

The Ethology of Domestic Animals, 2nd Edition

An Introductory Text

Per Jensen

*IFM Biology
Linköping University
SE-58183 Linköping
Sweden*



5.1 Introduction

A young sow approaches a site on the boundary between forest and open field where she had found some tasty roots the previous day. She is poised to start rooting the ground when she notices one of her group-mates, a large dominant female, approaching. Instead of digging for the roots, she turns away and continues along the forest boundary. Close by, a field ethologist, having studied the behaviour of this group of sows for several weeks, scribbles in his notepad. The young sow appears to have remembered where the good food source was, something that he had observed previously, but why did she not feed this time? Is it possible that she didn't want to reveal the location of the source to the approaching dominant sow? If so, wouldn't this suggest that she had some understanding of what would happen if she gave away her secrets?

This is not just a fanciful example; pigs show intriguing behaviour like this in controlled experimental studies (e.g. Held *et al.*, 2002). But it raises a number of important questions about the processes underlying the behaviour that we observe. How does the sow remember where food was? Does she form an association between a particular visual stimulus, a clump of trees, say, and food? Or does she have a complete mental representation of the area? Why does she not feed? Assuming that she recognizes her dominant group-mate, does she associate the dominant with previous painful skirmishes over resources and simply avoid her? Or does she actually understand what will happen if she started to feed, and perhaps even attribute food-pilfering intentions to the dominant sow?

These questions reveal that apparently 'clever' behaviour can be explained by a variety of putative underlying mental or 'cognitive' processes. These range from associative learning through to the capacity to form 'cognitive maps' or to have a 'theory of mind', abilities that involve quite complex mental representation of the outside world. Distinguishing between these explanations for observed behaviour is often not easy and is a theme that we will return to. However, our principal aim in this chapter is to consider the evidence for a number of different types of cognitive ability in domestic animals.

Before we go any further, what exactly do we mean by 'cognition'? Historically, the behaviourist school of psychology that dominated the study of animal learning for much of the 20th century, through the work of J.B. Watson, B.F. Skinner and others, sought to explain all behaviour without referring to unobserved mental processes. Indeed, it denied that it was possible to study these at all. However, the cognitive revolution of the latter part of the 20th century has re-legitimized the study of hidden mental processes through careful inference from observed behaviour. Consequently, for some authors, cognition refers to these mental processes, and the study of cognition seeks to understand how information is represented and manipulated in the mind, in stark contrast to the behaviourist approach. Others, however,

use the term in a broader sense to refer to all processes by which 'animals acquire, process, store and act on information from the environment' (Shettleworth, 1998).

In this chapter, we discuss a number of examples of animal cognition (*sensu* Shettleworth) but, where relevant, also consider the extent to which they can be explained by behaviourist and cognitivist theories. We should also emphasize that, when we refer to 'mental representations', we do not imply that these are consciously experienced by non-human animals in the way that we humans experience a thought or a feeling. This may be the case but at present we do not know. It is important to remember that the question of whether animals are consciously aware of their mental processes is distinct from the question of how these processes work. The study of cognition is concerned with the latter question only.

Learning and cognitive abilities should enhance the inclusive fitness of an individual, increasing its chances of contributing genetically to the next generation. Different aspects of learning will be of adaptive benefit to different species, making it very difficult to say whether one species is 'more intelligent' than another, although the capacity to learn will certainly be influenced by environmental and social complexity. Animals born into constant environments can survive well using innate responses but, when environments are varied and unpredictable, a wide range of learning abilities will be essential. The ancestors of our most common domestic mammals and birds will have faced many uncertainties, including food of variable quality or unpredictable distribution, predators with different appearances, location and habits, and complex social environments where the identities and roles of group members vary over time. This varied heritage means that domestic animals should easily be able to establish relationships between events and thus form associations that guide behavioural change.

We start by considering the associative learning processes underlying these abilities. We then consider memory processes, including the special example of object permanence, before discussing discrimination, generalization and category formation, social cognitive abilities and the relationship between cognition and emotion. Despite a long domestication history, we will see that domestic animals show surprising mental flexibility and complexity in the way that they interact with the environment and their social companions. Unfortunately, space constraints mean that we cannot address other topics. However, those that we do cover have relevance for domestic species, and we conclude the chapter by briefly discussing how an understanding of animal cognition influences our attitudes towards and understanding of animal welfare.

5.2 Associative Learning

Two main types of associative learning have been described and extensively studied. In classical, or Pavlovian, conditioning, an environmental event or stimulus is followed predictably by some other occurrence. Pavlov studied the effects of sounding a bell just prior to food arrival on salivation responses in dogs. The dogs naturally salivated to the smell or appearance of food, so salivation was described as an unconditioned response (UR) and food as an unconditioned stimulus (US). However, after repeated pairings of the bell with the food, the dogs salivated in response to the sound, i.e. the conditioned stimulus (CS). When an association is classically conditioned animals do

not acquire new responses or behaviours, so the conditioned response (CR) takes the same form as the UR. Such associations are acquired with ease. Companion dogs, for example, can become expert at detecting the subtlest signs that might predict their daily walk, without any formal training. The sight of a human picking up a lead (the CS) can set off a volley of anticipatory responses such as barking and leaping. Classical conditioning therefore allows animals to *predict* events, but it gives them little control or influence over the actual timing, quality or duration of their meals or walks.

Instrumental, or operant, conditioning is a second type of associative learning, whereby an animal directs a behaviour to a new part of its environment or learns to perform a new behaviour, to obtain a reward. Imagine, for example, a captive zoo-housed coati (*Nasua nasua*), presented for the first time with a cylindrical environmental enrichment device containing small food pellets that fall through holes only when the device is manipulated and moved in a certain way. The coati might initially approach the cylinder and perform a range of natural exploratory movements (URs). But, if one particular movement results in the acquisition of a food pellet (US), the coati will repeat the previous few movements it made, until it learns precisely which action (now a conditioned response, CR) reliably produces food. In this case, the animal gains not only the ability to *predict* what might happen next, but also the ability to *control* the timing and delivery of its own reward.

