pigs showed optimistic responses independent of the housing environment. This finding is not entirely unexpected since human judgement is also a product of trait effects and transient affective states.

Whilst not specifically a facet of personality, the abiltiy to empathise with others is needed to live successfully in social groups. Emotional contagion may assist in transferring information about emotional state to conspecifics. Demonstrating the presence or effect of emotional contagion and its messaging in animals is challenging. Adriaense et al., 2019 presented the first published investigation into the relationship between emotional contagion and judgement biasing. Demonstrator ravens were manipulated into oppositely valenced affective states. Observer ravens demonstrated pessimistic biasing after witnessing ravens in a negative affective state. However, the positive manipulation did not lead to optimistic reponses.

There are a couple of take-home messages from these studies. Firstly, assessment of personality traits using validated methods, with knowledge of links between certain traits and negative affective states, may allow for improved welfare by allowing for tailored selection to certain environments or roles (Barnard et al., 2018). Secondly, accounting for personality differences in experimental design could reduce the significant variability often seen in JBT studies, leading to improved reproducibility.

3.4.3.Laterality

A large number of studies evaluating the link between laterality and emotion have been conducted over the last few decades (Leliveld et al., 2013). The vast majority of these studies have examined the links with negative emotions such as fear and anxiety, but some investigation of assumed positive states has been conducted (Whittaker and Marsh, 2019). Davidson’s laterality-valence hypothesis proposes that negative emotions are controlled by the right cerebral hemsiphere, and vice versa for positive emotions (Davidson, 1995), although there is evidence disputing this neat separation from humans (Rogers, 2010). Since the laterality link with emotion is focussed on valence of response, the JBT would seem to be the ideal candidate for evaluating direction of effect further. However, whilst studies to date have demonstrated effects of handedness on judgement bias, too few studies have examined this to be able to draw any firm conclusions on specific linkages.

A possible link between pawedness and judgement bias has been shown in dogs, with left paw preferent dogs having a more pessimistic outlook than right or ambi-lateral animals (Wells et al., 2017). Similarly Gordon and Rogers, 2015 found that left-handed marmosets were more likely to show negative biasing.

Given, that both of these studies are supported by the Davidson hypothesis there is clearly merit in further investigating the linkage. Although, paradoxically further research to confirm these findings might actually lead to the proposition that time-consuming judgment bias testing be replaced with a far quicker investigation of handedness. However, since temperament, genetics, sex and the environment all influence laterality, the connection may not be that simple (McGreevy et al., 2010; Hopkins et al., 2013; Schneider et al., 2013).

4. Optimal test design to reduce confounding

4.1 Extinction of Response

A commonly reported problem with judgement bias tasks is the extinction effect. This phenomenon is seen as a result of animals learning that the intermediate, ambiguous probe is unrewarded and they therefore ceasing to perform the required learned behaviours (Brilot et al., 2010; Doyle et al., 2010b; Briefer and McElligott, 2013; Murphy et al., 2013; Freymond et al., 2014; Karagiannis et al., 2015). Chaby et al. (2013) noted this as a significant concern, advancing that only the first response to the ambiguous probe was based on the animal’s subjective experience. This led to the suggestion that separate analysis and presentation of results from the first ambiguous trial compared to subsequent trials, be performed, to account for this. Other studies have similarly reported reduced responses to the ambiguous probe over time in sheep, dogs and hamsters, suggesting that this is a cross-species concern (Doyle et al., 2010b, Starling et al., 2014, Bethell and Koyama, 2015).

