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Measuring Animal Welfare – Assessing Cognitive Bias as a Potential Approach

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Abstract

The evaluation of an animal's emotional state and its well-being poses a challenge to current research. Direct measurement of emotion is inaccessible, so assessment relies on measures of affective states that are predominantly influenced by emotions and important indicators. Studies that used physiological, cognitive or behavioural measurements have shown the assessment of cognitive and judgement bias to be a suitable method to gain insight into the affective state and welfare of animals. Although these method does not always allow a clear interpretation of the results with respect to the affective state, animals in discrimination tasks generally show a pessimistic judgement bias when they are in a negative affective state. This tendency agrees with cognitive theories stating that an individual's assessment of a situation gives information about the involved emotions. Therefore, the analysis of cognitive bias may allow assessing the influence of various factors on an animal's affective state and, if appropriate, creating conditions that result in a positive affective state for animals in husbandry. As it is our aim to highlight useful methods for determining the welfare of animals in husbandry, we here review underlying theories of cognition and affect, evaluate their relevancy to animal behaviour and give an overview of applicable methods and their outcomes.

Key words: Affective state, animal welfare, attention, emotion, judgement bias, memory

Introduction

Animals are part of our society and play an important role as livestock or companions. To meet their needs appropriately, an animal keeper needs to know under which husbandry conditions they feel well or unwell. Although an animal's affective state can give information about its welfare, the affective state is difficult to determine because the animal cannot verbally express its feelings. In this context, the evaluation of cognitive bias has proven to be useful for determining an individual's affective state. Cognitive bias is defined as a systematic tendency for positively or negatively biased perception. Cognitive bias is usually subconscious, is used to appraise circumstances efficiently to make a quick decision and leads to a judgement bias when an individual makes a decision in an ambiguous situation [1].

Materials and Methods

To find out how cognitive bias can give information about animal welfare, we searched the literature using the databases PubMed, BIOSIS, CAB and Google Scholar with the search terms cognitive bias, cognitive bias in animals, affective state in animals, animal welfare, attention, emotion, judgement bias in animals, and memory. We then selected studies on processes underlying cognitive bias and estimated the relevancy of cognitive bias to animal behaviour. To give an overview of applied experimental designs, we reviewed experimental settings and summarized successful applications.

Cognitive Theories

Before we can identify measures of cognitive bias that could be useful tools to determine the welfare of animals, we have to understand cognitive theories proposed in the context of cognitive bias. These theories will be introduced in the following subsections.

Cognitive theories of bias and emotional state

In animals as well as in humans, the processing of information follows specific

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computational rules that seem to be evolutionary adaptive [2]. In this evolutionary context, Haselton et al. [3] proposed that cognitive bias can arise from (1) heuristics, (2) error management effects or (3) experimental artefacts.

Judgement heuristics are often used when it is not possible, extremely complex or too time consuming to investigate all alternatives and rationally balance them before making a decision. In other words, heuristics are information-processing shortcuts *that are employed when making judgements under uncertainty [4]. Tversky and Kahneman [5] described three heuristics that underlie numerous intuitive judgements: (1) Representativeness, which is usually employed when individuals are asked to judge the probability that an object or event A belongs to class or process B. For example, one assesses the simularity of an individual described as "introverted, meek and solemn" to the stereotype of the occupational roles: farmer, salesman, pilot, librarian, physician and orders the occupations by the degree to which the individual is representative of these stereotypes. (2) Availability of instances or scenarios, which is often employed when individuals are asked to assess the frequency of a class or the plausibility of a particular development. For example, one may assess the risk of a heart attack among middle aged people by recalling such occurrences among one's acquaintances. (3) Adjustment from an anchor, which is usually employed in numerical prediction when a relevant value is available.* People make estimates by starting from an initial starting point, that for example maybe suggested by the formulation of the problem. When bias results from error management, selection favours bias toward the less costly error [6]. This selection means that costly reproductive errors are reduced if differences in the costs of errors exist. For example, men appear to overinfer sexual intent in women in response to cues such as a smile or freindlines.

In cases when an experimental artefact causes bias, apparent bias and errors are artefacts of research strategies. Here, bias results from the application of inappropriate norms [7].

