9 Memory and cognition in animal learning

‘If someone had bought a coat, but wasn’t wearing it, we’d say that he didn’t have it, but did possess it. — Well now, ask yourself whether knowledge, too, is something that it is possible to possess but not to have.’

Plato, *Theaetetus*, 197d

The meaning of memory

It is possible to use the word memory to refer to any conceivable kind of retention of information — wax tablets retain an impression of any words inscribed upon them, a lock stores an ability to recognize its key, and metallic oxides on videotapes or floppy discs can be made to function as memories for just about anything. The genetic material of all life forms can reasonably be regarded as consisting of memories of instructions for growth and structure, and the nervous systems of all animals as memories of instructions for behaviour. In some sense or other the brains of vertebrates record memories of events in the life of the individual animal. That is to say, events in the life of an individual animal will determine its future behaviour, and therefore a physical change must store information over the intervening period of time. But clearly, psychologists should want to know most about the kinds of changes responsible for human memory, and these are known to a large extent verbally and subjectively, and are therefore difficult if not impossible to be sure about in other species — which makes it dangerous to transfer the term memory to and fro between experiments on human and animal subjects.

For many years the dangers were acknowledged by reserving the term memory for the human case, allowing ‘learning’ to cover all cases of animal behaviour changed by prior experience. There is now however a very liberal use of terminology derived from work on human memory in the context of what was formerly called learning (e.g. Medin et al., 1976; Roitblat, 1982; Roitblat et al., 1984; Walker, 1983a). Is there any justification for throwing caution to the winds in this way?

Several of the experiments described later on in this chapter have attempted to replicate closely both the procedures and the results of investigations of human memory — thus we have probe recognition techniques revealing serial position curves in pigeons and monkeys (Sands et al., 1984). There is no ground for assuming that similar-looking curves in error data necessarily imply similar casual mechanisms (Gaffan, 1983), but it is certainly more excusable to be making hypotheses about memory mechanisms when specialized techniques provide ostensibly supportive data.

Other theorists (Wagner, 1981; Honig, 1981, 1984) have found it convenient to adopt the phrases and assumptions of human cognitive psychology, even when discussing data of a reflexive type: Wagner (1978, 1981) attributing modifications of shock-induced eyeblinking in rabbits to rehearsal in short-term memory, and Honig applying a theory of working memory to temporal discriminations made by rats. While in some instances borrowings of this kind may seem premature, there can be no denying that an enormous amount of new experimental work and theoretical discussion has been
stimulated by these theoretical developments, and therefore caution in accepting strong claims for animal memory mechanisms should be combined with tolerance for those who make them.

The wisest course, however, would seem to be to try to make distinctions between phenomena which most justify an appeal to memory mechanisms of a more or less human type, and those which can safely be attributed to humbler psychological processes, and perhaps left in the charge of some of the old favourites among principles of animal learning. For instance, the conditioning/extinction theory of animal discrimination learning, while failing to account satisfactorily for many of the more sophisticated achievements of higher vertebrates, may still be needed in cases involving their more basic responses (perhaps in metabolic and emotional conditioning) and might well provide the best explanation for all of the discriminatory performances of slugs (Sahley et al., 1981; Carew et al., 1983; see p. 353 below). As Thorndike (and Herbert Spencer and William James before him) was fond of pointing out, much human behaviour based on learning is habitual, in the sense that memories of the relevant prior experiences are either never available in the first place, or become progressively lost or unused. Since we do not need to explain all human learning in terms of memories it is unlikely that any concept of animal memory ought to be applied universally. Thus although there are advantages in the tactic employed by Roitblat (1982) and Hawkins et al., (1983) of referring to all effects of experience on later behaviour as representations, and all representations as memories, I shall try to differentiate between habit-based skills and automatic performances, and behavioural phenomena which seem to call more strongly for an explanation in terms of representations which are conditional and flexible tokens of prior experiences, not tied to any particular response output (Walker, 1983a). Weiskrantz (1985) has drawn a similar distinction between 'reflexive' and 'reflective' psychological processes, reflexive processes being associations, however complex, between a stimulus and a response to it, and reflective processes being associations in which learned information can be ordered and re-ordered without any behavioural response occurring. Weiskrantz (1985) and Johnson-Laird (1983) have both stressed that conscious human memories can be seen as a system that monitors stored categorical knowledge and associations, and that an enormous amount of extremely sophisticated cognitive processing can and does go on in the human brain, remaining forever unmonitored. A cognitive representation might thus qualify as a reflective process by Weiskrantz’s definition therefore without being subjectively and verbally remembered in the usual human sense, and to attribute any animal learning performance to retention of a cognitive representation does not necessarily imply that an identity with human psychological processes is being claimed (Terrace, 1985).

Nevertheless, a strong area of interest in studies of animal memory concerns questions about portions of brain anatomy that, when damaged, appear to result in disorders of memory in human clinical patients. The hippocampus, otherwise implicated in the storage of information about experienced events in theories of habituation (Sokolov, 1963, 1975; see pp. 50-2 in chapter 2) attracts most of this interest (O’Keefe and Nadel, 1978; Olton et al., 1979; Gaffan, 1977b; Gaffan et al., 1984c) although of course other brain structures, particularly the anterior thalamus, may lead to certain syndromes of memory loss when damaged and it is important to avoid the temptation of assuming that any single brain structure can perform a psychological function on its
own. The anatomical and the behavioural evidence concerning hippocampal function can however take up the whole of very large books on its own (e.g. Gray, 1982) and therefore I will say very little about it here; but I shall mention the hippocampus occasionally in passing, and it is worth bearing in mind that one of the reasons for distinguishing between habit and memory is that different kinds of brain processes are apparently required for each — certainly there is considerable evidence that human patients with severe disorders of memory can continue to exercise old skills, can learn new ones, and can acquire, for instance, the ability to play a new tune on the piano, without having the usual human ability to recall recent events. (Starr and Phillips, 1970; Cohen and Squire, 1980). Learning how is not the same as learning that.

Memories versus maps of mazes

One of the most familiar differentiations between response-based habits or gradually acquired skills on the one hand, and more cognitive representations of experience on the other, is that made by Tolman (1948) between stimulus-response association and ‘cognitive maps’ as explanations for the learning of mazes. In chapter 5 I concluded that there was overwhelming evidence, from the phenomenon of ‘latent learning’ by casual exploration and from ‘place-learning’ tests, that spatial representations of geographical information are commonly the basis for correct performance by rats given maze tests. It is not sufficient however to suppose that all maze-learning involves memories rather than habits and leave it at that. In some cases, of course, stimulus-response habits influence maze performance, especially after long training. But there is also a very productive distinction to be drawn between firmly fixed geographical knowledge and comparatively transient memories of spatial experiences. We would normally say that we know how to travel from home to work and back again, by a variety of routes, but say we may vaguely remember that the hotel was on the second street on the left coming up from the beach when revisiting the scene of a brief and long-distant holiday.

A not entirely dissimilar distinction is possible between the relatively well-learned and permanent knowledge that rats have of familiar mazes, and their memory of moment-to-moment changes in the location of food rewards in those mazes, and of their own recent activities in them. This distinction has come most to the fore in the context of the effect of brain lesions on maze performance, and in the context of performance on a particular kind of apparatus known as a radial maze (Olton and Samuelson, 1976), discussed in chapter 5.

Performance on a radial maze.

The radial maze was used in the first instance as a test of recent memory. Olton and Samuelson (1976) in a paper titled ‘Remembrance of places passed’ described the behaviour of rats place on an elevated maze of the design shown in Figure 5.1. The point of this apparatus is that it allows for a direct and straightforward assessment of a rat’s memory for where it has recently been. A rat is simply placed in the middle of the maze, with a single food pellet (out of sight) at the end of each arm. The most efficient thing for it to do is to go down each arm just once, retrieving all the food pellets with the minimum distance travelled. Olton and Samuelson found that with experience (after 40 tests) rats were almost perfectly efficient, choosing an average of about 7.5 arms in their first eight choices. Careful control tests established that they were not doing this by smelling the food, or smelling their own scent on previously used arms, but were using
geographical landmarks of some kind in the room where the maze was placed (called ‘extra-maze cues’) to supply place-memories of their previous choices. The controls included rebaiting already tried arms, and confining the rat in the centre of the maze after each arm was explored, during a short period in which individual arms of the maze might be swopped over, so than an already tried arm could be put in a not-yet-tried place (Olton and Collison, 1979). Rats sometimes adopt a stereotyped response strategy on the radial maze of always going into the next arm around in a particular direction, but this is not at all necessary for efficient performance, as may be gathered from several of the other experiments with the radial maze mentioned below.

Reference versus working maze memory

In discussions of human memory, a distinction is often drawn between short-term and long-term memory. A similar distinction is drawn between forms of cognition which may contribute to maze performance by animals, although different authors have used different terminology here. Honig (1978), Olton et al. (1979) and Olton (1979) draw a distinction between ‘reference memory’, which contains information used on most or many trials on the maze, and ‘working memory’, which contains only information pertaining to a particular trial — that is, on the usual radial maze, working memory contains a record of the places the rat has been to and eaten a food pellet, during that trial or run. Thomas and Spafford (1984) refer to ‘dispositional memory’ for long-term information, which conveniently links with the possibility of long-term control and may be partly accomplished via routine habits, and ‘representational memory’ for more vivid short-term cognitions. Walker and Olton (1984) have however stressed that long-term information may be in the form of relatively permanent cognitive maps rather than individual response habits, and this is important since it means we have to allow both for cognitive maps of the environment and for a working memory of recent movements within that cognitive map.

These terms are to some extent interchangeable — I would find ‘working memory’ versus ‘dispositional memory’ the most versatile contrast — but of greater moment than the terms themselves is the fact that experimental evidence supports a distinction between two types of process, whatever names they may be given. Olton and Papas (1979) provided such evidence with an experiment on a 17-arm radial maze, which differs from the 8-arm version only in having more arms. This makes it more difficult for the animals to perform perfectly; the usually quoted maximum level of performance is 15 different choices in the first 17 choices (Olton et al., 1977). Random selection of arms would allow for only 11 different arms in the first 17 choices, and it has been estimated that being able to make 15 out of 17 correct choices would actually require a memory of about 12 of the items (Olton, 1979). However accurate that may be, it is clear that performance on a 17-arm maze should be fairly demanding of memory capacity, and Olton and Papas complicated matters by using a procedure in which nine of the arms were always empty. Thus on a particular trial, a rat has to remember both not to go into any of the arms which have always been empty in the past, and not to go into any of the arms which always start off with food present but which have recently been visited. For some animals all the unbaited arms were bunched on one side of the maze; for the others they were randomly mixed with baited arms. The experimental data followed for two kinds, of distinction between ‘reference’ and ‘working’ memory. Entries into the never-baited arms could be counted as errors of reference, and entries into already tried baited arms could be counted as errors of working memory; both kinds occurred and working memory errors became more likely as successive choices were
made in a trial, whereas reference errors did not show this trend. (Reference errors were much more frequent in the ‘mixed’ group.)

