Behavioural Tests for Learning and Cognition in Humans and Animals

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9.1 Introduction

Anyone who has spent time with animals – be it professionally, as pets or simply through observing animals outdoors – has little doubt about their capacity to learn. For quite a while throughout history, however, humans were considered unique in many cognitive abilities that we now realize non-human animals may also possess. Tool use is a well-known example, where what was first considered as obviously unique to humans was later demonstrated in primates, famously by Jane Goodall (Goodall, 1986), and is now widely accepted also to occur in other species, including crows and possibly dolphins (Seed and Byrne, 2010). There is an increasing body of knowledge that many animals can perform complex learning tasks that can sometimes surprise us. Sheep can recognize other sheep from photographs (Kendrick *et al.*, 2001). Pigs turned out to be capable of learning complex cognitive tasks (Nordquist *et al.*, 2017). Indeed, the more research is conducted in animal cognition, the more capabilities are uncovered in species previously deemed 'lower' species; see, for instance, recent reviews on the cognitive capacities of fish (Salena *et al.*, 2021) and cephalopods such as octopus and squid (Schnell *et al.*, 2021).

In this chapter, I will discuss the importance of animal cognition to the field of animal welfare and will put the development of the field of animal cognition into historical perspective. The practicality of testing animal cognition will be illustrated with several tests frequently used in both humans and non-human animals, and I will end with some tips and recommendations for those wishing to embark on cognitive testing in relation to animal welfare.

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9.1.1 The importance of learning and cognition in animal welfare

In a field so broad as animal welfare, one can ask why it is important to study cognition in animals. After all, if an animal is healthy and seems happy, why is it important what its cognitive capacities are? Cognition is essential to both the animals themselves and to humans studying animals; this is visualized in Fig. 9.1. Cognition is essential to animals for two main reasons. First is the practical aspect: animals must have sufficient cognitive abilities to thrive in their own environments. Second, an animal's cognition is part of
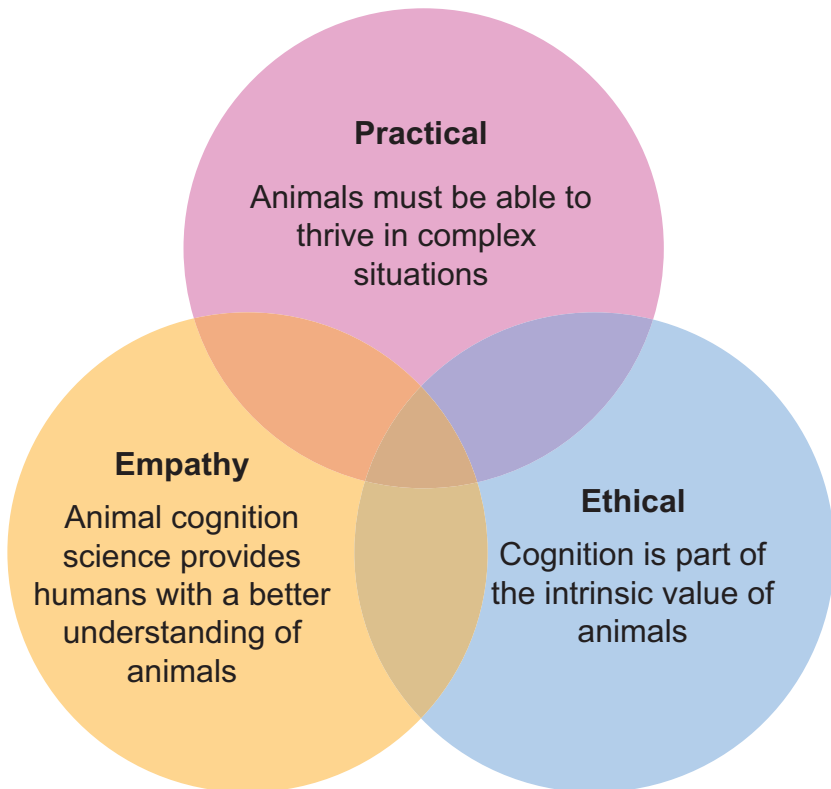
Practical

Animals must be able to thrive in complex situations

Empathy

Animal cognition science provides humans with a better understanding of animals

Ethical

Cognition is part of the intrinsic value of animals

Fig. 9.1. The importance of animal cognition within the field of animal welfare. There are three main reasons to study cognition in human-kept animals: (i) practical: humans keep animals in situations that can be complex for them; for example, farms are becoming increasingly complex, and we need to make sure that human-kept animals' intelligence is on a par with the challenges on farms; (ii) ethical: similar to other species-specific behaviours, the cognitive capacity of animals is part of their intrinsic value; if our breeding or management systems are changing the cognitive capacities of animals, this poses ethical issues; and (iii) empathy: by better understanding what animals are capable of, we as humans will be better animal stewards.

its intrinsic value. Intrinsic value refers to the value that an animal has as a living being, regardless of the value that humans may place on animals as a monetary commodity, a source of food or clothing, or a companion. This means that humans have ethical responsibilities regarding animal cognition. Just as other species-specific behaviours need to be taken into account when humans deal with animals, the cognitive capacities of animals must be taken into account. That ethical responsibility links the importance of cognition to the field of animal welfare research.