To use cognitive bias for measuring animal welfare, researchers must understand how bias arises. For example, feelings and moods can influence cognition and generate cognitive bias [8]. Cognitive bias can be positive or negative, and several authors defined different terms of cognitive bias. For example, Hertel and Mathews [9] categorized cognitive bias that arises from emotional states as (1) attentional bias, (2) interpretation bias and (3) memory bias.

Attentional bias is investigated by presenting cues that are irrelevant for the task but meaningful for affect and monitoring whether these cues influence the latency time of responses to intended targets. For example, in an emotional Stroop task, humans who were asked to name the colours in which words were written tended to respond more slowly when the word's content matched their personal concerns than when the word was not relevant to their psychological condition [10]. Also, anxious individuals shifted attention towards threat words, whereas non-anxious subjects shifted attention away from the threat term [11,12]. Furthermore, anxious individuals tended to interpret and remember ambiguous events more often as threatening whereas non-anxious subjects tended to perceive them as less threatening [13]. For example, non-anxious individuals were faster at endorsing words related to positive compared with negative inferences, whereas socially

anxious individuals were equally fast at endorsing positive and negative words. Thus, there is evidence that attentional bias and interpretative bias influence memory [14].

Paul et al. [15] similarly described the emotion-based ways of information processing and divided cognitive bias into (1) attention bias, (2) memory bias and (3) judgement bias. Thus, for example, the attention of anxious individuals is potentially directed toward frightening stimuli, and stimuli are increasingly perceived as frightening and stored as such in memory [12,16]. Consequently, fearful or depressed individuals often interpret ambiguous information negatively and make a negatively biased judgement in ambiguous situations [17–20]. This tendency is defined as negative cognitive bias. In contrast, positive cognitive bias describes the tendency to evaluate situations predominantly positively. The appraisal of a situation is therefore influenced by the emotional state, the directed attention and the memory processes [15]. Similar cognitive theories explain that changes in information processing occur in conjunction with changes in affective state and are part of the emotional process [16, 21,22].

Cognitive theories of affect

The affect infusion model

Forgas [23] proposed an integrative theory with the 'affect infusion model' to explain the role of affective states in judgement. He identified four judgement strategies: (1) The direct access strategy, based on the direct retrieval of a pre-existing, established judgement is most likely when the target is well known and the judgment has low personal relevance (2) The motivated processing strategy is employed when a judgement arises from a specific motivation. For example, sad subjects, that were asked asked to select a partner selectively looked for and found a rewarding companion, whereas subjects in other conditions chose task-competent partners. (3) The heuristic processing strategy is applied when the target is simple, the personal relevance of the judgment is low, the judge has limited cognitive capacity, and the situation does not demand accuracy or detailed consideration. (4) The substantive processing strategy is adopted when judges selectively and constructively process available information and rely on various learning, associative and memory processes [23]. In the affect infusion model, mood effects on judgement do not occur consistently. They occur mostly when constructive processing is used with affective priming (during substantive processing) and 'affect-as-information' judgement (during heuristic processing) [24–27].

Research on affective priming investigates whether the evaluation of a first stimulus – the prime – influences the processing of subsequent stimuli [28]. The 'affective primacy hypothesis' states that bias can arise when specific stimuli are presented subconsciously [29]. Referring to this hypothesis, Winkielman et al. [30] showed that subjects rated neutral Chinese ideographs more positively after viewing smiling faces than after viewing frowning faces, neutral polygons or blank slides.

The 'affect-as-information' approach implies that individuals do not merely judge on the basis of the recalled features of a target [31]. Rather, their actual emotional state influences their decision. Weather, for instance, can influence an individual's judgement. Humans in ambiguous situations tend to judge more positively during sunshine than rain [32].

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The mood congruity effect and the mood-state-dependent retention

Comparable to Forgas [23], Bower [33] claimed that the activation of an emotion node also spreads activation throughout the memory structures to which it is connected and described two basic phenomena. The first is the mood congruity effect, which is supported by other researchers [34, 35]. It states that individuals have the tendency to attend to events that match their emotional state. The recall of mood-congruent material predominates. For example, when we are happy, we are more likely to remember happy events than sad ones (for review see Blaney [36]). The second phenomenon, the mood-state-dependent retention, states that memories stored during a specific mood are recalled more readily when that mood is experienced again [36, 37]. Evidence from psychological studies confirms that emotional states tend to facilitate the retrieval of stimuli of the same emotional valence [38].

