

3 Mechanisms of Behaviour

Introduction

The sense organs described in the last chapter bombard the cat with data at every waking moment; somehow the important information must be filtered from the irrelevant (Dukas, 2002). This process may start in the sense organs themselves, as illustrated by pattern recognition within the visual system (see [Chapter 2](#), this volume), but much of it happens in the spinal column and the brain. The translation of sensory input into what we see as behaviour can occur in several ways, and at different levels of complexity. If there is a direct connection between the sensory information and the behaviour pattern, as is the case in simple reflexes, the reaction time will be short, but there will be little scope for flexibility in the response. If the information is thoroughly processed by the brain before any behaviour pattern is triggered, reaction time is likely to be longer, but the stimulus–response relationship can be considerably modified by learning. Some behaviour patterns are so essential for second-to-second survival that a cat could not afford to learn them from scratch; others have to be learned because the relevant sensory information is different for every individual – for example, the learning of routes around a home range. It is important for us to try to understand the mental, as well as the sensory, capabilities of the cat, to comprehend fully the subjective aspects of the world in which the cat lives. Every cat owner has ideas of how ‘clever’ their animal is, but these are usually built on anthropomorphic concepts, some of which are appropriate to a carnivore, but many of which are not.

This chapter deals with the role of the central nervous system and related physiological mechanisms in determining the behaviour patterns that we observe. Underlying rhythmical processes will be dealt with first, followed by the species-specific, reflexive patterns that confer some of the cat’s special abilities. Finally, more complex learning will be discussed, again emphasizing those abilities and constraints which seem to separate the cat from other mammals.

Rhythms of Behaviour

Cat behaviour is influenced by underlying rhythms in the endocrine and nervous system, which are themselves affected by external patterns, such as night and day, and seasonal changes in day length. The annual rhythms have not been studied in great detail, but the hormones adrenaline and noradrenaline vary considerably with the seasons (Randall and Parsons, 1987). Even at constant temperature, food intake peaks in the autumn and is lowest in the spring, while body weight is lowest in the summer and highest in mid-winter, suggesting that metabolic rate may also be subject to annual rhythms. Cats are also affected by daily (circadian) rhythms of activity that are endogenously longer than the normal day, at about 24.2–25.0 h (Johnson *et al.*, 1983), but are reset each day by the cycle of light and dark, so that in practice they repeat every 24 h.

Sleep

The cycle of sleeping and waking is very variable, but is almost always less than 24 h long, because cats tend to sleep for several short periods during both day and night, rather than in a single sustained session. Sleep has been studied extensively in the cat, and a particular area of the brainstem, the reticular formation, is known to be a major control centre. Nerve impulses from the reticular formation to the cortex keep the cat awake; these impulses are stimulated in turn by sensory input, both direct, from the sense organs, and also via the cortex in the case of learned signals, such as the visual characteristics of a potential threat. There are other interactions – for example, hunger and thirst tend to suppress sleep, acting mainly through the hypothalamus.

The rhythmic patterns in the brain during sleep can be recorded from the skin on the head. When a cat is awake, these electroencephalogram (EEG) patterns have low amplitude but high frequency, and vary greatly depending on how active the cat is, and what it is doing. The onset of sleep is marked by a change to a high-amplitude but much lower-frequency EEG, with occasional bursts of medium-amplitude, intermediate-frequency waves. The cat then looks as if it is asleep, but is readily woken. After about 10–30 min, the EEG changes again to low-amplitude, high-frequency patterns rather similar to those of wakefulness, but the cat is now difficult to rouse; this apparent anomaly has given rise to the term *paradoxical sleep* for this phase. After another 10 min or so, normal sleep is resumed, and the two types may alternate if the sleeping bout persists. During paradoxical sleep, there is an almost complete loss of muscle tone, although

individual muscles may contract suddenly, bilateral eye movements can be observed (hence this is sometimes also referred to as rapid eye movement or REM sleep) and the tail and whiskers may twitch (Oswald, 1962). All of this implies that cats in this state are dreaming, although we can have no direct evidence for this. Certainly paradoxical sleep seems to be more important than normal sleep, because the less sleep a cat has the greater is the proportion of the paradoxical phase.

The precise function of sleep (in mammals in general) still remains unresolved, even though the deleterious effects of sleep deprivation are self-evident. In kittens, the correlation between periods of sleep and both intense brain development and high synaptic plasticity suggests that sleep is indeed essential to memory formation (Frank, 2011).

Reflex Behaviour

Because the behaviour of mammals is so easily modified by experience, it is easy to lose sight of the fact that much of their minute-to-minute behaviour is controlled largely by reflexes. Before discussing the more 'intelligent' aspects of cat behaviour, some of the more pre-programmed patterns will be described. Many of these do not fit into the definition of a simple reflex, which is a brief, stereotyped motor output produced by a standardized input to peripheral receptors, acting by way of relatively simple nervous connections. One example of a simple reflex is the scratching response to irritation on a particular point on the skin; some other examples, from kittens, will be considered in the next chapter.

As the study of neurophysiology has become more sophisticated, it has been possible to study patterns of behaviour that are controlled by quite complex, interacting nervous connections; for the sake of simplicity, these will also be considered as reflexes. Many characteristic behaviour patterns can be considered as complex reflexes, because their form is largely independent from input from the forebrain, the part of the brain that processes much of the sensory information, and is responsible for most learned and 'conscious' behaviour. These include most aspects of locomotion, including walking and climbing, and the characteristic postures for urination and defecation, as well as the burying of excreta. The latter, for example, can occur with little or no feedback from the senses, as when a cat, after using a small litter tray, performs stereotyped scratching movements in thin air around the tray. Some patterns of agonistic behaviour, such as dilation of the pupils, piloerection, hissing, growling, tail

behaviour, such as dilation of the pupils, piloerection, hissing, growling, tail-lashing and protrusion of the claws, are also reflexive, although others, such as arching of the back, biting and striking out with the forelimbs, are elicited from the hypothalamus in the forebrain (see below). Similarly, some components of oestrous behaviour appear to be reflexive, including rubbing, rolling and calling, the oestrous crouch and treading with the hind legs, as well as parts of the after-reaction following mating (Bard and Macht, 1958).

Posture-maintaining reflexes

Postural control in the cat is maintained by two feedback systems, in addition to an anticipatory system that acts on input from the brain as soon as the cat 'decides' to change its position (Deliagina *et al.*, 2006). The simplest feedback system is in the trunk, where two closed-loop systems, one in the spinal cord and the other in the brainstem and cerebellum, correct for involuntary changes in posture, such as when one foot slips on a narrow perch.