There are a number of reasons why an understanding of animal cognition is important to the commitment of the field to improve animal welfare. First, better understanding of cognitive capacities allows humans to be better animal stewards by creating housing and management systems that match the cognitive capacities of animals: both by not overtaxing their cognition and also by providing sufficient challenge to their cognitive capacities. Second, a better understanding of animals leads to more societal concern for their well-being. It is not yet established that a better understanding of the cognitive capacities of animals leads to more empathy for those animals, but studies do point to the reverse situation being true: people tend to discount the cognitive capacities of animals that are to be consumed, compared with those that are not (Bastian *et al.*, 2012). Finally, cognition is an important proxy for internal state. Happy animals perform well, while compromised animals (i.e. animals in pain) perform more poorly (see section 9.2.3 on bias tasks below).

9.1.2 Historical perspective of associative learning and cognition in animals

The focus of the present chapter is on cognition research at the overlap between human and animal research. I will therefore outline the history of cognitive science from a psychological research standpoint, which focuses on understanding learning and the mind at a fundamental level. This type of research has been conducted in humans and in other animals. This is a different starting point compared with research from an ethological standpoint, which is geared more to understanding the animal itself. I will focus here on the history of cognitive research in animals that came from psychology, but this is not to dismiss the work of ethologists such as Niko Tinbergen (see Chapter 14, this volume), Jane Goodall, Irene Pepperberg or any of the other important contributions from ethology to understanding animal cognition.

Cognitive science within psychology was initially focused almost solely on understanding the human cognition. Psychology as a field started with early scientists such as Wilhelm Wundt, a German scientist in the late 1800s, whose primary interest was in understanding how learning takes place, and who studied this process in humans. He described (among other things) the process of 'apperception', in which past experiences colour

a subject's current perception (Mandler, 2011). Thus, from the start, the importance of internal states was recognized, with the potential for experience to alter cognitive abilities – much the same as current judgement bias tasks (see section 9.3.3). However, from the 1930s to the 1960s, the seminal work of B.F. Skinner on associative learning processes gave rise to 'behaviourism'. In behaviourism, (nearly) all behaviour is seen as the result of an animal receiving a reward or punishment for an action, and increasing or decreasing that behaviour accordingly. This extensively influential work was instrumental in understanding many fundamental learning processes but left little room for examining motivations or internal states of animals as conscious beings, despite the fact that this detached view of animals does not seem to have been Skinner's intention (O'Donohue and Ferguson, 2001).

In line with this shift to more 'hard' science in the psychology of learning, in the mid-20th century, psychology turned increasingly to quantitative measures such as latency times and correct choices in learning tasks to show how animals (including humans) learn, rather than qualitative reports. This corresponded with the rise of the analysis of variance (ANOVA) as a statistical method in psychology to parse out experimental effects, with all of the requirements the test entails in terms of independence of groups, ratio-level measures and normality of data distribution. This helped to lend credibility to the field of psychology as a 'real' science, which may not be a spectacularly good reason to adopt a methodology but was important to the maturation of the field nonetheless. The wider use of statistics in general, but ANOVAs specifically, was also instrumental in the development of ways to reliably test hypotheses about behaviour and cognition. The history of statistics in psychology is very readably discussed in Michael Cowles' book on this subject (Cowles, 2005).

The peak of the quantification movement in psychological research in animal learning was perhaps the introduction of the Rescorla–Wagner model. This model quantifies and predicts classical conditioning responses through the formula (Rescorla and Wagner, 1972):

$$\Delta V = \alpha\beta(\lambda - \Sigma V)$$

which specifies that the amount of learning (the change, Δ, in the predictive value of a stimulus, V) depends on the amount of surprise (the difference between what actually happens, represented by λ, and what is expected to happen, ΣV), with the learning rate included as α and the unconditioned stimulus used as β. While this view of learning as reducible to a formula was extremely helpful in understanding basic learning processes, and sparked many new areas of research (including having a strong influence on the development of artificial intelligence; Gershman, 2015; Hollis, 2019), reduction of learning processes to mathematical terms led to a distancing of behavioural psychologists from their subjects, the animals, and was perhaps

not helpful for the development of empathy of researchers for animals, or for viewing learning from an animal's perspective.

Starting in the 1990s, the role of individual variation in behaviour began to regain attention. In particular, the role of coping styles (Coppens *et al.*, 2010) made a strong contribution to examination of animals as individuals. It became clear that some animals show problem-solving strategies that are stable across time and correlate with, for instance, fear reactivity. As more stable traits were developed that differed among individuals within a species, the term 'personality' came more into use in animal research (Gosling, 2001; Stamps and Groothuis, 2010; Kaiser and Müller, 2021), and it has been observed that in some cases personality as defined by 'temporally stable behavioural traits' can also correlate with cognitive performance (Carere and Locurto, 2011).

From this background, with individual variation and cognitive performance only relatively recently regaining attention in animal cognition research, it is perhaps not surprising that it has taken some time to recognize that cognition is important to animal welfare as viewed from the perspective of the animal. Until recently, the study of animal learning and cognitive processes was mainly in the service of humans in order to uncover fundamental processes of learning, or in animal models of disease or disorder, but there was very little interaction between this large body of research, going back over a century, and animal welfare research. Fortunately, this is changing, and in the past decades, learning and cognition are increasingly seen as an integral part of animal welfare research.

