The complex interaction between genes and environment in Chapter 5 continues to affect the development of behaviour throughout the life of the animal, partly through maturation of sensory, motor and other physical systems, and partly through learning. Can we tease these two routes apart? Are there changes in behaviour that simply reflect physical maturation? If so, how are they brought about? If changes are instead due to experience, what processes underlie them? Animals seem to learn in many different ways, but are they really different or just modifications of the same basic process? Does an ability to learn quickly, or to learn complex tasks, equate to intelligence? Animals vary in their ability to learn. Why? Is there any evidence that such differences reflect adaptive specialisation? Play behaviour is a puzzling feature of development in many species. Explanations have suggested various roles in maturation and learning, but is there any consensus view?

The functional movements we call behaviour are the product of intricately coordinated sensory and motor systems (Chapter 3). In Chapter 5, we saw how the development of these systems, and therefore behavior, is influenced by genes through the cellular and biochemical events triggered by gene expression. Development, however, is an ongoing process throughout the organism’s life, with genes continuing to play a fundamental, shaping role. Because gene expression depends on environmental conditions, given genes give rise to different phenotypes according to prevailing resources and constraints. The development of behaviour is thus a complex and changeable interaction between organism and environment. This interaction is reflected in two ways: through maturation of the animal’s morphology and physiology, and through learning.

6.1 Maturation and behaviour

When animals emerge into the world, their physical systems may not be fully developed. This is especially true of altricial species (such as passerine birds and many small mammals) where the young are born or hatch at a relatively early stage of development. Even in precocial species such as guinea pigs and gazelles, however, where the young emerge at a relatively advanced stage, much may still need to be done before the animal’s physiology and behaviour achieve adult performance. Progress to maturity can affect behaviour in many ways.
6.1.1 Nervous systems, development and behaviour

For understandable reasons, developmental changes in the nervous system are often associated with changes in behaviour. Such associations are apparent even in the prenatal life of many species. Movement in embryonic Atlantic salmon (*Salmo salar*) is a good example (Abu-Gidieri 1966; Huntingford 1986; Fig. 6.1).

Movement at very early stages of development in salmon is limited to heart beats and twitches of the dorsal muscles. These are entirely muscular in origin (myogenic) and occur before the nervous system has formed. It is not until about half way through embryogenesis that the major motor systems differentiate in the spinal cord, and motor neurons establish contact with anterior muscles, allowing the embryo to flex its body. As neural connections extend down the sides of the body, the embryo becomes capable of the undulatory movements associated with swimming. Development of the sensory system and skin connections along the trunk follow soon after this, allowing responses to mechanical stimulation, while completion of neural circuits to the fins and jaws leads to their coordinated articulation and movement. Development of the nervous system

![Diagram](image-url)  
*Figure 6.1* The sequence in which behaviour develops in embryonic Atlantic salmon (*Salmo salar*) reflects the development of neural circuitry necessary for different patterns of movement. See text. From Goodenough *et al.* (1993), after Abu-Ghidieri (1966).
continues beyond hatching and is associated with the emergence of an increasing repertoire of behaviours (Fig. 6.1). The sequence in Fig. 6.1 may reflect an unsurprising relationship between neural connection, muscle function and movement of the affected part of the body, but it illustrates the progressive wiring up that shapes the animal’s behavioural capabilities, preparing it for the environment with which it will eventually have to cope.

Development, however, is not necessarily progressive. It is important to bear in mind that earlier stages of an organism’s life cycle are not some kind of imperfect protoadult, waiting to mature into their proper functional form. They are fully functional organisms in their own right, adapted to the particular circumstances of their time of life. This may entail specialisations that are transient, fulfilling a vital role then disappearing. The larvae of most metamorphosing insects provide clear, and sometimes extreme, examples, such as the cave-dwelling larvae of the fly *Arachnocampa luminosa*, which dangle luminous threads from an elevated web to catch prey, or the caterpillar of the butterfly *Aethria carinicauda*, building ‘fences’ of hairs along twigs to protect itself from predators during the pupal stage. Young vertebrates also show adaptive specialisations tailored to their early needs: the egg-eviction response of cuckoo chicks, and rhythmic head movements of many young mammals searching for their mother’s teat are examples. By definition, these early specialisations come and go as the animal matures. But how complete are the transitions; do they, for example, extend to underlying physiological mechanisms? Behaviours involved in hatching provide some indications.

Hatching is something an animal does only once, but it can require highly specialised anatomy and behaviour to be successful. After that, the specialisations are redundant and are not employed again. So what happens to the underlying machinery that coordinates them? Does it atrophy? Does it become used for something else? An innovative experiment by Anne Bekoff and Julie Kauer (1984) provides answers for hatching behaviour in domestic chicks. During hatching, the chick breaks free from the confines of its shell using a highly stereotyped sequence of body rotation and thrusts of the head and limbs. Since these actions are never seen again in the chick’s behavioural repertoire, Bekoff & Kauer wondered about the fate of the neural circuits controlling them, particularly the leg movements. To see whether capacity for the responses disappeared irreversibly, implying a loss of mechanism, they introduced chicks of up to 60 days of age into experimental glass ‘eggs’, carefully folding them into the hatching position, then recorded their behaviour and muscle movements. To their surprise, reincarcerated chicks quickly began to perform typical hatching movements, qualitatively and quantitatively matching the stereotyped patterns of true hatching. Thus, the machinery for producing the movements remained intact and functional long after hatching, even though the behaviour it controlled was not normally called upon again.

In other cases, the neural connections associated with particular behaviours disappear or are modified for different purposes. Obvious cases are organisms, such as butterflies and frogs, that metamorphose from larvae to a very differently organised adult form. Studies of changes in the nervous system in insects with complete metamorphosis have revealed some intriguing ‘conversion’ strategies in their neural circuitry. Levine & Truman (1985), for example, have shown that, in the tobacco hornworm (the caterpillar of the hawk moth *Manduca sexta*), all the motor neurons innervating the abdominal muscles are used again in the adult. Some continue to innervate the same muscles as before, which, surprisingly in view of the very different bodily appearance of the adult, retain broadly similar roles, but others lose their previous function in the caterpillar and grow new processes to serve newly formed muscles in the adult (Fig. 6.2). On the sensory side, most larval neurons innervating the sensory hairs atrophy when the caterpillar pupates,
but one group remains to serve specialised trigger hairs on the abdomen of the pupa. These hairs trigger a reflex – existing only during the pupal phase – which causes sudden flexion and serves as an anti-predator device. Thus neural and behavioural development across the metamorphic divide is a mixture of conservatism and innovation.

### 6.1.1.1 Environmental effects

As we might suspect from Chapter 5, physical maturation can be heavily influenced by the environment. This is certainly true for aspects of neural and sensorimotor development, as the acquisition of visual responsiveness in mammals demonstrates.

The eyes of many mammals develop their basic structure without any exposure to light, but normal function does not develop unless the eyes are ‘primed’ with certain kinds of visual experience. Blakemore & Cooper (1970) demonstrated this very clearly by exposing kittens to controlled visual environments during their early postnatal development. From the time their eyes opened at two weeks of age, kittens were kept in darkness except for brief exposure to an environment where they saw either vertical or horizontal stripes (Fig. 6.3a). After five months of this, the kittens were brought out into the real world where they generally appeared to cope normally. However, when Blakemore and Cooper tested their visual response to objects in different orientations, they found a dramatic difference between animals raised in the two environments. When presented with a rod held vertically, kittens raised with vertical stripes immediately paid attention to it and approached. Kittens exposed to horizontal stripes, however, failed to show any response. When the rod was held horizontally, the situation was reversed: the kittens exposed to the horizontal stripes responded, but not those shown vertical stripes.
To see why the kittens showed these restricted responses, Blakemore & Cooper looked at the arrangement of neurons in the cats’ visual cortex, the part of the brain eventually receiving information from the eyes (see Fig. 5.8). Each of the cortical neurons responds to objects in a particular orientation, so they fire in response to lines or edges presenting in that orientation (see 3.2.1.1). In the cortex of normally reared cats, there is a spectrum of responsiveness to different orientations (Fig. 6.3b), but in the kittens reared with vertical or horizontal stripes, the cortex appeared to be dominated by neurons sensitive to the orientation of the stripes. Thus kittens experiencing horizontal stripes had no neurons responding to vertically aligned objects or to lines or edges within 20° of vertical. In this case, therefore, early environmental influences appear to be critical in determining the functional development of visual perception, and thus the later response of the animal to objects in its world.

While the external environment may provide important cues during the development of the nervous system, internal cues may also be important, and illustrate the sometimes flexible nature of development at the cellular level. Bentley & Keshishian (1982) studied the development of neurons from the sensory hairs on the legs of developing grasshoppers. Like those of the cricket *Acheta domesticus* in 5.2.1, the sensory neurons grow out from cells in the hairs and establish connections with the CNS. Bentley & Keshishian, however, showed that the first axons to develop, the so-called ‘pioneers’, are guided in their quest by special cells that act as way-markers along the route. But, as the legs develop and grow, the intervals between these way-markers become greater and greater. Perhaps as a result, later axons do not appear to use them, but instead grow along the route already taken by the ‘pioneers’. Although the final result looks as if all the sensory axons developed in the same way, their developmental histories are in fact quite different. They also show a degree of flexibility, in that the way the synaptic connections with the CNS are formed as the sensory organs develop and their neurons reach their destination depends on which other cells are nearby at the time and what information is flowing from the sense organs. As we stressed in Chapter 5, therefore, the genetic prescription for development can establish contingency rules rather than laying down a hard-and-fast blueprint.

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**Figure 6.3** The visual cortex of kittens reared in an environment of vertical (a) or horizontal stripes became sensitive only to lines in the orientation experienced (b). The lines in (b) represent the preferred response orientation of cells in the cortex of kittens reared in each of the two environments. Modified from Blakemore & Cooper (1970). © Nature Publishing Group (http://www.nature.com/), reprinted by permission.
6.1.1.2 Brain development and behaviour

Needless to say, much of the behavioural change taking place during an animal’s lifetime relates to events in the brain. Much of this in turn involves learning, which we shall discuss shortly. Some changes, however, are associated with the ongoing physical development of the brain.

The direction of neural development in vertebrates is generally caudal-rostral (rear to fore). Thus lower brain structures develop before the higher regions. This is reflected in the presence and subsequent disappearance of neonatal reflexes in mammals (e.g. the grasp and nipple rooting reflexes in human babies and the lordosis response to maternal licking in neonatal rodents [Dewsbury 1978]), for which the excitatory centres are located caudally and inhibitory centres rostrally. The responses are therefore shown early on in development, before the inhibitory centres have matured, after which they are suppressed. Interestingly, some of the reflexes in humans can return in old age as a result of the deterioration of brain tissue and loss of higher-order control. Changes in other types of behaviour, such as locomotory activity, are also consistent with this pattern of brain development (Campbell & Mabry 1972, but see Randall & Campbell 1976).

Environmental factors are also important in shaping the brain and behaviour. The complexity of the environment in particular seems to have widespread effects, at least in mammals. For example, it is well known that so-called environmental enrichment (e.g. providing caged animals with toys or other objects) leads to structural changes in the brains of rats, including increased numbers of nerve cells, synapses and dendrites, particularly in the hippocampus and cortex (see 3.1.3.1). These changes can result in improved learning and memory (Rosenzweig & Bennett 1996; van Praag et al. 2000; Würbel 2001). Recent studies suggest that impoverished housing, especially involving social deprivation, can affect dopaminergic pathways between the cortex and striatum, leading to attentional deficits. Somewhat soberingly, the symptoms of this deficiency are the same as those used to model key attributes of schizophrenia in humans (Würbel 2001).

Impoverished environments can have other negative effects, including inducing stereotypical behaviour (see 4.3.2.1). Once fully developed, stereotypies persist, even under conditions where they would not normally be induced, suggesting chronic changes in underlying physiology (Mason 1991; Cooper et al. 1996). Indeed, behavioural and neurophysiological evidence associates stereotypy with changes in the basal ganglia, a region of the brain important in the initiation and sequencing of movements (Ridley 1994; Hauber 1998; Garner & Mason 2002; see 3.1.2.3). Once again, the changes involve dopamine, with stereotypies apparently developing in response to stress-induced sensitisation of dopamine target cells (Cabib 1993; Steiner & Gerfen 1998). Perhaps not surprisingly, therefore, stereotypies are often associated with other behavioural symptoms of basal ganglia disorders (Würbel 2001; Garner & Mason 2002).

6.1.2 Morphology, maturation and behaviour

Morphological change is an obvious feature of maturation. Size, physique, secondary sexual characters, genitalia and a host of other attributes change as the animal ages, and along with this come new opportunities and limitations for behaviour. The development of a particular behaviour pattern may track that of a specific structure or appendage which is critical for its performance. In the paddlefish (Polyodon spathula), a bizarre
inhabitant of the Mississippi and Ohio rivers of North America, feeding behaviour changes with the development of the gill rakers, comb-like bony structures projecting into the mouth from the gill arches (Rosen & Hales 1981). While juvenile paddlefish feed selectively on individual zooplankton, adults feed indiscriminately by simply opening their jaws and swimming through the water. The gill rakers strain food particles from the resulting inflow. Paddlefish can grow to over two metres in length, but the gill rakers start to appear as buds along the midline of the gill arches when the fish are about 10 cm long. At this stage, however, the fish are still selective feeders. By the time they reach 12–13 cm the buds line all the gill arches and have begun to increase in length. Nevertheless, this is not enough to allow effective filter feeding and the young fish remain selective. It is not until they reach around 30 cm that the gill rakers are sufficiently well developed for the fish to adopt the indiscriminate adult mode of feeding. Changes in feeding strategy thus track the development of the necessary anatomical structures. By way of contrast, the larvae of some insects sometimes carry out actions that are ineffectually premature; larval grasshoppers, for instance, silently perform the leg movements of song production long before the development of the necessary rasping mechanism (Weih 1951).