The second feedback system incorporates information coming from the head, specifically the vestibular (balance) and visual systems. The information produced by the balance organs has already been described (see [Chapter 2](#), this volume); it is relayed both to the cerebellum in the brain (see below) and also directly to some sets of muscles to form reflexes. Of these reflexes, the simplest are those that trigger contractions of the muscles that direct the eyes, because eye movements do not bring about changes in the orientation of the head to the body, and therefore do not in themselves trigger further signals from the balance organs. These vestibulo-ocular reflexes allow the gaze to be fixed while the head is moving slightly. As the head swivels, the direction and extent of the rotation is picked up by the semicircular canals and is translated into an exactly equal and opposite rotation of the eye. More prolonged turning, in which it would be impossible for the eyes to remain fixed on one point, results in intermittent repositioning of the eyes through repetitive compensatory movements known as nystagmus. These are rhythmic movements of the eyes, consisting of a slow deviation in one direction, matching the turning of the head, followed by a quick return to approximately the original position. This reflex allows for intermittent clear vision, whereas if the eyes were held stationary in the head, vision would be partially disrupted for the whole of the turn.

When a cat's attention is drawn to something to one side, its eyes will move first to look at the object, followed quickly by a rotation of the head, which must be accompanied by a counter-rotation of the eyes if the gaze is to remain on the object. This compensation is driven almost entirely by the vestibulo-ocular

reflex system. When a cat is moving, similar reflexes allow the gaze to be corrected for the effects of jolts and jerks due to unevenness in the terrain.

The vestibular system measures small, rapid changes in position or angle much more accurately than large, slow movements, and for the latter the simple reflexes described above would result in under- or over-compensation if used alone. The matching of visual and vestibular signals probably goes on all the time in a continuous learning process. To take an analogy from human experience, this adaptability is shown by the process of adjustment to the wearing of strong corrective spectacle lenses. When first worn, such lenses produce an apparently disturbed motion of the surroundings at the periphery of vision, due to a mismatch between the vestibular signals and the altered visual field, but within a few days these aberrations disappear.

The reflexes in the neck muscles are essentially an error-correcting system. Any rotational displacements of the head will cause the appropriate neck muscles to be activated, such that the disturbing force is counteracted and the head is restabilized. Since any movement of the neck muscles is likely to cause the head itself to move, triggering more signals from the semicircular canals, the detailed working of these reflexes is more complex than those involving the eyes. More complex still are those that trigger contractions of the body muscles, whose effects on the orientation of the skull are unpredictable. One of the simplest of these occurs at the beginning of a fall; within 70 ms of a cat losing its footing, signals from the otolith balance organs trigger extensions of the legs, as a preparation for landing (Watt, 1976). The semicircular canals stimulate reflexes that will tend to restore body position; for example, if the head rotates to the left, both front and hind left legs are extended, while both right legs are flexed. However, in many real instances the neck reflexes will act first, and thereby complicate the extent and direction of the body reflexes ([Fig. 3.1](#)).

	Labyrinth		
Neck	Head up	Head normal	Head down
Neck dorsiflexed			
Neck normal			
Neck ventroflexed			

Fig. 3.1. Interactions between the static labyrinthine reflexes and the neck reflexes, and their effects on the limbs. The central figure shows the normal resting posture. In the middle row (left and right) the labyrinthine reflexes operate alone; in the centre column (above and below) the neck reflexes operate alone. Their interactions are indicated in the four corner figures. See text for further interpretation (redrawn from Wilson and Melville Jones, 1979).

Locomotion

The basic patterns of locomotion are contained in spinal ‘programmes’ that produce the main features of rhythmic stepping for the various gaits described in [Chapter 1](#). The spinal cord contains specialized autonomous stepping generators for the hind limbs, and probably also for the forelimbs. Each of these contains the pattern for a complete step of a single limb, which can be speeded up or slowed down as necessary. Alternative neural pathways between these generators allow for the different ways in which the individual limbs follow one

another to produce the various gaits. Signals from proprioceptors in the limbs are integrated into the stepping cycle, their effects depending upon precisely where in the stepping cycle they occur. They also allow for corrections due to, for example, uneven terrain (Rossignol *et al.*, 2006), while the whole programme is activated and sustained by command signals from the brain (Grillner *et al.*, 2008).

During locomotion, cats tend not to fix their gaze on objects in front of them, but rather look downwards towards the ground, for periods of about 0.25 s at a time before shifting their gaze, sometimes blinking at the same time (Fowler and Sherk, 2003). Thus most of the visual information that they gather while moving is itself moving across their visual field. Cats are perfectly capable of tracking fast-moving objects by moving their heads, so they can presumably therefore do the same while moving. Keeping the head steady during locomotion appears to be essential for paw placement, since if the normal visual flow is disrupted by illuminating the ground with a strobe light, cats frequently tread on obstacles that they can easily avoid under normal illumination. Motion-sensitive neurons must therefore play a major role in foot placement.

Because they don't usually look at their feet while walking, cats must memorize two to four steps' worth of the ground in front of them. If they're distracted, this visual memory persists for only 2–3 s, consistent with being stored only in working memory. However, the memory that results from actually stepping over an obstacle with the forelegs can last for up to 10 min, as shown by the corresponding movement of the hind legs when the cat is distracted while the obstacle is beneath its belly (McVea and Pearson, 2007).

The orienting reflex

Cats, like most mammals including man, will rapidly orientate their sense organs towards any sudden event in the environment. This involves complex movements that are situation-specific and therefore far from rigid, so the term reflex is used here in its sense of the behaviour occurring very quickly after the onset of the stimulus. The motor patterns involved are not specific to either the quality or intensity of the stimulus, which can be provided by any one of the senses, or a combination. The most important features of the stimulus are its contrast and novelty; the ending of a continuous stimulus such as a drawn-out sound can evoke the same response as the beginning of that sound. If the same stimulus is repeated over and over again, the reflex becomes weaker and is finally not elicited at all. In the brain, one major effect is the dilation of the

cerebral blood vessels and constriction of the peripheral, which facilitates the transmission of information through the central nervous system, making the cat more 'attentive' (Sokolov, 1963). The essentially pre-programmed nature of this reflex can be illustrated by its invariant effects on the eyes. If an object appears suddenly in the visual field, the pupils dilate and the eyes automatically focus at their shortest possible distance, even if the object is actually far away. Non-visual stimuli have exactly the same effect on the eyes, whether they are odours, sounds or a light touch, always provided they occur with an element of surprise.

