Cortical Mechanisms and Cues for Action

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Cortical mechanisms and cues for action

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Monkeys have more highly developed brains and are more intelligent than rats; yet rats learn some tasks as efficiently as monkeys. For example, rats are as quick at discovering which of two doors hides food or how to open the doors. Presumably tasks of this sort do not greatly tax cortical associative mechanisms since the animals have only to cumulate facts about objects. It is argued that cortical mechanisms are crucial for the ability to relate together information that is presented at different times or in different places. After removal of parts of frontal cortex monkeys can still associate cues that are presented together but they are poor at relating cues that are presented apart.

Compared with monkeys rats have very underdeveloped brains. Even if a rat were as large as a rhesus monkey its brain would still be 3.2 times smaller (calculated from Eisenberg 1981). In the laboratory rat the neocortex (with the white matter) forms only 29.7% of the whole brain, whereas in a rhesus monkey the value is as high as 72.2% (calculated from Kruska (1975) and Stephan *et al.* (1981)). It would be reasonable to expect that the rat would lag considerably behind a monkey on tests of cognitive performance.

Yet on certain tests rats rival monkeys. On a visual discrimination task the animal must learn to associate one cue with food and the other with no food. In our laboratory both rats and rhesus monkeys (*Macaca mulatta*) have been given a simultaneous visual discrimination between black and white: the rats pushed doors on which the cue was displayed and the monkeys pushed plastic covers. Though the monkeys tended to learn faster there were rats that out-ranked some of the monkeys (figure 1).

The demands of the task can be increased by requiring the animal to perform one act to one cue and a different act to the other cue. We have taught a conditional problem of this sort to both rats and monkeys. The rats had to open a door by pushing it if it was white and pulling it if it was black (Passingham *et al.* 1985); the monkeys (*Macaca mulatta*) had to pull a handle if it was yellow and turn it if it was blue (Passingham 1985*b*). The task was more difficult than the visual discrimination; but still the rats learnt as easily as the monkeys (figure 2).

On both tasks the animals must form associations, and on both tasks the cues are arbitrary. Yet monkeys fail to outstrip the rats. In general different vertebrate species do not differ very markedly in the rate at which they solve discrimination problems or master the use of a manipulandum (Warren 1965). Why, then, do these tasks pose so little problem to the animal? The tasks are alike in that the animal must learn a property of an object. Either the object covers food or it is to be used in a particular way. Many problems that animals face in nature are of this sort: the animal must learn which foods are edible and how they are to be handled or opened. For example, monkeys deal with nuts and bananas in a different fashion. In the laboratory monkeys have little difficulty in learning discriminations if it is the foods themselves

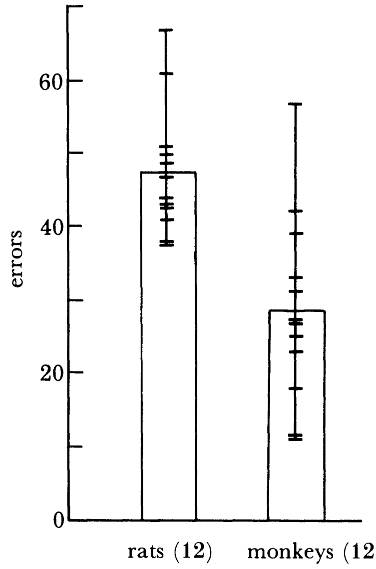

Figure 1. The mean errors to criterion for rats and monkeys to learn a simultaneous discrimination between black (positive) and white (negative). The bars give the scores for the individual rats or monkeys.

that they are given to discriminate or if the cue directly hides the food (Jarvik 1953; Cowey 1968). The animal's task is simply to remember information that is presented together in one place.

Tasks of this sort make few demands on higher cognitive mechanisms. It is usually supposed that one measure of higher intelligence is the capacity to grasp relationships (Thomas 1980). Thus the animal's ability is best tested not by asking the animal to learn that one object hides the food but by asking it to compare two objects and judge whether they are the same or different (King & Fobes 1982). The conditional problem can also be made more demanding. The animals in figure 2 were learning how to use an object on the basis of a property of that same object. The task is more taxing if the cue is separate from the object and the animals must therefore relate the nature of the cue to the usage of the object.