9.2   Concepts

Animal welfare

There are many definitions of animal welfare in use today (as described in Chapter 1, this volume). Most modern definitions in the field include adaptation or flexibility to adapt, and/or positive welfare indicators. For the current chapter, I will use the following definition, from Ohl and van der Staay (2012, p. 17):

An individual is in a positive welfare state when it has the freedom *adequately to react to*

- hunger, thirst or incorrect food;
- thermal and physical discomfort;
- injuries or diseases;
- fear and chronic stress; and thus,
- the freedom to display normal behavioural patterns that *allow the animal to adapt to the demands of the prevailing environmental circumstances and enable it to reach a state that it perceives as positive.*

Cognition

As with animal welfare scientists and defining animal welfare, cognitive scientists similarly struggle with a definition of 'cognition'. Indeed, there have been arguments from cognitive science to simply not define cognition and move on (Allen, 2017), or to accept multiple definitions as this does not inhibit the work of cognitive scientists (Akagi, 2018). For the sake of pragmatism, in the current chapter, I will use a broad definition of cognition. I refer to a definition relevant for comparative cognition (Buckner, 2015, p. 314), which poses that a 'general characteristic that nearly every test for cognition is meant to elicit is behavioural flexibility'. In this definition, responses in tests that contain a cognitive component contain at least a few of the following properties: context sensitivity, speed (with cognitive responses presumed faster than trial and error), class formation, higher-order and abstract learning, multi-modality transfer, inhibition, monotonic integration (i.e. ordering by size), and expectation generation and monitoring. For further explanation of these properties, see Buckner (2015).

Bias task

A bias task is a task where *affect* (how an animal is 'feeling') has an effect on performance of the task. Examples are judgement bias, where an animal has to choose between an expected positive or negative outcome of an action, and attention bias, where strong emotional stimuli, such as the threat of a predator, can cause animals to perform a task worse than without the predator.

9.3   Methodologies

Below, I will outline three types of tests that are used in both humans and animals, to serve as examples of tests that may tell us something about the fundamental cognitive capacities of animals related to animal welfare, or where cognitive performance may serve as a proxy to show the internal state of the animal. These examples were chosen because they cover different aspects of cognition and have been conducted in many species, but they are by no means more or less important than other tasks in investigation of animal cognition.

Delayed match tasks

Delayed match tasks are used to examine working (or short-term) memory. In these tasks, the subject is given a cue, followed by a delay. Following the delay, the subject must give a response based on the cue, so the subject must keep the cue in their short-term memory for the duration of the delay. The cues can be based on a sample (i.e. respond to a green light versus

a white light) or based on a location (i.e. respond to the left if the cue was on the left), and the task can be performed as a match (respond to the left if the cue on the left is given) or non-match (respond to the right if the cue on the left is given).

Delayed match tasks are used in humans to study the basic neurobiology of learning, for instance the role of the hippocampus in working memory using magnetic resonance imaging (O'Neil and Lee, 2019). Working memory as measured by delayed match tasks has been shown to be impaired by pharmacological interventions in healthy human volunteers (Jäkälä *et al.*, 1999). Humans born with low birth weight also show impaired performance in the task in adulthood (Daniel *et al.*, 2016; Mathewson *et al.*, 2020). This task has been used widely and extensively in laboratory animals to investigate fundamental learning processes and neurobiological substrates of learning using electrophysiology and psychopharmacology (Daniel *et al.*, 2016).

More recently, Teutsch and Kätzel (2019) developed a delayed match-to-place task (DMTP) in mice based on the five-choice serial reaction time set-up, which is considerably more complex than the typical two-lever DMTP set-up. This has the advantage of being able to more reliably exclude the animals using, for instance, body position as a marker to remember which cue requires a response. Given the increased complexity, however, the task has the distinct disadvantage that it takes several months of training before the mice are able to perform reliably. This trade-off is frequently seen in cognitive testing, where more detail requires longer and more intensive training, which is not always possible or feasible.

Set-shifting tasks

Set-shifting tasks include moving from rule learning based on one characteristic or modality, to another. The classic test of set shifting in humans is the Wisconsin Card Sorting Test, which was originally developed in the late 1940s (Berg, 1948). In this task, human subjects are given cards with one to four geometric figures (star, circle, square or cross) printed in one of four colours. Originally, these were physical cards, but currently the test is more often performed on a computer. Subjects are told to sort the cards, but not what the rule for sorting is, only 'correct' or 'incorrect'. The rule might be sorting by colour, by number of symbols (i.e. geometric figures) on the card, or by type of symbol; the subject is to discover the rule by trial and error. Once the subject has correctly discovered the rule, the sorting rule is changed without warning. For instance, if the sorting is first based on number of symbols, it is then based on colour. The ability of a subject to change the characteristic used to sort is taken as a measure of behavioural flexibility. Human subjects with a number of disorders thought to hamper their cognitive flexibility, including schizophrenia (Everett *et al.*, 2001;

Prentice *et al.*, 2008) and autism (Yerys *et al.*, 2009), score poorly on the parameters that measure set shifting in the Wisconsin Card Sorting Task.