The semantic and the distributed network models

Another model that explains the interaction between mood and cognitive processes is the semantic network model (see Bower [33]). It suggests that each emotion has a specific node in memory, which in turn connects with many related aspects that might evoke that emotion, such as autonomic responses, expressive behaviours and descriptions of situations [33]. However, Lewis and Critchley [39] stated that support for the semantic network model is weak for three reasons. Firstly, the influence of mood at the time of encoding on the brain activity during recall is not clear. It is debatable whether the involvement of the emotional system in the retrieval of emotionally valenced information differs for positive and negative valences. Secondly, there is no data suggesting a positive network to be more active in a happy mood or a negative one to be more active in a sad mood. Thirdly, no proof exists that emotional activity due to mood is associated with emotional activity during recall. For these reasons, the semantic network model is being questioned, and further research is needed.

The distributed network model also indicates that a unique network activates each item in memory, but closely associated units have overlapping networks [40]. Hence, activation of one item increases the chance of closely related ones also being activated. Plaut and Booth [40] furthermore evaluated their distributed network model against semantic priming (for a review see Neely [41]), which describes how the processing of a cue such as a word influences the processing of a subsequent word with a semantic relation to the first one. Accordingly, individuals responded faster to the word 'saddle' when the word 'horse' preceded it than when words without semantic relation came first. The presentation of a stimulus (prime) therefore influences the processing time of a subsequent stimulus (target). Although Borowsky and Besner [42] challenged this conclusion, Plaut and Booth [43] defended their model as being highly abstract in its applicability to lexical processing and stated that it nonetheless appears to capture important properties of human lexical processing.

Further studies claim that affect does not influence semantic memory processes [44] and that affect influences controlled but not automatic processing [45]. Storbeck and Clore [46] observed that positive affect activates semantic associations whereas negative affect inhibits their accessibility.

The relevancy of cognitive bias theories to animal behaviour

The question arises whether cognitive theories could be applied to animal welfare. How could cognitive bias arise in animals and possibly influence the results of behavioural tests?

According to the direct access strategy, individuals appraise a situation mostly via memory content. During a negative affective state, humans perceive situations negatively and store information accordingly in their memory [12]. These negative memories can then influence the appraisal of another situation and lead to a negatively biased perception. In discrimination tasks, the intermediate stimuli are usually unrewarded. It is possible that animals in a negative affective state increasingly store the associated experienced frustration in their memory, potentially leading to a pessimistic expectation when being exposed to subsequent intermediate stimuli. Possibly, a mood congruity effect occurs in this context. When animals are sad, they could be more likely to remember the sad event of an unrewarded, intermediate stimulus.

According to the motivated processing strategy, an individual is likely to improve its current mood [23]. In animals, this could mean that during a judgement bias task, they would try to optimize the outcome of positive events by exploring every feed bowl to maximize the possibility of a reward. This behaviour could not be observed so far. On the other hand, an animal trying to improve its current mood might try to avoid a negative event, for example the frustration of exploring a bowl and not receiving a reward. Harding et al. [47] observed in judgement bias tasks that animals in a negative affective state have a low expectation of a reward. It is possible that they try to avoid frustration when they are in a negative affective state.

According to the heuristic processing strategy, negative information is classified as less threatening when individuals are in a positive compared with a negative affective state [23]. Applied to an animal's behaviour in a judgement bias task, this would mean that the animal could handle frustration better and would be more likely to risk experiencing frustration of an unrewarded exploration when in a positive compared with a negative affective state. In fact, studies showed that animals approached a target faster and more frequently as a reaction to intermediate stimuli when they were in a positive affective state than when they were in a negative one [48–50].

According to the substantive processing strategy, memory content that is congruent with the current mood is easier to access than non-congruent memory content [23]. Possibly, animals in a positive affective state can more readily recall the experience of a reward and are therefore more optimistic to receive feed (as seen in several studies [48–50]) whereas animals in a negative affective state increasingly recall negative events like non-palatable food [19] or non-reachable food [51] and classify ambiguous stimuli as more negative.

Affective States in Humans and Animals

Several of the described mechanisms are fundamental to cognitive processing in animals as well as in humans. However, the way these mechanisms work may differ between animals and humans. For example, the appraisal of a situation and

implied decisions under uncertainty are influenced by the affective state, as shown by research with humans and animals [17, 47]. Nevertheless, differences in assessment exist. Animals appraise a situation on two levels (reviewed by Dantzer [52]): the sensomonitorial level (automatic triggering of reactions to adaptively significant stimuli) and the schematic level (automatic triggering of learnt reactions to previously encountered stimuli).