We have devised two tasks of this sort for monkeys. As before the animal has to pull or turn a handle, but the handle always has the same appearance. In one version the instruction is given by the colour of a plastic panel in front of the handle; the monkey starts the trial by

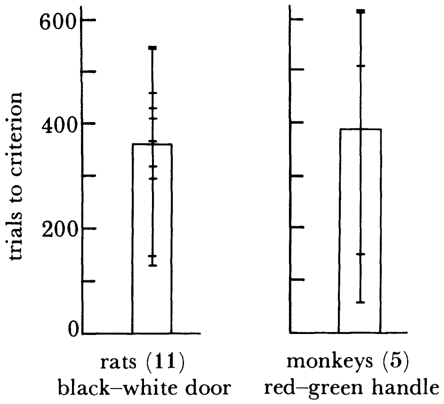

Figure 2. The mean trials to criterion for rats and monkeys to learn a visual conditional motor task.

pushing the panel to one side and must pull the handle if the panel was blue and turn it if the panel was yellow (Halsband & Passingham 1982). In an alternative version it is the colour of the background that provides the cue; the background is a perspex panel that is lit either blue (pull) or red (turn). The task is difficult to teach. We have trained eight monkeys (*Macaca fascicularis*) on the version with the background cue, and only four of them had passed in 1850 trials. Yet the four animals that failed had no trouble in learning to pull or turn the handle if it was the handle that gave the cue. We presented either a small or a large handle: if it was small they had to pull it, if large turn it. The animals took only a mean of 261 trials to master this problem. The animals find it easy to understand that the identity of the object is relevant to the way in which it should be handled; but they are slow to appreciate the relevance of environmental conditions or context.

1. Brain mechanisms

Cues for action

There is a way to test the claim that these tasks require different mental operations and thus differ in kind. This is to find an experimental manipulation such that animals who pass one task fail the other. One such manipulation is to tamper directly with the brain mechanisms themselves. We have been investigating the effects of removing premotor cortex (area 6) on the ability of monkeys to perform conditional motor tasks. Figure 3 shows the subdivisions of frontal cortex into motor cortex, premotor cortex and prefrontal cortex. After removal of premotor cortex monkeys (*Macaca mulatta*) had little or no difficulty in relearning the task if it is the colour of the handle that indicates whether it is correct to pull or turn (figure 4) (Passingham 1985*a*). Yet other monkeys (*Macaca fascicularis*) with a premotor lesion failed to relearn the task when the correct movement was signalled by the colour of the panel in front of the handle (Halsband & Passingham 1982).

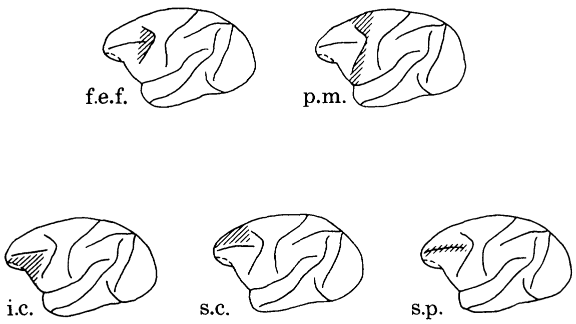

Figure 3. Location of lesions mentioned in the text for the macaque brain. p.m., Premotor cortex; f.e.f., frontal eye-fields; s.p., sulcus principalis; s.c., superior prefrontal convexity; i.c., inferior prefrontal convexity. The motor area lies behind premotor cortex in and in front of the central sulcus.

As a check a further comparison was made. Instead of requiring the animals to pull or turn they were required only to touch the object, but to do so sometimes with the left hand and sometimes with the right. Monkeys can be trained to use one or other hand according to a visual cue (McGonigle & Flook 1978). Two versions of the task were used: in one they were to use the left hand to push the object if it was object A and the right if it was object B; in