Grooming

Cats spend a great deal of their time grooming; of the half of their lives that is not devoted to sleep, oral grooming, supplemented by the occasional bout of scratching, can occupy as much as 10%. Cats' tongues incorporate cornified papillae that are specialized for cleaning the fur as they lick, and the small incisor teeth are also used. Although grooming is effective at removing ectoparasites such as fleas, it appears to be regulated by a programmed grooming generator, both in its timing and its typical form (Eckstein and Hart, 2000), rather than always being prompted by itching at a specific location on the skin. Cats often groom within a few minutes of waking, suggesting that this generator is 'catching up' after an enforced period of inactivity. The typical cephalocaudal sequence of grooming, starting with face-washing using the paws and then progressing to hind legs, flanks, neck and chest, anogenital area and then the tail, also suggests internal, rather than stimulus-driven, programming.

The Brain and the Control of Behaviour

The brain, and particularly the forebrain, exerts a controlling influence at almost every stage of the more complex reflexes. For example, the reticular formation in the brainstem not only controls sleep, but also the general state of arousal. It influences the impact of all the sensory systems on the cerebral cortex, and is particularly active during habituation, the process whereby the same stimulus, if repeated, elicits a weaker and weaker behavioural response. A second, parallel arousal system in the mid-brain mediates the effects of learned behaviour patterns (Colgan, 1989).

In addition to such non-specific effects, it has proved possible to group some behaviour patterns together, based upon the site in the brain from which they

originate. One of the best understood is the ‘quiet biting attack’, which is the psychologists’ term for the patterns seen in the latter stages of hunting, culminating in the kill. Groups of neurons in the hypothalamus and mid-brain control a whole sequence of events, each one of which contains several reflexes. In the order in which they occur, these are:

1. Stalking, sniffing and visually guided approach to the prey.
2. Visually guided orientation of the cat’s head to the target, assisted by tactile stimulation from the forepaw if this makes contact with the prey.
3. When the head reaches the target, precise orientation of the snout by tactile stimulation of a trigger zone on the face.
4. Opening of the jaws, in response to stimulation of a trigger zone around the lips.
5. Closure of the jaws when a trigger zone just inside the mouth is activated.

The hypothalamus has an important role to play in changing the thresholds for the component reflexes. For example, the seizing and biting reflexes are switched on, while others that would interfere with the capture of prey, such as the jaw drop reflex, are suppressed. The sensory inputs required at each stage can be defined precisely; the head-orienting reaction occurs in response to touch over an area of skin extending from just above the upper lip to the hairless area on the nose, and out to the side as far as the whiskers. Biting requires a touch on either the upper or lower lips, most effectively at the front of the mouth, but to a lesser extent around to the sides (Fig. 3.2). Persistent biting requires stimulation of the trigeminal receptors around the mouth, as well as touch receptors (Siegel and Pott, 1988).

Quite separate areas of the hypothalamus and mid-brain (specifically, the dorsal half of the periaqueductal grey) and the amygdala control a group of defensive behaviour patterns, including retraction of the ears, piloerection, arching the back, marked dilation of the pupils, vocalizations and unsheathing of the claws (Siegel and Shaikh, 1997; McEllistrem, 2004). Yet other areas of the brain control flight behaviour. Thus the way that many species-specific patterns are organized in the brain mirrors the groups in which we can place them, based on their functions in free-ranging animals.

Comparisons with other species

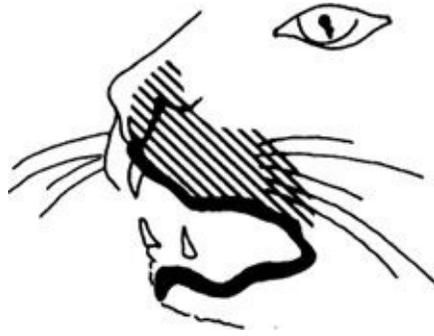


Fig. 3.2. Sensory fields that trigger the head-orienting (shaded area) and jaw-opening (solid areas) responses during prey-capture. The lower jaw also contains a less well-defined area (not shown) directing the head-orienting response (redrawn from Macdonnell and Flynn, 1966).

We can also deduce something of the special features of the cat's brain by making comparisons with other species. One concept that has proved successful in such comparisons is that of structural encephalization, which is defined as the enlargement of the brain beyond that expected from the size of the body, and is measured as an encephalization quotient (EQ) (Jerison, 1985). Large bodies need large brains because they have larger muscles and more extensive somatic sensory systems, but once this is allowed for some striking comparisons can be made. For example, deer, wolves, crows and lemurs all have roughly the same EQ, while hedgehogs have retained the lower EQ of the earliest mammals. This measure contains an element that could be defined as 'intelligence', but enlargement of the brain as a whole can also be due to specializations, such as an increase in the sensitivity of one or more of the senses, which will produce more information for processing. Some of the ecological factors that have been proposed as requiring an increase in EQ are movement in three dimensions (flying, swimming) compared with two (terrestrial); an active anti-predator strategy compared with a passive one (e.g. the hedgehog); and a long period of parent-young association for the transfer of skills (Shettleworth, 1984). More nebulous, but intuitively correct, is the idea that learning abilities differ between animals in terms of how flexible that learning can be. Higher primates can learn a wide variety of tasks and associations; the learning abilities of lower mammals seem to be more situation-specific, more constrained by the niche for which they have evolved. The former is likely to raise the EQ more than the latter. Thus EQ is built up from several components, which can have very different emphases in different species; overall the figure reflects an investment in information processing power, whether it be for learning, or for a special skill such as social

cognition, or for sensory ability. The first of these is the most flexible, the latter two are likely to be more niche-specific.

The brain of the domestic cat is very similar to that of other members of the genus *Felis*. The basic pattern appears in the fossil record some 5–9 million years ago; the brains of earlier cats, most of them sabre-toothed (the paleofelids), appear to have been organized along different lines (Radinsky, 1975). Two of the most striking features of the brain of the domestic cat are the enlargement of the cerebellum, coordinating balance and movement, and the large proportion of the cortex devoted to controlling movement; cats' brains reflect their athletic prowess. The part of the cortex that deals with hearing is well developed, but the olfactory bulbs are, compared with those of other carnivores, rather small. The felids as a family have rather little space for large olfactory bulbs in their comparatively short skulls; those that do have large olfactory bulbs, like the lion, have large home ranges, a trend repeated across all the Carnivora (Gittleman, 1991). The visual area of the cortex is less developed in the domestic cat than in some other felids, for example the jaguarundi, *Herpailurus yaguarondi*.

The cat's EQ is higher than for the majority of rodents, and about average for the carnivores. The dog family has the highest average EQ of any carnivore, some 25% higher than for the average felid; larger olfactory bulbs in dogs, reflecting a greater reliance on their sense of smell, are partly responsible, but the prefrontal cortex, which is thought to selectively inhibit primitive behaviour patterns, is also larger in some dogs. It has been suggested that such inhibition, for example the substitution of aggressive by submissive behaviour patterns, may be a component of the complex social behaviour seen in wolves and other canids.