Leventhal and Scherer [53] proposed a third level for human processing: the conceptual level (non-automatic, intentionally processed reactions). As an example for the lack of conceptual processing in animals, Dantzer [52] pointed out that a sow that receives no material for nest building may experience a negative affective state in consequence of not being able to build a nest or not having the opportunity to do so. However, because the sow had no expectation of fulfilling her motivation, she should not feel frustrated. With respect to this third level of processing and the role of cognitive bias in the context of animal welfare, it may be helpful to examine if affective states in humans and animals are comparable.

Methods to Determine Animal Welfare under Husbandry Conditions

Researchers have various means to evaluate an individual's affective state, its underlying mechanisms and its impact on the assessment of situations and judgement. In the following subsections, we will review results from three commonly used methods: brain imaging, neurobiological substrate analyses and behaviour tests.

Imaging of activated brain regions during affect

LeDoux [54] suggested – as an option to monitor an individual's emotional state – looking at the processes happening in the brain. As illustrated in brain imaging studies, the neural circuits that are involved in the processing of emotional information are conserved across species [55]. Correspondingly, studies with humans have identified a reward circuit located around dopamine neurons of the same fundamental circuit as that identified in experiments with animals [56].

However, interpretation of altered activity in specific brain regions is challenging. As Hayes and Northoff [57] explained, there is an overlap between reward processing areas and areas activated during the processing of aversion-related information. The prefrontal cortex and the amygdala seem to show activation during aversion processing, reward processing and ambiguous information processing; the orbitofrontal cortex shows altered activity during aversion processing and ambiguous information processing; the cingulate cortex and the prelimbic cortex show changed activity only during ambiguous cue interpretation [57]. Because of these overlaps, it is not easy to draw conclusions from activated brain regions on an individual's affective state and its welfare.

Evaluating neurobiological substrates during affective states

To get a detailed impression of the processes in the brain during affect, researchers have examined the role of neurobiological substrates [58, 59]. A lot of the relevant literature concerns the reward system, which often induces a positive affective state [60–63]. Although there is little research on neurobiological substrates regulating positive affect apart from reward, it is possible that positive affect and reward may be modulated by the same mechanisms [64].

The neurotransmitter dopamine plays a fundamental role in the reward system. Reward causes the release of dopamine from several brain stem sites, and dopamine antagonists disrupt reward signals [65]. The mesolimbic dopamine system is often associated with the rewarding effects of food, sex and recreational drugs [66]. Accordingly, it is possible, but still debated, that dopamine may have an effect on depression disorders [67, 68].

Shopsin et al. [69] showed that the neurotransmitter serotonin can be involved in affective states. Serotonin deficiency can be causal for the development of depression. Shopsin et al. [69] conducted their investigations by inducing serotonin deficiency and then using serotonin reuptake inhibitors. In depressed patients and patients who responded to serotonin reuptake inhibitors, the depression recurred after serotonin depletion [69]. In a visual discrimination task conducted with sheep, Doyle et al. [70] demonstrated that an administration of a serotonin inhibitor over the course of five days induced a pessimistic judgement bias in sheep. This finding further supports the involvement of the serotonergic system in judgement bias.

Similarly, noradrenaline reuptake inhibitors are administered as antidepressants. The evidence of noradrenaline being involved in depression is quite convincing [71]. Anderson et al. [72] investigated in rats if manipulation of the serotonin or noradrenaline pathway influences the affective state and thereby leads to cognitive bias in the expectation of a reward. They found that an acute treatment with fluoxetine (a selective serotonin reuptake inhibitor) and diazepam (a benzodiazepine) had no effect on the anticipation of reward whereas a treatment with reboxetine (a noradrenaline reuptake inhibitor) reduced it [72]. Similarly, Enkel et al. [73] showed that treatments with a combined noradrenergic–glucocorticoid challenge shifted response rates in rats to fewer positive and more negative responses to ambiguous cues.