Olton and Papas (1979) were interested in a second kind of distinction between reference and working memory errors. After training, they performed brain operations on all the rats, damaging parts of the hippocampal memory circuit (lesions to the fimbria of the hippocampus and of the fornix, the hippocampal output tract). Large memory-system lesions of this kind had much more effect on working-memory errors (increasing them substantially) than on reference-memory errors (which were unaffected). This supports an anatomical distinction between memory processes, with dysfunction of the hippocampal memory circuits strongly associated with errors attributable to lack of information about the recent past, with rats (Olton et al., 1979). There is plenty of evidence that ordinary radial maze performance shows a severe and enduring deficit after memory system lesions, even though response skills and habits remain unaffected (Becker and Olton, 1982; Walker and Olton, 1979; Walker and Olton, 1984).

Memory-system lesions cause deficits in temporary memory

Lesions to the septo-hippocampal structures and pathways in the rat limbic system produce deficits in performance on a variety of tasks, many of which involve memory for spatial information. O’Keefe and Nadel (1978) thus proposed that in animals the hippocampal system is responsible for the formation of cognitive maps — that is, it is devoted to spatial information, but not to other kinds of memories. There is considerable evidence, however, that this is largely an accidental consequence of the ubiquity of spatial tasks in tests of memory given to rats (Olton et al., 1979).

The general form of a test sensitive to memory-system damage in rats is to allow the animals to find food (Thomas and Spafford, 1984) or water (Sinnamon et al., 1978) in a particular location, on a particular day, and then to give them a choice between going to that or to an alternative location very soon thereafter. Rats can learn to accurately repeat their previous choice up to two hours after learning trials (Sinnamon et al., 1978), or can learn to repeat or not to repeat their immediately preceding choice in a T-maze, a few minutes later (Stanton et al., 1984); but these abilities are severely impaired by memory-system lesions, even though the usual dispositions involved in attempting to solve the task — running from the starting place to a goal site — remain unaffected.

In all these cases involving temporary memory for reward location, it is difficult to exclude the possibility that it is map-forming or map-reading abilities that have suffered, rather than a more general memory system. But there are other kinds of test in which spatial mapping abilities are less crucial, or in which they can be shown to be unaffected by memory-system lesions. Meck et al., (1984) used tests of stimulus duration discrimination based on choice of pressing one of two levers, with a single location of rewards, and concluded that memory-system lesions interfere with the retention of either spatial or temporal information over a short (5-second) delay even though there is no effect on discrimination of the duration of a sustained signal. Ross et al. (1984) used the Pavlovian conditioning procedure developed by Holland and Rescorla, (1975; see chapter 3, p. 86) in which lights and/or sounds are used as signals that food is to be delivered at an unvarying location, rats being observed to jerk their heads from side to side when a sound signals food, and to rear up on their hind legs at the illumination of a localized light source, when this is the signal. Rats with memory-system lesions appeared to be perfectly well able to learn simple associations and discrimination of this
type; but the lesions seemed to permanently prevent the formation of conditional
discriminations requiring the sensitivity to the joint presence of two signals separated by
a time interval (5 seconds again). Rats can usually learn that if a tone is sounded 5
seconds after a light signal has just been turned off, food is to be expected, but that the
same tone sounded without a prior light signal is to be ignored; hippocampal damage
prevented the initial learning or the subsequent continuation of this discrimination based
on a serial but separated compound positive signal (Ross et al., 1984).

Figure 9.1 A compound maze for working and reference memory.

Spatial habits can be distinguished from spatial memory. If rats are trained to run from all four start boxes, they can either be rewarded for always going north (relatively difficult) or for always going to the central goal box (relatively easy). Both these habits survive damage to the hippocampal memory system of the brain much better than the ability to choose whichever of 2 available paths from one of the start boxes had been taken a few seconds previously. After Walker and Olton (1984).

There are thus selective effects of memory-system damage on tasks not specifically spatial, but specifically requiring temporary retention of information over time intervals. Walker and Olton (1984) provide evidence that memory-system lesions do not prevent success on spatial tasks, if these make use of relatively long-term spatial knowledge. They used
a difficult form of maze with 12 separate locations divided into four starting points and eight goals (see Figure 9.1) In one spatial task, rats had to learn to always go to the centre goal box, being trained with two choices from each of three of the four possible starting places, and given transfer tests from the fourth. In a second spatial task, rats learned always to run in the same direction (say north in Figure 9.1) from three of the starting places (in this case finding food in three different goal boxes), being tested for transfer by being placed in the fourth starting box with the usual two choices available. Walker and Olton (1984) report that the same-direction task was more difficult to learn than the same-location task, but that rats could learn and transfer correct performance on both these tasks after memory-system lesions (fimbria/fornix). Similar lesions prevented correct performance on a spatially much simpler task, using just two goal boxes and two start boxes of the same apparatus, which required rats to choose (or not to choose) the goal box they had been rewarded in on an immediately preceding forced-choice information trial. Thus a distinction between working memory and reference memory is sustained for spatial tasks. It has to be admitted that the lesioned animals in one of Walker and Olton’s (1984) experiments took as long to relearn spatial tasks after brain damage as they had done to initially learn the same tasks before the operation and there may be some spatial tasks which are too difficult to learn after hippocampal damage. The Morris muddy-water test requires rats to learn to swim to an invisible underwater platform in a circular tank. Animals with severe hippocampal damage seem not to be able to do this (Morris et al., 1982). It may be that the only way for a rat to find the invisible platform here is to remember exactly where it was on immediately preceding tests, with respect to distant cues, dispositional habits being of less use for free-swimming than for running down narrow paths in mazes. In any event it is not necessary to assume that the hippocampal system is never useful in spatial tasks in order to reject the hypothesis that this brain structure is used exclusively for spatial knowledge.

Alternative views of connections between limbic systems and memory

I have endorsed the claim of Olton et al. (1979) that maze learning and other tasks performed by rats provide evidence for qualitatively different processes of memory, with brain systems centred on the hippocampus providing an anatomical key to the difference, as damage to these appears to selectively disturb the proper functioning of working memory, or the temporary information store. It is fair to say that there are conflicting claims. Gray (1982) has proposed an elaborate theory in which the septo-hippocampal system is functionally related to anxiety, although since the central assumption in’ this theory is that the septo-hippocampal system acts as a comparator for actual and expected events Gray is able to incorporate results which support the working memory hypothesis into his grander scheme. It is unlikely in the extreme that the limbic system as a whole is involved only with memory processes, since many kinds of motivation and emotion are related to limbic function as well (Green, 1987), but for present purposes, the main point is that some kinds of limbic damage produce selective behavioural effects, showing a distinction between long-term behavioural disposition and moment-to-moment temporary memory. Mishkin (1978, 1982) has on anatomical grounds suggested wider brain circuits, involving notably the amygdala, ought to be involved in all memory functions.

Outstanding alternatives to the working memory hypothesis remain O’Keefe and Nadel’s (1978) proposal that hippocampal damage always, and only affects spatial memory, Gaffan’s (1974) suggestion that the crucial distinction is between associative
learning and recognition memory, and Gaffan’s more recent alternative theory (Gaffan et al., 1984a, Gaffan, 1985) that the line is between the learning of stimulus configurations and the learning of conditional motor responses, with damage to the hippocampus producing only ‘an increase in confusability’, as normally it ‘keeps track of specific responses in specific contexts’. It is therefore premature to suppose that Olton et al’s (1979) working memory hypothesis is the final word on the matter, but some or other version of the temporary/long-term division of memory processes is likely to remain alive and kicking for a great deal longer (see Rawlins, 1985). We may note that the results reported by Gaffan (1977b, 1977c) still give some support to the notion of a temporary store for fairly recent experiences; while the new evidence provided by Gaffan (1985) does not unequivocally contradict it.

Gaffan (1977b) trained monkeys to observe the same 25 coloured slides every day, each presented twice in a random sequence, the animals only being rewarded if they pressed a response button several times during the second presentation of any slide. After considerable training they were able to distinguish between the first and second presentations of all individual slides with 90 per cent accuracy (during the middle part of the session) even when an average of nine other slides might have intervened between the two sights of the same picture. Disabling the hippocampus (by lesions of the fornix) produced a devastating loss in this ability, even though the monkeys were able to recognize the pictures and respond correctly when the same slide was shown twice in succession. A similar pattern of medium-term memory loss with intact very short-term recognition was apparent when monkeys were shown lists of one, two or three colours before a ‘probe’ item which they had to respond to differentially according to whether it had been on the list or not. (Gaffan, 1977c). Fornix lesioned monkeys had difficulties in identifying the earlier colours in lists of two or three, even though they were able to perform normally with lists of one. Difficulties in this sort of task are primarily due to interference between lists, which is especially prominent when lists of different lengths are used (Wright et al., 1984b; see below) and therefore it is difficult to sort out the relative contributions of absolute time values as opposed to number of confusable items as limiting factors in the hypothetical temporary store, as has been apparent for many years in studies of human short-term memory (Gregg, 1986).

Gaffan et al. (1984a, 1984b, 1984c) report the results of several experiments, which have led them to emphasize a distinction between the learning of actions and automatic dispositions to respond to standard stimulus configurations. In the first place several experiments show that fornix lesioned monkeys perform as normals on tasks in which varied stimulus rules have to be rote-learned. For instance, in a Wisconsin General Test apparatus (see p. 271) they learned to choose one member of five pairs of junk objects if they were given a free reward to start with, but the alternative member of these five pairs if they were not. This demonstrates an impressive storing of information, but it is of a long-term, dispositional or ‘reference memory’ kind and therefore is consistent with the view that only temporarily relevant information should become unavailable after this kind of memory system lesion (Walker and Olton, 1984; Rawlins, 1985). It was also the case however that fornix-lesioned monkeys performed unexpectedly badly on two tasks in which the nature of the response might plausibly be thought to be one of the items that needed to be remembered. In one task 60 objects were presented singly in random order each day, half with a reward under them and half not. Following this phase (which was split into six lists of 10), the same objects were presented as pairs. The monkey’s task was to choose only those
members of these pairs which had not just recently been rewarded. In this case lesioned animals performed badly, though not disastrously, while in an otherwise identical experiment in which the choice rule was to choose objects which had just been rewarded, they were not impaired. The problem for the working memory hypothesis is only to explain why no impairments were seen in the second case, but it would not seem particularly surprising if a rapid Thorndikean stamping in process provided a mechanism for repeating rewarded (but not unrewarded) choices in the absence of working memories of the previous choices themselves. A second task which proved difficult for fornix-lesion monkeys was to choose (in a WGTA) always the left-hand choice of one pair of objects, but always the right-hand member of a second pair. Thus correct choices were the left-hand member of A:B and B:A, but the right-hand member of C:D and D:C. It would have been difficult to predict that impairments of working memory should reveal themselves on this task but not the conditional choice among members of five pairs of junk objects referred to above (p. 314). However, it is clearly a task which involves conflicting rather than consistent cumulative response dispositions (sometimes A is chosen, sometimes B, sometimes the correct response is left and sometimes right) and therefore it is at least possible, if not conclusive, to suggest that unlesioned animals made fewer errors than lesioned monkeys in this case because they were able to consult working memories of the precise outcomes of individual previous trials.