In animals, the intradimensional–extradimensional set shift task investigates similar underlying constructs, namely the ability of an animal to learn to solve a task based on one modality, and then to change to another modality. In the most commonly used protocol, rodents are taught that a reward is in one of two dishes, covered with substrate. The rodents learn that the reward is always covered with either a specific substrate (coarse versus fine) or in a dish that contains a specific odour; thus, there is a task-relevant modality (i.e. tactile information from the substrate) and a task-irrelevant modality (olfactory cue). In this example, the animal needs to learn to respond to the correct substrate (tactile information given as the task-relevant modality) and disregard the olfactory cue (olfactory information as the task-irrelevant modality). After the first association has been learned to a performance criterion, the relevant and irrelevant modalities are switched. In this example, the rodent must now respond to the previously disregarded olfactory information and disregard the tactile information. In rodents, as recently reviewed by Tait *et al.* (2018), performance on set shifting has been shown to be impaired by a number of manipulations that would be expected to influence set shifting based on human literature, such as treatment with valproic acid (McKinnell *et al.*, 2021) and early-life lead exposure (Neuwirth *et al.*, 2019). Along with the wide use in more traditional laboratory animals, this task has recently also been adapted for use in sheep (Sorby-Adams *et al.*, 2021).

Bias tasks as a proxy for measuring affect

Assessment of subjective affect (i.e. how an animal 'feels') is notoriously difficult in animals. One cannot simply ask how they are feeling, of course. At the same time, subjective affect is an integral part of some definitions of animal welfare. For example, in the definition I use in this chapter, good welfare includes 'the freedom to display normal behavioural patterns that allow the animal to adapt to the demands of the prevailing environmental circumstances and enable it to reach a state that it perceives as positive' (Ohl and van der Staay, 2012, p. 17). When applying this definition to animal affect, there is an obvious component of subjectivity and individual response included, which is difficult to measure. The use of cognition as a proxy to reflect internal state is one approach to try to elucidate the inner emotional state of animals.

Judgement bias tasks are intended to investigate effects of affect on cognitive function, thus using cognitive performance as a proxy for subjective affect. Figure 9.2 provides a more detailed explanation of a judgement bias task. Basically, a subject is taught that one stimulus predicts a positive outcome (e.g. a high-frequency tone predicts a large reward) and a different stimulus predicts a negative outcome (e.g. a low-frequency tone
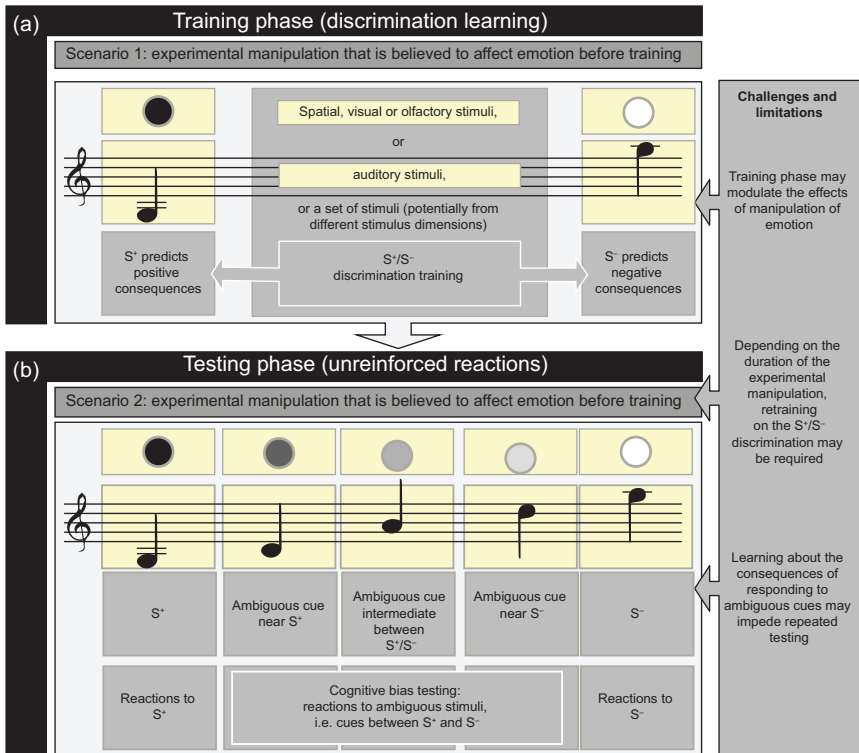
Fig. 9.2. Judgement bias training and testing. Schematic representation of judgement bias training and testing using visual, olfactory, spatial or auditory cues, or a combination of cues from different stimulus dimensions (inspired by Bateson *et al.*, 2011; Mendl *et al.*, 2011). The experimental manipulation that is believed to affect emotion precedes the training phase (a; scenario 1) or the testing phase (b; scenario 2). Refreshment of the discrimination acquired during the training phase may be necessary, if the experimental manipulation preceding phase (b) lasts for a longer time period. An example of scenario 1 is studying the effects of growing up in different housing systems, whereas scenario 2 might be applied in a study assessing the effects of shorter-lasting experimental manipulations, such as confinement, on emotion. Phase (b) may be repeated multiple times to test the effects of different experimental manipulations in the same animal. Specific challenges and limitations may be connected to the different phases. From Roelofs *et al.* (2016); reprinted under the terms of Creative Commons Attribution License (CC BY).