6.1.3 Maturation and motivation

The performance of a behaviour by a young animal may occur in a completely different context from that in an adult, suggesting differences in underlying motivation (Chapter 4). In young orange chromides (Etroplus maculatus), a species of cichlid fish, approach and ‘glancing’ behaviour (Fig. 6.4) are expressions of feeding (the fish skim mucus from the side of a parent), and approaches are made only to larger individuals. Overtly similar behaviour in adults is part of pairing or intrasexual competition, and is directed towards individuals of similar size (Ward & Barlow 1967).

Feeding behaviour in mammals provides other examples where underlying causal factors appear to change with age. Feeding actions in neonatal mammals, for instance, are unrelated to the degree of food deficit. Puppies fed through artificial nipples with large apertures, which thus obtain their required amount of milk quickly, suck more on objects unconnected with feeding than puppies given access to nipples with small apertures. Sucking in kittens is similarly independent of the rate of satiation over the first three weeks of life, and human babies actually suck more when satiated or aroused other than by hunger.

6.1.4 Life history strategies and foetal programming

Growth and maturation are not simply a function of an animal’s age. They also reflect its life history strategy, the adaptive allocation of resources to growth, survival and reproduction (2.4.5). Relative investment in different components of life history, and thus the timing of maturation and reproduction, vary between individuals in relation to a wide range of factors (see 2.4.5). Accordingly, behaviour is likely to develop along different lines and on different timescales in different individuals. A major factor influencing life history variation is maternal investment. Provisioning of eggs or foetuses in utero can have a profound effect on the competitiveness and reproductive potential of resulting offspring, and therefore their strategy for investing metabolic resources.
Extensive work in humans and rodents (e.g. Barker 1995; Phillips 1996; Rao 1996) has identified a crucial role of nutritional constraints and other mother/foetus conflicts in utero (Haig 1993; see also 5.3.1) in determining a suite of life history attributes in offspring. Patterns of growth and organ development, immune function, menopause and longevity all appear to be predictable from nutritional history in the womb (Barker 1995; Cresswell et al. 1997; Hales 1997; Langley-Evans 1997), the effects often extending down later generations (see Lummaa & Clutton-Brock 2002). This is sometimes referred to as foetal programming (Barker 1995). The effects are underpinned by various endocrine changes involving many different hormones, but particularly glucocorticoids, insulin and growth hormone.

Such shifts in development and metabolism, mediated by maternal condition, could account for early differences in apparent life history tradeoffs in some species (Lummaa & Clutton-Brock 2002). For example, Barnard et al. (1998) found that social status in randomly constituted groups of male outbred laboratory mice was predictable from the sex ratio in utero of their natal litters and its consequences for early suckling behaviour and rate of weight gain. High-ranking males tended to be those born of litters with a low male : female ratio that had suckled on more anterior teats and gained weight more quickly while with their mother. Heavier mothers (i.e. those in better condition) also lavished more attention on their pups. Although males did not develop aggressive dominance...
relationships in their natal litters, eventual high and low rankers showed the same difference in apparent immunity tradeoff as Barnard et al. had found in randomised groups in earlier studies (see 3.5.2.1): that is, future low rankers regulated immunodepressive hormone concentrations in relation to current immunocompetence (antibody levels), while high rankers did not (cf. Fig. 3.34). Since Barnard et al. (1998) had standardised postnatal litters to four males, their findings suggest that maternal condition influences investment in male offspring prenatally, and that this is reflected in the priority given by well-resourced pups to early reproduction (androgen-driven attributes) over long-term survival (immune responsiveness). Other studies have shown that the odours of male mice reared by well-nourished mothers are more attractive to females than those of males from undernourished females (Meikle et al. 1995), and that relationships between maternal investment, hormones and behaviour can programme later responses to stress (Würbel 2001). Key behavioural and physiological characteristics may thus be set environmentally before the animal ever ventures into the world.

6.2 Experience and learning

While many behaviours appear in their fully functional form without any previous practice by the animal, or develop in parallel with the animal’s morphology and physiology as it matures, many develop through accumulating experience and therefore the animal’s ability to acquire and retain information. The development of feeding skills provide some good examples.

Many small passerine birds, such as sparrows and tits, hold down food items with one or both feet while pecking and tearing at them. In great tits (Parus major), young birds attempt this at their first encounter, but their early efforts are clumsy and ineffective. The speed with which they acquire adult competence, however, depends on how much experience they have with suitable objects (Vince 1964). Improvement is thus not simply a consequence of developing musculature and grip. Similarly, red squirrels (Sciurus vulgaris) require experience in order to open hazel nuts efficiently. Young squirrels possess all the necessary gnawing and prising movements but cannot deploy them effectively (Eibl-Eibesfeldt 1963). Experienced adults usually gnaw a vertical furrow down the broad side of the nut, then drive their incisors into the aperture and prise the nut open, though some animals develop more idiosyncratic, but nevertheless effective, techniques. Naïve individuals gnaw haphazardly, sometimes creating several furrows until the nut happens to break. Improvement seems to involve learning that the nut breaks more easily when the furrow is gnawed parallel to the grain.

Some of the most detailed investigations of experience in behavioural development have involved bird song. Classic work with young male chaffinches (Fringilla coelebs) by the ethologist W.H. Thorpe and others (e.g. Marler 1956; Thorpe 1961; Nottebohm 1967) has shown that birds isolated from other conspecifics, so they hear no vocalisations by other birds, develop far simpler songs than normal adult males (Fig. 6.5a,c). Males reared with another of the same age end up with a song intermediate in complexity between those of isolates and normal adults (Fig. 6.5b,c). Hearing models is therefore important in the development of the young chaffinch’s song. But is that all that is important?

Chaffinch song develops through three well-defined stages. The first is known as subsong and is little more than a soft, featureless babble sung at the end of the bird’s first summer. In the following spring, subsong matures into the second stage, plastic
song, which is similar to the final full song in having most of the right syllables, but it lacks organisation into phrases. Once full song emerges, it remains unchanged through the rest of the bird’s life. This progression suggests the bird needs to practise its song and listen to the results in order to mimic the adult male model properly. To see how important such feedback is, Nottebohm (1967) deafened birds at different stages of song development. If birds were deafened as adults, when their songs had already matured, there was little effect on the song (Fig. 6.6a), but if they were deafened during plastic song (Fig. 6.6b), the final form of the song depended on how long they had been singing plastic song before the manipulation. If they had been singing for some time, subsequent full song was almost normal; if only for a short time, the song was less complex than usual. Birds deafened during subsong, however, ended up with little more than a long screech (Fig. 6.6c). The type of song chaffinches finally sing, therefore, seems to be a combined product of the songs they hear when young, and feedback from their attempts to match them.
So experience can play a crucial role in honing behaviour. Indeed, it may be the dominant shaping force in many cases. But how exactly does experience change behaviour? Is its potential open-ended, or are there limits to what it can achieve? These questions take us into the realm of learning.

### 6.2.1 Learning

A parallel is often drawn between learning and the evolution of behaviour by natural selection. Both are means by which behaviour ‘improves’ in the sense of becoming more effective at solving problems of survival and reproduction. Learning shapes behaviour within generations, while selection acts between generations. Ideas about learning have developed under many different theoretical frameworks, and its pioneers include some of the greatest names in the history of the study of behaviour – Pavlov, Thorndike, Watson,
Hull, Tolman and Skinner among them. Not surprisingly, therefore, its progress has been peppered with involved disagreements (see Bolles 1979 for a good historical perspective). Even a generally agreed definition of learning has proved elusive (Mackintosh 1983). In part the problem lies in distinguishing learning from other causes of behavioural change. An animal that begins to search for food in a particular location when it did not a few hours before may at last have learned where the food is, or it might simply be hungry now whereas it had not been earlier. Some careful experiments would be necessary to distinguish between these possibilities. Even where it seems obvious that experience has led to change, care may still be needed. Young birds, for example, cannot fly at first. Instead, they appear to practise the appropriate movements as they grow, until, after a few weeks, they have developed the capacity for flight. It thus seems reasonable to conclude that they learn to fly and that practice is necessary to develop the skill. However, Grohmann (1939) reared pigeons under confined conditions that prevented them practising flight movements. When he released them at the age they would normally be able to fly successfully, there was no difference in their proficiency relative to unconfined birds, suggesting practice was not necessary.

As Mackintosh (1983) argues, it is probably not helpful to worry too much about all-embracing definitions of learning. Instead it is more instructive to focus on the different situations in which learning occurs and the conditions necessary for its expression. This may encourage the view that learning is just an umbrella term for disparate, unrelated processes, but such might indeed be the case. It is certainly not obvious that the same process underlies learning to navigate a maze, associate particular food items with feeling ill or ignore innocuous noises in the environment. But equally there could be a common underlying mechanism, and many people have attributed superficially different forms of learning to the same basic process (see Mackintosh 1983; Roper 1983; Macphail & Bolhuis 2001). We shall return to this issue later. To begin with, however, we shall discuss different forms of learning using a slightly extended version of the classification proposed by Thorpe (1963). While the boundaries between Thorpe’s categories have blurred considerably in the light of subsequent work (as we shall see), their terminology still pervades the learning literature and remains a useful framework for discussion.

6.2.1.1 Habituation and sensitisation

Habituation and sensitisation both result from repeated exposure of the animal to a single event, and thus differ from other forms of learning where the animal learns about relationships between different events. In the case of habituation, the upshot is a reduction in response to the event; in sensitisation, responsiveness increases.

Habituation

Razran (1971) has defined habituation as ‘learning what not to do’. Animals are frequently bombarded with different stimuli emanating from the environment. The cost in terms of time and energy of responding to every one would be prohibitive, particularly since only a small proportion is likely to have a significant impact on their chances of reproducing. In Chapter 3, we saw how an animal’s perceptual systems filter out some of the noise in information received from the environment; habituation is a way of filtering out some more. More specifically, it eliminates responses to stimuli that are sometimes important, but that, in a particular instance, are not. Rustling leaves, for instance, may be worth reacting to, e.g. by orientating or hiding, because they sometimes indicate the approach
of a predator. Repeated rustling without the appearance of a predator, however, is probably just caused by the wind and can be ignored.

Habituation is stimulus-specific, so responsiveness is reduced only with respect to the habituating stimulus or something else very like it. This specificity is shown very clearly by habituation in territorial male three-spined sticklebacks (*Gasterosteus aculeatus*). When they allowed captive males to establish breeding territories, Peeke & Veno (1973) found they were initially very aggressive towards neighbouring individuals but that responsiveness quickly declined. This makes sense since there is no point harrying fish that are unlikely to be intruders. However, territory owners cannot afford to generalise habituation to all other sticklebacks because some of them will be intruders; habituation should thus be confined to neighbours. To test this, Peeke & Veno introduced ‘intruder’ fish in glass tubes to various locations in a territory owner’s tank. Owners were exposed to each ‘intruder’ for 30 minutes, given a 15 minute break, and then tested with one of four stimuli: (a) the same fish in the same location, (b) the same fish in a different location, (c) a different fish in the same location, and (d) a different fish in a different location. The results were clear cut (Fig. 6.7). Owners showed least aggression towards stimuli (a) and (b), though (b) elicited slightly more than (a), more aggression towards (c) and most towards (d). Thus decreasing familiarity with the stimulus, in terms of both individual and location, increased the tendency to override the previous habituation. However, it did not affect the rate at which habituation subsequently occurred: the lines in Fig. 6.7 all have approximately the same slope.

Figure 6.7 Habituation in territorial male three-spined sticklebacks (*Gasterosteus aculeatus*), measured as aggressive responses to (a) the same fish encountered in the same location as previously, (b) the same fish in a different location, (c) a different fish in the same location as a previous encounter, and (d) a different fish in a different location. See text. After Peeke & Veno (1973).
Of course, it is important to establish that habituation really is the result of learned non-responsiveness and not the upshot of something less interesting, such as fatigue or sensory adaptation. When we cease to become aware of our clothes shortly after putting them on, for example, the effect is due to sensory adaptation (sensory cells ceasing to fire) rather than habituation (learning to ignore the stimulation). Experiments with the sea hare *Aplysia* show how these other effects can be discounted (Kandel 1976). As we saw in 3.1.3.2, mechanical stimulation of the siphon in *Aplysia* elicits a gill withdrawal response. If the stimulation is applied repeatedly, however, the response rapidly wanes to give a typical habituation curve. If at this point a novel mechanical stimulus is applied somewhere else on the animal, responsiveness to stimulation of the siphon is immediately rekindled, thus ruling out fatigue or sensory adaptation as a cause of the initial decline.

Habituation seems to occur throughout the animal kingdom, and its demonstration in groups such as the Cnidaria (e.g. *Hydra*), which do not appear to be capable of associative learning (see 6.2.1.2), implies that at least some of the processes underlying habituation are not shared with conditioning. However, there is considerable debate about the distinction between habituation and more complex learning at the fundamental level of process (Mackintosh 1983).

**Sensitisation**

While repeated stimulation can result in a decline in some kinds of response, it can cause an increase in others. Wells (1978) found that the tendency for an octopus (*Octopus vulgaris*) to attack or withdraw from a neutral stimulus, such as a plastic disc suspended on a rod, could be enhanced by repeated feeding or shocking. The effects did not depend on rewarding or punishing the octopus for the response itself (food or electric shock could be administered at a different time and in an entirely different part of the tank), so were not due to conditioning (see below). Rather, repeated feeding or shocking seemed to increase the probability of their appropriate responses being elicited by a neutral stimulus. Such as effect is known as sensitisation. It is very important to distinguish sensitisation from conditioning effects because the two can produce overtly similar outcomes. As in the octopus example, teasing them apart requires careful control over the spatial and temporal relationships between stimulus and response (Evans 1966; Mackintosh 1983).