Gaffan et al. (1984b, 1984c) propose that the special property of memory that is affected by fornix lesions is memory of response actions as opposed to any kind of memory of the presence or absence of objects. It certainly seems to be the case that monkeys thoroughly trained before this lesion, even on quite difficult tasks, are able to sustain or even improve on a high level of correct performance. Monkeys shown two objects, say A and B, without any reward, but then rewarded if they choose these two from immediately following pairs with alternatives (i.e. from A with C and B with D), could perform this task at a level of 80 or 90 per cent correct after fornix lesions. Gaffan et al. (1984c) interpret this to mean that the lesions did not impair the working memory of the stimulus objects seen at the beginning of a trial, a conclusion it is difficult to avoid. However, it is not inconceivable that correct performance would be obtained on this task by an automatic learning strategy which did not require working memory. Whatever this might be, it did not appear to be possible when two monkeys were given a test which could be solved on the basis of memory of their own responses. At the beginning of each trial one object (A) was presented over a baited foodwell and the monkeys pushed it away in order to retrieve a peanut. Then a second object was presented 8 cm behind the baited foodwell — the animals reached out for the peanut but did not have to touch this second object (B). Then they were given a choice between A and B, the correct choice being to choose A, which they had just touched. The two animals were each about 10 per cent worse on this task after than before fornix lesions, and one of them was about 10 per cent worse on a more difficult version of this task (which the other animal could not perform even before the lesion). This is a rather limited amount of data on which to reject the more general ‘working memory’ interpretation of hippocampal function, but it may very well be that memory of the animal’s own activities often, but not always (e.g. Ross et al., 1984), forms a prominent part of the memory content which is disturbed by surgical damage to the hippocampal system.

Comparison of present with recent stimuli, and the serial position effect

The working memory hypothesis implies that the retention of temporarily relevant information over short periods (which may be in seconds, minutes, or even hours) is
subject to different constraints from those which apply to the longer-lasting retention of information in the case of motor skills, or of habits or dispositions of responding to standard stimulus configurations, even those which may take quite complex forms, as in a reference memory of spatial knowledge. Within this hypothesis, it is quite possible that several shorter-term processes contribute to working memory — for instance, there may be modality effects with special characteristics of short-term retention of visual auditory or olfactory information, and also stimulus dimension specificity, with selective attention to, for instance, the analysis of colour and shape (see pp. 275-9 above). In human short-term memory, there are undoubtedly many effects which depend upon verbal factors, and to some extent the whole system can be regarded as a device for the receipt and output of speech, involving a unique degree of similarity between stimulus items and response items. Tests of human memory may appropriately rely on measuring verbal recall. Mishkin (1982), among others, has proposed that all mental associations might be considered as forms of recall, and that therefore there is a neural hierarchy of separate systems for recognition of individual stimuli and associations with other events in animal brains, but for purposes of experimental measurement there are no worthwhile analogies to verbal recall available for studies of animal memory, except in ‘language-trained’ chimpanzees (see below).

Therefore, studies of temporary memory in animal learning have had to rely very heavily on recognition techniques, though it is of course possible to devise tests of an animal’s memory for its own recent actions (Morgan and Nicholas, 1979; Shimp, 1976, 1984).

*Delayed matching-to-sample procedures (DMTS)*

A standard procedure by which temporary retention of information may be investigated requires merely the insertion of

a delay between the sample stimulus and the two comparison choices in the matching-to-sample procedure described in the previous chapter (p. 278). If a centre key is lit red, but then goes out for a minute before two side keys are lit red and green, and a pigeon pecks the red side key reliably (but would equally peck green if the sample had been green), then we have good grounds for assuming that temporary information is retained in some way during the delay interval, although there is nothing in this basic result to indicate in what form the information is retained. The simplest suggestion is a trace theory, which supposes that an internal analogue of the sample decays gradually, and remains available at the time of choice to direct a matching (or non-matching) decision (Roberts and Grant, 1976). There has been general agreement, however, that theories of this type do not suffice even to explain the delayed matching performance of the pigeon, since for the pigeon ‘what’s past is prologue’, and sample stimuli initiate active remembering in specific codes of ‘what to do next’, as much as of ‘what just happened’ (Carter and Werner, 1978; Honig, 1981; Grant, 1981; Maki, 1981; Roitblat, 1982; Urcioli and Zentall, 1986).
The sort of performance which might initially suggest a simple trace theory is shown in Figure 9.2. Well-trained pigeons were shown single samples that might be red, green, blue or yellow, at various intervals before being required to choose between red/green or blue/yellow pairs of side keys (in random left/right positions) with the length of sample presentation time varied from day to day. As Figure 9.2 demonstrates, even without any delay (the choice being made available as soon as the sample was turned off), performance was only 100 per cent 'correct with the longest sample presentation of 14 seconds, declining to 80 per cent with 1-second samples; and this difference was retained when long delays were required, all samples being followed by less accurate choices as the retention delay was increased to 60 seconds. Such regular data, and the sharp drop in accuracy with delays of only a few seconds, suggest a process of temporal decay. No one doubts that time makes a difference, but there is considerable evidence against any simple form of trace decay. First there is a proactive interference effect, since if a wrong choice has recently or often been right it is much more likely to be chosen (Roberts and Grant, 1976). Second there are retroactive inference effects of the type that brief changes in lighting intensity during the delay interval have a detrimental effect on performance, whether the changes are increases (Grant and Roberts, 1976) or decreases (Cook, 1980). Third, surprising (relatively rare) samples are better remembered over longer delays than when the same samples are usual instead of unusual (Roberts, 1980; Grant et al., 1983), and fourth, there is a phenomenon called 'directed forgetting' (Maki, 1981), where on a proportion of trials a brief signal given after the sample normally indicates that there will...
be no choice to follow, and when choice stimuli are presented as probes after this 'forget' stimulus, accuracy is reduced.

These findings all suggest that what is remembered is not an automatic and passive trace of the sample. That what is remembered is not in fact coded in terms of the sample at all, but usually in terms of prospective choices, is indicated in the first instance by the lack of necessity that eventual choices bear any obvious relation to the sample. After a red sample the animal could be required to choose a vertical, not a horizontal black line, and after a green sample the (this sort of procedure may be referred to as a conditional discrimination, or as 'symbolic matching to sample'; Honig, 1984; Roitblat, 1982). Elaborations of this task to include a third easily confusible sample (e.g., orange) and a third easily confusible choice item (e.g., a nearly vertical line) allow for the observation that errors are more likely to reflect prospective coding of choices than retrospective coding of the sample, for both pigeons (Roitblat, 1982) and monkeys (Gaffan, 1977c).

Figure 9.3

Short-term visual memory in monkeys as a function of delay and interference.

If only one pair of coloured slides is presented to monkeys, and they are repeatedly required to choose whichever one of these two had just been shown to them a few seconds earlier, their choice accuracy drops precipitously after 10 seconds' delay. However, if slides were used only once per day ('trial unique'), or if the correct choice was always a novel slide, then 'short-term' memory could be measured in hours instead of seconds. See text. After Overman and Doty (1980).

The limits of temporary visual memory

The experimental procedures used to study retention over a delay by the conditional discrimination or matching-to-sample principles typically lead to the frequent presentation of the same small set of stimulus items, and typically suggest a retention span for accurate performance of the order of seconds for both monkeys and pigeons (D’Amato, 1973; D’Amato and Worsham, 1974; D’Amato and Cox, 1976; Roberts and Grant, 1976; Grant, 1981). Overman and Doty (1980) provided evidence to support the intermittently expressed suspicion that the second of these typicalities depends upon the
first. To produce the standard result they used one pair of coloured slides. One member of this pair was presented on a centre display panel, and the subjects (macaque monkeys) were required to touch this 9 times; it then went off, and after a delay the pair slide was projected on two side screens (left/right randomized) and a reward of orange juice could be obtained by pressing the member of the pair which had most recently been given as the centre sample. Under these conditions accuracy was only 70 per cent with a 5-second delay, quickly declining to chance levels of performance at 30-second delay intervals (Figure 9.3). At the other extreme, the same monkeys had previously been tested under the constraint that every trial began with a novel slide, never seen by the animal before, and after the delay interval there was a choice between this once-seen slide and an alternative never-seen picture (most slides were of human artifacts: a shoe, a mug, spectacles and so on). Here, by contrast, performance was relatively resistant to temporal delays, even when the animals were removed from the apparatus after seeing the sample, and returned to it an hour or a day later (Figure 9.3). Only slightly less resistant was the monkeys’ initial performance with a set of 100 slides used repeatedly for several days, but with each pair of slides being used only once a day. This would appear to be conclusive evidence that the time constraint on the memory processes assessed by sample and choice comparison procedures interacts very strongly with interference or confusability between alternative possibilities, at least as far as visual cognition in primates is concerned.

Memorable attributes

Allowing that there may be active retention of prospective codes during a delay interval, and that confusions between several physically similar possibilities may lower the accuracy of choices, does not amount to a very strong hypothesis about the properties of the memory process involved. However, it is likely that at least one more specific proposition about the nature of the remembered representations can be rejected, namely the idea that these are restricted to physical imagery of the sample or the choice stimuli. Parkinson and Medin (1983) suggest this on the basis of experiments on the role of the novelty or familiarity of the stimuli used in delayed-matching to-sample experiments with monkeys in the WGTA apparatus (see p. 271). Selections made from several hundred common manufactured objects repainted in uniform colours were used as stimulus categories: 10 objects seen repeatedly several times each day were designated ‘familiar’; stimuli seen once within a day and not re-used for several days were ‘novel’; and stimuli which were seen several times in a given day but only ever used on one day were termed ‘moderately familiar’. Overman and Doty’s (1980) result that accuracy is higher with novel than with familiar stimuli was replicated, but Parkinson and Medin (1983) also argued that the degree of familiarity itself became a discriminative cue, since the animals were highly accurate at always rejecting a novel choice, whether the sample had been itself novel, familiar, or moderately familiar. Also, with practice the monkeys became better at choices between a moderately familiar and a novel stimulus than they were at choices between two moderately familiar items. The experiment by Gaffan using repetitions of extremely familiar slides (1977a; p. 314) also suggests that fine distinctions in degree of familiarity can be available as cues for choice.

A much more direct suggestion that the immediate sensory properties of events are not the only contributors to memory processes can be obtained from the experiment of Weissman et al. (1980), who begin their report with a reference to William James’s
dictum that ‘a succession of feelings, in and of itself, is not a feeling of succession’. On the basis of a carefully designed experimental procedure they are then able to conclude that pigeons can, at least briefly, remember a feeling of succession. The birds were required to distinguish between the sequence of orange followed by green and that of green followed by orange, indicating this by pecking at a vertical line after the former, but at a horizontal line after the latter. The fact that they refrained from pecking at various alternatives offered to them (without reward), such as two green flashes followed by a vertical line, or two orange flashes followed by a horizontal line, was sufficient to establish that detection of the temporal order of the two-event sequences, rather than alternative sources of information, was responsible for their correct discriminations. It seems probable that various selected attributes of stimulus events and various relationships between them, such as those discussed in the previous chapter (bigger than, brighter than, etc.: p. 260) might be retained as part of working memory processes and that memorial coding should be selective in very much the same way that attention to and discrimination of the remembered events is selective in the first place.

The serial position effect in choice and recognition

In human verbal memory, an extremely reliable difference between the accuracy of recalling words from the beginning, middle and end of a memorized list has been obtained in countless experiments, and this serial position effect has occasionally been used to provide purely behavioural support for a distinction between long-term and short-term memory stores which might rest otherwise on neurological data (e.g. Kintsch, 1970). It is usually assumed that words at the end of a list are remembered well just afterwards because they are still available in some kind of short-term store, whereas words at the beginning of a list have been stored elsewhere, but have the advantage of being put there first, thus acquiring a certain distinctiveness, and also suffering least from proactive interference. On this model, hippocampally damaged human patients suffer most from interferences, or have difficulties inserting new items into long-term memories, and can thus remember only the very end, but not the beginning, of a long list, and that only just after hearing or seeing it (Milner et al., 1968; Weiskrantz, 1977).