predicts a small reward). The important response is then: what happens when the animal is given a stimulus in the middle (i.e. a mid-frequency tone)? Does the subject respond to the stimulus as if it expects a positive outcome or a negative outcome? In essence, is the glass half full or half empty? Figure 9.2 shows an example of the specific contingencies connected with responding to positive, negative and ambiguous cues. In humans,

judgement bias is seen to be affected by long-term negative affect, such as people suffering from depression (Mineka and Sutton, 1992). Judgement bias has been regularly used within the field of animal welfare as a proxy for measuring the subjective state of animals. It has now been tested in the context of animal welfare in a wide variety of animals, including, among others, pigs, sheep, chickens, rodents and hummingbirds. Recent reviews have examined the utility of the judgement bias paradigm for examining animal welfare and have covered the scientific literature quite extensively (see reviews by Roelofs *et al.*, 2016; Watters and Krebs, 2019; Mendl and Paul, 2020; Neville *et al.*, 2020).

Although there is certainly potential for this test to be useful, a number of hurdles are still to be overcome before the test can be practically implemented in animal welfare research. Judgement bias protocols require relatively long and labour-intensive training in learning tasks, making them impractical for use in more natural and/or farm settings. Recent efforts have also been made to design faster and more practical judgement bias paradigms (e.g. Hintze *et al.*, 2018), although the test will still need a great deal of refinement to be useful on a larger scale. Aside from practicality, the long training phase may be detrimental to interpretation of the results. The long training sessions may also provide enrichment with both relief from boredom and positive interactions with humans. This may mask effects of, for instance, housing conditions, as an animal that spends all day, every day in an impoverished environment will respond differently from an animal housed in an impoverished environment that is trained for an hour or two per day in an operant task.

Attention bias is similar to judgement bias in that it uses a proxy to elucidate emotional state. Where in judgement bias an operant task is used, which (by definition) requires training, in the attention bias task the amount of attention given to a threat versus a neutral or positive stimulus is measured. In general, humans and other animals will show a bias in attention towards a threat, compared with attention towards a neutral or positive stimulus. This bias is probably composed of both increased attention to the threat and decreased ability to disengage attention to the threat (Cisler *et al.*, 2009). In humans, anxiety disorders have been shown to increase the attentional bias towards threats compared with subjects without anxiety disorders (Bar-Haim *et al.*, 2007; Mobini and Grant, 2007), an effect seen already at an early age in humans (Puliafico and Kendall, 2006).

A common paradigm for attention bias in animals is the provision of a primary reward, such as food or water for bathing (in birds), in the presence of a predator or conspecific alarm calls (recently reviewed by Crump *et al.*, 2018). In primates, showing pictures of positively valanced stimuli (e.g. food) or negatively valanced stimuli (e.g. snakes) disrupts performance of a complex task more than neutral stimuli (Hopper *et al.*, 2021). Sheep paid less attention to a predator in the form of a dog, and were more likely to feed in the presence of the stimuli when given the anxiolytic diazepam

prior to testing (Lee *et al.*, 2016), supporting the influence of anxiety on task performance. In pigs, current housing conditions (but not early-life housing conditions) affect performance on attention bias tasks (Luo *et al.*, 2019).

9.4 Common Pitfalls in the Integration of Cognitive Research with Animal Welfare

The field of cognitive research in both humans and animals is vast and has a long history. Cognition research in animals was initially propelled primarily by basic questions about how cognition is fundamentally organized. At present, cognitive research in animals is most strongly in use in animal models for human disease with cognitive deficits, and this is likely to continue. The importance of cognition to animal welfare is starting to take hold in the field of animal welfare. This recognition is encouraging, but animal welfare researchers still have quite a way to go. There are a number of issues that generally impede the advancement of integration between broad cognitive research and cognitive research geared towards animal welfare.

The first hurdle is communication between fields. This is discussed at length in Chapter 2 (this volume), but I will address a few cognition-specific issues here. There is at present very little interaction between scientists working on cognition in animals as models for human disease and scientists working on animal cognition in animal welfare. Animal welfare research is a vastly smaller field than animal models of human disease. Animal welfare journals, consequently, generally have lower impact factors compared with those focused on human disease. This is a serious hurdle to scientists in the field of human disease who may want to work with animal welfare researchers or on animal welfare topics. Low-impact-factor publications will not help (and may even hurt) their careers at tenure review or other major milestones, and changing this viewpoint will require a more widespread change in valuation of scientific output. From the other side, animal welfare researchers can be strong in beliefs about animal welfare and mistrusting of the use of animals in models of human disease. This can be a hindrance to the openness needed to learn from another field. Furthermore, the huge volume of research in cognition in which animals are used as models can be daunting to dive into. More dialogue between the two areas could produce a more constructive discourse.

Second is the complexity of translation of tests from humans to animals, specifically for cognition. Cognitive tests in humans tend to rely on language, making translation to non-verbal animals difficult. One area of missed potential is in collaboration with scientists working on pre-verbal humans (young children). Dating back to the seminal work of Jean Piaget, cognitive testing in developmental psychology has been aimed at testing of

pre-verbal humans. There is much overlap in the difficulties of scientists researching neonatal abilities and the clinicians aiming to directly improve the welfare of neonates, and the science and practice of animal welfare. In one recent example where developmental psychology was taken to animal behaviour, teasing was reviewed in animals (Eckert *et al.*, 2020). Teasing in children is fairly well described developmentally, and requires the ability to understand what the to-be-teased partner is expecting in order to mislead them. There are a few examples, but at present there is too little interaction between these two fields, while there is much to be gained by both sides from the cross-pollination.