Learning and Intelligence

It is impossible to draw a sharp distinction between instinctive and learned behaviour in an animal as complex as the cat. Species-specific behaviour, such as vocalization, mating behaviour, some aspects of hunting and the reflexes displayed by kittens, are presumably based upon inherited patterns, but these are modified, supplemented and altered, in both the long and the short term, by learned components. Although the cat has been a favourite subject for the study of learning itself for more than a century, many of the earlier studies were conducted on indoor-reared animals, which are less adept at learning visual discrimination tasks than are cats that have grown up outdoors (Žernicki, 1993). Moreover, many have taken insufficient account of the evolutionary pressures

Moreover, many have taken insufficient account of the evolutionary pressures that have shaped the mind of the cat, compared with those that have shaped, for example, that of the rat or chimpanzee. While the vast majority of species are closely adapted to their current niches, their abilities to respond to sudden changes in those niches vary considerably. Animals relying largely upon instinct, or highly context-specific learning, will only be able to re-adapt at a pace determined by evolutionary mechanisms. Those with more extensive learning abilities can alter their behaviour patterns rapidly; they possess a capacity to solve problems by systems that have not been selected specifically by adaptation to current niches, but are available to cope with unexpected change.

The domestic cat seems to be a prime example of an adaptable species, given that it is able to move from total dependence on man to semi-independence and back, within a lifetime or at most a few generations. Such abilities are, almost by definition, not straightforward to assess, since their full value will only be expressed under circumstances of rapid change in the environment. However, certain mental skills, such as learning by imitation, and the formation of mental concepts, are likely to contribute to the flexibility required, and these are described in the section below on complex learning. On the other hand, cats are not infinitely flexible, for there is ample evidence that their learning abilities are species-specific at all levels of complexity, including straightforward associative learning.

Learning by association

At its simplest level, learning involves the linking together of previously unrelated stimuli, or between actions and the consequences of those actions. Even invertebrate animals are capable of this type of learning, and so it is hardly surprising that cats can form a wide range of associations of this type. Indeed, in the past the behaviourist school of animal psychologists has attempted to describe most learning at this level, but it is evident that many mammals, including cats, are capable of much more complex mental processes, some of which will be described in the next section. By contrast, popular accounts of cat behaviour tend to express learning in the terms of human subjective experience, almost as if cats were mentally defective people rather than highly adapted carnivores. Such controversies are far from new, as the following excerpt from Hobhouse (1915) will illustrate:

I once had a cat which learned to 'knock at the door' by lifting the mat outside and letting it fall. The common account of this proceeding would be that the cat did it in order to get in. It assumes the cat's action to be determined by its end. Is the common account wrong?

Let us test it by trying explanations founded on the more primitive operations of experience. First, then, can we explain the cat's action by the association of ideas? The obvious difficulty here is to find the idea or perception which sets the process going. The sight of a door or a mat was not, so far as I am aware, associated in the cat's experience with the action which it performed until it had performed it. If there were association, it must be said to work retrogressively. The cat associates the idea of getting in with that of someone coming to the door, and this again with the making of a sound to attract attention, and so forth ... Such a series of associations so well adjusted means in reality a set of related elements grasped by the animal and used to determine its action. Ideas of 'persons,' 'opening doors,' 'attracting attention,' and so forth, would have no effect unless attached to the existing circumstances. If the cat has such abstract ideas at all, she must have something more - namely, the power of applying them to present perception. The 'ideas' of calling attention and dropping the mat must somehow be brought together. Further, if the process is one of association, it is a strange coincidence that the right associates are chosen. If the cat began on a string of associations starting from the people in the room, she might as easily go on to dwell on the pleasures of getting in, or how she would coax a morsel of fish from one or a saucerful of cream from another, and so spend her time in idle reverie. But she avoids these associations, and selects those suited to her purpose. In short, we find signs on the one hand of the application of ideas, on the other of selection. Both of these features indicate a higher stage than that of sheer association.

Hobhouse evidently interprets his cat's behaviour as having purposeful elements. However, he does go on to offer an alternative explanation, which we would now class as behaviourist. This is based upon an association between the 'pleasure' of getting through the door and the action of lifting and dropping the mat, and no more. The action assimilates the character of its result and becomes in itself attractive to the cat.

Pavlovian learning

Even with such a simple sequence of events as this, psychologists do not fully agree on the precise details of the learning mechanisms involved. Their findings, usually based on simple tasks carried out under highly defined conditions, are not always easily interpreted in functional terms (i.e. the value to the cat of the type of learning observed). One of the simplest forms of learning is known as Pavlovian conditioning, named after the classic experiments of Pavlov, who trained dogs to anticipate the arrival of food in response to arbitrary signals, such as the sound of a bell or metronome. The dog has continued to be a favourite subject for this type of study, so some of the examples to be described, although drawn from the dog, will be assumed to apply to the cat also. The primary function of Pavlovian learning seems to be the acquisition of information about

stimulus relationships in the environment. One stimulus, the unconditioned stimulus (UCS), is normally linked to a particular motivational state, and releases an innate reaction, the unconditioned response (UCR); for example, the smell of food will result in salivation in a hungry animal. If a second stimulus, the conditioned stimulus (CS), occurs consistently with or immediately before the UCS, it will come to release the UCR even on its own; the UCR has become a conditioned response (CR). However, the UCR and CR need not be identical, although they are normally linked to the same type of motivation. For example, if the UCS is the pain inflicted in an attack by an aggressive tomcat, the UCR will most likely be flight. The victim will probably associate the appearance of the attacker (the CS) with the experience of the fight, and will respond appropriately (CR) on seeing the attacker again. However, this response may change with circumstances; if the CS is fairly distant, the CR may be to 'freeze' in an attempt to avoid detection, rather than to run away, inviting a chase (an example of an interaction between Pavlovian and instrumental learning). Such considerations, and more direct experiments, have led to the conclusion that in most cases the association built up in Pavlovian conditioning is genuinely formed between the CS and the UCS, and not between the CS and the CR; in ethological terms, if the UCS is a releaser, the CS is a learned releaser, bringing it under the control of normal motivational systems.

The interspecific differences that this can produce have been illustrated by a comparison between the learned feeding responses of cats and rats (Grasty and Vereczkei, 1974). The arrival of a food reward was signalled by 10 s of a clicking sound coming from a loudspeaker 2 m away from the food store. This combination caused the cats to run towards the sound, and some would search all around the loudspeaker, and even attempt to bite it. When this response was most intense, the cat would often not take the food reward at all, although after hundreds of further trials the feeding response was re-established. Under similar conditions rats would briefly turn their heads towards the sound, but would rarely approach it. For the rats, the sound was an initially irrelevant cue, but for the cats, which use auditory cues extensively while hunting, it was not, and evidently some conflict appeared between the apparent location of the 'prey', as indicated by the sound, and its subsequent appearance as food.