An influential model providing insight into the process of association formation was outlined by Rescorla and Wagner in 1972 (reviewed by Hall, 1994). This model describes many features of associative learning, although it provides no insight as to the neurological mechanisms involved. Repeated pairings of events result in associations with strengths that reflect the exact statistical probability that a CS (e.g. a bell sounding) or a CR (e.g. an action directed at a cylinder) will result in US arrival. The *contiguity* between two events is therefore more important in establishing an association than the absolute temporal relation between them. Usually, if a stimulus or response is followed rapidly by US arrival, a good association will be formed, because there is no time for intervening events to interfere with the predictive relationship. However, under some conditions, an association can be formed even if the CS precedes the US by many hours, provided the relationship between the two is statistically strong.

The best examples of delayed association formation come from ecologically appropriate situations. In food aversion learning, for example, an animal can ingest a novel (slightly toxic) substance and not feel sick for many hours. Once nausea sets in, however, it will be able to associate the sickness with the novel substance it ingested, rather than with any of the sights or sounds that it encountered in the intervening period. The novel food is biologically the most plausible predictor of sickness. The Rescorla–Wagner model makes a number of other predictions that have been valuable in explaining empirical data. For example, association ‘strength’ depends on factors such as the size or importance of the US, and the presence of existing associations (e.g. the bell that predicts food) can ‘interfere’ with the formation of new associations (e.g. that a light also predicts food) via processes called overshadowing or blocking (Dickinson, 1980).

Associative learning takes place only when an unconditioned stimulus is biologically meaningful: something the animal either wants, or wants to avoid. The unconditioned stimulus is often called a reinforcer. Some reinforcers result in *increased* performance of the behaviour under consideration. Appetitive reinforcers can be

positive, where the animal responds to gain more of the reinforcer (e.g. food), or negative, where the animal responds to avoid the reinforcer. Physical pressure, used in horse training, is a good example of a negative reinforcer. Horses will move forwards or sideways to obtain the reward of removal of the rider's leg pressure. In contrast, reinforcement that produces a *decrease* in the behaviour under consideration is known as punishment. For example, if a dog stops barking when it is shouted at, then shouting is a punishment for that animal. But there is nothing beyond an animal's own reaction that can be used to define a situation as good or bad in advance. A second dog may like its owner shouting and bark more whenever it is shouted at. For this second dog, barking is a positive reinforcer and not a punishment, whatever the intentions of the owner!

Other rewards such as social contact or neutral thermal conditions may be important in guiding learned behaviour, but they are difficult to use in experimental or training situations. Because of this, conditioned or secondary reinforcers, initially neutral but paired with a biologically meaningful stimulus, are often used when training animals. Interest in this area is exemplified by articles and books on 'clicker training' in the popular press. However, experimental studies of the efficacy of secondary reinforcers have not always shown that they promote the faster learning or greater retention sometimes claimed. Williams *et al.* (2004), for example, found that conditioned reinforcement did not improve learning acquisition, or resistance to extinction, in horses.

Associative learning: what is learned?

Studies of associative learning were the bedrock of behaviourist research and, in many cases, it was possible to explain changes in behaviour in terms of stimulus–response connections that required no reference to unobserved mental processes. However, this was not always so. For example, rats exposed to the coincidence of two biologically neutral stimuli – ‘tone predicts light’ – showed no change in behaviour, indicating to a behaviourist that nothing had been learnt. However, if the light then became predictive of electric shock, the rats subsequently showed avoidance behaviour to the tone as well. This could be explained by postulating that the rats formed mental representations of the relationships between tone, light and shock and were thus able to combine the information ‘tone predicts light’ and ‘light predicts shock’ (see Dickinson, 1980). A cognitivist perspective, therefore, accounted for the observed behaviour.

The cognitivist view further postulates that information acquired during associative learning can be stored in two different ways. *Declarative* representations, as in the above example, involve knowledge about things or relationships (e.g. the light predicts shock) that allow different representations to be combined in different ways, and confer flexibility in how the animal uses the information to guide a behavioural response (Dickinson, 1980). *Procedural* representations, on the other hand, involve knowledge about what to do (e.g. when the light is on, crouch), as in a simple stimulus–response connection, and can be used only in an inflexible way. There is some evidence that chickens may be able to integrate information about the location of a particular food type in a foraging arena, and the value of that food type, and use this information to guide their choices, suggesting that they may form declarative

representations (Forkman, 2001). If so, chickens and, very likely, other domestic species may be capable of more sophisticated forms of associative learning than the acquisition of simple stimulus–response relationships.

5.3 Memory

From a cognitivist perspective, associative learning involves changes to representations of information and the storage and retention of these – memory. Studies of learning and memory thus overlap, and to a certain extent the two phenomena are inseparable. However, memory research can be characterized by the types of question that it addresses, which include: (i) how is information acquired, stored and retrieved; (ii) for how long can information be retained; (iii) how large is the memory store; and (iv) what are the neural substrates of memory?

Memory research has also identified a number of different types of ‘memory system’. Working memory usually refers to the capacity to hold information in some form of cognitive workspace for a very short time (e.g. seconds). In humans, it has been suggested that a maximum of around seven pieces of information (e.g. seven numbers) can be held in working memory. In animal studies, the terms working memory and short-term memory are often used interchangeably to describe the storage of information over a few minutes to hours, as in when an animal is foraging for food and uses working memory to avoid revisiting locations that it has just searched. Long-term or reference memory holds information for much longer periods (days, months, years) and seems to have a virtually unlimited capacity. For example, there is evidence that some food-storing birds can remember the location of thousands of food-cache sites. Long-term memory also seems to require significant molecular and cellular events, including protein synthesis, in areas of the brain that are implicated in memory processes, such as the hippocampus, amygdala and medial temporal lobes. Although far from being fully understood, these can be conceptualized as the laying down of a ‘memory trace’.