Finally, cognitive testing in animals often relies on extensive training, elaborate set-ups and relatively subtle differences across many trials, and traditionally requires standardized set-ups with little variation in distractions such as background noise. All of these aspects make the use of cognitive testing outside laboratories challenging. This often leads to protests about the relevance of cognitive testing to animal welfare. If we cannot test cognition in relevant, real-world settings, what use are the results to improve animal welfare? In part, cognitive testing is about understanding the basic biology of the species we keep for companions, for food and for work in order to better meet their basic needs in practice. To some extent, cognitive testing will remain a laboratory discipline, geared towards better understanding of the cognitive abilities of animals. Better understanding then leads to more compassion on the one hand and opportunities to develop better management practices on the other. There are opportunities, however, to bring cognitive testing out of the laboratory. In conservation studies, the importance of animal cognition in human–animal interactions in the wild is gaining traction (Goumas *et al.*, 2020). In a recent example where cognition testing has made its way into ornithology of wild birds, wild collared flycatchers (*Ficedula albicollis*) were studied in an ingenious nest-box designed as a behavioural set-up (Morinay *et al.*, 2020). Similarly, squirrels have been tested in their own habitats (Chow *et al.*, 2021). More cognitive tests that can be performed in the home area, with animals freely deciding to participate or not, will certainly increase the utility of cognitive testing in natural and/or farm settings.

9.5   Conclusions and Tips

On a final note, I provide a few conclusions and practical tips for integrating cognitive research in animal welfare work. Cognitive testing takes time if you want results that can be interpreted. Involve a specialist to think through necessary controls and possible interpretations of results. Do not underestimate things like habituation to a test set-up or building in all of the steps needed to train an animal in a cognitive task. Habituation time can be considerably shortened by testing in a home

environment where possible, and testing in pairs when feasible. Faster learning of responses can be facilitated by making use of species-specific behaviours, such as rooting in pigs, digging in rodents or pecking in chickens, as responses. If using cues, make sure they are in a modality that is attractive to the species being tested. Even if a test is constructed optimally, the fact remains that cognitive testing in animals is nearly always time-intensive. The exact time required will differ among test and species, but cognitive testing takes easily a week and can take months for complex tasks. This needs to be taken into consideration when planning experiments.

A final issue is the need for recognition of the importance of cognition to animal welfare. Cognition is a much less obvious need of an animal compared with freedom from disease or a place to root (for a pig), scratch (for a chicken) or dig (for a rabbit). Within the field of animal welfare, there is increased attention to the need to examine cognition, as detailed at the beginning of the present chapter. There is, however, a lot of work to be done to educate non-researchers, such as the general public and policy makers, on why we should care about cognition in animals.

Further Reading

References that are recommended for further information are given in bold in the reference list.

References

Akagi, M. (2018) Rethinking the problem of cognition. *Synthese* 195, 3547–3570.

Allen, C. (2017) On (not) defining cognition. *Synthese* 194, 4233–4249.

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M.J. and van IJzendoorn, M.H. (2007) Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. *Psychological Bulletin* 133(1), 1–24. DOI: 10.1037/0033-2909.133.1.1.

Bastian, B., Loughnan, S., Haslam, N. and Radke, H.R.M. (2012) Don't mind meat? The denial of mind to animals used for human consumption. *Personality & Social Psychology Bulletin* 38(2), 247–256. DOI: 10.1177/0146167211424291.

Bateson, M., Desire, S., Gartside, S.E. and Wright, G.A. (2011) Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology* 21(12), 1070–1073. DOI: 10.1016/j.cub.2011.05.017.

Berg, E.A. (1948) A simple objective technique for measuring flexibility in thinking. *The Journal of General Psychology* 39, 15–22. DOI: 10.1080/00221309.1948.9918159.

Buckner, C. (2015) A property cluster theory of cognition. *Philosophical Psychology* 28, 307–336.

Carere, C. and Locurto, C. (2011) Interaction between animal personality and animal cognition. *Current Zoology* 57, 491–498.

Chow, P.K.Y., Clayton, N.S. and Steele, M.A. (2021) Cognitive performance of wild eastern gray squirrels (*Sciurus carolinensis*) in rural and urban, native, and non-native environments. *Frontiers in Ecology and Evolution,* in press.

Cisler, J.M., Bacon, A.K. and Williams, N.L. (2009) Phenomenological characteristics of attentional biases towards threat: a critical review. *Cognitive Therapy and Research* 33(2), 221–234. DOI: 10.1007/s10608-007-9161-y.

Coppens, C.M., de Boer, S.F. and Koolhaas, J.M. (2010) Coping styles and behavioural flexibility: towards underlying mechanisms. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365(1560), 4021–4028. DOI: 10.1098/rstb.2010.0217.

Cowles, M. (2005) *Statistics in Psychology: An Historical Perspective*, 2nd edn. Psychology Press, New York.