An important feature of the relationship between CS and UCS is that they must be contingent; if the pairing is unreliable, the response (CR) is considerably weaker than when the CS and UCS always occur together. This prevents the cat from acquiring false or poorly predictive information about its environment. Events that reliably do not predict the UCS are also learned, as can be shown in

two separate ways. First, if a CS is repeatedly presented in a way that does not predict the arrival of the UCS, then when the same CS is presented with the UCS it is difficult to establish the connection; the cat has already learned that the CS is an irrelevant cue, and so when its prediction value changes there is a delay before the new association is registered. Secondly, if the procedure described is performed in reverse, the association is rapidly ‘unlearned’ once it is no longer predictive. Furthermore, associations can be learned between two neutral stimuli (i.e. not releasers) that reliably occur together, even when neither brings about any overt behaviour. This can be shown by pairing just one of the two stimuli with a UCS, after which both stimuli will release the CR. This ‘behaviourally silent learning’ is of obvious value to, for example, a cat learning the topography of its home range, although cats also possess more advanced orientational abilities, which will be described in a later section.

Pavlovian learning is probably the basic mechanism behind many other behavioural phenomena, including taste aversion learning (discussed in [Chapter 6](#), this volume) and some aspects of foraging behaviour. For example, if cats form the equivalent of the ‘search images’ used by birds to detect cryptic prey (Zentall, 2005), they may do so by associations between the appearance of a specific prey type and its profitability. Specific features of the environment may come to be associated with particular prey types or prey densities. Moreover, Pavlovian associations can also prepare the cat for subsequent events so that they can be optimally exploited; for example, CSs indicating food bring about physiological changes that speed up digestion once the food is actually eaten.

Instrumental learning

These simple Pavlovian mechanisms should enable a cat to build up a much more organized picture of its world than would instinct alone, but they will not on their own produce the flexibility in behaviour that cats are evidently capable of. For the latter, a different type of learning is required, one that will enable the cat to predict the consequences of its own actions, and modify those actions based on past successes and failures. This is addressed by the psychological technique of instrumental learning, in which the subject has to respond in some way to a stimulus; correct responses are rewarded. Some of the earliest work in this area used cats as subjects, particularly the puzzle-box experiments of Thorndike (discussed in Hobhouse, 1915). Thorndike placed cats in cages from which they could escape by means well within their motor capabilities, such as clawing at a string, depressing a lever, pushing aside a swing door, and so on

(Fig. 3.3). The cats would claw and scratch indiscriminately at the sides of the cage, until by accident they performed the right action and gained their freedom. The time that it took the cats to escape declined with repetition, implying that the probability of performing the correct action was increased by each success. Some of the tasks set were quite complex; one latch required a simultaneous lift and push, and in other cages two or even three latches had to be opened in the correct sequence. Although not all cats could master these, all were opened by some. Taking an average of several animals, the skills appeared to be gained gradually, and Thorndike concluded that ‘The gradual slope of the time-curve, then, shows the absence of reasoning. They represent the wearing smooth of a path in the brain, not the decisions of a rational consciousness.’ However, individual animals did not behave quite in this probabilistic way. Some did take a little less time to escape on each successive attempt, but many seemed to improve their performance quite abruptly, and then never make another mistake, even with an interval of several months between trials. In fact, rapid (one-trial) learning is nowadays not thought to be good evidence for conscious thought. Many animals learn crucial associations, such as the toxicity of particular foods, after only one experience; in this situation the potentially lethal consequences of eating the same food again are likely to outweigh the risk that, after only one encounter, the animal has learned the wrong connection.

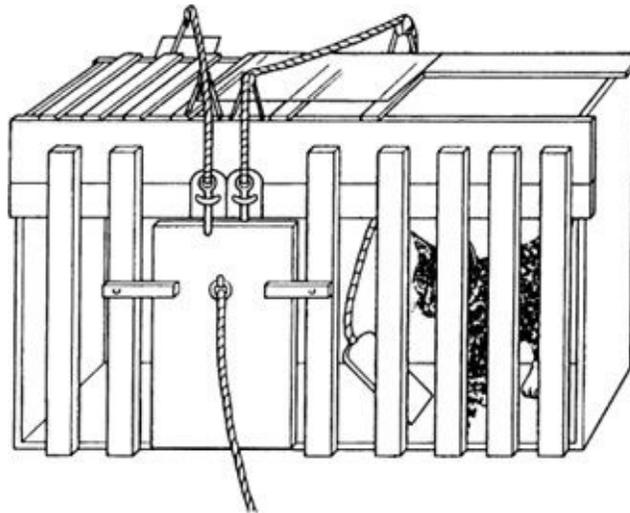


Fig. 3.3. An example of one of Thorndike's puzzle boxes (from McFarland, 1985).

Thorndike's idea that random behaviour patterns were shaped by successes gave this type of process its alternative name, 'trial-and-error learning'. The

apparently random behaviour of the cats when first put into the cages, together with the results of many other such experiments on other species, helped to establish the notion that almost any behaviour could be shaped in this way, minimizing the value of instinctive behaviour. However, it is now clear that species-specific behaviour patterns have a clear role to play in providing the behaviour that is to be shaped, in directing the attention of the cat towards the task to be performed, and in providing an assessment of the value of the reward for correct performance. These *species-specific constraints* presumably ensure that in the real world, outside the narrow context of the typical instrumental learning paradigm, the most ecologically functional skills are acquired. Thus it is much easier to train a cat to obtain a food reward by using a normal component of hunting behaviour, such as hooking back a bolt with its paw (the movement used to dislodge prey that takes refuge in a crevice), than by some arbitrary but straightforward action, such as pushing an identical bolt inwards. In the cage experiments, Thorndike found that certain actions of the cat could not be trained; for example, if the cat dislodged the latch by accident with its tail, it did not appear to learn anything about the location of the latch or the type of actions likely to open it on subsequent trials. Also, if the cat was allowed to escape every time it performed some arbitrary action, such as grooming, the frequency of grooming did not increase; the connection between the action (grooming) and the reward (escape) was never made. The type of incentive is also important. For young cats, although food is a powerful reinforcer, other activities, such as manipulation of simple objects like a ball or a crumpled piece of paper, or exploration of an unfamiliar space, are also adequate rewards for a discrimination task (Miles, 1958).