Despite the findings of Chaby et al. (2013) in a rat study, extinction was not observed in the Brydges et al. (2011) rat study. Neither was it observed in subsequent studies utilising the same JBT design (Brydges et al., 2012; Barker et al., 2016; Barker et al., 2017a). This discrepancy may have resulted from the training protocol used in these studies. In the original Brydges et al., 2011 study, a training phase immediately prior to the testing phase was recorded, which was not documented in the Chaby et al. 2013 study. This particular phase involved removing the reward (either preferred or less preferred) from a normally rewarded training trial. It is suggested that this action encourages animals to learn that not every trial is rewarded, reducing the chances of extinction when it comes to the ambiguous probe (Barker et al., 2016). It is also important to note that these unrewarded training trials occurred for a limited period (5 days), and took place after the animals had already demonstrated their ability to perform the task to the researchers established criteria. This is important, as unrewarded trials in the early stages of the study could hamper animals' learning, and subsequent performance of the JBT.

The possibility of extinction suggests that the judgement bias test has relatively low repeatability, and will be of particular concern when there is repeated exposure to the ambiguous probe as part of ongoing welfare assessment, to increase statistical power (Barker et al., 2018), or when animals act as their own controls (Walker et al., 2014). To counter concern some studies have introduced partial reinforcement of the ambiguous probes (Bateson and Matheson, 2007; Matheson et al., 2008). However, it could be argued that this action permanently alters the reward status of the intermediate stimulus for the animal, rendering its presence no longer 'truly intermediate'. The animal learns that the intermediate stimulus results in a higher chance of a reward being offered, than the 'negative' stimulus, and their judgement to ambiguity changes accordingly.

Extinction of learning is unlikely to be completely eliminated as a potential confounding factor in traditional JBT test design, it may however be managed through experimental design considerations (Doyle et al., 2010b). The optimal method to do this may be through combination of methods to include the use of unreinforced training trials (Brydges et al., 2011), not allowing animals to act as their own controls (Barker et al., 2016), increasing the occurrences of reinforced training between testing sessions

(Doyle et al., 2010b), and confirming differences in outcomes from the first exposure to the ambiguous stimulus compared to subsequent exposures (Chaby et al., 2013).

A novel, recently reported method to overcome this concern has been to intentionally train animals to recognise the cues presented in the task and make associations between these cues and the probability of reward or punishment. (Lecorps et al., 2019b). The task then no longer relies on ambiguity interpretation. This test was successfully validated in calves expected to be in pain because of disbudding. Whilst this is a departure from the foundational psychological theories of cognitive bias in ambiguity judgements from which animal JBTs derived (Amir et al., 2005; Iigaya et al., 2016), the method clearly shows promise. Further investigation and validation of this alternate strategy is needed.

4.2 Parameters measured in the tests

Typically studies using JBTs tend to report either latency to perform the required learned behavior (see e.g. Boleij et al., 2012, Kloke et al., 2014, Carreras et al., 2015,Scollo et al., 2014), or choice (optimistic or pessimistic) which may be presented as percentage of total number of tests (see e.g. Brydges et al., 2011, Barker et al., 2016). A number of studies also use a combination of these outcomes.

Time taken to achieve a task (latency) has traditionally been used in behavioural tests conducted on animals. There is good evidence that latency to approach a novel object indicates an animal’s preference, and therefore decreased latency to approach an object can identify a decreased desire for that object (Bateson and Kacelnik, 1995). However, the use of latency as an outcome measure may suffer from similar confounds as go/no-go test designs (Hernandez et al. 2015). Decreased motivation (Karagiannis et al., 2015), inactivity (Salmeto et al., 2011; Hymel and Sufka 2012), or other confound such as a difference in body size and strength (Roelofs et al., 2019) may reduce latency to approach an object, but an active ‘optimistic’ choice may eventually be made (Roelofs et al., 2019, Barker et al., 2018). Decreased latency may also be seen as a result of repeated exposure and loss of ambiguity as discussed earlier. In a JBT design where latency alone is used, decreased latency in response to the ambiguous probe is taken to be indicative of negative affective state. However, when decreased latency does not correlate with the performance of the behaviour normally associated with the less-positive (negative) reward in an active response task, as was seen in Barker et al., 2018, determining valence of affective state is challenging. This raises a fundamental issue with JBTs that whilst it is normally assumed that one behaviour performance represents a ‘positive’ affective state, and the other a ‘negative’ state, affective state occurs on a continuum between these extremes. Since there is currently no accepted baseline against which to categorise affective state as positive or negative (Bethell, 2015), these tasks may in fact be contrasting a highly positive state with a less positive or neutral state, or any other position on this continuum. With this in mind, perhaps concerns around use of latency are unfounded. A decrease in latency to perform a behaviour when compared across time, or between groups, indicates a shift in the negative direction, with the absolute categorisation of affective state being immaterial given the nature of JBTs.