A negative judgement bias was also found in congenitally helpless rats, a genetic animal model of depression [73]. Thus, both environmental and genetic factors may induce the same judgement bias. Furthermore, von Frijtag et al. [74] proved that a defeat against a rival rat and subsequent single housing led to changes in plasticity of the hippocampus and to a reduced expectation of reward. The effect was reversible through the administration of the antidepressant imipramine, which raises the concentrations of serotonin and noradrenaline for three months. Harmer et al. [75] showed that an acute treatment with antidepressant drugs in humans induced a positive bias in emotional processing but had no subjective effect on mood. Importantly, this finding contradicts traditional models of antidepressant action by suggesting that antidepressants alter the processing of affective stimuli rather than influencing mood directly (for comparison see [76–79].

The impact of neurobiological processes on affective states is out of question and should be taken into account when evaluating an individual's welfare. Because neurobiological substrate analyses are applicable to both humans and animals, they could help interpret results from behaviour tests to evaluate affective states and welfare.

Behaviour tests

In humans, it is relatively easy to evaluate what circumstances cause positive or negative affective states because humans can be asked about their experiences, their feelings and their perception of a certain situation. In contrast, the interpretation of physiological and neurobiological measurements in terms of the emotional state of animals is limited. Thus, this field of research brought forward several innovative study designs.

Dating back to the 1950s, research has shown that a change in judgement can be a result of the affective state. As Brown et al. [80] found out in this context, the affective state influences the startle response in rats. The startle response, provoked by a suddenly occurring event (e.g. shot from a toy gun), occurred faster and with greater intensity when a negative affective state predominated than when a positive affective state prevailed [80].

In this regard, Von Frijtag et al. [74] demonstrated that in rats that experienced a defeat against a rival and afterward were kept alone in cages for three months, the expectation of a reward (sucrose) was reduced for up to three months. This and similar findings stimulated the interest in the influence of affective states on behaviour. A potential model for the assessment of psychopathology was developed, and a number of methods are now available to manipulate an animal's affective state and monitor its influence on the animal's expectation in ambiguous situations. We will introduce selected methods and give detailed examples in the following subsections.

A discrimination task to assess affective states in animals

In general, experimental designs to investigate cognitive bias in animals are based on a discrimination task. The animals initially learn to discriminate between two stimuli. One stimulus is associated with a positive event, such as a reward. The other is associated with a negative event, such as no reward, a reward of lower value or an aversive experience. These stimuli can be acoustical (tones of different frequencies [47, 81]), visual (cards of different brightness [19, 20] or different locations in a room [50, 82]), sensory (sandpapers of different granularity [49]) or olfactory (different odours [83]). When the animals have completed the training and are able to discriminate between two stimuli, their affective state gets manipulated.

Methods used to generate a negative affective state are: unpredictable, aversive events [47, 84, 85], removal of environmental enrichment [19, 51], warning cry of a conspecific and frightened eyes of a conspecific [86], shearing [87], social isolation [88–90], bright illumination [83], shaking [91], defeat against a rival [74] and neuromodulators that mimic stress [73]. Practices applied to induce a positive affective state are: environmental enrichment [48, 50, 92], successful foraging [93], olfactory enrichment with essential oils [94], administration of antidepressants [73] and the ending of an aversive event [85]. Following this manipulation, intermediate stimuli between the two learnt stimuli are presented, and it is evaluated whether the animals classify the ambiguous cues as a positive or negative stimulus.

Go/no go and go/go method

The first experimental design developed as a discrimination task was used by Harding et al. in 2004 [47] and characterized as a go/no go method. Rats were taught to press a lever when they heard a specific tone in order to receive a reward and to ignore the lever when another specific tone sounded in order to avoid the aversive event of random noise. When they responded correctly to more than 50% of the tone stimuli, half of the rats were confronted with up to two unpredictable stressors daily, a procedure that can cause depression in rats and should evoke a negative affective state in the animals. After nine days, it was tested how the rats interpret intermediate tones, which were between the two learnt tones. Compared with the rats from the control group, those from the unpredictable treatment group showed a lower expectation of a reward: they pressed the lever less frequently or after a longer latency time [47]. These results indicate a negative affective state in these rats, leading to a judgement bias. Based on the work of Harding et al. [47], further tests on cognitive bias in animals were conducted, and the experimental design was enhanced.

One could argue that the go/no go method of Harding et al. [47] can be imprecise because the decision is counted as positive only when the animal definitely expected a reward and decided to press the lever. When the animal hesitated too long or did not react in the given time, a negative decision was registered. To create the necessity for an active decision in the expectation of a positive or negative event, variants of go/go methods were developed. Enkel et al. [73] for example used a study design in which rats had to actively press a lever in order to receive a reward or to avoid punishment.