Working, short- and long-term memory abilities have been demonstrated in a variety of domestic species, often using ecologically relevant spatial tasks such as remembering the location of food. Pigs show a well-developed spatial memory; they can be readily trained to search an arena each day for food in a novel location, retain that memory over the next 1–2 h and revisit the same (re-baited) location when allowed back into the arena. They demonstrate good working memory in that they usually avoid returning to previously visited locations during the few minutes of each search of the arena, and this is not due to following a simple ‘turning rule’ (e.g. always moving to the left of the site that has just been visited). They easily remember that day’s correct location over a 2 h retention interval, and improving performance over consecutive days indicates that they learn that the first search of each day involves finding the new location of food, while the second search involves remembering where food was on the first search, thus indicating good reference or long-term memory of what the task is all about (Mendl *et al.*, 1997).

Cattle and sheep also perform well in spatial memory tasks. For example, cattle can develop good long-term memory of where high- or low-quality food is in a radial-arm maze, showing a preference for high-quality sites and avoiding low-quality ones. In the case of high-quality food, this memory persisted for at least 30 days in one

study, while memory-aided avoidance of low-quality food locations appeared to decline during the same period (Bailey and Sims, 1998). Sheep can also develop good long-term memory of the location of high-yielding areas in large arenas (e.g. 160 m × 160 m), and this ability allows them efficiently to exploit different quality pastures (Dumont and Petit, 1998).

These examples of spatial memory probably involve associative learning processes that link visual, olfactory or other spatial cues with food reward. Distant visual cues are often used by animals to orient themselves and solve these tasks, but there is also evidence that cattle and sheep can use visual cues close to the food source itself to guide their searching. Whether these species can develop ‘cognitive maps’, mental representations of the spatial environment that allow them to make novel short cuts, remains to be discovered.

Another ecologically relevant ability, memory for other individuals – or at least for cues from those individuals such as facial appearance – has also been studied in domestic species. One study demonstrated that sheep could discriminate between pairs of conspecific faces as evidenced by learning to associate one member of each pair with a food reward. They also appeared to be able to generalize from frontal views to profiles, and they were able to perform accurately on these discriminations after 2 years, although there was a decline in performance, and it is possible that they were mainly remembering the task and could have performed equally well on new face pairs (this was not reported). Neurophysiological evidence indicated that neurons in the temporal and medial prefrontal cortex of the brain, which fire when sheep view a familiar conspecific, continued to fire in response to specific facial images, even after 8–12 months in which that individual had not been encountered (Kendrick *et al.*, 2007).

While the capacity of domestic species to store information in memory is not in doubt, the variables that affect the selection, storage and retrieval of memory have received less attention, but are critically important in determining what is remembered and how well (see Fig. 5.1). Clearly, we don’t remember everything that happens to us. In fact, if we did, it might drive us crazy. There is increasing evidence that, just as biologically meaningful unconditioned stimuli trigger associative learning, the events that are prioritized for storage in memory are also ‘important’ ones, those which are most likely to impinge on survival and reproductive success and, probably through ‘evolutionary design’, also have emotional impact. In support of this idea, moderate elevations of ‘stress hormones’, such as cortisol or adrenalin, as would probably occur in response to significant events, can aid consolidation of information into memory, probably through direct or indirect action on brain structures such as the amygdala and hippocampus. Furthermore, a study of pigs indicates that information that is more costly to forget, in this case because forgetting it increases the time taken to obtain food, is indeed encoded more effectively in memory (see Mendl *et al.*, 2001).

Information stored in memory may ‘decay’ with time, in that it is less readily retrieved as time passes. One process that may contribute to this is termed retroactive interference and occurs when new information presented to the animal apparently interferes with the stored representation of similar information. For example, pigs that have been trained to remember the location of food in an arena appear to have this memory disrupted if they are exposed to the arena again (without being allowed to search it) prior to being tested for memory retrieval (Mendl *et al.*, 2001). One explanation for this is that the memory trace of the original information is ‘reactivated’ from a ‘dormant state’ when the animal encounters a relevant cue. Once reactivated, the