A method reported that may avoid some of the concerns around the use of absolute latency as an outcome measures is to use some form of index which normalises the animal’s responses to the ambiguous probe based on their latency to repsond to the positive and negative stimuli. This would presumably account for differences in agility and motivation between animals (See e.g. Henry et al., 2017; Barnard et al., 2018; Horback and Parsons, 2019).

4.3. Other Methodological Issues

There are a number of other methodological issues to consider in JBT testing. Some of these may be eliminated through choice of alternate test or careful experimental design. Food is commonly used as a reinforcer in JBTs since animals are generally highly motivated to acquire it. The use of food rewards has been discussed extensively elsewhere (Mendl et al., 2009). However, there are a few salient issues based on factors presented here. There is evidence to suggest that elevated glucocorticoids, released during a stress response, motivate animals to consume food (Dallman, 2010,Willner et al., 1998). This increases the incentive value of food rewards used, therefore animals in a negative state may respond with seemingly optimistic biases (Hernandez et al. 2015). A similar concern exists when considering animals that have suffered early life adversity since they may be underweight, and consequently highly motivated for food (Brydges et al., 2012), as well as having heightened HPA axis responsiveness (Plotsky et al., 2005). Social status may also affect JBT outcomes when food reinforcers are used. Dominance status is associated with other behavioural traits such as being more risk prone and food-motivated, although it is not clear whether dominant rank acquisition favours reward-seeking behaviour or occurs because of it (Davis et al., 2009; Lozano-Montes et al., 2019). Therefore, in dominant animals an optimistic response may not actually reflect the subjective experience of being in a positive emotional state.

Related to laterality many animals have side biases in motor behaviour or perception of stimuli on opposite sides (Rogers, 2000). To our knowledge this has not been investigated specifically in the context of JBTs but it is postulated that these biases may influence spatial task performance, especially in prey species. In the authors' experience, there may also be more practical reasons for side biases; in creating a JBT arena for larger animals, usually situated in a room or open space, it is easy to overlook facets of the environment that may be imperceptible to human observers but of importance to animals. Differences in shadowing, airflow or noise may influence approach to the reinforcer. Randomisation of side of positive and negative positions across the animals to be tested can reduce the impact of this in JBT findings but is unlikely to completely mitigate the impact.

5. Conclusion

Whilst the JBT is now well-established as a tool for measuring valence of emotional response across a range of species, results are sometimes contrary to those expected based on physiological principles and corroborating behavioural data. Some of these unexpected results may arise due to significant inter- and intra-animal variation, as well as facets of test design. This review has proposed that animal-based factors including sex, social status, early life experience, genetics, personality and laterality may all lead to unanticipated responses that do not necessarily relate to current state effects. Test design features, for example the use of food reinforcers when animals have suffered early life adversity, may also exacerbate some of these factors. Whilst test design may be able to be modified to minimise these concerns, animal biology cannot be changed.

It is our proposition that 1) researchers consider undertaking dedicated study to investigate the impacts of these inherent biological factors on various types of JBT across a range of species, 2) that the impact of these factors are considered in experimental design and analysis, by documenting their presence, and including them, for example, as covariates in statistical analysis of results. These refinements will increase the reliability of JBTs for animal welfare assessment and as a reference for developing new welfare biomarkers, particularly those for positive affect.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. AW is supported by an Australian Government, NHMRC Peter Doherty Biomedical Research Fellowship (APP1140072).

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Figure Legends