As Mackintosh (1983) points out, there is some conflict between the concepts of habituation and sensitisation. How can two diametrically opposite effects arise from the repeated presentation of a given stimulus? The fact is, however, they can, and careful scrutiny of the animal’s response can reveal them. It is commonly the case in habituation experiments that the animal’s responsiveness to a stimulus at first increases, and only later decreases in a classical habituation curve (Groves & Thompson 1970). One distinction between the two processes may thus be that sensitisation occurs only for the first few presentations of the stimulus, while habituation continues for as long as the stimulus is presented (Mackintosh 1983). The strength of the stimulus also appears to be a factor. Sensitisation seems to be more pronounced the stronger, or more significant, the stimulus; thus food and electric shock are typical examples of stimuli which, if repeated, lead to sensitisation. Weak stimuli appear less likely to produce sensitisation, and habituate rapidly with little evidence of an initial increase in response.

**6.2.1.2 Associative learning**

Sensitisation may underlie the enhanced performance of some behaviour patterns, but we usually think of new responses being acquired, or existing ones enhanced, through
processes of **associative learning**. Here, some action or stimulus of hitherto little significance takes on significance as a result of suddenly having some important consequence. Accidentally treading on a mound of soft earth, for example, yields an unexpected bonanza of nutritious ants’ eggs, or the silhouette of a large bird flying overhead is quickly followed by an alarming attack. If the consequences reliably flow from the action or stimulus each time it occurs, a long-term association may develop and the animal alters its behaviour accordingly. Thus it becomes more likely to trample a mound of earth on encounter, or dive for cover when a large bird flies over. In the terminology of learning theory, the animal’s behaviour has become **conditioned** by the events it has experienced. Experimental approaches to conditioning typically rely on arranging temporal relationships between two events, E1 and E2, and observing changes in behaviour as a result of exposing animals to the relationship. Two categories of conditioning are generally recognised depending on whether E1 is a neutral stimulus, usually some extraneous environmental event or object, or the animal’s own actions. In the first case, learned outcomes are usually referred to as **classical conditioning**, in the second, **operant** or **instrumental conditioning**. However, as we shall see, the two may not be as distinct as their labels imply.

**Classical (Pavlovian) conditioning**

Classical conditioning stems from the pioneering work of the Russian physiologist Ivan Pavlov in the early part of the twentieth century. A stimulus that initially does not elicit a response comes to do so by association with a stimulus that does. This new property of the stimulus is thus **conditional** on its association with an established stimulus–response relationship. The stimulus is therefore referred to as the **conditional stimulus** (CS) and its elicited response the **conditional response** (CR). By the same token, the stimulus in the established stimulus–response relationship is the **unconditional stimulus** (UCS) and its response the **unconditional response** (UCR). The relationships between these components are summarised in Fig. 6.8, using Pavlov’s classic study of the salivation response in dogs as an example. Importantly, while the CR is functionally similar to the UCR, there may be subtle qualitative and quantitative differences between them that beg some questions about the process of stimulus–response association.

The temporal and/or spatial association of the CS with the UCS is known as **reinforcement** (Box 6.1), with the close proximity between the two eventually leading the animal to anticipate the UCS on perceiving the CS, and hence perform the CR. Thus pairing the bell with the presentation of meat powder in Fig. 6.8, leads the dog to expect meat powder on hearing a bell, and so salivate. The important relationship in classical conditioning is therefore that between the two stimuli; reinforcement occurs even if the animal does not perform the CR (in early exposures, the CS is almost always ineffective at eliciting the CR). This contrasts with operant conditioning where the animal experiences the reinforcing stimulus **only** if it performs the CR.

Pavlov found that almost any stimulus could become a CS, as long as it did not evoke too strong a response of its own, as might an urgent desire to escape from the experimental apparatus for example. Even pain could be used to elicit salivation in his dogs. In many cases, dogs also **generalised** from the CS to other similar stimuli. Animals conditioned to salivate in response to a pure tone of a specified frequency would also salivate when other tones were played, though the response was often weaker, a phenomenon known as **generalisation decrement**. With persistent exposure to one particular tone, however, dogs became more **discriminating**, i.e. they were less likely to generalise the CR to different stimuli. Perhaps not surprisingly, discrimination can be enhanced if, as
well as being rewarded for responding to the correct stimulus, subjects are also punished for responding to incorrect ones.

From the discussion so far, and indeed intuitively, we might expect that the CS has to precede the UCS if stimulus association is to occur. In fact, this is not so, although the relative timing of the two stimuli does affect the efficacy of the association. Figure 6.9 shows a number of possible temporal relationships between the CS and UCS. Of these, conditions (a) and (b), sometimes called delayed conditioning, in which the UCS at least partly precedes the CS, are the most effective. Perhaps surprisingly, simultaneous conditioning (d), where the CS co-occurs with the UCS but does not precede or extend beyond it, is very ineffective, more so even than backward conditioning (e), the effectiveness of which can be increased by making the UCS contiguous with the CS. We shall return to the issue of pairing the UCS and CS and its implications for conditioning a little later. Of some interest, particularly with respect to some rhythmic behaviours (see 3.4.1), is so-called temporal conditioning, where the CR relies on presentation of the UCS at predictable time intervals and the intervals themselves act as a CS (Fig. 6.9).
Excitatory and inhibitory conditioning

In most conditioning, the CS indicates the likely occurrence of the UCS, a situation referred to as excitatory conditioning. However, sometimes the CS can indicate that the UCS is likely to be absent, in which case the process is known as inhibitory conditioning.

The eye-blink response in rabbits is a good example of excitatory conditioning. The response can be conditioned to the presentation of a brief tone followed by a mild mechanical shock to the cheek. The intensity of the shock is just enough to elicit a blink, and a few pairings with the tone (which does not normally result in blinking) is enough to turn the tone into a CS for the response. Figure 6.10 shows some typical results, in which the percentage number of times a conditioned blink response occurred is plotted for successive blocks of 100 trials. The likelihood of response increases sharply at first, but then levels off in an asymptote, a stable level of responding for the particular experimental
conditions. To the right of the figure, there is a rapid decline in the CR when the CS is no longer paired with shock. This is known as response extinction. Extinction does not simply eradicate the CR and leave the animal as if conditioning had never occurred, however. If the animal is later presented with the CS again, the CR shows spontaneous recovery, though not to its original level (the recovered CR also extinguishes more rapidly the next time pairing with the CS ceases). An extinguished CR can also be recovered by presenting a novel stimulus along with the CS. Thus an extinguished salivation response in dogs can be rekindled by pairing the buzzer or bell CS with a flashing light, an effect Pavlov referred to as disinhibition. While extinguished responses can be recovered, repetition of the UCS–CS association beyond the level that maximises performance of the CR (overtraining) can increase resistance of the CR to extinction in the first place.

Excitatory conditioning is a means by which one stimulus comes to indicate another, and is concerned with the animal predicting things that are likely to happen in its environment. Equally, however, stimuli may predict that certain things will not occur in the environment. In the real world, this may be important, for example in choosing feeding places that are safe from predators, or steering clear of migration routes that do not cross sources of water. An experiment with pigeons shows that animals are perfectly capable of this kind of inhibition conditioning.

Hearst & Franklin (1977) looked at the responses of pigeons to two illuminated keys in a Skinner box. The keys lit up one at a time, and in random order, for 20 seconds, with an average of 80 seconds between successive illuminations. Food was periodically delivered into a hopper during the interval, but never when either of the keys was lit. Hearst & Franklin observed the movements of birds around the Skinner box during each session to see whether their responses to the keys changed with time. In early sessions, pigeons seemed indifferent to the keys and disregarded them whether or not they were lit. As time went on, however, they developed a marked tendency to move away from a key when it was illuminated. One interpretation of this is that the pigeons learned that lighting a key signified the absence of food and that moving away indicated conditioned withdrawal from a negative stimulus. That the tendency to move away was stronger when food was delivered more frequently during the interval between illuminations (thus emphasising its absence during illumination) adds support to this conclusion (Fig. 6.11).
Adaptive significance  Intuitively, a learning capacity that enables the animal to predict events in its environment would seem to be useful, and it is not difficult to imagine reproductive benefits accruing from it. Surprisingly, however, relatively few studies have set out to test this explicitly. While psychologists have speculated for many years about the adaptive value of conditioning, interest has generally remained theoretical rather than experimental. An exception is the work of Karen Hollis at Mount Holyoke College, Montana (see e.g. Hollis 1982, 1999). For the best part of 20 years, Hollis has been interested in the functional significance of classical conditioning and has conducted extensive experiments using territorial defence, and mating behaviour in fish as model systems. Figures 6.12 and 6.13 below show some results from her experiments with blue gouramis (*Trichogaster trichopterus*), close relatives of the familiar Siamese fighting fish (Hollis 1999).

In Hollis’s experiments, male gouramis were trained to expect a rival male or a female (UCS) after the presentation of a brief light stimulus (CS). In later tests, these classically conditioned males, along with control males that had either been exposed to the light stimulus without the appearance of another fish, or had experienced other fish with no preceding light, were given a light cue and then presented with a rival or a female. The conditioned males showed pronounced differences in response compared with the two control groups. When the light came on in rival male treatments, conditioned males rapidly approached it with a full frontal threat display. When the rival itself appeared, they were therefore already responding aggressively. Consequently, conditioned males delivered more biting attacks (Fig. 6.12a), and other aggressive responses such as tail-beating, to the rival than either of the control groups, and so won more contests (Fig. 6.12b). The priming effect of the light thus appeared to give the conditioned males a marked advantage in aggressive disputes.

A similar advantage accrued in encounters with females. Males conditioned to expect a female after a light stimulus were more likely than control males to show courtship appeasement instead of aggression (Fig. 6.13a). They were also more likely to build a nest over the two hours subsequent to encountering a female (Fig. 6.13b). As a result, they coupled more often and sired more offspring (Fig. 6.13c). Conditioning therefore had a very direct effect on their reproductive success.
Classical conditioning underlies adaptation in many different contexts. Aposematic signalling (8.3.5.3), for example, where distasteful, or otherwise noxious, prey adopt garish colour patterns that are highly memorable, results from naïve predators having an unpleasant experience when they first encounter such prey, and rapidly learning to associate the experience with the colour pattern (e.g. Martin & Lett 1985). As a result, predators avoid anything bearing the pattern in the future, to the advantage of both themselves and the erstwhile prey. Other (noxious or non-noxious) prey species can then...

Figure 6.12  (a) Compared with unconditioned fish (plae bars), male blue gouramis (Trichogaster trichopterus) delivered more bites towards a rival male when they had been conditioned to expect another fish after a light stimulus (dark bars). (b) They also (dark bars) won more contests than unconditioned controls (pale bars). After Hollis (1999).

Figure 6.13  Male blue gouramis conditioned to expect a female after a light stimulus (dark bars) were less likely to be aggressive towards females (a), more likely to build a nest (b) and ended up producing more young (c) than unconditioned fish (pale bars). After Hollis (1999).
capitalise on this avoidance conditioning by adopting the UCS of the bright colour pattern and avoiding predation themselves, thus driving the evolution of Müllerian, Batesian and other forms of mimicry (8.3.1).

**Surprise, attention and conditioning**  Classical conditioning results from a developing association between a UCS and a CS, or between the CS and a response. For much of its history it was assumed that conditioning would come about whenever the UCS and CS were paired. During the 1970s, however, views began to change, and it is now believed that the important attribute of the UCS is not that it is paired with the CS, but that it is in some way surprising or unexpected, so heightening attention which can then be focused on the CS.

Animals do not attend equally to all the stimuli reaching them (see also 3.2.1). Pigeons in a Skinner box prefer to peck the lighted key of a pair, for example, and cats attend more to movement than to colour. An important effect of differential attention is that it can bias the capacity for different stimuli to form stimulus–response associations. The past history of other stimuli in the environment can be a major factor in this. If stimuli $A$ and $B$ are presented together, but stimulus $A$ has been reinforced in the past, it may prevent the development of a stimulus–response association with stimulus $B$, a phenomenon known as *blocking*. Sometimes, the effectiveness of a stimulus is merely reduced when it is presented together with others, with the effect depending on the relative strengths of the other stimuli. Miles & Jenkins (1973), for example, found that tone stimuli were more effective than lights of different intensity when the latter were similar and difficult to tell apart. When the lights were easily distinguishable, however, lights were better than tones. In this case, one stimulus is said to *overshadow* the other (here tone first overshadowed light, then vice versa). As a rule, the more intense of any pair of stimuli tends to overshadow the less intense stimulus (see also Box 7.4).

Attention can also depend on *relationships* between stimuli. Thus pigeons presented with circles or triangles on red or green backgrounds can be trained to attend to shape when a blue light is shining, but to background colour when the light is yellow. This is known as *conditional stimulus control*. Sometimes animals can be trained to discriminate between two stimuli (see later) by using an already effective stimulus and *transferring stimulus control* to one of the new stimuli, often by ‘fading in’ the new stimulus over the effective one once the animal is attending to it. *Feature-value effects* (the attention-grabbing effect of some distinct feature of a stimulus – e.g. a spot on a Skinner box key) also influence the effectiveness of stimulus conditioning.

While the animal’s attention can be influenced by many factors, one property that is argued to underlie attention is the element of surprise. Several theories of learning have stressed the importance of surprise in conditioning (e.g. Mackintosh 1975; Pearce & Hall 1980; Wagner 1981), but the most influential has been that of Rescorla & Wagner (1972).