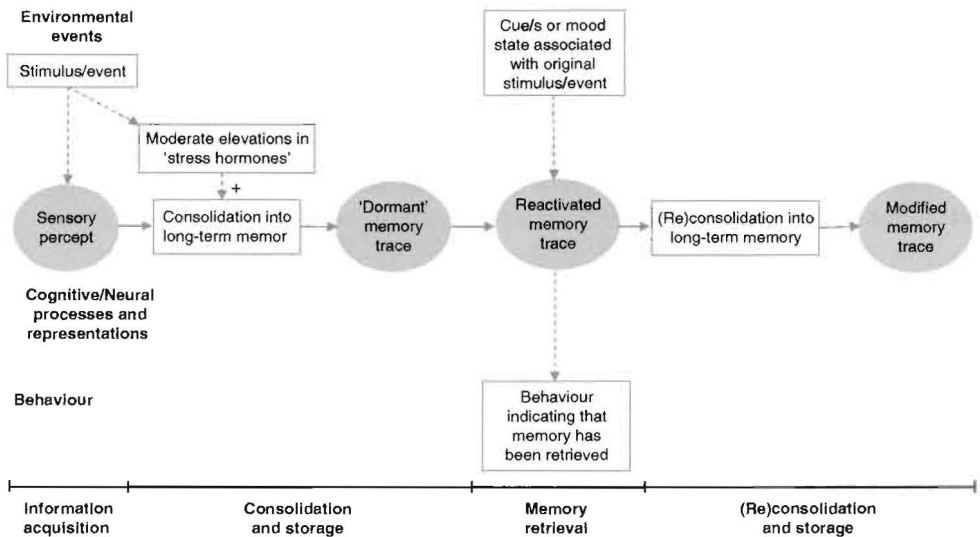


Fig. 5.1. Schematic representation of some of the events that are thought to occur when information is acquired, stored and retrieved in memory. A stimulus or event is perceived and a representation of this is consolidated into long-term memory as a neural ‘memory trace’. This involves molecular processes, including protein synthesis in cells, and can be facilitated by moderate elevations in ‘stress hormones’, ensuring that important or emotionally salient events are given priority in memory. When a cue related to the original stimulus and/or a mood state associated with the original stimulus is encountered, the ‘dormant’ memory trace appears to be reactivated, as evidenced by behaviour indicating that the memory has been retrieved. New information present at this time may then be incorporated into a newly consolidated memory trace, which may thus be slightly, or even greatly, altered from the original memory.

memory trace is then ‘labile’ and vulnerable to alteration by new information, before it is stored again in a dormant form. It is possible to investigate this idea because the (re)storage of longer-term memories requires protein synthesis in specific brain areas, and this can be temporarily stopped using protein synthesis-blockers.

Using such techniques it has recently been shown that a ewe’s memory trace of her lamb does indeed appear to be reactivated by cues from the lamb, and can then be disrupted such that her subsequent ability to recognize the lamb deteriorates (Perrin *et al.*, 2007). These and other findings emphasize the complexity of memory processes (see Fig. 5.1) and help to explain how memories can be interfered with and decay, and also how human memories can change and become embellished with time.

Retrieval of memories can be triggered by presentation of appropriate cues, such as the context in which an event took place or the smell of another individual, and there is some evidence that information with a particular affective value (e.g. anxiety-inducing) is more readily retrieved when the subject is in a congruent state (see Fig. 5.1). There has been limited research on how retrieval is affected by these variables in domestic species. However, one study of laboratory rats found that short-term memory for another individual appeared to be unaffected by whether the individual, or a representative odour cue, were re-encountered in the same context as originally or in a different, but familiar, context (Mendl *et al.*, 2001). Whether animals can retrieve

memories in the absence of an overt cue, so-called ‘recall’ in contrast to cue-driven ‘recognition’, is of course very difficult to test. Furthermore, exactly what is retrieved remains mysterious. Whether animals have vivid conscious recall of events that happened to them in the past, termed ‘episodic memory’ in humans, remains unknown and perhaps unknowable, although there is increasing evidence that at least some species, including laboratory rats, may be able to remember not just what happened where, but also when it happened.

5.4 Object Permanence

Object permanence is the awareness that objects are separate entities that continue to exist when out of sight of the observer, and can be thought of as a specific type of memory. The development of this awareness in humans was studied by Piaget, who noted that babies of less than about 8 months of age sometimes behaved as if an object no longer existed when it was hidden behind a screen (reviewed by Pepperberg, 2002). These infants did not try to search for the object and behaved as if ‘out of sight’ was ‘out of mind’. In contrast, older babies would search for a toy or other object obscured by a screen or a blanket. Piaget suggested that object permanence became increasingly sophisticated as children aged, culminating in the ability to infer where objects were, even after a series of invisible displacements. Improved techniques for studying human babies have shown that they may develop these abilities much earlier than originally thought.

In the light of these improved techniques, it is interesting to consider whether domestic animals have object permanence and, if so, at what level of complexity. The developmental sequences described for humans are unlikely to be relevant to precocial species such as horses or chickens, but object permanence can still be examined within a comparative framework. Parrots can accomplish sophisticated invisible displacement tasks (Pepperberg, 2002), whilst dogs (Fiset *et al.*, 2007) and chickens (Freire *et al.*, 2004) are adept at finding objects that have been hidden inside or behind visible containers or screens, even if they have to take detours or move out of sight of the container as part of the retrieval process. The ability to retrieve a hidden object depends not only on some form of awareness that it still exists, but on developmental experience with occluded objects (Freire *et al.*, 2004) and on a variety of spatial memory and navigation processes (see Fig. 5.2).

5.5 Discrimination, Generalization, Categorization and Concept Formation

Discrimination allows distinctions to be drawn between objects or stimuli that differ in particular features. There appear to be natural biases in the ease with which different species attend to and use different stimulus features for discrimination, which almost certainly depend on adaptive ecological history. In tests where both the appearance and relative position of buckets are potential cues indicating food availability, horses preferentially utilize the positional cues (Hothersall *et al.*, 2009). In chicks the situation is more complicated, in that the right brain hemisphere preferentially attends to position-specific cues, whereas the left hemisphere attends to object appearance (Regolin *et al.*, 2004).