Kesner and Novak (1982) described a procedure that would be theoretically capable of revealing serial position effects in rats, and report results, replicated by Cook et al. (1985), suggesting that it does so in practice. A radial maze (p. 144 above) is used, equipped with doors enabling the experimenter to allow access to only one of the eight arms at a time. A rat may thus be given the chance to enter the arms in a particular random order, and then given a choice between two of them, being rewarded only if it chooses the one it has least recently entered. After training animals to choose the first rather than the seventh arm in any random previous list of arms entered (an easy discrimination first, see p. 265 chapter 8) Kesner and Novak (1982) compared rats’ performance in choosing the first over the second, the fourth over the fifth, and the seventh over the eighth, of any preceding list, finding that choices between the middle pair were at chance levels, but that the earliest of the first and last pairs could be chosen successfully, by normal rats. On the other hand, animals with hippocampal lesions never performed above chance on the first pair, and could only manage the last pair if tested just after they had experienced it. Slightly different methods of immediate testing have confirmed that more information is retained by rats about places in a maze they have most recently visited than about places visited earlier (Roberts and Smythe, 1979).
A more elaborate technique for obtaining serial position effects from visual recognition performed by monkeys was reported by Sands and Wright (1980a, 1980b). The animals were first trained on a simultaneous same/different discrimination, using 211 coloured slides of objects such as flowers, fruit and human artifacts. Slides were presented in pairs, one above the other. When an identical pair was shown, the correct response was to move a lever to the right, and if, alternatively, the slides were obviously different, the same lever was to be pushed to the left. Various food rewards were given intermittently for correct responses. With sufficient training on this same/different principle, it was possible to move on to what is referred to as 'serial probe recognition', in which a 'list' of 10 slides were shown serially on the top screen, followed by a single slide on the bottom screen, and occasional rewards were obtained by pressing the lever to the right if the bottom slide had appeared on the previous top list, and to the left if it had not. The data resulting from this training are shown in Figure 9.4, along with data obtained from a single human subject performing without any reward or previous experience on the task. A more pronounced bowing of the serial position curve is apparent for the rhesus monkey than for the human subject, due no doubt to the ceiling affect produced by the greater accuracy of the latter. When the list was lengthened to 20 slides, the human and monkey curves became more similar.
What should be concluded from this result? First, we must note that both primacy and recency effects in similar procedures have been reproduced in other monkeys by Roberts and Kraemer (1981) and by Wright et al. (1984a) and in a chimpanzee by Buchanan et al. (1981), and that therefore the effect shown in Figure 9.4 is replicable. But does this mean that, as Wright et al. (1984a, p.527) conclude, such primacy and recency effects make it more likely that ‘animals process information and think in ways basically similar to humans’? Only up to a point. Gaffan (1983) argues that quite different factors might be responsible for the production of the primacy effect in the monkey procedure and in human verbal learning, on the grounds that the monkeys were allowed to initiate all lists by depressing their lever on hearing a ‘ready’ signal. It is certainly true that this is likely to enhance attention to the first items on the list — one of the reasons for requiring animals to make a response before or after a stimulus is presented is to make sure that they notice it. However, as Wright et al. (1983) do not fail to mention in their rejoinder to Gaffan (1983), the primacy effect in human learning may be due to a variety of factors, among them greater attention paid to the beginning of a list, and the combination of both recency and primacy effects is unlikely to have a single cause in any species. There must surely be extra factors to consider in human performance: a superficially trivial matter mentioned by Santiago and Wright (1984) is that animals have difficulties in ‘trial separation’ whereas humans bring to all experiments a whole set of expectations, sets and attributions which may influence even the most basic of conditioning processes (Lowe, 1983; Davey, 1986). The now unfortunately common practice of referring to a hypothetical process of animal memory as ‘rehearsal’ should not disguise the fact that some at least of human verbal learning depends on a unique articulatory loop, to say nothing of deeper and more mysterious linguistic matters. Nevertheless, providing one retains a sense of proportion, it is not merely reasonable but obligatory to consider whether some of the phenomena of human cognitive performance might share both properties and causes with similar happenings observable in humbler species, and Sands and Wright (1980a) have every justification for urging that models of memory for complex images have much to offer to the comparative psychologist.

One of the strongest empirical points made by Sands and Wright (1980a) was that monkeys are more strongly influenced than people by the problems of confusion (‘proactive interference’) that arise from using the same stimulus items repeatedly. This seems to apply also to pigeons, since Santiago and Wright (1984) discovered that pigeons given the opportunity to look through a window of a Skinner box at the same slides as those used in parallel experiments on monkeys, projected on similar screens, were able to develop roughly similar serial position curves in the serial probe recognition procedure (see Figure 9.5). It should at once be said that Wright et al. (1984a, 1984b) were more than adequately seized by the differences between pigeon and monkey capabilities. (i) The birds showed little sign of generalizing their same/different responses (on right and left-hand keys) to new stimuli, whereas monkeys eventually showed near perfect transfer to completely new pairs of slides. (ii) The pigeons have so far only performed above chance on lists of four, whereas monkeys have got up to lists of 20. (iii) Monkeys appear to tolerate longer delays between the end of a list and its probe. (iv) Unlike the monkeys, pigeons demonstrated only random responding when lists of variable length were used. (v) As a plus for the pigeons, they showed no sign of developing the short cuts, circumventing the purpose of the experiment, which had to be guarded against in monkeys, such as memorizing correct responses to individual probes whenever this is possible, or making fast and correct ‘different’ responses to probes
based on novelty. (vi) Summarizing these differences, Wright et al. (1984b) suggest that monkeys are better able than pigeons to quickly and flexibly adopt new and efficient cognitive strategies.

Therefore, the similarity of the data for monkeys and pigeons in Figure 9.5 should not be taken as reflecting a similar similarity in overall cognitive capacity. But it serves to indicate strongly that there may be reasonably general principles behind primacy and recency effects in probe recognition performance, of the archetypal form that the recency effect is based on a short-term or more transitory store, since it is a decreasing function of delay, whereas the primacy effect is related to interference, attention, or possibly some form of consolidation, since it actually increases with time past since the list was seen, during the intervals under consideration.
Figure 9.5 Serial position effect in pigeons and monkeys as a function of probe delay.

Serial position curves for 4 pigeons (above) and 2 monkeys (below) obtained using the same stimulus materials (coloured slides of objects) in lists of 4, and with various delays intervening between the list and the probe test, at which the animals were required to indicate whether a probe stimulus had been present in the previous list. See text. After Santiago and Wright (1984) and Wright et al. (1984a).
The ecology of memory

It is not immediately obvious that the variations in memorial accuracy that produce the serial position effect have in themselves a useful function. It is more likely that they reflect general principles of the operation of memory mechanisms, which arise from natural necessities, but which are not specialized to particular species or particular tasks. It is a very general feature of perceptual systems that a change in stimulation is strongly marked, especially if it represents an increase, and thus the special attention given to the beginning of a list, in either storage or retrieval, is to be expected. Similarly, it would be difficult to design any perceptual system without some form of transitory sensory buffer, and recency effects should not therefore come as any surprise in studies of animal memory.

However, although specialized laboratory testing of memory may seem both very general and very artificial, few doubt that both the acquisition of a long-term store of knowledge (reference memory) and memory in the form of running commentaries on recent events (working memory) may serve useful purposes in real life. In the natural life of animal species the most obvious function of both kinds of memory is producing optimum patterns of foraging for food (Olton et al., 1981; Krebs and Davies 1983; Olton, 1979). We may imagine a hypothetical animal which learns that food may be temporarily available at 10 different locations with a much larger territory (reference memory) and also takes note of which of these have been recently exploited (working memory). A special case of memory for food locations arises when animals themselves place food in particular hiding places, returning to retrieve it at a later date. The hoarding of nuts by squirrels is an example, though not one usually taken to indicate very efficient use of memory. In other species, however, rigorous experimental testing has indicated that memory for the location of hoarded food is very accurate. Shettleworth and Krebs (1982) studied the behaviour of captive marsh tits (Parus palustris — actually a woodland bird) in an artificial aviary, in which old tree branches had a total of 97 holes drilled in them and were covered with cloth flaps. An experienced bird placed in the aviary with a bowl of hemp seeds would hide 12 seeds in some of these hiding places (as well as eating other seeds) within seven or eight minutes. It was then removed from the aviary for two or three hours, before being allowed a 12-minute recovery test to see how many of the seeds it had stored it could find (the bowl of free seeds having been taken out). The average performance of four birds on this task was 8 out of 12 seeds recovered, with a total of 30 of the hiding places inspected, over a total of 12 tests each. This is very much less than perfect, but substantially better than chance. The birds did better at the beginning of a test — five of the first 10 holes inspected had seeds previously hidden in them, but there was no relation between the order in which seeds were stored and the order of their recovery. Occasionally the birds missed a seed even though they inspected the hole it was in.

In the course of a second experiment (Shettleworth and Krebs, 1982) birds were given two hiding places, a couple of hours apart — in each case a bowl of seeds was available and they were allowed to hide eight seeds before being removed. Then they were given a 12-minute retrieval test three hours after the second hiding phase. The first additional result here was that the birds almost never attempted to put two seeds in the same hole, even in the second hiding phase — this strongly suggests that they were avoiding already used sites, although the chances of revisiting one of the previous eight sites is fairly low, even at random. A second additional result was that some birds showed a tendency to find first those seeds which they had hidden last (that is, in the
second storage phase). The data were not unequivocal for these additional results (the experiment was curtailed by the advance of spring — the birds only bother to hide food in the winter) but there seems little doubt that ‘marsh tits can use memory for individual storage sites in recovering hoarded food’ (Shettleworth and Krebs, 1982). For this species and other extremely small tits the rigours of winter must combine with the dangers of heat loss (due to their high surface area/volume ratio) to make it worthwhile for them to exploit occasional superabundant food sources by systematic caching. It is not clear, however, whether this requires a specialized development of memory capacities, as opposed to the specialized behaviour of hiding as well as eating food.

Crows, jays and other corvids often perform well on tests of learning and memory (e.g. learning sets, see p. 274). It appears that a certain North American corvid, Clark’s nutcracker, may have developed a spectacular memory for the location of stored food, since in order to cope with the harsh winters of alpine environments it may store upwards of 30,000 pine nuts in 2,500 locations during the autumn, returning to these throughout the winter, during its early breeding season, and in some cases much later in the following year (Van der Wall, 1982; Balda and Turek, 1984; Kamil and Balda, 1985). Studies of individual captive birds suggest that non-local landmarks of some kind must be used in coding the location of food stores, since birds performed accurately if experimenters removed food or pushed away local signs when pine nuts had been buried under sand, but made systematic errors if obvious features of the test environment, such as logs and stones, were all moved (Balda and Turek, 1984). Since in the wild food caches are often retrieved when buried under snow, it seems necessary to assume that this species forms a particularly detailed cognitive map of its surroundings, possibly with food caches referred to particular large landmarks or ‘focal points’ (Balda and Turek, 1984).