**Rescorla–Wagner theory:** Two assumptions are fundamental to Rescorla–Wagner theory. First, repeated pairing of the CS and UCS will lead to an increase in the strength of association between them. However, this will not continue indefinitely but will be limited by the strength of the CS–UCS association relative to that of the UCS. Second, when there is an increase in the strength of the association, the increase will not be by a fixed amount. Rather, it will be determined by the *difference* between the present strength of the CS–UCS association and the *maximum* possible strength of the UCS. Thus, when the difference is large, as at the start of the conditioning process, the increase in associative strength is correspondingly large, but once a strong association has formed, there can be little further change. These assumptions can be expressed as a simple equation (Box 6.2).
Underlying theory

Box 6.2 The Rescorla-Wagner model

The Rescorla–Wagner model assumes that the degree of increase in a CS–UCS association depends on the difference in the current strength of the association and the maximum possible strength of the UCS. This can be expressed in a simple equation:

$$\Delta V = \alpha (\lambda - V) \quad (6.2.1)$$

where $V$ is the strength of the CS–UCS association, $\Delta V$ the change in strength of the association over a given time (or trial), $\lambda$ the magnitude of the UCS (and thus the maximum strength of the CS–UCS association) and $\alpha$ the magnitude of the CS ($\alpha$ takes a value between 0 and 1 and does not vary during conditioning).

Application of the equation is very straightforward. If we assume at the outset that $\alpha$ is, say, 0.2, and the CS has no prior association with the UCS (i.e. is novel), then on the first CS–UCS pairing, the value of $V$ will be zero. The value of $\lambda$ can be set arbitrarily at 100. From the equation, the increase in strength of association over the first pairing will then be:

$$\Delta V = 0.2(100 - 0) \quad \Rightarrow \Delta V = 20$$

For the second pairing, $V$ takes the value 20 (the increment over zero in the first pairing), so the next increment will be smaller:

$$\Delta V = 0.2(100 - 20) \quad \Rightarrow \Delta V = 16$$

and so on for the third ($V = 20 + 16 = 36$):

$$\Delta V = 0.2(100 - 36) \quad \Rightarrow \Delta V = 12.8$$

and successive pairings.

Figure (i) (a) The change in the strength of the CS–UCS association predicted by the Rescorla–Wagner equation for two intensities of CS ($\bullet$: $\alpha = 0.8$; $\bigcirc$: $\alpha = 0.2$). After Pearce (1997). (b) The development of conditioned suppression of emotional behaviour in rats trained to the same UCS but exposed to different strengths of CS (white noise). After Kamin, L.J. and Schaub, R.E. (1963) Effects of conditional stimulus intensity on the conditional emotional response, *Journal of Comparative and Physiological Psychology*, 56, 502–7. Copyright © 1963 by the American Psychological Association. Adapted with permission.
One interpretation of the above is that the difference in strength between the UCS and the CS–UCS association ($\lambda$–V in Box 6.2) indicates the degree to which the UCS is unexpected or surprising. The greater the difference, the greater the surprise when the UCS comes along. Various aspects of the UCS and CS are likely to influence the effect, as shown in Box 6.2. However, the situation in the real world is unlikely to be quite as straightforward as this because at any given time a range of different potential CSs is likely to be impinging on the animal when the UCS is presented. According to Rescorla & Wagner it is how well this combination of stimuli predict the UCS that determines how surprising it is. This becomes important more formally when animals are conditioned to a compound stimulus, for instance a light and buzzer presented together. As we saw above, various relationships between the components of such stimuli can influence the development of conditioned associations through blocking, overshadowing and other effects. A Rescorla–Wagner account of these differs from the conventional interpretation. Take blocking, for example. The account earlier implied that blocking is due to a previously formed association (say with a light) distracting the animal from forming an association with a new CS (say a buzzer) when the two CSs are presented at the same time.

**Testing the model**

Various experimental studies have tested the Rescorla–Wagner model by attempting to manipulate the value of different parameters in the equation. Figure (i)a, for example, shows the change in associative strength predicted by changing the value of $\alpha$ (intensity of the CS), and Fig. (i)b, the outcome of an experiment in which rats were conditioned to suppress ‘emotional’ behaviour (defecation) in response to different intensities of white noise (Kamin & Schaub 1963). Similar outcomes are predicted and found when the intensity of the UCS is varied (Fig. (ii)a,b).
Rescorla & Wagner would argue instead that pretraining with the light ensures the UCS is predicted by the compound light–buzzer stimulus. The UCS is therefore unsurprising, and so prevents the formation of an association between itself and the buzzer.

While the Rescorla–Wagner view has been very influential, and generally well supported by experimental evidence, it is not without problems. Not all aspects of blocking and overshadowing, for example, are consistent with it, and it does not fully account for the role of surprise in conditioning (see e.g. Dickinson et al. 1976). Various developments of, and alternatives to, the Rescorla–Wagner model have been proposed and have met with some success, but no single theory as yet caters satisfactorily for all aspects of conditioning. A good discussion of the issues can be found in Pearce (1997).

**Operant (instrumental) conditioning**

In operant or instrumental conditioning, the delivery of the reinforcer (E2) is associated with the animal’s performance of some activity (E1) rather than another stimulus in the environment. Instead of starting out with a UCS-linked UCR, which becomes associated through experience with a novel CS, the animal becomes conditioned through initially chance reinforcement to respond to a previously ignored stimulus. For example, a hungry animal wandering about in search of food is likely to perform a range of behaviours. If one of these happens to procure food, and is associated with finding food sufficiently often, the animal learns, through a process of trial-and-error, to perform the behaviour regularly in that particular situation.

Pioneers of the field include E.L. Thorndike and B.F. Skinner, whose ‘puzzle box’ and Skinner box respectively have provided paradigms for the experimental investigation of operant conditioning. In Thorndike’s puzzle box (Fig. 6.14a), an animal obtains a reward...
by tripping a particular catch or treadle which opens a door and allows it to escape or gain access to food. In Skinner’s modern equivalent of the puzzle box (Fig. 6.14b), the animal obtains food, water or access to some other resource, by activating a lever, button or panel on the wall of the box and being rewarded on some preprogrammed schedule.

Thorndike (1898) was the first to suggest that operant conditioning reflects learning about responses, and that, when a response is followed by a reinforcer, a stimulus–response (S–R) relationship is strengthened (Thorndike’s Law of Effect). For a rat that has to press a lever for food, the stimulus may be the lever itself, and the response the action of pressing it. Each successful press strengthens the association between the sight of the lever and the act of pressing. Thus, as encounters with the lever accumulate, so the tendency to press it increases, eventually reaching some asymptote. Animals can be taught to perform novel and sometimes complicated behaviours in order to receive a reward, a process known as shaping. Skinner (1953) likened shaping to a sculptor moulding clay. At first any coarse approximation of the desired outcome is reinforcing, but reinforcement soon demands closer and closer matching to the required outcome to be effective.

**Reinforcement schedules** In the real world, rewards rarely follow every performance of a behaviour, but are instead intermittent. Thus a bumble bee probing a flower receives nectar on most occasions, but sometimes another bee has beaten it to the reward and the flower is empty. The frequency with which a particular behaviour is rewarded is referred to as the reinforcement schedule. A large body of work shows that reinforcement schedules have important and predictable effects on the strength, rate of performance and resistance to extinction of conditioned responses. We shall discuss just a few examples.

**Continuous reinforcement schedules**, where each performance of a behaviour is rewarded, not surprisingly tend to produce the strongest and most consistent responses and are generally used in initial shaping procedures. **Fixed ratio schedules**, in which the animal has to respond a certain number of times before being rewarded, encourage high rates of response because the faster the animal responds the sooner it obtains a reward. As Goodenough et al. (1993) put it, fixed ratio schedules are like piecework in factories, where an employee is paid on completion of a given number of items and therefore strives for a high rate of production. **Variable ratio schedules** also generate high rates of response. In this case, the number of responses required for a reward varies randomly. The response rate is high because, once again, faster responses mean quicker rewards, but responses are more resistant to extinction than those of fixed ratio schedules because random unrewarded gaps are an inherent feature of the schedule and thus less likely to be a disincentive. Variable ratio schedules are therefore like gambling machines: there is an average level of reward, but the payout in relation to expenditure is unpredictable.

**The nature of stimulus–response associations** Early views of operant conditioning saw the outcome of responses as automatically reinforcing any preceding S–R association. However, several lines of evidence suggest this is too simplistic, and contrary views abound. One problem is distinguishing empirically between operant and classical causes of conditioned responses. **Autoshaping**, where an animal is induced to respond to a Skinner box key, or other device, by highlighting the device in association with a reward, is a good example. Opinion is predominantly in favour of a classically conditioned (CS–UCS association) account of autoshaping, but the animal may instead learn that the response causes the reward to become available, so reinforcing an operant S–R relationship. One way to decide between these two possibilities is to look at the effects of an omission schedule (see 4.2.1.1) on the development of the response.
Instead of rewarding a response each time it is performed, an omission schedule delivers a reward when the response does not occur. Thus the response will never be followed by a reward, which therefore cannot strengthen a preceding S–R relationship. If autoshaping is a result of an operant S–R association, then it should be ineffective under omission schedule conditions. Williams & Williams’s (1969) experiment in 4.2.1.1 used just such a procedure to look at pigeons pecking at an illuminated key in a Skinner box. As we saw there, imposing an omission schedule on a key-light, key-peck association did little to abolish the conditioned pecking response. One conclusion, therefore, is that the remaining loose and intermittent pairing of the key-light CS with the food UCS was sufficient to generate the pecking CR, which thus came about by classical conditioning (Pearce 1997). Detailed video analysis of pigeons pecking keys during autoshaping supports this conclusion further by showing that the kind of peck delivered depends on what the bird expects as a reward (Moore 1973). When it is pecking a key for food, the peck is brief and forceful, the bill is opened at the instant of contact and the eyes are shut (Fig. 6.15a) – just like a peck at real food, in fact. When the same key is pecked for water, the response is longer and less forceful, the bill is opened only slightly on contact, the tongue is extended, and the eyes stay open (Fig. 6.15b) – just as when actually drinking. This suggests that the pigeon treats the key as if it is food or water. Thus it is not learning an association between pecking the key and reinforcement (operant conditioning), but between the key itself and reinforcement (classical conditioning).

Classical and operant conditioning may also act in combination, rather than as alternatives, to produce a CR. Mowrer (1960), Konorski (1967), Rescorla & Solomon (1967) and others have argued that classically conditioned motivational factors might play a role in operant conditioning. A CS might, for instance, lead to an arousing representation of the UCS which then has a preparatory effect on the CR. Experiments have supported this idea by showing it is possible to manipulate the strength of an operant response by presenting a classically conditioned CS at the same time (Lovibond 1983).

**Discrimination learning** So far we have looked at the role of reinforcement and associative learning in the context of responses to one particular stimulus, albeit sometimes a compound stimulus. In many situations, of course, animals are faced with choices of stimulus. Which they choose may depend on subtle differences in the reward offered by each stimulus and the animal’s ability to learn the appropriate associations. Such *discrimination learning* has been subject to extensive investigation and become fertile ground for arguments about learning theory in general. The following are just some of the issues.

**Matching:** Making a choice often involves experience with alternative reward schedules over a period of time, rather than an instantaneous decision. Thus the relative rate or duration of reinforcement offered by the various options becomes important. Nevertheless, preferences can sometimes be expressed quickly, after as little as one inter-reward interval in some cases (Mark & Gallistel 1994).
Herrnstein (1961) and Catania (1963) found that pigeons presented with two different rates of food reward (concurrent variable-interval schedule) in a Skinner box delivered most pecks to the key yielding the greater rate or duration of food presentation. However, they did it in a way that matched proportionately the distribution of rewards across the two keys (Fig. 6.16). This result has now been found so consistently in so many species and contexts that it has become referred to as the matching law (Box 6.3; Williams 1988; Shettleworth 1998). Animals match responses to more or less any measure of reinforcer – size, rate, duration or delay – and matching is sufficiently well established to be used as a diagnostic in assessing how animals value options (Hamm & Shettleworth 1987). The ‘matching law’ also has obvious functional implications, since it relates to the reward maximisation models of optimal foraging theory (e.g. Staddon 1983; Shettleworth 1998; Fantino 2001; see Chapter 8) and the distribution of predators across resource patches (Shettleworth 1998; Chapter 7). A problem with the idea that matching maximises reinforcement, however, is that rewards are sometimes maximised by allocating more (if not all) effort to the option yielding the greater reinforcement (so-called overmatching). At other times the animal would do better by responding more to the poorer option (undermatching). Which the animal should do (match, overmatch or undermatch) depends among other things on the context (e.g. social vs solitary foraging [Gray 1994; Thuijsman et al. 1995]) and predictability of the concurrent schedules. We shall return to this problem again in Chapter 8.