Instrumental learning methods have been used extensively to probe the sensory and mental capabilities of cats; examples of the former have been described in [Chapter 2](#), and the latter will be explored in more detail in the following section. To provide information on the way that the cat makes everyday decisions about its actions, more complex schedules of reward and response are required. For example, one common procedure is to reward two distinct responses simultaneously, either pairing each with a reward of different value or rewarding different proportions of the two responses. In many species, the strategy that is adopted can depend on the type of stimulus (e.g. visual or spatial) used to indicate the reward, presumably reflecting species-specific propensities to learn links between food and its sensory characteristics. The types of strategy adopted by the animal can give some idea of the way it might behave in the field when confronted with prey items of different nutritive value,

or that are more or less easy to catch. One set of trials that mimicked the latter situation (Warren and Beck, 1966) can be used to illustrate the procedure and its possible results. Cats were rewarded intermittently for choosing one of a pair of visually distinct wooden blocks (for example, one triangular and black, and the other circular and white). If only one block was rewarded (reinforcement ratio 100:0), the cats rapidly learned to respond only to that block. If both were rewarded equally (50:50), responses were, on average, also equal. A 90:10 ratio resulted in all cats responding in the same way as to the 100:0, a strategy known as *maximizing*, because by this means the maximum number of food rewards is obtained within a session. The more complex reinforcement ratios of 60:40, 70:30 and 80:20 produced some very individual-specific shifts in strategy. Particularly at the lower ratios, most cats distributed their responses within 5% of the reinforcement ratio, a strategy known as *matching*. The ratio at which each cat switched strategies varied considerably, some maximizing at 60:40, others matching up to 80:20. The mechanism behind matching seemed to be a simple one; most cats persevered in responding to the stimulus that had produced food on the previous attempt, only switching to the other when this prediction failed to pay off. The origins of the individual differences could not be determined, but may have been due to the cats' previous learning experiences.

It is difficult to extrapolate from the results of such trials to real foraging decisions, because they still contain an element of artificiality, in that the cats obtain a great deal of their daily food intake away from the training procedure, so their motivation may not be the same as if they were foraging. In other species, closed-economy experiments, in which animals have to do work for all their food, have produced some conclusions that are opposed to those obtained from trials like the one described above (Davey, 1989). Very few trials of this type have used cats, but there is some evidence that the maximizing strategy can be subservient to a direction-stable strategy in which each cat has a preferred foraging route (see [Chapter 7](#), this volume).

Various extensions of instrumental learning are used when cats are taught to do tricks (McGreevy and Boakes, 2007). It is sometimes claimed that cats cannot be taught tricks, but what is usually meant by this is that cats cannot easily be taught by the same methods as dogs. Most dogs are very attentive to their trainers, and can be rewarded by positive social contact alone. Cats are much less likely to be interested in the training process for its own sake, and usually need to be rewarded with food or other incentive such as play. The sooner the reward is given after each correct response, the more easily cats will learn the correct association. Instrumental learning tests also show that cats, in common

with most mammals, remember tasks for much longer if they are only rewarded for a proportion of correct solutions (an intermittent reinforcement schedule): introducing intermittent rewarding once a behaviour is learnt can be used to fix the results of such training. These simple techniques can be used to reinforce normal behaviour patterns, which can also be trained to be shown on cue by only reinforcing responses shown after the cue is presented. Patterns that are not entirely natural can be trained by progressively rewarding responses closer to the desired behaviour, known as *shaping*. To take a simple example, cats will not usually jump over an obstacle if they can walk round it. To train a cat to jump on request, it can first be rewarded for walking over a stick that is lying on the ground, then for stepping over it when it is raised slightly. As the stick is raised further, the cat is rewarded for jumps only. Once the habit has been established, it can be made more persistent by rewarding only a proportion of successes. More complex tricks often have to be built up a step at a time using gradual shaping of responses.

Because the timing of reinforcement is important in establishing a desired response, a *conditioned reinforcer* is sometimes used to avoid delays associated in providing a reward. Conditioned reinforcement is where a previously neutral signal (e.g. a sound) is reliably associated with a primary reinforcer, for example food. Once this association is established, the sound can be used to signal a correct response, even where the trainer is at a distance from the cat, and any delays associated with getting out and providing a food reward are avoided. With patience, cats can be trained to show complex behaviours involving quite long chains of shaped behaviours. However, training sessions generally need to be short and the reward valuable to maintain interest in the task.

Complex learning

The cat is no longer a favourite subject for the study of learning – much more is known about the specific abilities of pigeons, rats and monkeys – and so the account that follows is by no means a complete description of feline intelligence.

Complex stimuli

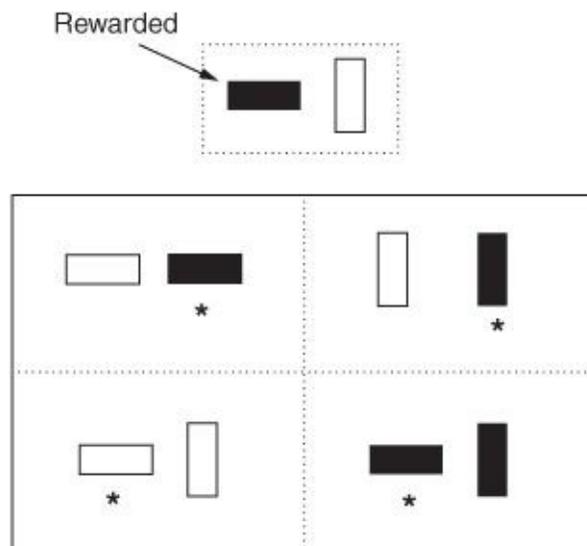


Fig. 3.4. One example from the sets of discriminations that show that cats can learn two attributes of a visual stimulus simultaneously. Young cats were rewarded for responses to the left-hand figure in the upper box, and once trained were tested for preferences between the four pairs in the lower box. Each of these differed in either brightness, or orientation, but not both. The cats tended to make choices (starred) indicating that they had learned that the rewarded object had been both shaded and horizontal (redrawn from Mumma and Warren, 1968).