A comparison of applied study designs shows that the go/go task, which requires an active response to positive and negative stimuli, is possibly more suited for assessing judgement bias than the go/no go task. Pessimistic judgement bias indicates impaired animal welfare. The go/go task can help prevent that a behavioural inhibition due to emotions (resulting in no reaction or a delayed reaction) is counted as false pessimistic choice.

Experimental designs measuring judgement bias

Following, we review a selection of judgement bias tasks and their outcomes with particular relevance to animal welfare. A visual discrimination task was used by Bateson and Matheson [19] and showed that a decline in environmental quality leads to pessimistic bias in birds. In the experiment, starlings were trained to discriminate between a white and a dark-grey cardboard. Palatable mealworms were placed behind the positive stimulus, whereas non-palatable mealworms were located behind the negative stimulus. Subsequently, unrewarded intermediate stimuli were presented (cardboards in different shades of grey between white and dark-grey). Those starlings that had recently experienced a reduction in the quality of their environment classified fewer of the intermediate stimuli as positive and more of them as negative.

With a similar experimental design, Brilot et al. [20] evaluated cognitive bias of starlings and the link to stereotypical behaviour. Removal of environmental enrichment did not lead to negative cognitive bias; instead, pessimistic bias occurred in individuals that showed stereotypic behaviour. However, when intermediate shades of grey were presented to the birds, changes in latency times occurred [20]. The authors assumed the birds rapidly learnt that intermediate shades were unrewarded [20].

Individual differences in the occurrence of pessimistic bias were also found by Mendl et al. [95] in dogs. In a spatial discrimination task (the experimental design of a spatial discrimination task is described after the next paragraph), these researchers observed that dogs showing social separation-related behaviour showed pessimistic cognitive bias and were therefore in an underlying negative affective state [95].

The fast learning of unrewarded stimuli described by Brilot et al. [20] was also observed by Doyle et al. [84] in spatial discrimination tasks with sheep. During the investigations, Doyle et al. [84] created a negative affective state through long-term exposure to unpredictable, aversive events; their results showed that stressed sheep approached buckets in ambiguous locations less frequently than control sheep, which had not been exposed to the aversive events. However, this effect did not occur for all ambiguous bucket locations, and Doyle et al. [84] suggested that the animals rapidly learnt which intermediate stimuli were not rewarded.

The spatial discrimination task was first used by Burman et al. [51] in 2008 to evaluate whether rats in a positive or negative affective state react differently to ambiguous location-based stimuli. To create two groups with differing affective states, half of the rats experienced a reduction in environmental enrichment. All rats then began a training in which they learnt that a feed bowl placed in a specific location would grant them free access to the feed. Placed in another specific location, the feed was behind a grid and not reachable. It was assumed that the rats were able to discriminate between the two locations when they showed a longer latency time to reach the unrewarded than the rewarded location. Then, the feed bowl was placed in intermediate locations between the two learnt locations. In the location near the unrewarded one, a longer latency time for the rats with reduced enrichment was noted compared with the rats that had been kept in an enriched environment. Burman et al. [51] concluded that the rats with the longer latency time showed a higher expectation of an unrewarded event, which correlates with a negative affective state.

Burman et al. [96] used a similar concept when they tested the effect of different illumination on the emotions of rats. One group learnt the spatial discrimination in bright light. Afterward, three intermediate locations were presented in low light. In the other group, the conditions were reversed. In the first group, significantly shorter latency times were recorded compared with the second group. Burman et al. [96] interpreted the outcome by explaining that the bright light initially created fear. The decline of fear in low light provoked a positive affective state and therefore an optimistic expectation.

The effect of different illumination was also investigated by Boleij et al. [83]. BALB/cJ mice (with high initial anxiety) were tested in a discrimination task under aversive white light conditions. They showed a longer latency to approach the ambiguous stimulus, which is assumed to correlate with a more pessimistic expectation, compared with mice tested under less aversive white light conditions. Additionally, Boleij et al. [83] tried to train mice to discriminate between two odours. Whereas BALB/cJ mice learnt the discrimination and showed intermediate reactions to the ambiguous cues, 129P3/J mice (with low initial anxiety) did not discriminate between the cues. The BALB/cJ

mice judged the intermediate stimulus as negative under both test conditions. This mouse stem could be used to evaluate emotional states, but further research is necessary.