Choice and reinforcement schedule control: While response matching with concurrent variable interval schedules may seem intuitively sensible, there are problems beyond the departures from expectation touched on above. If very different reinforcers or reinforcement schedules are used, the subsequent measure of choice may be confounded by the nature of responses to the particular reinforcers or schedules used (so-called reinforcer- or schedule-control). For instance, a predator may spend more time hunting for food during the day than it does sleeping, but we cannot infer from this
Underlying theory

Box 6.3 The matching law

Animals tend to distribute their responses across options according to the relative rate at which they are reinforced (see text). The distribution of choices thus matches the distribution of rewards, a relationship referred to as the matching law and expressed as:

$$\frac{R_1}{R_1 + R_2} = \frac{r_1}{r_1 + r_2}$$  \hspace{1cm} (6.3.1)

where \( R \) denotes response rate, \( r \) reinforcement rate and subscripts alternative reward schedules. A similar matching relationship applies to the amount of time an animal spends responding to each of the two alternatives. While the equation above applies to relative response rates to two concurrent options, it can be modified easily to cater for absolute response rates to each option by introducing a constant \( k \), the maximum overall rate of responding by the animal in the given situation (thus, here \( k = R_1 + R_2 \)). The constant is independent of the number of options available. Substituting \( k \) in the equation gives:

$$\frac{R_1}{k} = \frac{r_1}{r_1 + r_2}$$  \hspace{1cm} (6.3.2)

so, the response rate for each option is:

$$R_1 = \frac{kr_1}{r_1 + r_2}$$  \hspace{1cm} (6.3.3a)

and

$$R_2 = \frac{kr_2}{r_2 + r_1}$$  \hspace{1cm} (6.3.3b)

While these equations predict many aspects of choice on concurrent schedules, they do not predict all and have been modified in various ways to widen their applicability. For example, there are problems when either \( r_1 \) or \( r_2 \) are zero (i.e. there is only a single schedule). To get round this, Herrnstein (1970) argued that there is strictly no such thing as a single schedule, because there are almost always other reinforced behaviours (e.g. daydreaming, defaecating, scratching an ear) going on simultaneously with the schedule presented by the experimenter. Thus there is always a choice of some kind. Herrnstein therefore introduced a further term, \( r_0 \), into the equation to cater for ‘other’ reinforced responses outside the design of the experiment. The equation for \( R_1 \) thus becomes:

$$R_1 = \frac{kr_1}{r_1 + r_2 + r_0}$$  \hspace{1cm} (6.3.4)

Herrnstein (1970) increased the generality of the equation yet further by introducing a final constant, \( m \), which allows for interactions between multiple concurrent schedules. Thus:

$$R_1 = \frac{kr_1}{r_1 + mf_2 + r_0}$$  \hspace{1cm} (6.3.5)

The matching law is sometimes stated in a generalised form that can be applied across experiments as:

$$\log(R_i/R_j) = \log k + b \log(r_i/r_j)$$  \hspace{1cm} (6.3.6)

where \( b \) is an additional scaling parameter fitted to each data set.

Based on discussion in Fantino & Logan (1979) and Baum (1974).
that the predator prefers hunting to sleeping. The requirements of hunting behaviour mean that it must be performed more often and for longer than sleeping. Similarly, reinforcement schedules may produce different levels of response as a result of their intrinsic structure. We have seen this already in the relative response rates on concurrent variable ratio and fixed interval schedules. Inferring choice on this basis would clearly be dangerous.

**Learned ‘concepts’**: Experiments in which animals are required to discriminate between more or less complex stimuli have led some authors to suggest that they are able to acquire sophisticated concepts, such as the idea of shape, colour, flowers or wetness. Perhaps the most striking example is Irene Pepperberg’s African grey parrot (*Psittacus erithacus*) Alex. Like many parrots, Alex has been taught to talk, but Pepperberg has used this over many years to probe his understanding of the world around him. Her experiments suggest that Alex has acquired, and can articulate, an astonishing range of concepts, from relatively basic things such as colour, shape and number, to the decidedly more abstract properties of sameness and difference (e.g. Pepperberg 1991). However, other species have also demonstrated impressive abilities in this direction, if via more conventional experimental methods. Pigeons are a noteworthy example.

Using Skinner box procedures, Herrnstein et al. (1976) presented pigeons with photographs of various scenes projected above a key that they had to peck to obtain a reward. The birds were given the task of distinguishing between pictures that contained a certain feature and those that did not. The feature could be anything (e.g. human beings, fish, leaves, water, abstract shapes [see Watanabe et al. 1993]). Pigeons turned out to be astonishingly good at the task, not just recognising the relevant feature, but recognising it in almost any form or context in which it was portrayed. Thus they could correctly identify a ‘human being’ whether it was a close-up of someone’s face, a picture of a person sitting on the floor or a crowd scene. Pigeons are also extremely good at recognising complex abstract shapes in different orientations (Fig. 6.17; Hollard & Delius 1982), a task commonly used in human intelligence tests.

People have made various claims for these seemingly impressive examples of discrimination. Some see them as evidence that other animals are able to form concepts in much the way we can; others view them as no more than discrimination learning with unusually complex stimuli (Wasserman & Astley 1994). Yet others rule the ability of non-human species to form concepts out of court on principle, on the grounds that concepts can be defined only by language (Chater & Heyes 1994). Certainly we have to be careful how we interpret the animals’ responses. We cannot, for example, conclude that Herrnstein et al.’s pigeons saw the slide images as pictures in any sense that we would recognise. Indeed, it is not necessary for animals to see the images as representations of objects at all in order to be able to classify them. The available experimental evidence suggests that pigeons responded to Herrnstein et al.’s photographs simply as patterns of coloured patches. Even monkeys tend to respond at this level. D’Amato & van Sant (1988) trained capuchin monkeys (*Cebus apella*) to discriminate between slides with and without people. Like pigeons, the monkeys performed the task very well, but careful analysis revealed they were basing their discrimination at least partly on the presence or absence of red patches. Slides containing other kinds of red patch, such as a slice of watermelon or dead flamingo, were treated as slides with people. As Shettleworth (1998) argues, what animals are doing in these kinds of experiment is best interpreted operationally rather than in terms of hypothetical mental processes, even though these processes might indeed exist. Thus category discrimination with broad stimulus generalisation, rather than concept learning, is probably the safer interpretation of the results.
We can begin to understand why pigeons might have this capacity for complex visual discrimination learning by considering their normal way of life. Pigeons have evolved for flight and rely very heavily on visual information. We might therefore expect them to be able to pick out important visual features in a fast-moving, fast-changing environment. Trees must be recognised in the distance as diversely shaped masses, but also closer to as the bird selects a roosting site and swoops into the foliage to alight. Looked at like this, the pigeons’ apparent ability to categorise is arguably more to do with perception and sensory processing than it is with mental sophistication (Manning & Dawkins 1998). Nevertheless, there do appear to be some basic similarities in the way pigeons and humans classify images that suggest a degree of congruence in cognitive processing (Delius 1992).

6.2.1.3 Latent learning

The status of Thorpe’s fourth category of learning, that is whether it should or should not be regarded as a form of associative learning, has been a matter of some debate. The crux of the issue is the absence of any obvious reinforcement behind the learned associations. If a rat or mouse is placed in a maze that contains no reward, the animal nevertheless investigates the apparatus, running up and down the various alleys and dead ends, and inspecting the empty goal box. When required at a later date to navigate the maze for a food reward, such individuals do better than naïve animals experiencing the maze for the first time. Figure 6.18 shows the results of a classic early experiment along these lines by
Clearly the animals learned something on their initial visit to the maze even though they received no reward for their effort. For many years, learning theorists preferred to treat such latent learning as a separate category of learning, but as views about the role of reinforcement in operant conditioning changed, so did opinions as to the associative nature of latent learning. As long ago as 1970, Hinde argued that latent and operant learning differed only in the timing of their expression; both involved memorising aspects of a situation, but only in operant learning was memory translated into action straight away.

As in classical and operant conditioning, there are interactions between latent learning and other forms of learning. This is reflected in events in the CNS. Ohyama & Mauk (2001), for example, found that conditioning of the eye-blink response in rabbits (see Fig. 6.10) depended on changes in the interpositus nucleus of the cerebellum. However, these changes were preceded by latent changes in the cerebellar cortex that had important effects on the magnitude and timing of the conditioned response. Experiments in which the two regions of the cerebellum were reversibly disconnected showed that learning of the temporal characteristics of a tone CS took place in the cortex prior to the appearance of any conditioned blink response. The latter appeared only after changes in the responsiveness of the interpositus nucleus. In other cases, for example in honey bees, the neuronal basis of latent learning appears to be distributed and connected with circuits affecting other forms of learning (Menzel 2001).

Adaptive significance

The adaptive value of latent learning is not difficult to imagine. A knowledge of the home area, its food sources, hiding places and escape routes, would pay obvious dividends when needs arose. An experiment with white-footed deermice (Peromyscus leucopus) by Metzgar (1967) provides a rather stark illustration. Metzgar introduced pairs of mice into a room containing a screech owl (Otus asio). One of each pair had previously had the opportunity to explore the room for a few days, while the other was unfamiliar with it. The owl caught a mouse on 13 out of the 17 trials in the experiment; of these, 11 were
mice that had not previously been in the room. An almost inescapable conclusion, there-
fore, is that prior experience with their surroundings gave the familiarised individuals an
advantage in avoiding attacks by the predator.

Sometimes important spatial information is gleaned passively as the animal moves
around its environment over time. On other occasions it seems to be acquired during
specific reconnaissance activities, as, for example, in the orientation flight of the female
digger wasps as they leave their burrows to hunt (Tinbergen 1951; see also 5.1.1.3).

6.2.1.4 Insight learning

Classical and operant conditioning are often referred to as ‘simple’ associative learning
(Mackintosh 1983), implying that some animals are capable of other, more complex,
forms of learning. One of these is what Thorpe and others have called insight learning.
‘Insight’ refers to the rapid apprehension of solutions to problems – too rapid to be due
to normal processes of trial-and-error. It is the equivalent to our own ‘Aha!’ experience,
where the answer to a problem occurs to us in a flash, even though we may have been
wrestling with it fruitlessly for days. However, while responses may be too rapid for
physical trial-and-error procedures to have taken place, the animal may have run through
trial options quickly in its head. Once again, we are back with the problem of the
animal’s private mental processes and how to infer them from the indirect evidence of
behaviour (see 4.2.1). Nevertheless, if we accept the possibility of mental trial-and-error,
we acknowledge that the animal has at least some capacity for reason, a capacity that is
doubtfully distinguishable from insight (Manning & Dawkins 1998).

Several well-known experimental paradigms have been used to assess reasoning and
insight. We have seen some already in the detour experiments and cognitive maps in
Chapter 4 (4.2.1.2). Perhaps the best-known, however, are Wolfgang Köhler’s (1927)
experiments with chimpanzees. Köhler studied a captive group of chimpanzees in
Tenerife during the First World War. He set them various problems, typically requiring
them to obtain food that was out of reach beyond the bars of their cage, or suspended
from the roof. Various items were available to the animals in their cage, and they
quickly learned to use these in novel and inventive ways to get to the food (Fig. 6.19).
For example, they used bamboo poles as rakes to pull in food on the ground outside. If
the poles were too short, they joined two together to make them long enough. To try to

Figure 6.19  Chimpanzees joining
poles together and stacking boxes to
get at food that is out of reach. After
Eibl-Eibesfeldt (1975) from Köhler
(1927).
get at food suspended from the roof, the chimpanzees positioned wooden boxes underneath and climbed up on them. If one box was not good enough, they stacked another on top of it until they could jump up and grab the food. Köhler noticed that these solutions often appeared to occur suddenly to a particular animal. For instance, a male called Sultan tried unsuccessfully for over an hour to obtain food with two bamboo poles that were each too short. He appeared to give up the endeavour and sat lethargically on the ground playing with the poles. Suddenly, while he happened to be holding a pole in each hand, he apparently realised that the end of one could be inserted into that of the other, so making a longer implement. Immediately he rushed to the bars of the cage and used the connected poles to pull in the food. On a number of occasions the poles separated mid-operation, but Sultan quickly recovered the lost component and refitted it to the end of the other pole, thus suggesting he understood the functional potential of joining the two together.

Köhler interpreted the behaviour of his chimpanzees in terms of their having perceived new relationships between stimuli (the poles) and outcomes (getting at the food), relationships they had not experienced previously. In his view, they were reflecting on the problem as a whole and deducing novel solutions. However, this is not a universal view. Others have explained results such as Köhler’s as the consequence of previously learned associations. For example, the chimpanzees that moved boxes into place then climbed on them might previously have learned the two responses separately, then just put them together. This idea has been tested in pigeons.

Pigeons do not usually move boxes around and climb on them, but they can be trained to do so. Epstein et al. (1984) rewarded pigeons for pushing a box towards a green spot on the floor, but not for pushing a box when there was no green spot. In a separate regime, pigeons were trained to sit on a box to peck at a banana suspended above. When birds that had received both kinds of training were put in a room without a green spot, but with both a box and a suspended banana, they responded very like Köhler’s chimpanzees. While at first they attempted unsuccessfully to stretch up from the floor and get the banana, they eventually shuffled the box along underneath the banana, climbed up and pecked it. Birds trained either to peck a banana, but not to climb on a box to do it, or to push a box to a particular spot, but not to peck at a banana, were unable to put the two skills together and get the banana. They either stretched repeatedly, but ineffectually from the floor, or they pushed the box aimlessly around without climbing on it. Thus, apparently insightful behaviour can be generated from preceding learned S–R relationships.

**Learning sets**

Very often, we solve a problem quickly by applying our experience with similar problems in the past. Past experience allows us to perceive general rules that apply across the board, even though each individual problem we encounter may be different in detail. Thus, once we have been shown how to solve simultaneous equations with a handful of examples, we can solve any others that come our way (or some of us can). In recognising and applying a general principle like this, we are said to have formed a **learning set** (Harlow 1949). Other animals seem to be able to form learning sets too.

In his early experiments with monkeys, Harlow (1949) presented subjects with pairs of dissimilar objects, say a matchbox and an egg cup, one of which concealed food. The positions of the two objects were alternated, but food was always under the same one, and the monkeys soon learned which it was. Harlow then changed the objects for two entirely different ones, say a building block and half a tennis ball, and repeated
the procedure. Again the monkeys learned which object concealed food, but took about the same time to do it as previously. After several dozen such trials, however, they became much quicker at learning which was the right object (Fig. 6.20). While the objects in the problem continually changed, the monkeys had learned the general solution to it, that is: ‘choose the same object each time if it yields food in the first trial, but change to the other object if it doesn’t’, a strategy known as *win–stay, lose–shift*. Many other species have since been shown to adopt a *win–stay, lose–shift* solution in similar circumstances.