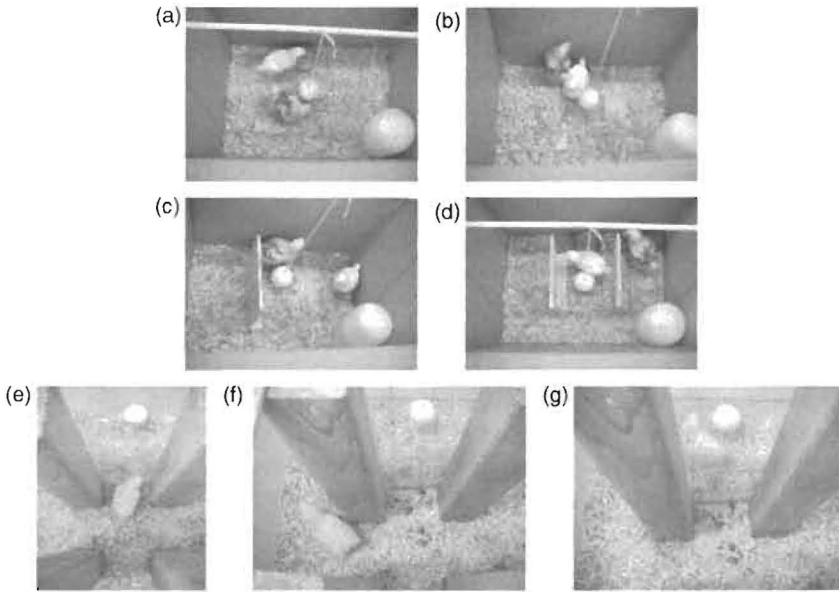


Fig. 5.2. Experience of occlusion of objects at around day 11 of life is important in the development of object permanence abilities in chicks. Freire *et al.* (2004) kept chicks from 8 days of age under conditions that permitted different opportunities to move out of sight of a yellow tennis ball on which they had previously been imprinted. Chicks were housed in pens with either: (a) no screens, (b) two transparent screens, (c) one opaque and one transparent screen or (d) two opaque screens. Chicks with opaque screens spent most time out of sight of the ball, and subsequently made fewer errors in locating the ball in a detour test (e, f, g).

Discrimination also enables animals to fine-tune their behaviour in response to environmental cues. A dog may learn that barking results in attention from the owner when the TV is off, but not when the TV is on. The status of the TV therefore controls the behaviour of the dog, much as a laboratory rat might discriminate by performing an operant response in the presence of one stimulus but not another. Generalization is the converse tendency to attend to shared features within a range of stimuli. Generalization enables animals to respond to new stimuli adaptively, provided sufficient shared information exists with previously encountered stimuli. The adaptive balance between discrimination and generalization depends on precise circumstances. A riding school pony, for example, has to respond appropriately to a variety of riders using leg, seat and hand cues in different ways. The adaptive response of the pony is to generalize and respond in the same way to a broad range of different cues. For an advanced dressage horse, such generalization would be disastrous and dressage riders aim for precision and consistency in their aids in order to foster discrimination and avoid generalization.

If the shared features of a class of stimuli are based on physical similarities such as colour, size or shape, then the processes of discrimination and generalization can result in category formation. Horses can categorize trained and novel images according to whether they have open centres or are solidly black, when procedures are used that control for confounding variables such as the overall areas of black and white in the stimuli (Hanggi, 1999).

Categorizing stimuli according to abstract principles such as properties that result from *relationships* between stimuli, e.g. 'bigger than' or 'paler than', is cognitively more demanding. Well-designed experiments have demonstrated that primates, parrots and pigeons can form such relational categories, but there is limited information about the abilities of domestic animals on these tasks. The only relational category that has been studied to any real extent in domestic animals is the 'same/different' category. This can be examined using matching-to-sample or non-matching-to-sample tests, where an animal capable of this degree of abstraction should be able to select a stimulus that is the 'same as' or 'different from' one previously viewed. Same/different categorizations have been difficult to demonstrate in some species, but studies using olfactory stimuli in rats and auditory stimuli in dogs have recently shown more success, and such methods could fruitfully be adapted to examine abstract categorization abilities in other domestic animals.

An entirely abstract category could be called a 'concept' or an 'idea of a class of objects', where stimuli are included on the basis that they stand for the same idea and not that they resemble each other physically in any way. Concept formation, especially in animals that have no language, is of great theoretical interest but few studies have been conducted with domestic animals, and developing viable methodologies remains a challenge (Lea *et al.*, 2006).

5.6 Social Cognition

For many species, the social environment is highly complex and changeable, and some of the most interesting examples of cognitive abilities arise in this context. Notably, social learning facilitates the acquisition of new behaviours in many domestic animals. Social learning occurs when a naive animal (the observer) acquires information from a knowledgeable conspecific (the demonstrator), resulting in faster or more effective learning by the observer, often with greatly reduced costs. Sometimes, the demonstrator simply draws the observer's attention to a previously unnoticed stimulus, and subsequent acquisition of a new response by the observer behaviour then takes place by normal instrumental conditioning. But social learning can also occur via processes that are cognitively more demanding, including imitation, where an animal copies the physical movements of a demonstrator; and emulation, where it reproduces the results of a demonstrator's actions (Whiten *et al.*, 2004).

There is good evidence that most domestic animals employ social learning in some situations, but the processes involved have perhaps been most studied in chickens (reviewed by Nicol, 2004), where, in early life, chicks are sensitive to social guidance about which foods they should and should not ingest. Hens attract their young to food with a complex display of staccato food calls and pecks to the ground. The hens' display is more intense in the presence of high-quality food items, if the chicks move away or if the chicks make apparent 'errors' in the objects they peck at. Older chickens will learn to eat, but not to avoid, novel-coloured food after watching a knowledgeable demonstrator. The relationship between the observer and demonstrator birds is very important, as hens are more likely to acquire new behaviours after watching socially dominant demonstrators than social subordinates.

As well as transmitting information about food availability or quality, animals communicate with each other about predator presence and identity, and about their own internal reproductive or emotional state (Manteuffel *et al.*, 2004). Traditional

texts hint that animals such as chickens might be rather inflexible in their communication abilities but, as seen by the responses of hens to the feeding behaviour of their chicks, communication can be both subtle and flexible. Another example comes from the alarm-calling behaviour of cockerels, who give different types of calls in response to perceived aerial or ground predators, and modulate their calling depending on the type of 'audience' that may be listening. Cockerels are most keen to impress novel female chickens and call more in their presence than in the presence of familiar females or novel birds of a different species. In addition, both male and female (broody) bantam chickens adjust their alarm calling according to the size of the aerial predator relative to the size of their own growing chicks. Alarm calls were given only in response to small hawks when chicks were very young and vulnerable (Palleroni *et al.*, 2005).