Ecologically meaningful cues are rarely simple; they may differ from their background, and other less relevant cues, in several ways, for example size, shape, brightness, colour, characteristic movements, sounds and odours. A great deal is known about the ability of cats to identify stimuli that differ in only one sensory dimension, but much less about the analytical processes they use when confronted with complex stimuli. Some idea of these processes can be gained from experiments carried out to detect the more relevant of a pair of cues presented simultaneously (Mumma and Warren, 1968). Three-month-old cats were trained to distinguish between rectangles that differed in both orientation and brightness, and were then tested to see which one they preferred of pairs of rectangles that differed in either orientation or brightness (Fig. 3.4). These preferences showed that both cues had been learned simultaneously by most kittens, although there was the expected variability in accuracy; there was no evidence that some had relied more on one than the other, as rats tend to do. The relevance of particular shapes has also been examined, and one cue that cats seem to pay great attention to is whether figures are open or closed. For example, they learn to discriminate circles from U-shapes much more quickly than from triangles (Fig. 3.5). The basis for this seems to be the ratio between

the area of a shape and the number of sides that it has (Warren, 1972). When irrelevant cues are presented along with relevant ones, cats are better than rodents at singling out the predictive one. For example, from a set of wooden triangles and circles that could be black or white, and one of two sizes, only triangular or circular shapes were rewarded with food. The cats learned that it was the shape that was the discriminating feature, and there was no difference in the speed of learning between cats trained with pairs of triangles and circles which were always the same shade and size, and cats trained with pairs of triangles and circles the shade and shape of which changed from session to session (Warren, 1976). The errors that cats make in such trials seem to originate in their initial preferences and aversions, which they rarely overcome as completely as monkeys do when trained on the same problems.

The concept of oddity

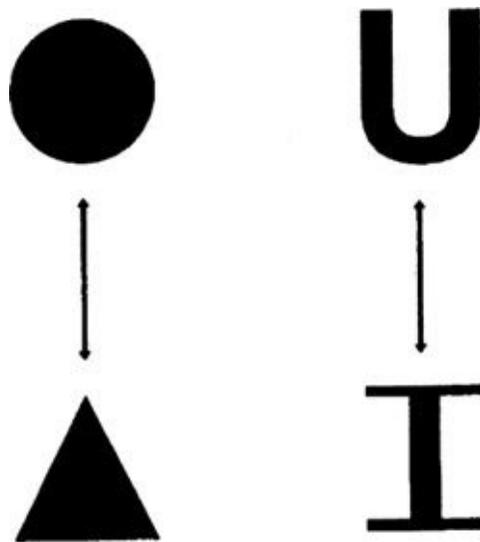


Fig. 3.5. Examples of shapes that cats find easy to discriminate from one another, the exceptions being the pairs connected by arrows.

The precise extent to which cats can generalize from one discrimination to another is still unclear. One such generalization is that of oddity. Chimpanzees can quickly grasp the idea that they are to pick out the non-matching object in a group of three in which the other two objects are identical. Cats take much longer to learn this, and are prone to mistakes. In one set of trials, five 9-month-old cats were initially trained to discriminate the odd one (for example, a

triangle) of three objects (the other two being, for example, circles), when the same set of three objects was presented at each session (Warren, 1960). Once each cat had successfully learned that it should look for the triangle, one of the circles was removed from the set and was replaced by a triangle; in other words, the oddness was transferred from the triangle to the circle. The odd object was still the one that was rewarded; initially the cats preferred either of the two triangles, because that shape had previously been associated with food, but quickly turned their attention to the circle, which was now the odd object. This reversal was repeated 20 times, and each time the cats followed the change, although one of the five was consistently more accurate than the others. This part of the procedure demonstrates that the cats could discriminate the objects from one another even when two were identical, but it does not demonstrate learning of oddity itself. In the second part of the procedure, the triangle/two circles and circle/two triangles combinations were presented in a random order, and one cat, the best performer in the preliminary trial, learned that it was the odd one out, rather than either of the shapes themselves, that signalled food. This cat could also rapidly generalize from this pair of shapes to others; presented with random orders of two new shapes in groups of three, it made fewer and fewer errors each time the pair of shapes was changed for a new pair, showing that it had grasped that the salient cue was oddity. That the cat that mastered the oddity problems was also the best at recognizing objects suggests that these two types of learning are linked. It is also possible that all the cats had the concept of oddity, but could not be persuaded to demonstrate it by object discrimination.

Object permanence

Similar problems may lie behind apparently conflicting findings relating to the extent to which cats understand where objects have been hidden. Such skills would be highly adaptive for a carnivore hunting in cover, and so we should expect cats to be highly aware of the most likely location of prey that has gone to ground, or has moved after disappearing behind cover. A theoretical framework for the concept of object permanence, devised by Piaget for recording the development of human infants, has been used to quantify the abilities of cats and is therefore worth summarizing in its basic form. In the first two stages of development, infants show little interest in objects, and when an object is hidden, they stare at the point from which it disappeared, rather than looking round for it. Stage 3 is marked by the ability to discriminate partly hidden objects, and to recognize the part that is visible as belonging to the original whole. Stage 4 introduces the concept of permanence for the first time; objects

that disappear are searched for, indicating that the infant realizes that they still exist. However, in a series of tests with the same object they tend to search the place where the object has been hidden most often, rather than the place where they have just seen it hidden; a previously successful action is repeated, akin to the result expected from instrumental conditioning. Reliance on immediate perception is established in stage 5, and more complex problems can also be solved. These include *sequential visible displacement*, in which an object is hidden in several places in turn, the solution being to look in the place closest to where it was last seen, and *single invisible displacement*, in which an object is hidden first in the hand, and then the hand is placed under a cover. When the hand is withdrawn and shown to be empty, the child should look under the cover. The final (sixth) stage completes the mental concept of object permanence, in which the child can follow *sequential and successive invisible displacements*. In the first, an object is hidden in the hand, put under one cover, shown to be under that cover, palmed again and hidden under a second cover. Infants at stage 5 tend to look under the first cover. In the successive displacement, the object hidden in the hand is moved from one cover to another, and left under the last before the empty hand is displayed; again, infants that have not reached this stage tend to start by looking under the first cover.

The extent to which cats can be persuaded to demonstrate their abilities in this area seems to depend a great deal on the protocol that is used. Cats appear to be easily fooled by the classic sequential invisible task: if a piece of food is made to disappear behind one barrier, then moved concealed inside a container first into the open and then behind another barrier, where it is made to reappear and then disappear, most cats will look behind one or other of the screens, but show no strong preference for either (Goulet *et al.*, 1994). Their behaviour suggests that they don't realize that the two objects they have seen are actually one and the same.

However, if invisible displacements are made more ecologically relevant as far as their hunting behaviour is concerned, cats do appear to be able to make predictions about where a potential prey item might have hidden itself. Using the apparatus shown in [Fig. 3.6](#), Dumas (1992) was able to show that if a cat has to lose sight of a prey object in order to reach it, the cat does have an idea where the prey has gone if it subsequently finds that it has hidden itself. Moreover, given a choice of routes to hidden prey, cats do not always take the most direct route, possibly a tactic for confusing the prey item (Dumas, 2000). The locations where prey has disappeared are generally stored in working memory only (10–15 s) presumably because it is not worthwhile for the cat to continue to look for

highly mobile prey for much longer than this (Fiset and Doré, 2006).