Crump, A., Arnott, G. and Bethell, E.J. (2018) Affect-driven attention biases as animal welfare indicators: review and methods. *Animals* 8, 136. DOI: 10.3390/ ani8080136.

Daniel, T.A., Katz, J.S. and Robinson, J.L. (2016) Delayed match-to-sample in working memory: a BrainMap meta-analysis. *Biological Psychology* 120, 10–20. DOI: 10.1016/j.biopsycho.2016.07.015.

Eckert, J., Winkler, S.L. and Cartmill, E.A. (2020) Just kidding: the evolutionary roots of playful teasing. *Biology Letters* 16(9), 20200370. DOI: 10.1098/ rsbl.2020.0370.

Everett, J., Lavoie, K., Gagnon, J.F. and Gosselin, N. (2001) Performance of patients with schizophrenia on the Wisconsin Card Sorting Test (WCST). *Journal of Psychiatry & Neuroscience* 26(2), 123–130.

Gershman, S.J. (2015) A unifying probabilistic view of associative learning. *PLOS Computational Biology* 11, e1004567. DOI: 10.1371/journal.pcbi.1004567.

Goodall, J. (1986) *The Chimpanzees of Gombe: Patterns of Behavior.* Harvard University Press, Cambridge, Massachusetts.

Gosling, S.D. (2001) From mice to men: what can we learn about personality from animal research? *Psychological Bulletin* 127(1), 45–86. DOI: 10.1037/0033-2909.127.1.45.

Goumas, M., Lee, V.E., Boogert, N.J., Kelley, L.A. and Thornton, A. (2020) The role of animal cognition in human–wildlife interactions. *Frontiers in Psychology* 11, 589978. DOI: 10.3389/fpsyg.2020.589978.

Hintze, S., Melotti, L., Colosio, S., Bailoo, J.D., Boada-Saña, M. *et al.* (2018) A cross-species judgement bias task: integrating active trial initiation into a spatial Go/ No-go task. *Scientific Reports* 8(1), 5104. DOI: 10.1038/s41598-018-23459-3.

Hollis, G. (2019) Learning about things that never happened: a critique and refinement of the Rescorla–Wagner update rule when many outcomes are possible. *Memory & Cognition* 47(7), 1415–1430. DOI: 10.3758/ s13421-019-00942-4.

Hopper, L.M., Allritz, M., Egelkamp, C.L., Huskisson, S.M., Jacobson, S.L. *et al.* (2021) A comparative perspective on three primate species' responses to a pictorial emotional stroop task. *Animals* 11(3), 588. DOI: 10.3390/ani11030588.

Jäkälä, P., Sirviö, J., Riekkinen, M., Koivisto, E., Kejonen, K. *et al.* (1999) Guanfacine and clonidine, alpha2-agonists, improve paired associates learning, but not delayed matching to sample, in humans. *Neuropsychopharmacology* 20(2), 119–130. DOI: 10.1016/S0893-133X(98)00055-4.

Kaiser, M.I. and Müller, C. (2021) What is an animal personality? *Biology and Philosophy* 36, 1.

Kendrick, K.M., da Costa, A.P., Leigh, A.E., Hinton, M.R. and Peirce, J.W. (2001) Sheep don't forget a face. *Nature* 414(6860), 165–166. DOI: 10.1038/35102669.

Lee, C., Verbeek, E., Doyle, R. and Bateson, M. (2016) Attention bias to threat indicates anxiety differences in sheep. *Biology Letters* 12(6), 20150977. DOI: 10.1098/rsbl.2015.0977.

Luo, L., Reimert, I., de Haas, E.N., Kemp, B. and Bolhuis, J.E. (2019) Effects of early and later life environmental enrichment and personality on attention bias in pigs (*Sus scrofa domesticus*). *Animal Cognition* 22(6), 959–972. DOI: 10.1007/s10071-019-01287-w.

Mandler, G. (2011) *A History of Modern Experimental Psychology: From James and Wundt to Cognitive Science*. MIT Press, Cambridge, Massachusetts.

Mathewson, K.J., Maurer, D., Mondloch, C.J., Saigal, S., Van Lieshout, R.J. *et al.* (2020) Visual configural processing in adults born at extremely low birth weight. *Developmental Science* 23(2), e12890. DOI: 10.1111/desc.12890.

McKinnell, Z.E., Maze, T., Ramos, A., Challans, B. and Plakke, B. (2021) Valproic acid treated female Long-Evans rats are impaired on attentional set-shifting. *Behavioural Brain Research* 397, 112966. DOI: 10.1016/j.bbr.2020.112966.

Mendl, M. and Paul, E.S. (2020) Animal affect and decision-making. *Neuroscience and Biobehavioral Reviews* 112, 144–163. DOI: 10.1016/j.neubiorev.2020.01.025.

Mendl, M., Paul, E.S. and Chittka, L. (2011) Animal behaviour: emotion in invertebrates? *Current Biology* 21(12), R463–R465. DOI: 10.1016/j.cub.2011.05.028.

Mineka, S. and Sutton, S.K. (1992) Cognitive biases and the emotional disorders. *Psychological Science* 3, 65–69.

Mobini, S. and Grant, A. (2007) Clinical implications of attentional bias in anxiety disorders: an integrative literature review. *Psychotherapy: Theory, Research, Practice, Training* 44, 450–462.