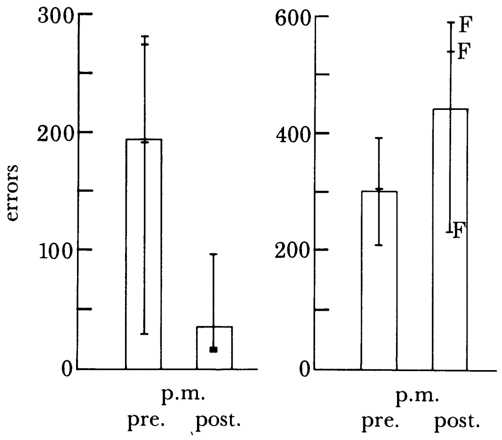

FIGURE 4. Errors to criterion for monkeys with premotor lesions (p.m.) to learn two versions of a visual conditional motor task. For figure on left cue is given by colour of handle. For figure on right cue is given by colour of panel. pre., preoperative learning; post., postoperative retention. Note that the scale for the ordinate differs for the two figures. F, failed in 1000 trials.

the other version they were to push a clear panel with one hand if the bulb behind it was lit red and with the other hand if the bulb was lit green. It was very much more difficult to teach the second than the first of these tasks (figure 5). After the removal of dorsal premotor cortex (and the frontal eye-fields) monkeys (*Macaca mulatta*) had no trouble in learning the use of the correct hand to push the objects; yet they were very poor at learning to push the panel according to the background illumination (figure 5) (Halsband 1982). They could base their action on the identity of the object being used but not on the environmental context.

This dissociation between tasks would be of little interest if it was simply that the monkeys failed to notice the cues unless they were properties of the objects being used. It is implausible that the monkeys would fail to notice the coloured panel as they had first to push it to one side, but the issue is open to test. We need to show that the animal can use the cue if given a different task. Thus Petrides (1982) has reported that after removal of premotor cortex (area

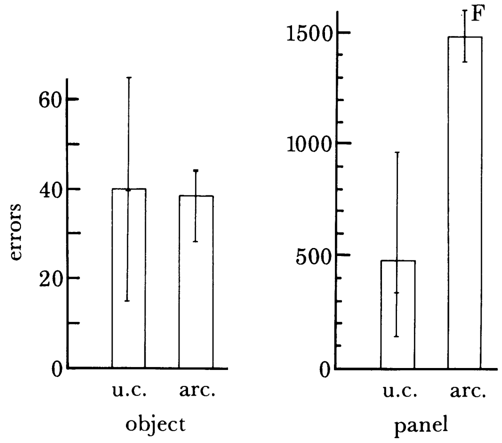

FIGURE 5. Errors to criterion for monkeys with dorsal arcuate lesions (arc.) to learn two versions of task cueing the use of the left or right hand. For figure on left cue is given by the colour and shape of the object. For figure on right cue is the background illumination. Note that the scale of the ordinate differs for the two figures. u.c., Unoperated control; F, failed in 3500 trials.

6 and area 8) monkeys fail to learn to make one of two movements depending on which of two objects appeared in the background; yet the same animals could learn whether or not to touch a rod depending on the object presented at the back. In the first case, but not the second, the object acts as a prompt as to *which* act is to be performed. The animals noticed the cue but they could only use it to tell them whether food was available or not, not what movement to perform.

There is a third way of showing that monkeys with lesions in premotor cortex can use cues to guide their actions so long as the cues are provided by the object being manipulated. This is to require that they move a handle on the basis of prior information about how the handle could be moved. We taught monkeys (*Macaca mulatta*) to reach through a hole and to squeeze or turn a handle that they were unable to see. On each trial the handle was initially locked so that only one of the two movements could be made. The animal was thus forced either to squeeze the handle by flexing the fingers or to turn it by rotating the wrist. Five seconds later it placed its hand on the handle again and was given a free choice of making either movement. The monkeys were rewarded for repeating the movement they had just been forced to make. when the animals had learnt the task dorsal premotor cortex was removed in three animals, together with the tissue in the anterior bank of the upper limb of the arcuate sulcus (Passingham 1985*b*). Although one of the three animals was impaired two of the animals relearnt with few errors; and all three animals relearnt much more quickly than before operation (figure 6). Yet the task is a difficult one; before the operation it took the six animals a mean of 675 trials (352–995) to learn the task.