Complex and flexible communication does not, however, mean that domestic animals possess language abilities. Language requires that new meanings can be generated by an almost infinite rearrangement of discrete symbols (such as words), or from rearrangements of symbol order (as in grammar). There is considerable debate about the extent to which symbolic use in chimpanzees and parrots meets these (admittedly anthropocentric) criteria for 'language', and there is no hint of current evidence that any domestic species possess such specialized abilities.

Perhaps the most advanced form of social cognition is the ability to 'put oneself in another's shoes' – for example, to take their visual perspective, to empathize with them, to understand that they have a mental state like oneself and even to use this knowledge to deceive them. Not surprisingly, it is very difficult to study these abilities involving high-level mental representations, and also to be sure that any behavioural evidence for them cannot be explained by 'simpler' associative learning processes. Primatologists research, and argue about, this area, but there have been only a few studies in domestic animals. As in the example at the start of this chapter, pigs can show behaviour that allows them to minimize exploitation of their knowledge of where food is in a foraging arena by another individual (see Fig. 5.3). However, although this may indicate a sophisticated understanding of the intentions of the other animal, it is more likely that this 'clever' behaviour is the result of the knowledgeable animal avoiding a competitive encounter with its larger companion over food, having learned by association that it is likely to lose out (Held *et al.*, 2002).

One technique designed by primatologists to reveal more precisely what one animal understands about another's knowledge has been adapted for pigs and dogs. Here, the subject animal chooses to use one of two individuals as a guide to where the food is. The subject is unable to see where food is being placed in an arena, but can see that one of the individuals (the 'knower') has visual access to this baiting event while the other (the 'guesser') does not. The question is whether the subject then uses information provided by the 'knower' to locate food, which would indicate some understanding of the relative knowledge of the two individuals. One out of ten pigs made this 'correct' choice (Held *et al.*, 2001), while no dogs did when tested with conspecifics, though they did when tested with human partners (Cooper *et al.*, 2003). Despite well-designed experiments, it is still difficult to rule out the possibility that animals showing the correct response were doing so on the basis of previously learned associations rather than by taking the visual perspective of the other individual. For example, they may have learned that another's gaze direction or visual access to an event is a good predictor of subsequent behaviour. Dogs, at least, are highly sensitive to gestures and even the glancing behaviour of humans.

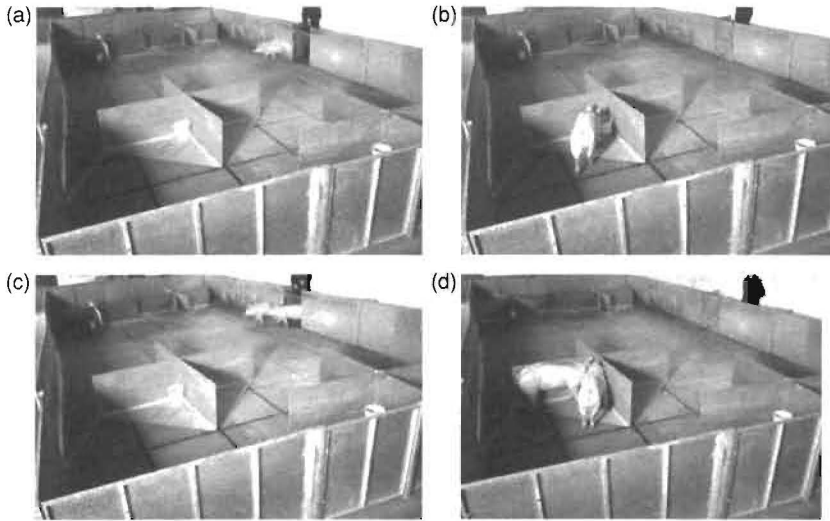


Fig. 5.3. Pigs undergoing a competitive foraging task. The animals are trained and tested daily in a foraging arena. (a) On the first trial of the day a pig enters the arena to search for food placed randomly in one of eight buckets; (b) it finds the food and eats it. It has previously been trained that, on the next trial a few minutes later, food will be in the same location as on the first trial; (c) the 'informed' pig is now introduced to the arena with a heavier companion, which has been trained that there is food in the arena, but does not know where it is; (d) if the companion follows the informed pig to the correct bucket, it is able to displace it and steal the food. Over many days it is possible to observe how the behaviour of the two pigs changes as first the companion learns to follow the informed pig to the food and then the informed pig develops behaviours which minimize the chances of the companion pig stealing its food (see Held *et al.*, 2002).

5.7 Cognition and Emotion

One recent area of interest has been in the use of cognitive measures as potential indicators of emotional states in animals. Emotions are states like happiness, sadness, fear and anxiety. Understanding these states in animals is critical to a better understanding of animal welfare. We consciously experience emotions, but we cannot be sure that animals do. Nevertheless, emotions are also accompanied by behavioural and physiological changes (e.g. an urge to flee, raised heart rate), and we can use these as proxy indicators of animal emotional states. The problem is that these measures may not always reliably reflect whether an emotion is positive or negative ('valence'), and are often species specific and therefore difficult to generalize a priori to other species. There are also few measures of positive emotions (Paul *et al.*, 2005).

Human studies have shown that cognitive processes may both influence and be influenced by emotional states, suggesting that they may be useful and novel indicators of animal emotion. For example, when an event happens there is evidence that people perform an extremely rapid series of stimulus checks (e.g. how familiar is it? How predictable is it? How sudden is it?), and the outcome of these 'cognitive appraisals' influences the emotion that is experienced. Particular emotions appear to be associated with specific stimulus characteristics, and it is possible that animals exposed to such

stimuli may also experience similar emotions. If so, the behavioural and physiological responses they show to these stimuli will provide good indicators of the corresponding emotion. Current work with sheep is investigating this possibility and is showing, for example, that stimuli differing in suddenness and novelty do indeed produce different behavioural and physiological response profiles (Boissy *et al.*, 2007).