Concepts for orientation

Familiarity with the environment implies that cats have some kind of concept of the way that the components of the world around them fit together. This has been investigated by examining the ways that cats find their way around. There are several possibilities, incorporating different levels of sophistication. The simplest type of orientation relies on direct perception of the goal ('the rabbit warren is in the bank that I can see at the other side of the field'), or a step-by-step route based on landmarks ('if I go to the oak tree that I can see, and turn left, I will then be able to see the warren'). Many animals, including some invertebrates, use such orientation systems, which are generally simple to use but prone to error ('the oak tree has been felled, so I can no longer find the warren'). Cats rely on egocentric cues ('to my left') in simple situations where they are unlikely to lead to error (Fiset and Doré, 1996), but they are also capable of constructing cognitive maps of their surroundings, particularly if they have been able to explore them thoroughly (Poucet, 1985). Although they can construct mental maps based on a brief view of relevant features, these are not remembered for more than a few minutes. Mapping leads to the possibility of taking short-cuts ('last time I went to the warren I went to the oak tree and turned left, so this time I will go diagonally across the field and through the hedge; the warren is just beyond the hedge'). It also permits the rapid choice of optimum routes; given a choice of ways to an invisible goal, cats almost always prefer the shortest one. If there are several routes of roughly the same length, the one that starts off in the direction closest to the direction of the goal itself may be preferred, a common human habit also. Minimizing the number of twists and turns in the route after that is also a factor that determines a cat's choice, but a relatively unimportant one.

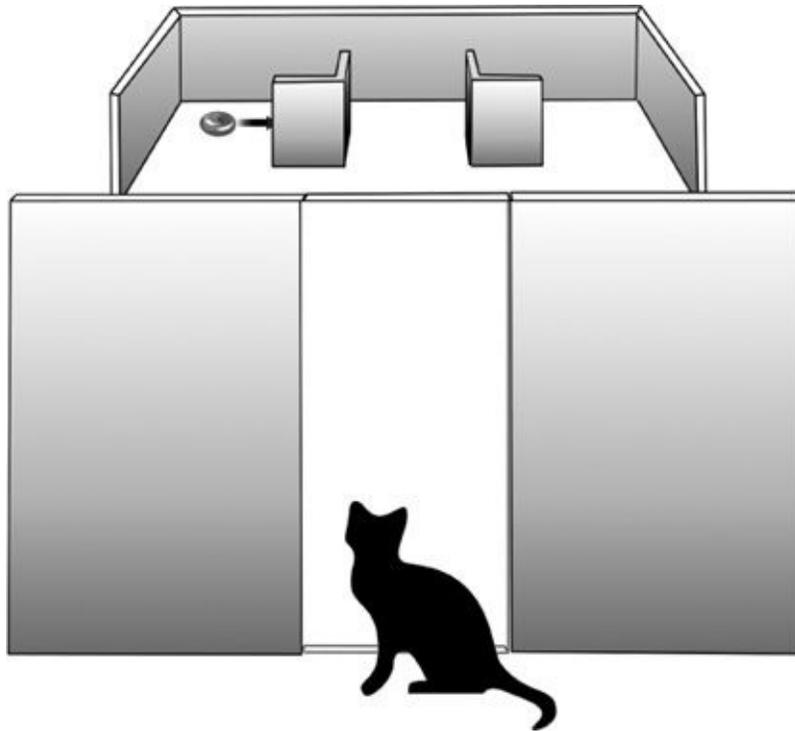


Fig. 3.6. An apparatus used to test cats' ability to follow invisible displacements. The cat starts as shown, from where it is able to see a piece of food through a transparent centre section of a screen that is otherwise opaque. Once the cat has started approaching the food, and is behind one or other of the opaque sections, the food is moved (using transparent strings) behind the inner 'hiding' screen (redrawn from Dumas, 1992).

Concepts of time and physics

Cats are capable of discriminating short time-intervals; they can tell the difference between a sound that lasts 4 s from one that lasts 5 s, and can also learn to delay their response to a stimulus by several seconds, again to an accuracy of about 1 s. This implies the existence of an internal clock that times the duration of both internal and external events; this could be used, for example, in assessing the rate at which particular feeding strategies produce food. Another skill which would be useful in this context is the ability to count, and it is thought that cats do have some kind of abstract conception of number, although attempts to demonstrate this have not proved recognition of numbers greater than about seven.

Cats' comprehension of causality, while little studied, seems rudimentary at best. In a string-pulling task (Fig 3.7), most cats can easily be trained to retrieve

a piece of food by pulling on a single string, but seem unable to work out which of two parallel or crossed strings is attached to food and which is not (Whitt *et al.*, 2009) – dogs also fail at the crossed-strings task but can solve the parallel-strings problem.

Finally, it is worth returning to the question of how cats obtain the information on which learning is based. Trial-and-error is a time-consuming process, and in a social animal a great deal of time could be saved by watching the ways that conspecifics solve problems. Cats are certainly capable of this, even when they are adult (John *et al.*, 1968), although it has been argued that the actions of the conspecific merely help to focus the cat's attention on the problem to be solved. Some are apparently able to 'work out' exactly how to perform a task simply by watching an experienced individual carry out that task, and then repeating the actions they have seen. Learning of this kind is essential in the most intense period of the cat's social life, its life as a kitten with its mother and siblings.

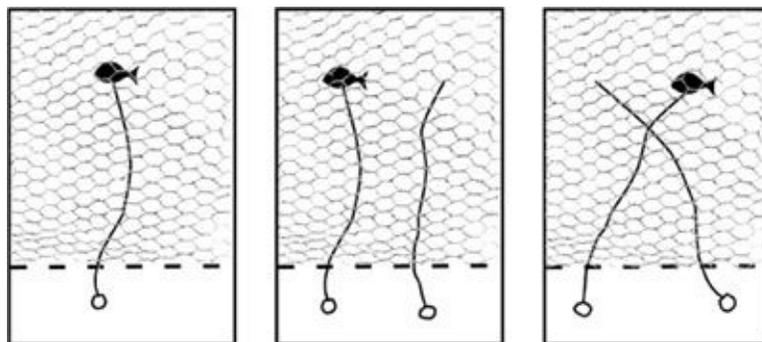


Fig 3.7. Arrangements of strings, handles and food rewards in a string-pulling task – the cat has access only to the area in front of the dashed line, the remainder being enclosed in a box with transparent sides and a mesh cover (redrawn from Whitt *et al.*, 2009). Cats can be trained to obtain a food reward by pulling the string out from the covered box (left), but when presented with two strings, one baited and the other not, seem incapable of selecting the correct string, whether the strings are parallel (centre) or crossed (right).