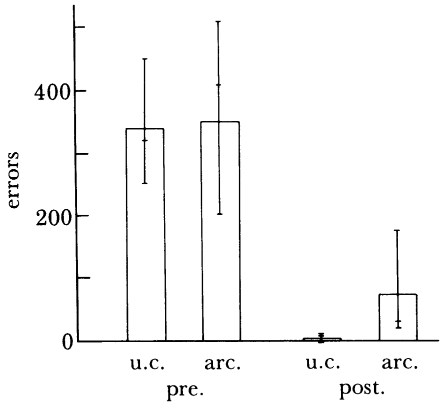

FIGURE 6. Errors to criterion for monkeys with dorsal arcuate lesions (arc.) to learn a motor conditional task in which the cue was a movement (squeezing or rotating a handle). u.c., Unoperated control; pre., preoperative learning; post., postoperative retention.

It seems that the animals understand the relation between the proper use of an object and the nature of that object but not between the use of the object and the environmental context. A similar dissociation can be demonstrated in the case of visual discrimination tasks such as the black–white discrimination discussed earlier. Mishkin *et al.* (1982) have given monkeys two tasks. On the first the animal is presented with pairs of objects and must learn which object is associated with food. Each pair is presented for just one trial a day so that 24 h separate each trial. On the second task the monkey is given an object and then 10 s later required to pick that object out again from a pair. After removal of medial temporal structures monkeys were very poor at the second task but had no trouble with the first. Yet the first task required that the animals retain what they learn over 24 h while on the second task memory was tested over 10 s.

The matching task differs in one crucial respect (see Honig 1978; Rawlins 1985). *Within* each trial the animal must relate one object (the sample) to other objects presented at a later time (the choice objects). On the discrimination task the animal does not have to put together information in this way. The same event repeats on different trials, for example food is found under one object; and the animal has only to record and cumulate the number of occasions on which this event recurs. In the experiment of Mishkin *et al.* (1982) the monkeys with medial temporal lesions could accumulate information about the properties of objects (that they were associated with food) but were poor at comparing objects presented at different times.

Thus the brain treats quite differently the task of learning about the properties of objects (association with reward or correct usage) and the task of relating one object or cue to the task of dealing with another object. In the first case the association is made between information that is presented in the same place and at the same time. The animal must simply remember that information and cumulate its knowledge over trials. In the second case the association is made between information that is presented apart. The animal must perform the cognitive operation of relating the bits of information so as to identify the current situation.

Spatial contiguity

Things and events can be related in space or time. It is possible to dissociate the cortical mechanisms that handle spatial or temporal relations. Experiments can vary the separation between cues in space or the interval between the presentation of a cue and the time at which the animal must respond.

Thus spatial contiguity can be varied by presenting a task on which the animals have the choice of opening the food well on their left or right. A visual cue, say a colour, tells them where the food is to be found. In the contiguous version of the task the cue is visible by the food wells; in the discontiguous version the cue is placed centrally and the animals must first take note of it before responding to the food wells.

Passingham (1971) taught monkeys (*Macaca mulatta*) conditional tasks in which the cue was contiguous with the place to which the animals responded. There were two tasks. In one the cue was a colour: if the board in which the food wells were located was orange the food was on the left; if blue on the right. In the other task the cue was a spatial one: the animals were given a choice between two objects, A and B; if the objects were on their left A was correct and if the objects were on their right then B was correct. In four monkeys dorsolateral frontal cortex was removed, including the frontal eye-fields (figure 3). Yet these monkeys learnt the task as quickly as unoperated animals whether the cue was colour or spatial position (figure 7). They had no trouble in associating the cue with the correct choice if the cue was clearly evident as they opened the food well.

But monkeys with lesions in the frontal eye-fields are impaired at learning to locate food if the cue is presented somewhere other than the point to which they respond. Milner *et al.* (1978) taught monkeys (*Macaca fascicularis*) to choose between left and right on the basis of a central colour cue. After the bilateral removal of the frontal eye-fields (figure 3) the monkeys were slow to relearn the task. That it is indeed the location of the cue that is crucial was clearly demonstrated by Lawler (1980). She directly compared contiguous and non-contiguous