That species other than those which habitually hide food may possess memory for food location in considerable detail is illustrated by the semi-naturalistic experiments reported by Menzel (1973, 1978) on chimpanzees who were thoroughly familiar with the test environment of a 1-acre field, having already lived in it for a year before the tests began. One straightforward test was to carry a single chimpanzee around the field to watch while 18 pieces of fruit were hidden by another experimenter in holes in the ground, tree stumps and so on, all the other animals having been removed and caged outside, allowing the observation that when all the animals (six) were put back in the field a couple of minutes later, the observer chimpanzee could demonstrate its remembered knowledge of the location of food by finding it (on average 12 out of 18 pieces), the uninformed animals providing a control comparison (and typically finding only one piece between them). The chimpanzees, like nutcrackers (Balda and Turek, 1984), are capable of re-organizing spatial knowledge, since they recovered hidden food according to a least distance principle rather than in the order in which it was hidden (except when the food was half food and half vegetables, in which case they travelled greater distances in order to be able to recover fruit rather than vegetables first). Another example demonstrating some use of geometry was obtained when the experimenters adopted the device of hiding only two pieces of food, at symmetrically opposite locations about the midline of the field, drawn from the point where all animals were released into it, but with the exact position of the hiding places varying considerably from trial to trial. The same procedure of showing only one chimpanzee the hiding places on a given trial was used, but in this case the control
animals were able to improve their performance by watching the test animal and, on seeing it find one of the two food locations, running directly towards the symmetrically opposite one (Menzel, 1978, p. 409).

Inference and intentional communication in Anthropoidea

Menzel (1978) reported a number of results which confirm the essential features of the observations of Kohler (1925): chimpanzees, given suitable opportunities for play and practice, demonstrate manipulations of objects which appear to indicate considerable knowledge of spatial relationships, and insights into how these may be altered. Thus some of Kohler’s apes used sticks to drag in otherwise out-of-reach bananas on the ground outside their cage, and piled up old crates to reach an out-of-reach banana suspended from the roof.

The Anthropoidea is the suborder of primates made up of New World monkeys (Ceboidea, e.g. marmosets, capuchins and squirrel monkeys), Old World monkeys (Cercopithecoidea, e.g. rhesus, Japanese, pig-tailed or other macaques, baboons, guenons and langurs), and the Hominoidea superfamily which includes lesser apes (gibbons and siamangs), great apes (gorillas, chimpanzees and the orang-utan) and all the Hominidae, of which the only surviving species is Homo sapiens. The other primates, prosimians, including the lemurs of Madagascar, bush babies and tarsiers, are mostly nocturnal, lacking colour vision, and smaller-brained than the Anthropoidea, and are phylogenetically earlier and more remote from human ancestry. On the grounds of both behaviour and anatomy, it is clear that the great apes collectively are more closely related to the present human species than any other group of animals, although opinions vary as to which one of four great apes (chimpanzee, pigmy chimpanzee, gorilla and orang-utan) should receive the dubious accolade of being most human.

The chimpanzee is usually given the edge by anatomists and physiologists, and is in any case selected most often for study by comparative psychologists partly because of its availability. Because of its close biological relationship to people, some comparative psychologists have been tempted to assume that a reverse-Tarzan effect should be possible, that is that by rearing a young chimp in the company of a human family, it should be possible to inculcate in it all significant human qualities, up to and including articulate speech. However, the husband and wife teams of Kellogg and Kellogg (1933/1967) and Hayes and Hayes (1951), though observing for several years the development of lively, sociable and otherwise imitative infant chimpanzees, were unable to report any significant progress by these animals towards the acquisition of a human language. (More recent accounts have been given by Kellogg, 1968 and Hayes and Nissen, 1971.) The Hayeses were initially encouraged by the fact that their animal, Viki, appeared to go through a ‘babbling’ stage of experimental noise-making when a few months old, but their efforts to explicitly train up normal speech had minimal success. It is now believed that the shape of the chimpanzee throat precludes the production of more than a single general-purpose vowel, but that a range of consonants should be anatomically possible (Lieberman, 1977). However Viki appeared to have great difficulty in establishing any voluntary control of the vocal apparatus. In order to assist with consonant production, the experimenters manually held Viki’s lips together. Viki subsequently demonstrated a surely adequate degree of motivation by holding her lips in the required position with her own hands. However, by the time of her death (at age 6½), she had, by even the
most charitable criteria, learned only seven words. ‘Mama’, ‘Papa’, ‘up’ and ‘cup’ were approximations to vocal English, used in approximately correct contexts. Three sounds which she produced spontaneously in the first instance, two clicks and a ‘tsk’, were trained as requests for a ride in the car, a cigarette, and to go outside. No other investigator, before (Furness, 1916; Cunningham, 1921) or since (Premack, 1976; Gardner and Gardner, 1971; Patterson, 1978) has claimed that intensively trained young simians can better Viki’s limited performance, and it seems safe to conclude that the motor skills necessary for learned vocalization are beyond the capacities of the great apes.

Inappropriate anatomy, and the lack of specializations for the voluntary control of tongue, palate, lips and lungs, might conceivably prevent the acquisition of speech without rendering impossible meaningful communication via other modalities, as certainly may be the case for human beings with similar motor handicaps. Similarly inhibition of speech in human children by profound deafness may necessitate recourse to visual sign languages. Herculean efforts have therefore been expended in attempts to train chimpanzees up to human levels of competence in the use of gesture sign language (Gardner and Gardner, 1969, 1971, 1985), communication by the manipulation of plastic tokens (Premack, 1971, 1976); and communication via special symbols on computerized keyboards (Rumbaugh and von Glaserfeld, 1973; Savage-Rumbaugh et al., 1980; Savage-Rumbaugh et al., 1985).

There is now a very extensive literature on these attempts, which has frequently been reviewed (e.g. Terrace et al., 1979; Passingham, 1982; Walker, 1986). No detailed account of this research will therefore be given here. A very general conclusion is that, although there is much of interest in the data gathered, there is little to suggest that the natural abilities of apes verge on human competence, requiring only a helping hand from a persistent experimenter to reveal much more than is immediately obvious; and much which supports the hypothesis of Lenneberg (1967) and Chomsky (1976) that linguistic ability depends not only on biological specializations of hearing and voice, but also on genetically determined intellectual capacities of some kind which are not shared by any non-hominid primates. The communicative performance of trained apes differs from human speech in, among other possibilities, modality (it is not vocal); syntactic complexity (it is not sequentially ordered); disengagement from context (reference is usually to present or imminent stimuli); and separation from tangible goals (communication in apes is typically impelled by ulterior motives, and is rarely an end in itself).

However, attempts to train apes in language-like communication, and spin-offs from these attempts, have raised a number of questions about the limits of animal learning, and the transition between basic and universal associative processes and primate cognitive superiorities (Rumbaugh and Pate, 1984). Although apes cannot talk, or communicate in an equivalent manner with gestures, this does not necessarily mean that all their learning abilities can be adequately accounted for in terms of mechanisms available to invertebrates, or even in terms of mechanisms available to the pigeon or rat. Terrace et al., (1979) were inclined to the view that, since their gesture-trained chimpanzee, Nim Chimpsky, failed to produce evidence of sentence construction, the associations they observed between certain gestures and appropriate objects referred to did not differ from associations between discriminative stimuli and instrumental responses and rewards obtained in Thorndikean experiments (see p. 118). Savage-Rumbaugh et al., (1983) have however given both a theoretical and an experimental
demonstration that there is a wide variety of possible kinds of association between a
gesture and an object, or a visual symbol and an object. Simple labelling demands an
association between symbol and object, but ‘reference’ as an act of naming involves
considerably more than knowledge as an association. The conclusion supported by
Savage-Rumbaugh et al. is that ‘symbolization
is not a unitary skill but rather a combination of diverse productive and receptive skills’: it is possible however to suppose roughly that naming usually involves an agreement
among several participants that a particular symbol ‘stands for’ a corresponding object
or event, with all parties knowing that the symbol is only a symbol, but a real event is not.

The most rudimentary form of reference is perhaps to draw someone else’s
attention to a particular object by pointing at it, or holding it up for inspection. Children
often do this before they know conventional names for individual objects. Without
special training, young chimpanzees do not point things cut with the arm or finger, but
they do exhibit objects by holding them out to a human companion. After a certain age
children hold things out to give as well as to show, but this seems not to happen with
chimps, since it is reliably reported that psychologists are frequently bitten when
assuming that they are intended to take possession of objects held out in this manner
(Savage-Rumbaugh et al., 1983, p. 462).

Thus although chimpanzees can be trained by rote-learning to associate a set of
visual symbols or gestures with a set of objects, they do not normally demonstrate what
these authors take to be the preliminary features of the ‘protodeclarative’ in the human
child: indicative pointing, giving objects to others, and the use of nonsense vocalization
in association with these activities. Further, chimpanzees may after learning a set of
symbols in one context, be unable to transfer this training to another. Often they are
trained to give the symbol for a food object under conditions when they always receive
that food object after they have named it. Not surprisingly, they then become confused if
they are shown chocolate, and produce the chocolate symbol, but receive beancake. If
chimpanzees are trained in a productive skill, that is to produce consistent symbols for
real objects which they are shown (either by gesturing, or by pressing the correct key on
a keyboard), they do not necessarily perform correctly when tested on a corresponding
receptive task, namely selecting a single item from a collection when given the symbol.
A similar dissociation may however be observed in very young infants; Rice (1980)
trained normal 2- and 3-year-olds who did not

already know this to say the right words when shown red, green and yellow objects.
Some infants took hundreds of trials before they did this correctly, and after that still
performed at random when asked to choose named objects — choosing at random when
asked ‘Give me the red one’ yet responding correctly when asked ‘What colour is this?’
Even as adults, these skills are in one sense highly separated, since brain damage (for
instance, after strokes) may frequently affect productive but not receptive skills or vice
versa, as in the traditional classification of Broca’s and Wernicke’s aphasia (Goodglass

Whatever the final verdict on these matters, it is obvious that the human act of
naming involves more than a simple association between two events, and most probably
requires a whole complex of social skills and cognitive assumptions. Nevertheless, two
chimpanzees, Austin and Sherman, who had previously demonstrated a functional form
of communication between themselves (Savage-Rumbaugh et al., 1978b) by requesting
and donating various tools required to procure concealed foods, satisfied what Savage-
Rumbaugh et al. (1983) regarded as fairly stringent criteria for an act of naming which includes intentional reference to objects. In the first experiment the animal subject had to look at a table on which an experimenter had placed a selection of five to seven foods, changed from trial to trial. Then it had to walk round a screen to a keyboard out of sight of the foods, key in a particular item (by pressing a single key), return to the table, and pick up the item it had previously indicated. When this was done correctly the subject was allowed to share the indicated food with the other chimpanzee. This provides additional evidence to that previously reported for ability to label previously seen food objects (Savage-Rumbaugh et al., 1978a) since the stimulus for the choice of label was not simply a single object but the animal’s own decision about its intended future choice from among a given selection.