A high-pressure situation prior to a judgement bias test led to more positive assessment of situations in sheep. This shift was shown by Doyle et al. [88] after social isolation and by Sanger et al. [87] after shearing. Briefer and McElligott [97] made similar observations with goats. In a spatial discrimination task, they evaluated the effect of a long period of poor welfare (> two years) on judgement in ambiguous situations. No overall effect could be detected, but female test goats from the poor conditions showed more optimistic expectations than the control goats, suggesting a more positive assessment due to the reduction of stress. Male test goats showed a mood similar to that of the control goats [97]. Obviously, all of the animals recovered from the neglect, and possibly, sex differences were relevant.

In contrast, the previous experience of agitation or pain seems to create a lasting negative bias. For example, Bateson et al. [91] reported that agitated honeybees exhibited pessimistic cognitive bias, and Neave et al. [85], who investigated how pain affects cognitive processes in animals, found negative cognitive bias in calves following the painful process of hot iron disbudding. This pessimistic bias indicates that pain created a negative shift in the affective state of the calves.

Burman et al. [93] illustrated the link between a recently experienced feeling of success and a subsequent evaluation of ambiguous stimuli. Dogs were trained on a visual discrimination task, and half of the dogs experienced successful foraging prior to the judgement bias test. The dogs with this positive prior experience showed a significantly longer latency time in the reaction to intermediate stimuli than those without prior positive experience [93]. Unexpectedly, the dogs with successful foraging experience had a lower expectation to receive feed. It seems that an emotional event immediately prior to a judgement bias test can provoke a contrary emotion during the task. Animals that experienced a positive event had a lower expectation of reward in a subsequent judgement bias task [93], whereas animals having experienced a negative event showed an increased expectation of reward [84, 87].

Like the study by Burman et al. [93], other studies investigated positive affective state and its influence on expectation. Matheson et al. [48] for example found optimistic cognitive bias in starlings with enriched environment. The birds judged intermediate stimuli more frequently as being associated with a food outcome when they were housed in enriched compared with standard cages. This finding was confirmed by Brydges et al. [49], who, with the help of a sensory discrimination method, found out that environmental enrichment created a positive affective state and therefore an optimistic reaction to ambiguous stimuli in rats. The rats were trained to discriminate between smooth and rough sandpaper. When they chose one, they received a reward of higher value (white chocolate) than when they chose the other (rewarded with cereal with honey). When the rats had learnt the discrimination task, some animals were moved into enriched cages and presented with sandpapers of intermediate granularity. The rats previously housed in standard cages and then transferred to enriched cages showed more optimistic responses than the control rats that remained in standard cages.

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Another experimental design, used by Brilot et al. [86], included pictures of eyes that provoked fear when presented to starlings. As a positive stimulus, a picture with hidden eyes was shown. Pictures with semi-transparent eyes were the intermediate stimuli. In addition, acoustic signals such as characteristic warning cries or random noise were used to further influence the affective state of the starlings. However, the starlings assessed positive and intermediate stimuli in the same way [86]. Thus, this method seems rather inappropriate to verify cognitive bias in birds.

Salmeto et al. [89] isolated chickens for a short period to create a fearful affective state. Other chickens were isolated for a long period to cause a depression-like affective state. Subsequent judgement bias tests demonstrated a pessimistic mental attitude in the shortly isolated chickens and an even more pronounced one in the chickens that had been isolated longer [89]. Therefore, this method seems appropriate to create a negative cognitive bias in birds.

In studies with pigs and dogs, the method of isolation did not create a negative cognitive bias. Düpjan et al. [90] used a spatial discrimination task to evaluate the affective state of domestic pigs. Following the training, half of the pigs were socially isolated several times and then presented with stimuli in three intermediate positions. Additionally, the cortisol level in each animal was determined every morning. Neither the behaviour tests nor the cortisol levels indicated cognitive bias in the isolated pigs [90]. Thus, we hypothesize that isolation of the pigs caused neither acute stress (which, according to Doyle et al. [88] could have led to a higher expectation of reward) nor chronic stress (which could have created a negative emotional state and therefore have led to a lower expectation of reward, as well as changes in the cortisol levels). Similarly, an affective state of anxiety was not induced by separation in a study with dogs. Müller et al. [98] applied a judgement bias task during the owner's absence and during the owner's presence. The dogs showed no differences in their reactions to ambiguous stimuli, indicating either that the dogs were used to the absence of their owners or that only a moderate state of anxiety was provoked, which did not influence the outcome of the task [98].