Animals can also just as easily learn the opposite strategy — *win–shift, lose–stay* — if they are subjected to so-called ‘repeated reversal’ training. In this case, the object concealing the reward is swapped once the animal has learned which to go for. Thus if the animal learns that A conceals a reward but B does not, the reward reverts to A, and so on.

**Learning sets and intelligence** While learning ability as a whole features prominently in arguments about intelligence, learning sets have commanded particular attention in this respect. Harlow (1949) went so far as to say that acquiring learning sets ‘transforms the organism from a creature that adapts . . . by trial and error to one that adapts by seeming hypothesis and insight. (Learning sets) are the mechanisms which, in part, transform the organism from a conditioned response robot to a reasonable rational creature.’ The idea that animals can learn underlying principles rather than just immediate stimulus–response relationships has obvious appeal in the context of intelligence. Moreover, the shape of the error curve over successive trials seems to provide an objective relative measure of ability that is independent of absolute levels of response. That is, regardless of how well or poorly different species learn in the first problem, we can ask whether they improve over successive problems and eventually get it right on the second trial of each new task. The more they do, the more intelligent we consider them to be.

Early comparative studies of mammals encouraged this view. Figure 6.21 shows performance in visual learning set tasks for a range of mammal species (Warren 1965). As we might expect, Old World rhesus monkeys did better than New World squirrel
monkeys, which in turn did better than marmosets, cats, rats and squirrels. The order sits comfortably with our notion of an evolutionary ladder of intellectual prowess ascending from humbler mammals to primates. Such an interpretation, however, would be highly dangerous. For one thing, as Warren himself noted, the various species in Fig. 6.21 were tested in very different ways, thus introducing all sorts of confounding effects into the comparison (Warren 1973). Another problem is that learning sets can depend on the sensory modality of the task. The rats in Fig. 6.21, for example, did rather poorly on their visual discrimination tasks, barely rising above chance levels even after several hundred attempts. However, with spatial discrimination tasks, rats acquire learning sets within 50 trials (Zeldin & Olton 1986), and fare even better in olfactory discriminations (Eichenbaum et al. 1986). Further problems arise when other species are slotted into the comparison. Other mammals, for instance, do not fall where expected in the order of performance in Fig. 6.21 (Macphail 1982), while some birds seem to do as well as rhesus monkeys (Kamil 1985).

These and other difficulties led Macphail (1982, 1985, 1987) to suggest that all non-human vertebrates are in fact of equal intelligence (the so-called ‘null hypothesis’ of vertebrate intelligence). Absurd as this suggestion might seem at first, diverse taxa do actually share important fundamental features of learning and memory, and the argument is not as easy to dismiss as one might imagine (Macphail & Bolhuis 2001). Take perhaps the most obvious objection to the ‘null hypothesis’, that species have become specialised during evolution to occupy very different niches each requiring different learning capabilities and cognitive skills (see 6.2.2). At one level this is certainly true. We have seen already that scatter-hoarding birds have a special kind of memory (3.1.3.1), and that cognitive maps tend to be possessed by animals foraging out from a central location, such as a hive (4.2.1.2). But these arguments ignore the fact that even very different niches can impose similar basic demands on mental processes. Classical conditioning is a good example. The potential for a stimulus to predict an event can exist...
in almost any kind of environment, and a capacity to learn the appropriate associations would benefit any organism living in them. Accordingly, the same basic rules of classical conditioning have been found to apply across vertebrates (Macphail 1982) and in the various invertebrate species that have been tested appropriately (e.g. Walters et al. 1981; Menzel et al. 1993; Dukas 1999). Indeed, the basic principles of associative learning in general appear to be distributed widely across taxonomic groups (Domjan 1983; Roper 1983). The same argument can be applied to other cognitive abilities (Pearce 1997). However, that is not to say there are no important differences between species. Subtle differences seem to exist, for example, in the precise mechanisms by which associations are formed, and these can result in different outcomes in appropriate experimental tests (Pearce 1997). It is also important to test animals with procedures appropriate to their sensory modalities and other physical attributes (tasks requiring manual dexterity are fine for chimpanzees, but no good for goldfish) in drawing fair comparisons, and to acknowledge that natural selection has shaped learning and memory to function under different ecological conditions. Unfortunately, experimental evidence that caters for all these caveats is still patchy (to say the least), so the jury will be out for some time yet on Macphail’s ‘null hypothesis’. But, despite its seemingly unlikely claim, Macphail’s argument cannot be dismissed lightly.

**Social learning**

Thorpe included imitation in his definition of insight learning, by which he meant a heterogeneous range of behaviours involving some degree of copying from other individuals (Box 6.4). Social companions, or indeed any other individuals, can be a rich source of information about how to behave. By exploiting this information, an animal can save time and energy that it would otherwise have to invest in learning the task for itself. The responses of others might also save its life if they trigger appropriate action when a predator is around. Such arguments help us to understand why **social learning** might spread through a population. But social learning has also been studied for what it might tell us about the capacity for imitation and its implications for rational understanding on the part of the animal.

So what kinds of things are learned socially and how might they benefit the learner? Among the obvious contenders are skills associated with finding and consuming food, avoiding predators, choosing a mate and communicating. However, we must bear in mind that social information may be made available incidentally, such as the loud rustling made by a squirrel rooting through fallen autumn leaves, or strategically, as when a male bird of paradise displays to a female to persuade her to mate (the distinction between ‘cues’ or ‘signs’ [Seeley 1989; Hauser 1996] and signals [Dawkins 1993b]; see Galef & Giraldeau 2001 and Chapter 11). Of the contenders above, feeding behaviours have perhaps received the most detailed attention (see Galef & Giraldeau 2001 for a brief review).

**Social learning and feeding behaviour**

Foraging efficiency appears to be one of the main selection pressures favouring social aggregation among animals (see Chapter 9), and social information about the whereabouts and quality of food is a major factor enhancing feeding efficiency in foraging groups. Norway rats (*Rattus norvegicus*) are a good case in point.

Norway rats are colonially living omnivores that eat virtually anything, but are good at avoiding things that make them ill. Naïve young rats thus have a lot to learn about what is and what is not good to eat. Not surprisingly, therefore, rats seem to be adept at
Experience and learning

picking up social information about foodstuffs. In fact, pups begin to learn about food and develop later feeding preferences while still in utero (Galef 1996a). They continue to learn from their mother while suckling because flavours of foods ingested by the mother find their way into her milk (Galef & Sherry 1973; see Hudson et al. 1999 for similar learning in rabbits \(Oryctolagus cuniculus\)). Once they have weaned, the newly independent young rats begin to leave the nest and forage near other conspecifics, or areas recently visited by conspecifics. All these routes help to ensure that young rats are educated in their choice of food. However, pioneering experiments by Jeff Galef at McMaster University have shown that there is more to the social guidance of foraging in rats than just early familiarity.

Galef surmised that the breath of an animal that had just fed could carry olfactory information about recently ingested food. Other individuals could then pick up this information and make use of it. Rats are good candidates for this because they frequently sniff the facial area of other rats they encounter. Galef & Wigmore (1983) therefore set up a simple experiment using pairs of animals in which one individual (the \textit{demonstrator}) was fed rodent pellets that had been flavoured in a distinctive way, for instance with cocoa or cinnamon. The other rat (the \textit{observer}) was then exposed to the

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**Some definitions**

**Box 6.4 Types of imitation**

Thorpe (1963) included a range of social effects on behaviour in his definition of imitation.

*Social facilitation*

An animal may already possess a particular behaviour in its repertoire, but becomes more likely to perform it as a result of seeing it performed by another individual. If a bird is given water, for example, others that see it bathing may start to wash themselves even though they had water present all the time. Similarly, satiated rats may start to feed again if they see a hungry individual eating. The infectiousness of yawning is a familiar example in humans.

*Local enhancement*

Animals may direct their activities towards a particular part of the environment as a result of responses by others. The spread of milk bottle opening in tits is an example (see text), but the effect is widespread in foraging behaviour and can be important in locating concealed or novel feeding sites (see Chapter 9).

*True imitation*

Thorpe reserved the term ‘imitation’ for ‘the copying of otherwise improbable utterances or acts’. Vocal mimicry in birds and food-washing in primates are frequently-cited apparent examples. The key distinction between true imitation and local enhancement is that, in the latter, the observer has learned something about the environment (i.e. something has happened here) but not necessarily behaviour (it happened because \textit{A} did this). The existence of true imitation and its implications for intelligence in non-human animals are the subject of ongoing debate (see text).
demonstrator before being given a choice of foodstuffs (Fig. 6.22). As Fig. 6.22 shows, when observers were exposed to cocoa-fed demonstrators, they predominantly chose cocoa in the preference test. When the demonstrator had been fed cinnamon-flavoured pellets, the observers preferred cinnamon.

Clearly, then, feeding preferences in rats can be influenced by social information. But is this any more than a brief localised effect, or can it result in ‘cultural traditions’ within groups of animals? To find out, Galef & Allen (1995) established rats in groups of four and trained them to prefer one of two diets (pellets flavoured with Japanese horseradish or cayenne pepper) by making them ill when they ate the other kind. They then gradually replaced animals in these ‘founder’ groups with naïve rats until the group comprised animals that had never experienced illness after eating either of the diets. The results were
clear. Rats maintained the dietary preferences of their predecessors even though there was no longer a disincentive to reinforce it. The preference was maintained for four generations of naïve rats in one case, and was transmitted even when new group members had not fed in the presence of established animals but had merely interacted with them.

Social learning in other contexts  Experiments based broadly on the demonstrator–observer principle have tested for social learning in other contexts. Eberhard Curio and coworkers, for example, looked at socially transmitted mobbing responses in birds. Blackbirds (*Turdus merula*) were set up in the ‘teacher–pupil’ apparatus in Fig. 6.23 (Curio et al. 1978). The ‘teacher’ bird was presented with a stuffed owl in the central chamber, and responded with the characteristic mobbing call normally elicited by predators in the wild (see Chapter 9). This stimulated mobbing behaviour in the ‘pupil’ out of sight on the other side of the apparatus. The ‘pupil’, however, was presented not with an owl, but with a non-predatory stimulus such as a harmless bird or plastic bottle. The result was that the ‘pupil’ became classically conditioned to mob the neutral stimulus when later encountered on its own. When conditioned ‘pupils’ then became ‘teachers’, they transmitted their novel, culturally acquired image of a predator to new ‘pupils’, a ‘tradition’ that could be perpetuated for up to six ‘generations’ of birds (Curio et al. 1978).

Mating preferences can also be influenced by social example. While partners of the opposite sex may be chosen on the basis of various individual attributes (Chapter 10), simply seeing others of the same sex attending them may be enough to influence preferences. Some of the evidence for, and debate surrounding, such mate choice copying is discussed in 10.1.3.2.
Imitation We have seen that various sources of information can lead to social influences on behaviour. In few of the above examples, however, would we be tempted to suggest that animals were directly imitating the actions of others. Imitation is at once of great interest, because it might suggest advanced appreciation of how things can be achieved, but is difficult to demonstrate unequivocally, because of the many other ways social learning can resemble it. The famous potato-washing Japanese macaques (*Macaca fuscata*) (see Itani & Nishimura 1973; Nishida 1987) are a salutory example.

A colony of macaques on Koshima Island in Japan was provided with sweet potatoes. While the monkeys happily ate them, the moist tubers frequently became covered with sand. In 1953, however, a female called Imo was noticed taking sandy pieces of potato to a stream and washing them clean. Very quickly, the behaviour spread through the colony (Fig. 6.24), initially to individuals associated with Imo, but then further afield. The spread was almost universally interpreted as an innovative behaviour by one individual being imitated by others. However, several factors militate against this conclusion (Galef 1996b; Shettleworth 1998). For one thing, transmission by imitation should start slowly, because there are few exemplars to copy, then speed up as more and more individuals demonstrate the skill. This is clearly not the case in Fig. 6.24 (though see Lefebvre 1995). The more or less constant (and rather modest) rate of spread in the Koshima macaques is more consistent with individuals learning the skill independently (Shettleworth 1998).

A second point is that washing food may not be as remarkable as the macaque story implies. Indeed it may be something that individual monkeys pick up for themselves quite easily. This latter conclusion is supported by evidence from several species, in which the juxtaposition of dirty food and water, and a widespread tendency to play with objects in the water, frequently led to washing behaviour (e.g. Visalberghi 1994).

Many other claims that animals imitate have foundered on the same kinds of criticism (see Shettleworth 1998; Heyes et al. 2000; Galef & Giraldeau 2001), one of the best-known being the puncturing of milk bottle tops by blue tits (*Parus caeruleus*) to get at cream (Fisher & Hinde 1949; Hinde & Fisher 1951). The local spread of puncturing behaviour after it first appeared in the early–mid-twentieth century in the UK was initially attributed to birds copying one another. Later teacher–pupil experiments with
parids in the laboratory, however, suggested that birds simply learned the skill independently after having encountered already opened tops (Sherry & Galef 1984, 1990).

So is there any good evidence for true imitation? The question is not easy to answer, as a glance at the ongoing debate will verify (see e.g. Zentall 1996; Shettleworth 1998; Heyes 1993; Heyes et al. 2000 for a flavour). The most promising evidence, however, comes from a procedure known as the two-action test (Heyes 1996).