A second and similar experiment used an object set of photographs of 20 foods and 10 objects; two experimenters (one of whom placed a random selection of five objects on the table each trial, and the other, who did not know which five objects were present, to receive the animal’s eventual choice); and a longer distance between the table of objects and the remote keyboard. Pains were taken that all these trials were ‘blind’, that is, that human experimenters could not inadvertently signal to the animals which objects they should choose or which key they should press. The task also differed from the first in that the food rewards given to the animal did not correspond to the objects previously indicated. Possibly because photographs of food were used, whereas sometimes real objects rather than photographs of objects were present, the choices were more often of non-food objects than of foods. Thus on a typical trial the animal would inspect a table on which was present a straw and a wrench, and photographs of cake, melon and banana, walk round a screen to a distant keyboard (sometimes after the animal had reached the keyboard it would have to return to the table to refresh its memory), press the arbitrary visual pattern for ‘wrench’, return to the table, select the wrench, take the wrench around another screen to an experimenter who knew only that ‘wrench’ had been indicated, and receive praise and yoghurt.

This sort of one-word indication of intended action is one of the earliest vocal skills achieved by human children and the surprise is perhaps only that its demonstration in chimpanzees should have been so long delayed — these animals were 9 and 10 years old and had been in training together for eight years. It does not of course follow that the eight years of training were all necessary, but the trouble taken over this result does not suggest that more creative and lengthy conversations with chimpanzees will readily be achieved. Is it possible therefore to conclude that the obvious superiority of humans at human language tasks should be attributed to a core of grammatical or syntactical competence, rather than to a larger plexus of social, emotional and vocal predispositions? There is no reason to suppose that human predispositions for language do not include all the above and more besides, and it is unlikely that the difficulties encountered by those trying to train non-human primates in language arise from a single cause. The detection of grammatical regularities by human infants may require the utilization of a powerful

and special-purpose problem-solving device (Wexler, 1982), but the normal routines of early life and more particular forms of support in social relationships no doubt aid its activities (Bruner, 1983; Harris and Coltheart, 1986). It is certainly unlikely that merely the detection of word order (or morpheme order) supplies a great deal of force in itself to language-learning in human infants. No theory should come to harm, therefore, from the discovery that apes, having become sensitive to a limited number of visual or gestural
symbols, can detect limited changes to the order within two— or three-symbol messages.

Muncer and Ettlinger (1981) trained a single 5—year-old female chimpanzee for one year in the production and comprehension of a small number of the hand and arm gestures which make up the American Sign Language used with the human deaf. Correct use of the prepositions ‘in’ and ‘behind’ was trained by rewarding the animals for using the correct function word, with the correct order of nouns, in describing displays such as ‘apple in bag’, or ‘apple behind bag’ (the bag was transparent). Comprehension of similar phrases was taught by compliance with instructions always beginning with push — thus ‘push apple in bag’, ‘push bag behind apple’. Double-blind trials were given regularly both in training and in the subsequent tests. These were made up of a small number of probe trials, on which words were presented in novel orders. There were 14 of these new sequences, of the form ‘bag in box’, ‘bag behind box’, and ‘push apple behind box’, ‘push bag behind peanut’. Performance on these novel trials was significantly better than chance, though far from perfect. The chimpanzee appeared to have little difficulty in always putting the preposition second, in groups of three signs, and in fact more errors were due to choice of the wrong preposition than to errors of sequence, possibly because both ‘bag in box’ and ‘bag behind box’ entail the occlusion of the bag by the box. In any event, in this limited context the chimpanzee’s syntactical abilities were not negligible.

In a second experiment, the same chimpanzee was trained in similar fashion to produce and comprehend gestures for ‘and’, ‘or’ and ‘not’. Presented with displays of four items, the animal might be instructed to ‘take peanut and carrot’, while leaving the other two (perhaps a banana and an apple), or alternatively ‘take peanut or carrot’. For production of ‘and’ the animal had simply to put this between 2 appropriate object gestures when 2 objects were presented. For production of signs for ‘or’ and ‘not’, the chimpanzee was encouraged to gesture ‘Graham not take Banana’, or ‘Graham take banana or apple’, if one or two items were present respectively, by being allowed to take herself what Graham left. Selfishly, the chimpanzee, Jane, failed to produce the sign for ‘or’ correctly even after six months of training, but comprehension for all three gestures appeared to be good. Comprehension test trials were therefore given in which, for the first time, ‘not’ was combined with ‘or’ or ‘and’, using objects not previously experienced with conjunctions; these took the form of instructions such as ‘not paper and bag’ or ‘not paper or bag’. The reader may care to consider for a moment which responses should be regarded as correct in these circumstances. The chimpanzee’s response was to refrain from taking raisins from objects signed immediately after the gesture for ‘not’, but to pick up the raisins placed on all other objects. This would seem to me to be one plausible interpretation of the ‘not’ sign, given that there was nothing which corresponded to a set of brackets. However, Muncer and Ettlinger intended that ‘not paper or bag’ should mean neither object should be responded to, and therefore conclude that a response to the second object indicates a ‘failure to negate conjunctions’. It certainly seems likely that a very simple strategy, of not taking rewards from the first object after ‘not’ was responsible for the chimpanzee’s choices, and this also appeared to apply when instructions of the type ‘not A and not B’ were successful in preventing responses to both objects. However, it should be noted that even the application of this simple rule (to novel combinations of ‘not’ with objects) placed a load on visual memory, since the serial gestures were transitory. The results of the first experiment, in which ‘in’ and ‘behind’ were applied correctly, suggest that the chimpanzee was capable
of interpreting order of gestures in visual memory in terms of object relations in space (and vice versa), and this represents a considerable cognitive, if only a trivial syntactical, achievement.

Theoretical interpretations of ape-training experiments
There are a number of theoretical questions which arise from the limited success of experiments in training apes to communicate, most of them not within sight of being clearly answerable. (i) The most secure conclusion at present is that the innate difference between the other Anthropoidea and Homo sapiens with regard to propositional communication and thought can be only a little blurred by the best efforts of the latter to educate the former; (ii) despite this, special coaching of young apes promotes intellectual accomplishments not normally exhibited spontaneously; (iii) there being little basis for comparison, it is not clear whether this is possible because apes have innate abilities which are significantly in excess of those of other large mammals; (iv) it is uncertain whether the special coaching of apes allows already present cognitive processes to be revealed to human observers, or whether the artificial educational procedures build in new mental strategies which could never arise in their absence.

Communication in non-primate mammals
The successful employment of sheepdogs and working elephants to perform economically productive tasks, and also the use of performing animals such as dolphins or seals for the purposes of human entertainment, all require some degree of comprehension by the animals concerned of human commands (e.g. Williams, 1950). There is considerable difficulty, however, in determining whether such reliable following of instructions is due to instrumental learning of the Thorndikean type — that is, stamped-in routine responses to discriminative signals — as opposed to psychologically more complex transmission of information about goals to be achieved. Productive skills of course suffer from the same ambiguity, but the combination of both receptive and productive use of meaningful signals, as appears to be demonstrated in certain of the chimpanzee experiments (e.g. Savage-Rumbaugh et al., 1978b) is more impressive than the following of instructions alone, especially as the instructions given to domestic and working animals are usually of the very simple ‘go’, ‘stop’, ‘turn left’, ‘turn right’ type, which are easily interpretable in terms of conditioned responses to stimuli.

Various experimental studies have however suggested that non-primate mammals may be trained in comprehension exercises not wholly dissimilar to some of those given greater publicity when performed by chimpanzees, although in neither case is any strong theoretical conclusion made possible. Schusterman and Krieger (1984) used a specially developed system of gesture-signs, composed of both arm and hand positions, of a trainer sitting on the side of a pool (very like a whole-word, sitting semaphore), to convey three-sign instructions to California sea lions. The first sign was always a ‘modifier’ such as black, white, grey, large, small; the second was a noun indicating which of several items floating in the pool was to be operated on — including pipe, ball, disc, waterwings and chlorox bottle; and the third was the required action — such as flipper-touch, tail-touch, mouth-touch, fetch, or toss. After two years on gradual training with these signals, one animal was judged to follow correctly 190 three-sign combinations, involving five modifiers, 10 objects and five actions, and another 64 three-sign combinations, involving two modifiers, eight objects and six actions. Very small pieces of fish (15 g) were given for correct responses. It is certainly possible to
view this kind of training as merely a very elaborate form of stimulus-response, instrumental conditioning, but whether or not this is appropriate, successful performance undoubtedly requires (a) significant short-term visual memory, to allow a series of signs to be responded to jointly, and (b) a highly conditional relationship between the immediate stimulus objects (balls, bottles, and so on, since several different objects were always present) and the organized response categories, as both the gesture-signs and the stimulus objects jointly determined motor actions. The internal organization of a large number of putative stimulus-response associations becomes a separate problem from merely that solved by the existence of a mechanism for forming associations, and thus to some extent behavioural complexity alone is a criteria for cognitive achievement.

Herman (1980) reported rather similar learned instruction-following in a bottle-nosed dolphin, again demonstrating at least an extremely flexible and large capacity for forming associations. The same dolphin was also successfully trained in a limited type of sign-production in object labelling (Richards et al., 1984). The animal was first trained to mimic vocally computer-generated sounds within the range of its whistle mode of sound production, but unlike any noises it had previously been heard to make. Then, by presenting a certain object together with one of the computer-generated sounds, as a condition for reward, and then requiring the correct sound to be present for reward, but decreasing the probability that it would be made artificially, the animal was persuaded to produce five sounds selectively according to which of five object categories it observed (ball, pipe, hoop, frisbee and person). There were however no checks that these vocal labels served any referential functions (of the kinds discussed by Savage-Rumbaugh et al., 1983; see p. 335ff) and the five associations are therefore of less theoretical interest here than the cognitive skills of sound mimicry and object recognition. It is however worth noting that the range of learned behaviours of this kind is much greater in dolphins and seals than it is in rats and pigeons (or in invertebrates), and that quantitative factors in learning may be important as an underlay for the achievement of performances which appear qualitatively more impressive.

The brain size, both absolutely and in relation to body weight, of marine mammals (typically over 1,000 grams for dolphins and several hundred grams for sea lions) would provide an anatomical substrate for the storage of large quantities of information. It is far from being the case, though, that learning abilities are always perfectly correlated with brain size. Imitation of human vocalization, which is beyond the ability of chimpanzee, partly because of limitations of their vocal organs, is well within the specialized capabilities of parrots and mynah birds. Such imitative species usually have average to high brain/body weight proportions by mammalian standards, even with the necessary mathematical adjustments for scale (Jerison, 1973), but in absolute size, the brain of even a large parrot is small by mammalian standards. A budgerigar, with a brain of 1 gram, can produce far better imitations of human speech sounds than any chimpanzee, with a brain of hundreds of grams. The vocal imitation should clearly be regarded as a specialized, though not a negligible, skill. Its use gives an appealing apparent plausibility to tests of cognitive discrimination conducted on parrots, since they can give clearly formed verbal answers to verbal questions. Thus Pepperberg (1981) trained an African grey parrot to give appropriate vocalizations when presented with 40 kinds of object — a performance quantitatively in excess of that so far observed in the bottle-nosed dolphin (Richards et al., 1984). Later, the same parrot was trained to give
different answers when presented with the same object (e.g. a yellow triangle) depending on whether it was asked ‘what colour?’ (answer ‘yellow’) or ‘what shape?’ (answer ‘three-corner’) — an arbitrary imitation of human answers given in training). The experimental controls in this investigation leave something to be desired, and Pepperberg (1983) claims only limited accuracy and understanding by the bird with the two perceptually easy dimensions of colour and shape. However, the study serves at least as a reminder that the rote-learning of large amounts of information is not confined to large-brained mammals (see also Vaughan and Greene, 1984).