The stocking density at which captive animals are held may be another factor with influence on the affective state. Scollo et al. [99] investigated the influence of stocking density on the affective state of pigs with a spatial discrimination task. Two treatments were applied to calculate the area required (A), the space allowance coefficient (k) and the bodyweight (BW) by the equation $A = k \times BW^{0,667}$. One treatment provided a space of k = 0.030, complying with the required European Union minimum standard, whereas the other treatment provided a space of k = 0.048, following the recommendation of the Scientific Panel on Animal Health and Welfare of the European Food Safety Authority. Although the results indicated that the higher stocking density did not lead to cognitive bias due to a negative affective state, differences in learning behaviours between treatments were found [99]. Further research could shed light on the effects of stocking density on learning behaviour.

Whereas neither social isolation nor high stocking density provoked negative cognitive bias in pigs [90, 99], Douglas et al. [50] showed that enriched housing systems led to positive cognitive bias in pigs. For five weeks, they kept one group of pigs in enriched environment and another group in standard housing conditions. All animals were then trained on an auditory discrimination task with a go/no go procedure, and afterward, the environmental conditions of the pigs were changed. Both groups approached the hatch more frequently and faster when presented as intermediate stimuli while the pigs were housed in an enriched environment compared with a standard environment [50].

The affective state of rhesus macaques was also evaluated in an enriched environment and compared with their affective state after a health check. Bethell et al. [100] trained the monkeys on a discrimination task via touch screen. In a subsequent judgement bias test, the monkeys had a lower expectation of reward and therefore responded less frequently to intermediate stimuli after the health check than during the phase of enrichment [100]. Thus, non-human primates show changes in affective state following standard husbandry procedures such as health checks.

In grizzly bears, this method initially failed to demonstrate cognitive bias. However, when the bears spent a longer time pacing prior to testing, they subsequently showed more optimistic judgement in the test [101]. Judgement possibly varies in situations causing anxiety, during times of increased activity, during sexual arousal or in anticipation of feeding, and data could indicate a negative or positive mood [102–106]. Thus, the combination of physiological measurements with behavioural observation could help to evaluate results.

Conclusions

In most of the herein reviewed studies, the animals were more pessimistic in a judgement bias task when they were in a negative affective state and more optimistic when they were in a positive affective state. Cognitive theories argue that an individual's assessment of a situation gives information about the involved emotions. Thus, the evaluation of cognitive bias may allow an objective assessment of the affective state of animals.

However, the methods to assess cognitive bias and the obtained results have to be interpreted carefully. Physiological parameters possibly vary depending on the circumstances (such as situations causing fear, times of increased activity, state of sexual arousal or imminent feeding times), and physiological data could variably indicate a negative or positive mood. The combination of physiological or neurobiological measurements with behavioural observations could help draw realistic conclusions on an animal's affective state.

Additionally, this review shows that the quality (positive or negative) and degree of cognitive bias arising in response to traumatic events or social isolation can differ between animal species. A method that seems to create positive cognitive bias in various species is the provision of environmental enrichment. The possibility of increased locomotion is a substantial component in enriched environments and can induce a positive affective state in animals.

Furthermore, individual differences in the motivation to feed, the need for movement or the attention span, as well as different personalities and sex differences, have to be taken into account. Thus, it could be useful to test every subject under different conditions to create a before-and-after comparison concerning the development of cognitive bias instead of testing one group

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against another. Moreover, test conditions should be as equal as possible between treatments to exclude the influence of factors such as temperature, time of day or feeding motivation on the animal's decision.

A comparison of applied study designs shows that the go/go task, which requires an active response to positive and negative stimuli, is possibly more suited for measuring judgement bias than the go/no go task. The go/go task can help prevent that a behavioural inhibition due to emotions (failure to act) is counted as false pessimistic choice.

Altogether, the assessment of cognitive bias seems to be a useful approach to determine the affective state of animals, which is crucial information for improving the welfare of animals under husbandry conditions. The numerous studies that have been carried out draw an increasingly precise picture of applicable methods. We look forward to further research that aims to identify a validated method for measuring animal welfare.

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