The principle of the two-action test goes back to Thorndike (1911), who put chicks in a puzzle box with two possible, and equally easy, escape routes. The chick was allowed to watch one of the routes being used and then given a choice itself. If it chose the route it had seen demonstrated, instead of choosing either at random, then the chick was capable of imitation. Later refinements of these kinds of test met with varying success depending on the species and task concerned (see Galef et al. 1986). However, an experiment with rats by Heyes & Dawson (1990) has provided strong evidence for imitation through observation. Demonstrator and observer rats were established in a partitioned cage as in Fig. 6.25. The demonstrator had been conditioned to push a hanging pole in one direction (right or left) to obtain food, and the observer was allowed to watch the demonstrator work for a sequence of 50 rewards. The observer was then moved into the demonstrator’s erstwhile compartment and allowed to push the pole. Importantly, observers received a reward whichever way they pushed the pole, but despite this, they showed a significant tendency to push it in the direction shown by the demonstrator (Fig. 6.25). This is an important result because it suggests that the observer rat had learned not simply to push the pole for food, but to push it in a particular direction with respect to the body of the demonstrator. Further refinements of the experiment confirmed the outcome and showed crucially that the pole had to be moved by a demonstrator (automatically controlled movement was ineffective). The conclusion that rats were imitating the demonstrator is thus difficult to resist.

While a version of the two-action test has also provided convincing evidence of imitation by chimpanzees (Whiten et al. 1996), studies of other primates have not (Call & Tomasello 1995). Even in chimpanzees imitation was confined to directing attention towards appropriate targets rather than mimicking the actions needed to deal with them (goal emulation) (Whiten et al. 1996). This contrasted starkly with the performance...
of children in similar tests. The status of true imitation among non-human species thus remains equivocal.

**Teaching** It is clear that animals of various kinds can learn from the actions of others, albeit with different implications for the mental processes involved. While it is helpful at a descriptive level to refer to demonstrators and observers, or tutors and pupils, this is a far cry from suggesting that demonstrators or tutors set out to *teach* their acolytes. They are simply doing what they do and incidentally making information available, even if the situation is deliberately rigged to that end by an experimenter. Curio et al.’s mobbing blackbirds above are a good example. But if social learning is advantageous, it is not difficult to imagine circumstances in which it would pay one individual actively to teach another certain skills, perhaps how to deal with a particular food, or negotiate a difficult obstacle. Parents and offspring are the most obvious candidates for this kind of relationship. So do any other animals teach?

To answer this, we must first decide what would constitute teaching. Caro & Hauser (1992) suggest that, to be regarded as teaching, an animal must change its behaviour in the presence of naïve individuals in such a way as to facilitate their learning. There should be some cost to the didactic act to the teacher, but also some reproductive benefit, hence the intuitive likelihood of it occurring between close relatives. The most likely contexts in which teaching might evolve are those where complex skills must be learned but take a while to perfect – hunting skills, for example. There is much anecdotal evidence that predators, from domestic cats to cheetahs (*Acinonyx jubatus*), meerkats (*Suricata suricata*) and ospreys (*Pandion haliaetus*) (Caro & Hauser 1992), teach their offspring about what to catch and/or how to catch it. Chimpanzees also appear to teach infants the knack of using tools to crack nuts, for instance by providing tools when infants are next to a suitable anvil, or orientating nuts properly when infants fail to crack them (e.g. Boesch 1991). Some of the examples are compelling, but evidence that the various parties are benefiting from the acts in each case is often lacking, and we must remember that many complex behaviours can mature adequately without specific experience (6.1).

Perhaps surprisingly, given their lowly reputation in the intelligence league, a promising example comes from domestic chickens. Sherry (1977) looked at food-calling behaviour in mother hens. Here, the mother bird adopts a characteristic posture and utters a distinctive call while repeatedly picking up and dropping food items and pecking the substrate with food in her bill. Chicks are attracted by the display and, through local enhancement (Box 6.4), start to peck at the food. The display appears to be costly to the mother (it takes time and energy away from her own feeding and may attract predators), but chicks do seem to learn about food from items presented by hens (Suboski & Bartashunas 1984). Food-calling thus appears to meet the important criteria for teaching.

### 6.2.1.5 Imprinting

The final category of learning in Thorpe’s classification is **imprinting**. Imprinting was first identified by Lorenz and has long been considered to show characteristics that set it apart from other kinds of learning, including long-lasting effects, irreversibility and occurrence during some kind of **critical period** in the animal’s development. However, these distinctions have been softened somewhat in the light of more recent work. It is clear that they often depend on how responses are measured, and that they vary with the life history strategy (and thus the premium on rapid early learning as opposed to ongoing
development throughout life) of the animal. It is also clear that, despite the absence of obvious reward, and its somewhat unusual features, imprinting has much in common with associative learning (e.g. Hollis et al. 1991; Bolhuis 1999) and most people would now no longer make a hard and fast distinction between the two.

Imprinting is a narrowing of the range of stimuli that elicit a particular social response. The process takes place early on in the animal’s life and seems to be directed towards a mother object (filial imprinting), though other social stimuli, such as siblings, can play a similar role indirectly, and sensitive learning periods also occur in other behavioural contexts (e.g. navigation [Gagliardo et al. 2001; see Chapter 7]). Quite what counts as a mother figure can be surprisingly open-ended. Domestic chicks and ducklings, for instance, have been imprinted on objects ranging from people and canvas hides to balloons, matchboxes and blocks of wood. However, birds often show naïve preferences for certain characteristics such as colour, shape, size and movement, and can rapidly develop preferences that steer them towards their real mother figure rather than arbitrary objects (Hampton et al. 1995; Bolhuis 1999).

While imprinting initially relates to a parent object, it can also influence later social preferences, particularly choice of a mate (sexual imprinting). Schutz (1965), for example, reared mallard (Anas platyrhynchos) ducklings with foster parents of a different species. When the mature birds were later released into a mixed species flock of ducks and geese on a lake, many attempted to mate with birds of their foster species. However, the tendency was more pronounced among drakes, possibly because females of many of the duck species were drab and difficult to tell apart, making it advantageous to have a reliable pre-set yardstick for the ‘correct’ species. Females, in contrast, can choose between drakes that are brightly coloured and differ markedly between species. In species where both sexes are drab, such as doves, both males and females acquire their sexual preferences through early imprinting. The long-lasting influence of imprinting is emphasised by the ineffectiveness of so-called ‘counter-experience’ experiments, where birds reared by a different species are paired for long periods with conspecifics, to overcome preferences for mates of the foster species. This behavioural evidence is now supported by neurological studies. Rollenhagen & Bischoff (2000) suggested that sexual imprinting in male zebra finches (Taeniopygia guttata) is a two-step process, with a period of acquisition early in life, and a process of stabilisation during the first attempts at courtship. During the stabilisation phase, they found that neurons in two areas of the forebrain (referred to as ANC and HAD) changed morphologically, increasing their spine density as the process progressed. Neurons in two other areas (MNH and LNH) showed a corresponding decrease in spine density. Both sets of changes appear to be underpinned by androgen secretion, since anti-androgen treatment abolishes them. However, further experiments by the authors suggested that, of the two, changes in the MNH and LNH played the greater role in the overall imprinting process.

Critical periods

Its occurrence during a well-defined critical (or sensitive) period was long regarded as a defining characteristic of imprinting. While imprinting undoubtedly takes place early in life, however, perceptions about the nature of critical periods have changed considerably since the early days of ethology. It has become clear, for example, that the evidence for a sharply defined period depends on how responses are measured. In ducklings, plotting the period in terms of percentage following responses after a single exposure to an object gives a much more sharply defined period than the percentage of birds following
during their first exposure (Fig. 6.26). Social factors can also play a role: chicks kept singly remain responsive to moving objects much longer than those kept in groups, perhaps because the latter imprint on one another (Guiton 1959). Such imprinting between siblings may facilitate a cohesive response by the brood where only some chicks have imprinted on the mother (Boyd & Fabricius 1965). Interactions between developmental age (age since conception) and postnatal/hatching age in narrowing responsiveness can further complicate things (e.g. Gottlieb 1961; Landsberg 1976).

In the light of this kind of evidence, Bateson (1979) put forward a more open-ended model of critical periods, drawing an analogy with the carriages of a train (Fig. 6.27). The train represents a developing animal travelling one way from ‘Conception’ to a place where it vanishes from the tracks. Each compartment and its occupants reflect a behavioural system that is sensitive to the external world at a certain stage of development, represented in Fig. 6.27 by the sudden opening of opaque compartment windows. In the extreme situation (Fig. 6.27a), all the windows are closed for the first part of the journey, but are flung open at a particular moment to expose the occupants and then closed again. The occupants of all the compartments are thus exposed to the world at the same time. Alternatively (Fig. 6.27b), the windows of different compartments may be opened and closed at different times, so that different behavioural systems become sensitive at different stages of development. A third possibility (Fig. 6.27c) is that the windows of a compartment are opened but never closed. Here, any end to the critical period results from changes to the occupants (behavioural systems) themselves rather than a cut-off mechanism. Clearly, then, several arrangements could generate critical periods, each differing in timing and discreteness. The key to understanding them lies in the mechanisms underlying the onset and termination of sensitivity.

The onset of heightened sensitivity to environmental cues can be due to internal and/or external factors. In many cases, it begins as the relevant sensory and motor systems of the animal reach an appropriate stage of development, with sensory experience shaping
the development of neuromuscular systems (6.1.1) to impart a permanent influence on subsequent adult behaviour (Pytte & Suthers 2000). Hormonal changes can also bring about changes in sensitivity (3.3.1.2). These endogenous changes then interact with environmental cues to define a period of sensitivity in the development of particular behaviours. For instance, visual filial imprinting in chicks begins once birds are able to register and respond to visual stimuli, but experience with light is needed to seed the onset of a critical period (Bateson 1976).

Two mechanisms have been suggested to account for the decline in sensitivity at the end of a critical period. The *internal clock hypothesis* assumes a wholly endogenous mechanism (see 3.4) that switches the period off independently of external cues. The *competitive exclusion hypothesis*, on the other hand, assumes that certain external factors play a crucial role by effectively closing down the potential for others to influence responses (thus if the image of its mother influences the growth of neural connections in its brain, a chick’s responsiveness becomes tailored to the maternal image and therefore less likely to respond to other images, such as that of an adult duck [Bateson 1987]. This is similar to the exclusion effects that can operate between elements of compound stimuli [Bolhuis 1999]).

**Adaptive significance**

So what is the function of imprinting? It seems to be a curious half-way house between hard-wired inflexibility and open-ended learning. If it is important to narrow responses to certain restricted stimuli, why not go the whole hog and evolve a hard-wired template? The answer seems to be that target stimuli for imprinting, while discrete as categories (own vs other species, mother vs not mother), vary in their characteristics within categories. Thus there is no way an individual can predict exactly what its mother, say, will look like in advance. Her unique features need to be learned. Thus there is a tradeoff between focusing quickly on the right object, and catering for unpredictable variation within classes of object.
Many explanations of imprinting suggest species recognition as the driving force, usually to ensure appropriate mating (e.g. Irwin & Price 1999). This becomes especially important in, for instance, brood parasites, where young are reared entirely by a different species and may rely on auditory imprinting to establish a ‘password’ recognition template for conspecifics (e.g. Hauber et al. 2001). Bateson (1983), however, argues for a rather more refined function based on kin discrimination (see 9.3). He sees imprinting facilitating kin discrimination at two levels: first in establishing a parent–offspring bond as a coevolution between offspring survival and discriminating parental investment, and second by allowing individuals to optimise their degree of inbreeding/outbreeding by choosing mates that differ from close kin by an appropriate degree. Several lines of evidence support the optimal inbreeding/outbreeding idea, as we shall see in Chapters 9 and 10.

6.2.2 Learning and adaptation

While the analogy between learning and natural selection as processes of adaptation (6.2.1) stands superficial scrutiny, there is an important qualification: learning is itself an adaptation shaped by natural selection and can be shown to have the genetic basis necessary for selection to act (Chapter 5). The ability to adjust behaviour more or less flexibly in the light of experience is adaptive in just the same sense as camouflage or defending a territory – it helps the animal survive and reproduce. To do this, however, learning must be tailored to the reproductive needs of the animal, and these, of course, vary enormously both within and between species. Thus we should expect to see evidence of adaptive specialisation in learning capabilities. Indeed, we have already come across some examples, for instance in food-hoarding birds, where prodigious feats of spatial memory reflect neuroanatomical specialisation of the hippocampus (3.1.3.1). But much of what we have discussed in this chapter has suggested generalised features of learning that apply across the board to all species and circumstances. So, is learning a general property of living organisms, or is it a heterogeneous collection of specialisations?

6.2.2.1 Ethology, psychology and laws of learning

This question has a long history that goes back to the debates between ethologists and psychologists in the middle of the last century (1.3). As with other aspects of behaviour, ethologists looked at learning in a naturalistic perspective, concerning themselves mainly with questions of function. Much information was therefore acquired about context-dependent aspects of learning, such as habituation, song learning and filial and sexual imprinting, but little attempt was made to seek common features between them. Psychologists, on the other hand, were more interested in mechanism, and adopted a highly analytical approach in contrived laboratory settings to try to uncover the basic principles that lay behind learning (Roper 1983). This learning theory approach focused almost exclusively on associative learning, though more recent work implies that other apparent categories of learning can be brought within its ambit (e.g. Hollis et al. 1991; Schmajuk & Thieme 1992).

**General process theory and the principle of equipotentiality**

A main plank of learning theory has been the idea that all instances of associative learning involve the same basic underlying mechanism (Roper 1983), a position known as
general process theory. This idea, while rarely stated explicitly, has provided much of the impetus for the laboratory-based approach of learning theory: if there is a common process underlying learning, it is more likely to be revealed under controlled conditions where species-specific idiosyncrasies can be minimised (Dickinson 1980). It also justifies the predominance of a handful of stock laboratory species as experimental subjects, since if learning is the same in all animals, experimenters can confine themselves to the most convenient species for their work.