Visual inference and reasoning

Communicative skills are one thing, internal manipulation of mental symbols another. At least, one should expect that to be the case with species in which language is not obviously the main vehicle of thought. Several tests have been designed to discover not whether a chimpanzee exhibits explicit linguistic skills, but whether it is capable of solving intellectual problems which can be of other kinds.

Transitive inference

One kind of inferential and logical extrapolation is of the type that if A is greater than B, and B is greater than C, this contains the implication that A is greater than C, even if no perceptual comparison between A and C is possible. There is some disagreement as to whether people detect such implications on the basis of linguistic formulae or because of some more concrete internal imagery (Clark and Clark, 1977). Gillan (1981) reports examples of choices by a chimpanzee without special training in communication, which he believes demonstrated a form of transitive inference. If this is the case, the choice must certainly represent transitive inference on the basis of figural, rather than linguistic, mental models (Johnson-Laird, 1983). The aim of Gillan’s training (1981) was to set up an arbitrary selection of colours in an internal ordered series, the test of this series being choices between colours not paired together before. Thus, in a random series of trials, a chimpanzee was trained to choose orange from orange/white, white from white/red, red from red/black and black from black/blue (by putting food in only one of pairs of containers presented with coloured lids). Strictly speaking, there is no logical reason for concluding anything from such a series of trials, apart from noting the relative frequency of food location in each individual pair. However, since orange is always rewarded, and blue is never rewarded, it would be possible to code appropriate choices on a single scale of preference with the order orange, white, red, black, blue — this would be a more economical way of representing previous experience than memories of the outcome with each pair. A consequence of this sort of mental scale of preference should be that white is preferred to black, if these two colours are presented together, even though no experience has been gained with exactly this pair. Only one chimpanzee out of the three studied by Gillan (1981) in fact chose white over black consistently in this sort of test. But for this animal strong and statistically reliable choices suggestive of internal serial ordering of colours was obtained even when a longer sequence was used. (One other animal made similar choices after longer training.) The most revealing control test was that, if the linearity of the inferred sequence was distorted by contradictory trials with the two end-points — that is, in the example above, if blue was rewarded in blue/orange pairings, then the inferred preference (of white over black) disappeared. This supports the hypothesis that the chimpanzee is capable of constructing an internal mental model from a limited sample of experience, the mental model determining

**Analogical reasoning**

A form of reasoning quite different from transitive inference, frequently elicited by paper-and-pencil tests of human intelligence, requires, at least ostensibly, a comparison between two instances of an abstract two-point relationship. Thus, ‘hand is to arm as blank is to leg’ demands a comparison between arms and legs, with respect to the relationship of extremities to limbs, but might conceivably be solvable in a less formal way, by more concrete mental analogies. However, according to Premack (1983), chimpanzees can only solve this sort of problem if they have had formal training in the use of symbols to denote the logical relationships of similarity and dissimilarity. It may be, therefore, that what appears to us subjectively to be concretely obvious may in fact depend upon covert use of abstract, linguistically coded concepts of likeness.

Analogical reasoning was reported by Gillan *et al.* (1981) for the chimpanzee Sarah, who had experienced thorough training with the use of plastic tokens to indicate other objects and relations between them 10 years previously, with intermittent use of the plastic tokens for the concepts of ‘same’ and ‘different’ in the intervening period (Premack, 1971; Premack and Woodruff, 1978; Woodruff *et al.*, 1978; Premack *et al.*, 1978). This animal was thus already extensively trained to place the token ‘same’ between two identical objects, or between an object and another token normally associated with it (as its ‘name’), with similar but contrasting use of the token for ‘different’. For the analogies training these tokens for likeness and difference had to be applied either with geometric figures (differing in size, shape, colour and marking) or with household objects already familiar to the animal (most of whose 16 years had been spent in academic captivity). The chimpanzee was able to answer questions of analogy in two related ways, which I shall describe in the case of examples of household objects.

The chimpanzee’s task (Gillan *et al.*, 1981) was always to produce a consistent array of four objects with ‘same’ or ‘different’ tokens placed between them. Thus if given on one side apple peel together with a peeled apple, and on the other orange peel with a peeled orange, and the two tokens to choose from, the correct response (successfully made) was to insert the ‘same’ token in the middle. In the alternative form of the test, the ‘same’ token was already present, with a banana and banana peel on one side of it, and an orange alone on the other, a choice having to be made between orange peel and a peeled orange for the completion of the array (the animal’s choice, judged correct, being the peel: thus orange peel is to orange as banana peel is to banana).

A range of problems of this type were tested, Sarah being correct in her choices more often than not, but making the occasional apparent error. Given a paintbrush and a piece of painted wood on one side and a piece of marked and torn paper, she choose tape rather than the correct crayon — the target relationship being ‘marking’. This might cast some doubt on the validity of the correct choice of tape to go with marked torn paper when the comparison was with a torn cloth together with a needle and thread — the target relationship being ‘repair’. On the other hand, who is to say that a paintbrush should not be construed as ‘repair’? Clearly the interpretation of the roughly 80 per cent correct choices made by the animal is exceedingly difficult — a variety of cognitive strategies, all falling short of human understanding, may have been employed by Sarah, based on her extensive previous experience. It is however very hard to imagine an explanation for the relatively accurate performance in terms of simple conditioning
processes along the lines of the theory of discrimination learning put forward by Spence (1936) and Hull (1952), and to a large extent the intercourse with common objects and tools as well as arbitrary indicators for the concepts of ‘same’ and ‘different’ ought to qualify as an analogy for human reasoning, at least by comparison with an analogy to conditioned spinal reflexes.

In 1983, Premack reported that Sarah was the only chimpanzee to have performed successfully on the above tests of analogical reasoning (and that by comparison with the performance on similar tasks by human infants, she was at the 6—year-old rather than the 4—year-old level). However,

there was one other test which three ‘language-trained’ (with plastic tokens) chimpanzees passed, while four similar but not thus trained animals failed. They were presented with two objects from a meaningful series of three, for example, an apple and a knife, and given the opportunity to complete the series, for example by choosing a cut apple to add instead of alternatives of a cut orange, or an apple with a nail in it. Premack (1983) supposed that the ‘language-training’ facilitated performance on this task by enhancing an already present abstract mental code. Alternative, or complementary, possibilities are that: (i) since the training with tokens took the form of placing objects in meaningful arrays, the attentional and conceptual learning involved in this transferred fairly directly to the choosing of correct items to make up meaningful groups of three; and (ii) in the case of extensive training with tokens for ‘same’ and ‘different’, the mental representations of these tokens supply a completely new abstract code, which serves as a new tool for thought, and enables animals thus trained to make conceptual choices not otherwise available to them.

Biological bases of animal cognition

One sort of basis for conditioning, learning, and cognition, is the anatomical apparatus of the central nervous system, without which there would be little by way of suitable phenomena available for study. Oakley (1979a, 1983, 1985) has provided several surveys of relationships between the central nervous system and learning and memory, and I shall not pursue this topic in detail here (see Walker, 1983a, chapters, 4,5,7 and 8). The main organizing principle adopted by Oakley (1979a, 1983) has, however, been alluded to in previous chapters (3, 4 and 5) and is worth emphasizing again now: different sorts of internal computation, of different orders of complexity, can be expected to be performed at successive levels of the vertebrate brain. Rather different mechanisms for accomplishing superficially similar behavioural ends may therefore be employed by disparate vertebrate species, and we are entitled to expect, on these grounds alone, that the capacities of a chimpanzee for

receiving, ordering and interpreting the results of life experience will not be identical to that of a lamprey or tadpole, because very different weights apply to the functions of the cerebral hemispheres in the two cases. It might not be worth belabouring this point were it not for the fact that Macphail (1982, 1985) is not entirely alone in seeking to minimize, or to ignore, the factor of species differences in animal learning and cognition (e.g. Mackintosh, 1974, 1983; but see Mackintosh et al., 1985). The evidence from cross-species comparisons of cognitive abilities, like the evidence from comparative studies of brain size (Jerison, 1973), remains equivocal and ambiguous in many respects, but we can rest assured that even the most ardent advocates of species equality in learning are as unlikely to produce data demonstrating analogical reasoning about household objects from laboratory rats and pigeons as they are to produce evidence for
the serial position effect using lists of four coloured slides from the sea-slug *Aplysia*, or from lampreys or tadpoles.

An alternative theoretical basis for biological differences in psychological processes which ought to be more fundamental than brain mechanisms, but which in practice is far more elusive, concerns the evolutionary rationale for species differences, either in terms of the functioning of psychological processes in behavioural ecology or in terms of phylogenetic development. This perhaps is best left as a goal for the future, since there is so little agreement on either the possibility or the desirability of this kind of theoretical basis for psychological matters, but one or two attempts to construct theoretical frameworks for cross-species comparisons may be mentioned. Although obscure, Piaget’s *Biology and Knowledge* (1971) has the virtue of emphasizing natural continuities in information processing mechanisms, while clearly not losing sight of human cognitive excellences (Boden, 1979). The continuities are empirically confirmed by findings such as those reported by Redshaw (1978), who gave tests of intellectual development designed for human babies to infant gorillas in the first year of life. Human babies progress in a predictable order through tasks such as: following moving objects with their eyes; finding a toy after it has been hidden behind a screen; pulling in a toy resting on a flannel; and knowing to desist from pulling the flannel in the same task when the toy is held just above the flannel. Gorilla babies progress through exactly the same tasks in very much the same order, but at a slightly faster rate, failing on only one or two of the tests used for human infants up to the point, at about 18 months of age, when human infants begin to acquire speech, but gorilla infants don’t. Like chimpanzees, the gorillas do not spontaneously point to familiar persons, or hand over toys to human observers (as babies do), activities which have been mentioned above as aiding the development of spoken communication (Savage-Rumbaugh *et al.*, 1983). Neither did the infant gorillas observed by Redshaw (1978) use sticks to retrieve otherwise out-of-reach toys, or pile up building blocks into towers, although adult chimpanzees will gradually learn to do these things to obtain food (Kohler, 1925).