Just as cognitive appraisals may influence emotional state, so emotional state affects cognitive processes including attention, memory and judgement. For example, people in a negative affective state are more likely to interpret an ambiguous event negatively, and to anticipate negative rather than positive things happening (Paul *et al.*, 2005). These emotion-related ‘cognitive biases’ have been explored in animals using discrimination learning protocols in which subjects are trained to make response A to stimulus X in order to acquire a good thing (e.g. food), and response B to stimulus Y (in the same sensory modality as X) in order to acquire a less good thing (e.g. less food) or avoid a bad thing (e.g. noise). Once trained, the subjects are presented with ambiguous stimuli (intermediate between X and Y) to see whether they perform response A, indicating that they categorize the stimulus as predicting a good thing (‘optimistic’), or response B, indicating a ‘pessimistic’ judgement of the stimulus (see Fig. 5.4). The prediction is that subjects in a putative negative affective state are more likely to show ‘pessimistic’ responses. Results indicate that this is the case in species including rats, starlings and dogs (e.g. Harding *et al.*, 2004), raising the possibility of using cognitive bias as a novel indicator of animal emotion.

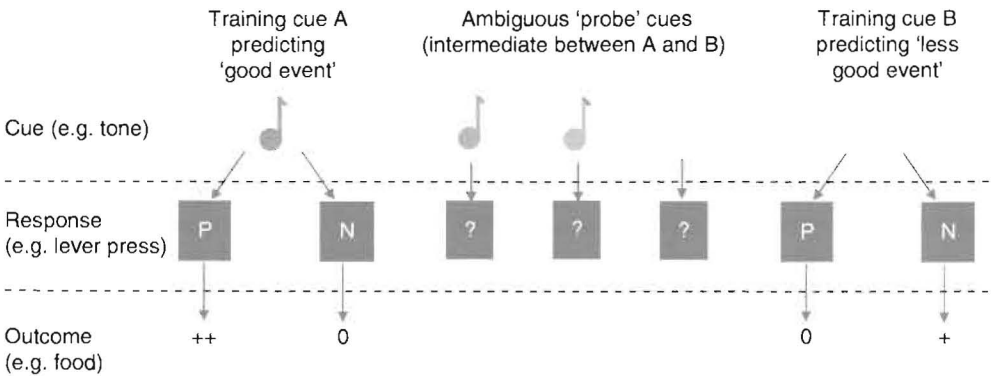


Fig. 5.4. One example of a procedure for a cognitive bias task. In this ‘judgement bias’ task, the animal is trained that when training cue A (e.g. a tone of a specific frequency) is presented it must perform response P to acquire a good reward (e.g. several pellets of food), while when training cue B (e.g. a tone of a different frequency) is presented it must perform response N to acquire a less good reward (e.g. one pellet of food). Once trained to this task, it can be assumed that performance of response P indicates anticipation of a good event, whilst performance of response N indicates anticipation of a less good event. The animal is then presented with ambiguous cues (tones of intermediate frequency) and its responses to these are recorded. The prediction is that animals in a negative mood state are more likely to categorize the ambiguous cues as predicting a relatively negative event and hence are more likely to show response N. This ‘pessimistic’ judgement bias compares with negative cognitive biases observed in people in negative mood states. Variants on this procedure include making training cue B predictive of a negative event (e.g. noise) which can be avoided by performing response N (e.g. Harding *et al.*, 2004).

5.8 Animal Cognition and Animal Welfare

There is growing interest in understanding the cognitive abilities of domestic animals. Once we appreciate that they do not simply respond to their environments, to each other or to us, with a set of simple, fixed or ‘unthinking’ responses, we may want to rethink their place within our ethical frameworks. We may admire and appreciate their complexity just as we might admire great paintings or diverse and complex landscapes, and perhaps accord them greater respect or protection on these grounds alone.

Nevertheless, their cognitive abilities also have a more direct impact on their welfare. For example, behaviours such as cannibalism in chickens are facilitated by prior observation of companions (Cloutier *et al.*, 2002). Only by understanding the mechanisms of social learning in large flocks might it be possible to reduce the transmission rates of these harmful behaviours. In a different context, it is sometimes argued that animals cannot be trusted to make rational or considered choices in preference tests, because they are incapable of ‘weighing up’ the consequences. Studies of cognition can be used to investigate these claims. In one experiment, it was shown that feeding decisions were not guided solely by immediate considerations. Chickens were able to show a degree of ‘self-control’, selecting a strategy that meant they had to wait for a large reward rather than receiving a smaller but immediately available reward (Abeyesinghe *et al.*, 2005).

This type of evidence can give us a little more confidence in the use of preference tests to assess animal needs and desires. It also demonstrates that animals are able to measure the passage of time, and other studies have shown that, for example, pigs can learn to choose a location where they will be confined for a shorter period of time over one where confinement lasts longer (Spinka *et al.*, 1998). If animals can use cues to anticipate the duration of events, this might be used to ‘reassure’ them that an upcoming procedure will soon be over.

Finally, the types of cognitive abilities that domestic animals possess are relevant to the types of situations in which they might suffer. Although there is no compelling reason why *any* of the complex learning or cognitive abilities already described should be accompanied by subjective experiences or consciousness, it is usual to give domestic animals the benefit of the doubt and concede that consciousness is logically possible, or even likely. If so, then an animal that can remember past, stressful, events may have reduced welfare many days or weeks after the event itself ended. It is even possible that animals may generate ‘innate’ mental representations of things they have never encountered in their own lifetime, so that an animal kept in social isolation could still, conceivably, ‘miss’ the company of others. And an animal that can anticipate future events may be able to anticipate its own future. Much work remains to be done.