Morinay, J., Cauchard, L., Bize, P. and Doligez, B. (2020) The role of cognition in social information use for breeding site selection: experimental evidence in a wild passerine population. *Frontiers in Ecology and Evolution* 8, 559690.

Neuwirth, L.S., Masood, S., Anderson, D.W. and Schneider, J.S. (2019) The attention set-shifting test is sensitive for revealing sex-based impairments in executive functions following developmental lead exposure in rats. *Behavioural Brain Research* 366, 126–134. DOI: 10.1016/j.bbr.2019.03.022.

Neville, V., Nakagawa, S., Zidar, J., Paul, E.S., Lagisz, M. *et al.* (2020) Pharmacological manipulations of judgement bias: a systematic review and meta-analysis. *Neuroscience and Biobehavioral Reviews* 108, 269–286. DOI: 10.1016/j.neubiorev.2019.11.008.

Nordquist, R.E., Meijer, E., van der Staay, F.J. and Arndt, S.S. (2017) Chapter 39 – Pigs as model species to investigate effects of early life events on later behavioral and neurological functions. In: Conn, P.M. (ed.) *Animal Models for the Study of Human Disease*, 2nd edn. Academic Press, London, pp. 1003–1030.

O'Donohue, W. and Ferguson, K.E. (2001) *The Psychology of B.F. Skinner*. SAGE Publications, Thousand Oaks, California.

Ohl, F. and van der Staay, F.J. (2012) Animal welfare: at the interface between science and society. *Veterinary Journal* 192, 13–19.

O'Neil, E.B. and Lee, A.C.H. (2019) Examining the representational content of perirhinal cortex and posterior ventral visual pathway regions when maintenance of visual information is interrupted. *Cortex* 121, 16–26. DOI: 10.1016/j.cortex.2019.08.008.

Prentice, K.J., Gold, J.M. and Buchanan, R.W. (2008) The Wisconsin Card Sorting impairment in schizophrenia is evident in the first four trials. *Schizophrenia Research* 106(1), 81–87. DOI: 10.1016/j.schres.2007.07.015.

Puliafico, A.C. and Kendall, P.C. (2006) Threat-related attentional bias in anxious youth: a review. *Clinical Child and Family Psychology Review* 9(3–4), 162–180. DOI: 10.1007/s10567-006-0009-x.

Rescorla, R. and Wagner, A.R. (1972) A theory of Pavlovian conditioning: variations in effectiveness of reinforcement and nonreinforcement. In: Black, A.H. and Pokasy, W.F. (eds) *Classical Conditioning II: Current Research and Theory.* Appleton-Centry-Crofts, New York, pp. 64–99.

Roelofs, S., Boleij, H., Nordquist, R.E. and van der Staay, F.J. (2016) Making decisions under ambiguity: judgment bias tasks for assessing emotional state in animals. *Frontiers in Behavioral Neuroscience* 10, 119. DOI: 10.3389/fnbeh.2016.00119.

Salena, M.G., Turko, A.J., Singh, A., Pathak, A., Hughes, E. *et al.* (2021) Understanding fish cognition: a review and appraisal of current practices. *Animal Cognition* 24(3), 395–406. DOI: 10.1007/s10071-021-01488-2.

Schnell, A.K., Amodio, P., Boeckle, M. and Clayton, N.S. (2021) How intelligent is a cephalopod? Lessons from comparative cognition. *Biological Reviews* 96(1), 162–178. DOI: 10.1111/brv.12651.

Seed, A. and Byrne, R. (2010) Animal tool-use. *Current Biology* 20(23), R1032–R1039. DOI: 10.1016/j.cub.2010.09.042.

Sorby-Adams, A.J., Schneider, W.T., Goncalves, R.P., Knolle, F. and Morton, A.J. (2021) Measuring executive function in sheep (*Ovis aries*) using visual stimuli in a semi-automated operant system. *Journal of Neuroscience Methods* 351, 109009. DOI: 10.1016/j.jneumeth.2020.109009.

Stamps, J. and Groothuis, T.G.G. (2010) The development of animal personality: relevance, concepts and perspectives. *Biological Reviews* 85(2), 301–325. DOI: 10.1111/j.1469-185X.2009.00103.x.

Tait, D.S., Bowman, E.M., Neuwirth, L.S. and Brown, V.J. (2018) Assessment of intradimensional/extradimensional attentional set-shifting in rats. *Neuroscience and Biobehavioral Reviews* 89, 72–84. DOI: 10.1016/j.neubiorev.2018.02.013.

Teutsch, J. and Kätzel, D. (2019) Operant assessment of DMTP spatial working memory in mice. *Frontiers in Behavioral Neuroscience* 13, 193. DOI: 10.3389/fnbeh.2019.00193.

Watters, J.V. and Krebs, B.L. (2019) Assessing and enhancing the welfare of animals with equivocal and reliable cues. *Animals* 9, 680. DOI: 10.3390/ani9090680.

Yerys, B.E., Wallace, G.L., Harrison, B., Celano, M.J., Giedd, J.N. *et al.* (2009) Set-shifting in children with autism spectrum disorders: reversal shifting deficits on the Intradimensional/Extradimensional Shift Test correlate with repetitive behaviors. *Autism* 13(5), 523–538. DOI: 10.1177/1362361309335716.