As Roper (1983) emphasises, it is important to be clear what ‘the same basic underlying mechanism’ means in this context. From the discussion in Chapter 3, one might be forgiven for thinking it meant the neural and other physiological hardware of learning. Not so. Learning theorists have traditionally eschewed ‘nuts and bolts’ interpretations. Instead, their ‘underlying mechanisms’ owe more to the ‘software’ explanations of Chapter 4, being concerned, as we have seen, with the relationships between input variables (stimuli and events and the way in which they become paired) and output variables (observed behaviour) as mediated in black box fashion by the internal systems of the animal.

Over time, the rules that underlay these relationships became formulated into basic laws of learning. These related to the effects of stimulus strength, the interval between unconditioned and conditioned stimuli, the relative intensities of the components of compound stimuli, and so on, many of which we have discussed already. Alongside general process theory, the principle of equipotentiality held that all stimuli and events could become associated with equal ease in all species. In other words, animals could learn to associate anything. Note that equipotentiality and general process theory are not the same thing. General process theory does not assume animals can learn anything, merely that where learning does take place it follows the same basic rules (Roper 1983).

Constraints on learning

The first serious challenge to general process theory and equipotentiality came from within learning theory itself during the mid 1960s (see also 1.3.4). In what turned out to be a set of landmark experiments, Garcia and coworkers (e.g. Garcia & Koelling 1966; Garcia et al. 1966, 1972) tested the efficacy of various punishers in causing rats to avoid certain foods. In Garcia & Koellings’ experiment, two punishers (nausea and electric shock) were paired with two novel water stimuli. Water was either ‘bright’ and ‘noisy’ (there was a flash of light and a loud click when the rat contacted the spout of the bottle), or ‘tasty’ (the water was flavoured with saccharin). Although both punishers produced conditioned aversion, their effectiveness depended on the kind of water the rat encountered. Nausea (induced by X irradiation) was effective only when paired with ‘tasty’ water, while shock was effective only with ‘bright–noisy’ water (Fig. 6.28a). The rats thus appeared to associate only punishers and water cues that had some functional complementarity – a gustatory cue with a gastro-intestinal punisher, and a mechanical cue with a mechanical punisher. Interestingly, birds, which hunt food visually, do seem able to pair visual cues with induced sickness effects (Martin & Lett 1985). Nevertheless, birds show similar limits to association in other contexts. For example, Stevenson-Hinde (1973) trained chaffinches to perform various tasks in order to obtain food or hear a burst of recorded song. She found she could train them to land on a particular perch to hear song, and to peck a key for food, but it was extremely difficult to get them to perch for food or peck for song.
Garcia & Koellings’ results, which have since been corroborated by other studies and extend to operant conditioning procedures (see e.g. Breland & Breland 1961; LoLordo 1979), clearly challenge the principle of equipotentiality, since rats manifestly failed to associate certain pairs of stimuli. They therefore did (could?) not learn just anything. Garcia’s work also challenged one of the so-called laws of associative learning under the general process theory umbrella, namely that the interval between pairs of events must be brief (no more than a few seconds long) for an association to be learned. Garcia et al. (1966) manipulated the delay between a rat consuming a particular food and becoming ill. Once they had recovered from the punisher, rats were offered the same food again and their response noted. The results of the experiment, and subsequently of several others (e.g. Smith & Roll 1967), showed that aversion to the food could be learned even with several hours’ delay been ingestion and the animal feeling ill (Fig. 6.28b).

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Garcia’s work suggested that, far from being a uniform, generalised property of living organisms, learning is constrained by the particular requirements of different animals. Animals could not learn everything with equal facility; they learned what they needed to learn in a fashion that served the purpose. Biases and predispositions abounded (Box 6.5). While these effects have widely been referred to as constraints on learning, the phrase is perhaps not entirely apposite, since it implies that its design features serve only to limit learning. As Bolles (1979) points out, they can also facilitate it, sometimes to a pronounced degree, as in concept learning in pigeons and spatial memory in seed-hoarding birds. Perhaps the best way to think about learning is to view it as a means of working out

Figure 6.28 (a) Aversion learning in rats, where nausea or shock punishers were paired with sweet-tasting water or water associated with noise and flashing light. Nausea paired with sweet taste and shock paired with noise and light were the only combinations effectively suppressing water intake. After Garcia & Koelling (1966). (b) The strength of food aversion learning (suppression of eating) in relation to the interval between eating test food and nausea in rats. Control animals ate the food without being made ill. After Smith & Roll (1967).
Underlying theory

Box 6.5 Constraints on learning

The ‘constraints on learning’ literature discusses a number of aspects of behaviour that bear on the outcome of learning experiments. Among the best-known accounts are those of Breland & Breland (1961), students of B.F. Skinner who used operant conditioning techniques to train animals for commercial purposes.

Using standard operant procedures, the Brelands were able to induce animals of various species to perform unlikely tricks. However, the ease with which tricks could be acquired often depended on the natural behavioural characteristics of the animal in question. In one case, a raccoon (*Procyon lotor*) was being trained to put coins in a ‘piggy’ bank as a shop window gimmick to attract investors. While the animal could be trained to do this, the procedure was not straightforward. Instead of simply dropping the coin in the bank, the raccoon would repeatedly dip it in, retrieve and fondle it, then dip it in again before eventually letting it go and being rewarded. The behaviour was reminiscent of the way raccoons often wash food and clean it before eating. In learning the trick, therefore, the raccoon brought some of the baggage of its normal feeding behaviour into play as well, making it an unsuitable candidate for the window job. The Brelands had similar problems with pigs, which insisted on rooting with their snouts when approaching the money box.

In other cases, it has proved difficult or impossible to condition particular responses at all. Shettleworth (e.g. 1975, 1978), for instance, tried to condition a variety of responses (rearing, scatching, digging, washing and so on) with different reinforcers (food, nest material, direct brain stimulation) in hamsters. Scrabbling, rearing and digging turned out to be easily conditioned with most reinforcers, while washing, scent-marking and scratching proved highly resistant whichever reinforcer was used. Two things could explain this. Either hamsters have a *learning deficit* and are unable to form stimulus–response associations for these behaviours, or they have a *performance deficit*, and can learn the association but not alter their response. Experiments with scratching in rats initially suggested the former (Morgan & Nicholas 1979). However, Pearce *et al.* (1978) found that scratching could be conditioned if rats were fitted with a mildly irritating Velcro collar. Thus they concluded that a performance deficit (absence of the necessary causal factor – an ‘itch’) was the more likely explanation.

Failure to learn may also be due to selection against learning. One of the reasons avoidance learning often depends on the kind of stimulus used (see text) is that natural hazards, such as predators and poisons, may leave little room for learning. One mistake and the animal is dead. The resulting intense selection is likely to lead to hard-wired rather than learned responses (the reaction of naïve kiskadee (Aves: Tyrannidae) chicks to the colour patterns of coral snakes is a good example [Smith 1977]). Avoidance may thus become highly stereotyped, so that animals show *species-specific defence reactions* (SSDRs). In rats, SSDRs consist predominantly of fleeing or freezing, so when expecting a threatening stimulus, these are the only responses available. This may explain why rats can associate noxious stimuli and running in a wheel, but find it difficult to pair noxious stimuli with pressing a bar: activities akin to bar-pressing do not fall within their repertoire of avoidance reactions (see Bolles 1979).

Based on discussion in Bolles (1979) and Roper (1983).
how the world works. If learning has evolved for this purpose, then the properties of learning should reflect those of the problems it is designed to overcome. Thus associative learning should be geared to real cause and effect relationships in the animal’s environment, so making some associations easier to form than others. In the real world, causes usually precede effects, so conditioning is more likely when E1 occurs before E2. Certain kinds of effect (e.g. nausea) tend to result from certain kinds of cause (e.g. ingestion of contaminated food), so these are the relationships that are learned most easily. Operant conditioning seems to be easier to bring about when responses relate to technical skills (e.g. learning to deal with different types of food) needed in the natural environment.

6.3 Play

A prominent feature of development in many species (see Bekoff & Byers 1998) is the performance by young animals of seemingly purposeless activities collectively called play (Fig. 6.29). Kittens frequently ‘attack’ small, moving objects, batting them about with their paws. Young monkeys and baboons chase each other and engage in mock fights. Puppies chase their tails. Play is one of the most familiar aspects of development in animals (largely...
because it occurs in our most familiar companion species), even though its distribution across species is very patchy. However, it is also one of the hardest to explain.

Even defining play is difficult because it covers such a wide range of behaviours, including social interactions, manipulation of inanimate objects and individual movement patterns (so-called social, object and locomotory play; e.g. Burghardt 1998). Since it is not clear that these have the same functional or developmental significance (Burghardt 1998), Bekoff & Byers (1981) advocated a neutral definition of play as: ‘motor activity performed postnatally which appears to be purposeless and in which motor patterns from other contexts may be used, often in modified form and/or altered temporal sequencing’. This highlights the central problem with play, which is its apparent purposelessness, but obvious cost. Playing consumes energy, with estimates ranging from 5% to 20% of the energy not required for growth and metabolism. In keeping with this there is evidence that play is reduced when energy is limited. Lambs, for example, play less when the ewe’s milk supply is inadequate (see Fagen 1977). However, in other cases, for instance domestic cats, restricted maternal resources stimulate more object play by young, arguably to prepare them better for fending for themselves (Bateson et al. 1990).

These kinds of difference between species may reflect differences in life history strategy and the likely later benefits of play (Fagen 1977). Play can also incur significant physical costs, with injuries being a common consequence of chases and mock fights, and cavorting individuals exposing themselves to predation. Harcourt (1991), for instance, found that, while young fur seals (Arctocephalus australis) spent only 6% of their time playing, some 86% of casualties to predatory sealions (Otaris flavescens) were playing when attacked. So what kinds of benefit might overcome these potential costs?

Most of the suggested benefits relate to advantages later in adult life. The fact that play often incorporates various components of adult behaviour suggests young animals may gain from practising them early on. Certainly there is evidence that early performance of motor activities enhances neuromuscular development and that play may form a developmental continuum in this respect with prenatal movements (Bekoff & Byers 1981). There is also little doubt that practice can improve specific skills (see 6.2). What is not clear, however, is whether playful practice enhances later performance. Some argue that playfulness is unnecessary – if you need to practise, practise seriously; playing just wastes additional time and energy. Another argument against the practice-makes-perfect hypothesis is that play sequences are often very similar to their eventual adult form, so there is not much to improve by practising. Evidence from young carnivores suggests that any later advantage from playing is small and individuals lacking experience of play soon make up any deficit (Caro 1980, 1995). Conversely, play behaviours may be so dissimilar from their later equivalents that their function cannot be one of practice. Byers & Walker (1995) review some of the relevant studies.

Another possible function of play is to generate new behaviour patterns so that the animal is better able to deal with eventualities. By allowing free combination of different activities, play might come up with novel sequences for tackling new or existing problems. Spinka et al. (2001) take this argument a stage further and suggest that a major function of play is actually to generate novel situations which the animal can then get used to handling – a kind of confidence-building exercise in other words. Of course, there is always the counter-argument that novel spin-offs from play are just incidental rather than an indication of underlying function (e.g. Symons 1978).

Finally, several hypotheses suggest that play enhances socialisation, the main arguments being that it helps the development of communication and reduces aggression, thus facilitating the establishment of social bonds (see Symons 1978; Biben 1998). Again, however, the evidence is patchy and equivocal.
The diversity of form and context in play defies simple pigeonholing. While it is clearly an important element in the development of many species, the bottom line is probably that there is no single function to play, but rather a mix of functions that varies from species to species. A good idea of the state of the debate can be gained from the volume edited by Bekoff & Byers (1998).

### Summary

1. **The development of behaviour reflects a complex interaction between organism and environment.** There are two broad ways in which this interaction is expressed: through maturation of the organism's physical systems and accompanying sensory and motor capabilities, and through learning.

2. Developmental changes in motivation and behaviour may reflect development and differentiation in the nervous system and changing hormone profiles. Changes in the organism's morphology as it grows may also lead to behavioural change. However, many physical maturation effects are confounded with increased experience, and the two may be difficult to distinguish as agents of change.

3. Growth and maturation take place in the context of the organism's life history strategy. Behavioural development thus reflects the different investment priorities of different individuals. Life history strategies, and therefore behavioural development, can be influenced by maternal investment, both prenatally (through foetal programming) and postnatally.

4. Many behaviours depend on experience and learning to develop properly. There appear to be several different types of learning but there is considerable debate about the extent to which these reflect different underlying processes. Much of this debate has centred on associative learning and the nature of classical and operant conditioning, though other forms of learning may also share properties with associative learning.

5. Apparently more complex forms of learning, such as insight, concept learning and the acquisition of learning sets, have been argued to reflect intelligence. However, many seemingly sophisticated learning outcomes can be explained in terms of basic learning processes and definitive experiments are still required in many cases.

6. While psychologists long sought general laws of learning, it is clear that learning shows adaptive specialisation and that organisms differ in what they can learn and how easily they can learn it. The 'constraints on learning' literature provides numerous examples. In the context of associative learning, constraints on learning undermine the principle of equipotentiality (animals can learn associations between anything), but offer less of a challenge to general process theory (where it occurs, learning always follows the same basic rules).

7. Play is an obvious feature of behavioural development in many species, especially mammals. However, while it seems to be a costly activity, its functional significance remains unclear. Many features of play suggest some form of preparation for adult behaviour, but evidence that playfulness *per se* enhances adult performance is weak.
Further reading