References

- Abeyesinghe, S.M., Nicol, C.J., Hartnell, S.J. and Wathes, C.M. (2005) Can domestic fowl show self-control? *Animal Behaviour* 70, 1–11.
- Bailey, D.W. and Sims, P.L. (1998) Association of food quality and locations by cattle. *Journal of Range Management* 51, 2–8.
- Boissy, A., Arnould, C., Chaillou, E., Desire, L., Duvaux-Ponter, C., Greiveldinger, L., Leterrier, C., Richard, S., Roussel, S., Saint-Dizier, H., Meunier-Salaun, M.C., Valance, D. and

- Veissier, I. (2007) Emotions and cognition: new approach to animal welfare. *Animal Welfare* 16(S), 37–43.
- Cloutier, S., Newberry, R.C., Honda, K. and Alldredge, J.R. (2002) Cannibalistic behaviour spread by social learning. *Animal Behaviour* 63, 1153–1162.
- Cooper, J.J., Ashton, C., Bishop, S., West, R., Mills, D.S. and Young, R.J. (2003) Clever hounds: social cognition in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science* 81, 229–244.
- Dickinson, A. (1980) *Contemporary Animal Learning Theory*. Cambridge University Press, Cambridge, UK.
- Dumont, B. and Petit, M. (1998) Spatial memory of sheep at pasture. *Applied Animal Behaviour Science* 60, 45–53.
- Fiset, S., Beaulieu, C., Le Blanc, V. and Dube, L. (2007) Spatial memory of domestic dogs (*Canis familiaris*) for hidden objects in a detour task. *Journal of Experimental Psychology: Animal Behavior Processes* 33, 497–508.
- Forkman, B. (2001) Domestic hens have declarative representations. *Animal Cognition* 3, 135–137.
- Freire, R., Cheng, H.W. and Nicol, C.J. (2004). Development of spatial memory in occlusion-experienced domestic chicks. *Animal Behaviour* 67, 141–150.
- Hall, G. (1994) Pavlovian conditioning. In: Mackintosh, N.J. (ed.) *Animal Learning and Cognition*. Academic Press, San Diego, California, pp. 15–43.
- Hanggi, E.B. (1999) Categorization learning in horses (*Equus caballus*). *Journal of Comparative Psychology* 113, 243–252.
- Harding, E.J., Paul, E.S. and Mendl, M. (2004) Cognitive bias and affective state. *Nature* 427, 312.
- Held, S., Mendl, M., Devereux, C. and Byrne, R.W. (2001) Behaviour of domestic pigs in a visual perspective taking task. *Behaviour* 138, 1337–1354.
- Held, S., Mendl, M., Devereux, C. and Byrne, R.W. (2002) Foraging pigs alter their behaviour in response to exploitation. *Animal Behaviour* 64, 157–166.
- Hothersall, B., Harris, P.A. and Nicol, C.J. (2009) Foals preferentially utilise relative spatial cues over visual cues in a discrimination learning task. *Animal Cognition*. In press.
- Kendrick, K.M., da Costa, A.P., Leigh, A.E., Hinton, M.R. and Peirce, J.W. (2007) Sheep don't forget a face. *Nature* 447, 346.
- Lea, S.E.G., Wills, A.J. and Ryan, C.M.E. (2006) Why are artificial polymorphous concepts so hard for birds to learn? *Quarterly Journal of Experimental Psychology* 59, 251–267.
- Manteuffel, G., Puppe, B. and Schon, P.C. (2004) Vocalisation of farm animals as a measure of welfare. *Applied Animal Behaviour Science* 88, 163–182.
- Mendl, M., Laughlin, K. and Hitchcock, D. (1997) Pigs in space: spatial memory and its susceptibility to interference. *Animal Behaviour* 54, 1491–1508.
- Mendl, M., Burman, O., Laughlin, K. and Paul, E. (2001) Animal memory and animal welfare. *Animal Welfare* 10, S141–S159.
- Nicol, C.J. (2004) Development, direction and damage limitation: social learning in domestic fowl. *Learning and Behavior* 32, 72–81.
- Palleroni, A., Hauser, M. and Marler, P. (2005) Do responses of galliform birds vary adaptively with predator size? *Animal Cognition* 8, 200–210.
- Paul, E.S., Harding, E.J. and Mendl, M. (2005) Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews* 29, 469–491.
- Pepperberg, I.M. (2002) The value of the Piagetian framework for comparative cognitive studies. *Animal Cognition* 5, 177–182.
- Perrin, G., Ferreira, G., Meurisse, M., Verdin, S., Mouly, A.M. and Levy, F. (2007) Social recognition memory requires protein synthesis after reactivation. *Behavioral Neuroscience* 121, 148–155.

- Regolin, L., Marconato, F. and Vallortigara, G. (2004) Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). *Animal Cognition* 7, 162–170.
- Shettleworth, S. (1998) *Cognition, Evolution, and Behavior*. Oxford University Press, Oxford, UK.
- Spinka, M., Duncan, I.J.H. and Widowski, T.M. (1998) Do pigs prefer short-term to medium-term confinement? *Applied Animal Behaviour Science* 58, 221–232.
- Whiten, A., Horner, I., Litchfield, C.A. and Marshall-Pescini, S. (2004) How do apes ape? *Learning and Behavior* 32, 36–52.
- Williams, J.L., Friend, T.H., Nevill, C.H. and Archer, G. (2004) The efficacy of a secondary reinforcer (clicker) during acquisition and extinction of an operant task in horses. *Applied Animal Behaviour Science* 88, 331–341.