As growth (and formal education) proceeds, the differences between ape and human young of course expand enormously: without minimizing these it was possible for Piaget (1971) to conclude that the development of cognition in the two cases has some common biological roots, with more primitive forms of learning of a sensory-motor kind, in particular associations formed in classical or instrumental conditioning being retained when higher forms of cognition, depending on the internal classification, comparison, and ordering of perceived objects, are successively added in. The details of these theories are perhaps less important than the fact that experimental classification and comparison of animal learning abilities is possible when tests of the development of object perception are conducted. Gradual development of the concept of object permanence can be observed in kittens as well as chimpanzees, at least up to the point of the recovery of play-objects hidden under cloths (Gruber *et al.*, 1971). With infant monkeys it is still possible to use tests of object perception roughly similar to those employed with human babies, and to observe a form of object permanence of some cognitive significance (Wise *et al.*, 1974). The experimental limit of this, which would appear to require both good visual memory and some form of visual inference, is the ‘empty container’ test. A peanut is put into an opaque container, such as a large cup, within an infant monkey’s sight; the container is then
slowly passed behind a screen, afterwards being turned towards the monkey so that it can see whether the peanut is still there or not. If, on seeing that the container is empty, the animal immediately looks behind the screen for the peanut, it has passed the test. Premack (1983) termed this sort of performance in young chimpanzees ‘natural reasoning’, and found that both language-trained (with plastic tokens) and non-language-trained chimpanzees performed at roughly the same level as 4- to 5-year-old children on several different tests of this kind. In one of these, the chimpanzee watches while an apple is put in one bucket, and a banana in another. It is then briefly taken away, returning to find a human individual standing between the buckets and eating either an apple or a banana. Older chimpanzees, and children, immediately go to the bucket in which the other type of fruit had been put; younger ones learn to do this very quickly. Obviously one of the reasons for getting this task wrong could be a failure of memory. However Premack (1983) found that younger subjects were more likely to give wrong responses because they did not seem to make a ‘similarity assumption’ — the hypothesis (not necessarily correct) that the banana being eaten is the same one that had recently been put in a bucket. This assumption of object similarity — or of consistency and stability in the environment, and relatedness between events — is even more apparent in a more complicated test used by Premack (1983). In this, the animal is shown one or two pieces of the same kind of fruit in the trainer’s hands. Then the trainer goes to a different room, or out to a field, and puts whatever fruit there is in a container, in the absence of the animal, going back, manifestly empty-handed, to the animal, which is then taken out to the container to see a single piece of fruit removed from it, and confiscated. Now, if the chimpanzee had seen only one piece of fruit in the first place, it merely grooms itself or stares into the distance. If, on the other hand, two pieces of food had been in the possession of the trainer to begin with, the chimpanzee goes directly to the container to retrieve the piece of fruit which remains in it.

It would of course be possible to perform correctly on this task, given enough training, by differential habits controlled by the two initial stimuli of one and two pieces of fruit. It is however likely that both children and apes react to the problem by incorporating such isolated stimulus events into a more coherent narrative, or network of related events, though not necessarily to the same degree. A particular narrative constraint on a series of simple events, or, alternatively, a development of the concept of object permanence which occurs at a relatively advanced age in human children, demands that a given object does not spontaneously change certain of its quantitative characteristics over time. Thus 7- or 8-year-old children, but not 3- or 4-year-olds, know that orange juice poured from a wide to a narrow glass must in some important sense remain ‘the same’ (provided none is spilled or added), and passing a range of such tests, for conservation of volume and number over a variety of physical transformations, is heralded as an important stage in cognitive development (Piaget and Inhelder, 1969). It is thus of interest that two individual female chimpanzees, Sarah trained with plastic tokens as symbols, and Jane trained with a limited number of sign-language gestures, have satisfied reasonably rigorous tests for conservation of volume (Woodruff et al., 1978; Muncer, 1982), without much special training. By explicit and protracted training on rewarded and unrewarded choices between changed and unchanged displays, Pasnak (1979) demonstrated that rhesus monkeys were capable of arduously acquiring the habit of paying attention to whether an experimenters did or did not add or subtract something to the volume of one of two displays (whether of modelling clay, straws, sponge cubes, or
of many other substances) before further changes to the shape of the displays were made.

All of these experimental details could be regarded as supporting the uncontroversial claim that the biological function of the vertebrate brain is to regulate the animal’s interaction with the external world, if not Piaget’s (1971) particular discussions of this function. A necessary addition to this bald truism is however some or other scheme for classifying the variety of ways and means by which the useful regulation of animal behavior is brought about. The experiments and theories reviewed in previous chapters have presented many possibilities, with emphasis on a cognitive dimension or hierarchy, ranging from simple reflexes to complex ideas. Concern with species comparisons and evolutionary progression has always suggested at least one more dimension of classification: that ranging from the utterly innate to the entirely learned. There is sometimes a temptation to conflate these two dimensions — supposing that all reflexes are innate, and all complex ideas learned. The evidence is quite to the contrary, much experimental work on conditioning and habituation (chapters 2, 3 and 4) demonstrating that the most reflexive of behaviors (including knee-jerk spinal reflexes and internal metabolic processes) are subject to learning, since they become attached to widely varying sets of controlling stimuli, depending on life experiences; while most work on memory and cognition in animal learning suggests that the more complex the mental operation, the more likely it will be constrained by species membership, and thus by inherited predisposition if not by inherited mental content.

Many learning theorists have been guilty of ignoring both variations in information-processing capacity, as between single reflex circuits (Hull, 1943; Carew et al., 1983) and the possibilities presented by whole brains, as well as of ignoring information-processing specializations (such as colour vision in birds and primates, echolocation in bats and dolphins, speech in Homo?) whose style and range of operation must be unlearned, even if all the information thus gathered is not (Fodor, 1983). However, most of the guilty parties have been apprehended (Seligman, 1970) and current trends are towards far more realistic incorporation of biological facts of life into idealized and relatively abstract accounts of the learning process (Lea, 1984a; Krebs and Davies, 1983; Staddon, 1983; Staddon and Simmelhag, 1971).

The evolution of learning

Increasingly, attention is being given to the more fundamental question of how and why the learning process itself should have evolved (as an alternative to the more reliable but less flexible instinctive methods of producing useful behavioural strategies: Maynard-Smith, 1984). Plotkin and Odling-Smee (1981) provide a necessary overview of the problems of applying evolutionary theories to behavioural and psychological questions. They propose that these problems should be made explicit by distinguishing several different levels in a ‘multi-level, multi-process model of evolution’. The first level of this is that at which natural selection operates on the genes — often the only level considered even in analyses of behaviour (Maynard-Smith, 1984; Hamilton, 1964). The second level they call ‘variable epigenesis’: genes are only important in so far as they direct growth and bodily change, and normal growth (epigenesis) is determined by many other factors (including nutrition, temperature, chance) as well. At a third level they put all forms of learning, by which the individual organism is to some extent affected in its own experience of life, rather than by the genetic consequences of the experiences of its
ancestors; and at a fourth level, the ‘cultural pool’, by means of which the mechanism of individual learning becomes a means of transmitting information both across and within generations, while bypassing the relatively slow and painful route of genetic selection.

It is undeniable that processes denoted as learning stretch from changes barely distinguishable from physical growth and maturation (especially early in life) to the nowadays virtually instantaneous transmission of information that may be made possible by human rumour, fashion, scholarship or science. Within the biological context of learning theories, the lesson has gradually sunk in that the animal world contains a hierarchy of strategies for behavioural change, many individual strategies all serving roughly the same purpose and many individual strategies accomplishing a broadly similar function, all being possible in the same species. Thus it is biologically possible to arrange for the decline of responsiveness to a repeated stimulus by a mechanisms of sensory adaptation, by a process more like response fatigue, or by a more complicated procedure of setting up a central representation of the detailed characteristics of sensory input which will allow a repeated stimulus to be recognized as familiar. All these operations might be performed for a single item of behaviour, inexorably linked to only one form of stimulus input, even though a sufficiently rich internal representation of familiar stimuli should qualify as an advanced form of memory. Similarly, to allow individual responses of muscles or glands to become triggered by many alternative inputs, according to various and unforeseen circumstances of life, a number of associative mechanisms might be employed: arrangements might be made for links to be formed between stimulus inputs adjacent in time, between the response as made and whatever input happens then to be present, or between central representations of the environment as perceived and global emotional or cognitive states. And for actions and reactions to change, as surely they should, as a consequence of the costs and benefits which they immediately bring, in so far as these can be assessed by the evaluative procedures of a given brain, then alterations might be made, on the basis of their results, to one or all of reflexes, impulses, habits and intentions.

The detailed evidence in previous chapters suggests that any laboratory study of learning is likely to call into play a large number of these possible processes of behavioural change, crossing boundaries between functional categories such as habituation or anticipatory conditioning, as well as between putative levels of complexity such as reflexive and cognitive learning. However this does not mean it is impossible to separate out such processes, according to experimental variables of species, physiology and behavioural procedure. A simple example discussed in this chapter (p. 310) is that the process of conditioning signal A for a standard motivating event may no longer apply when what is required is the conditional relationship that stimulus A should serve as a signal if and only if stimulus B is present as well. This is the biological range of learning in microcosm — in the animal kingdom as a whole there is clearly a somewhat more vivid contrast between learning processes which change reactions to the world by means of minor adjustments to the strengths of certain reflexes, and those by which an animal internalises knowledge about the world in ways which lead to theories of its mental models or cognitive representations. Although the evidence is as yet fragmentary rather than systematic, it is possible to argue that progressive changes in the course of evolution are reflected in the degree to which species can acquire internal knowledge of the experienced environment, as well as the degree to which they demonstrate physical mastery of it. (Gottlieb, 1984; Mackintosh et al., 1985; Rensch, 1959; Walker, 1986). Whether this argument is correct
in the sense that progressive changes are actually visible in the capacities of monkeys and apes, but not of fish or frogs, to perform the experimental tasks involving memory and inference, is still in doubt (Passingham, 1982; Macphail, 1982, 1985). However, it is certainly safe to claim that any more advanced or more cognitive learning abilities that may be used by primates or other mammals must co-exist with older and simpler associative mechanisms, since these undoubtedly remain (Oakley, 1979a, 1985).

Irrespective of any hierarchies within processes of animal learning, there is a distinction between human verbal and cultural learning and all other possibilities that should arouse little dissent. However the question of whether there are nevertheless points of contact between human skills and principles of conditioning has never been easy to resolve. The learning-theory tradition of Pavlov and Thorndike is of course to see most if not all of human psychology as more elaborate and extreme manifestations of universal underlying necessities. Some subtler account is now clearly called for in order to accommodate both the objections from above, that history and civilization make human learning less biological, and the objections from below, that genetically inherited species differences of some kind mean that human cognition is biologically not dependent on learning (Chomsky, 1976; Fodor, 1983), or that all cross-species comparisons are invalid (Seligman, 1970; Hodos and Campbell, 1969; Johnston, 1981).

If a hierarchy of processes of learning is involved in the biological context, it is perhaps easier to propose that learning processes collectively provide the interface between the natural physiology of human growth and form and the cultural possibilities that limit the relevance of any strictly biological approach to human learning. Since, from the time of William James and Sigmund Freud, it has been unexceptional to assume that human psychology itself is composed of more varied and less refined preliminaries than the end-product of rational thought, it is in some ways surprising that there should be any resistance to the assumption that the components of human habits and motives are not necessarily all immune to natural influences.

Therefore the surrender of general process learning theorists to the claims of species-specializations and human cultural uniqueness does not need to be permanently abject. Principles of learning are not fundamental to everything else in the way that Pavlov (1927), Hull (1943) and Skinner (1953) supposed that they must be, but neither are they biological curiosities that apply only in arbitrary laboratory procedures. If there is a multitude of specialized forms of learning appropriate to a variety of ecological niches, if there is a range of learning strategies between invertebrate reflexes and the social awareness of primates, and if human intellectual abilities will always have to be a special case — then this means that Pavlov and Skinner were wrong in some of their claims, but not that all subsequent theories of learning are doomed to be equally mistaken. Modern emphases on the ecological details and biological functions of natural behaviours, and on differences obtainable in laboratory experiments between reflexive associations and more cognitive forms of learning and memory, both lead to ‘divergences of theory and practice, with a wider spread of types of investigation than I have been able to cover in this book. The divergence is in some ways less satisfying than the simple underlying certainties which all theorists seek for, but the compensation for the variousness of explanation, that now seems inevitable, may be that the variousness is closer to the truth.