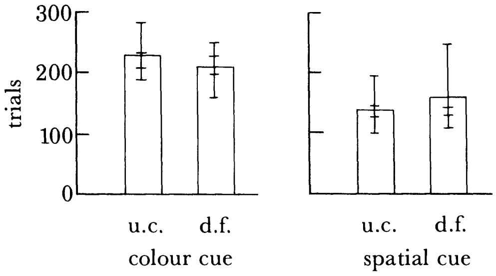

FIGURE 7. Trials to criterion for monkeys with dorsolateral frontal lesions (d.f.) to learn two versions of a conditional task. For figure on left cue is colour, for figure on right cue is spatial. For details see text. u.c., Unoperated control.

versions of the task. A cue, black or white, told the animal whether to open the left or right panels. After removal of the frontal eye-fields on both sides the monkeys (*Macaca mulatta*) learnt easily if the panels gave the cue but they were impaired if they had to use a central cue.

This would not be worthy of note if it were simply that these animals failed to notice the cue at all if it was placed centrally. But we know that the animals did notice the cue since to start the trial they had to push the centre panel to retrieve half a peanut. It is more likely that they failed to pay further attention to the cue once they looked to the left or right. After removal of the frontal eye-fields monkeys tend to neglect visual stimuli and are slow when required to search for them in an array (Latto 1982; Collin *et al.* 1982). They detect stimuli that are presented on their own, but will ignore one stimulus if at the same time another stimulus is presented elsewhere (Rizzolatti *et al.* 1983). In the human clinical literature a defect of this sort is termed an ‘extinction’ defect.

Temporal contiguity

Temporal contiguity can be varied by presenting the cue either at the time the animals makes its choice or in advance of this time. If the tissue is removed in sulcus principalis (figure 3) monkeys (*Macaca mulatta*) can still choose accurately between two food wells on their left and right so long as the cue is present at the time of choice (Passingham 1985*a*). A light appeared either on the upper or the lower of two central panels and the monkey started the trial by pressing the relevant panel. If the upper panel was lit the monkey had to open the left hand door, if the lower panel the right hand door. The monkeys could learn the task normally after the operation even though there was a spatial discontiguity between the spatial cue and the doors to which they responded (figure 8).

Yet monkeys with this lesion fail to learn the task at all if the cue is presented a second or two before the time at which they are allowed to respond. On the standard delayed response task the spatial cue is presented by allowing the animal to watch a peanut being placed in the food well on the left or the right. After removal of the tissue in sulcus principalis monkeys (*Macaca mulatta*) perform at chance or near chance levels (Goldman *et al.* 1971). On the delayed spatial conditional task the animals must choose between left and right on the basis of a non-spatial cue such as a colour or pattern cue, the cue no longer being present at the time of choice. If electrical stimulation is applied so as to disrupt the activity of the tissue in sulcus principalis monkeys (*Macaca mulatta*) are very poor at this task (Cohen 1970).

Damage to other areas of prefrontal cortex also impairs the ability of monkeys to respond

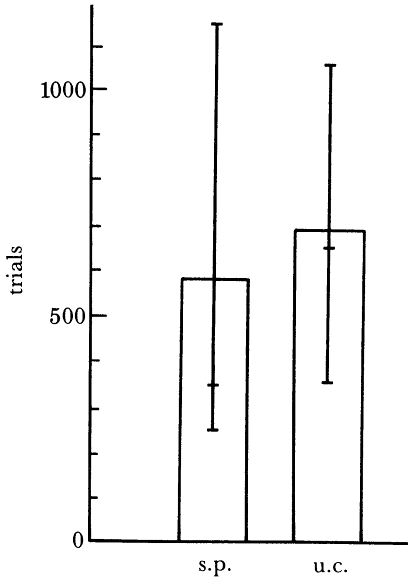

FIGURE 8. Trials to criterion for monkeys with lesions in sulcus principalis (s.p.) to learn a spatial conditional with no delay. u.c., Unoperated control.

accurately on instruction from cues that are no longer available. After removal of the tissue of the superior prefrontal convexity (figure 3) monkeys (*Macaca mulatta*) are poor at a counting task (Passingham 1978). This requires them to press a lit key and to continue pressing until the light goes off; they must then press a second key the same number of times without any further cue as to when to stop. After removal of the tissue of the inferior prefrontal convexity (figure 3) monkeys (*Macaca mulatta*) are poor at a colour matching task (Passingham 1975). On this they must press a central key which is lit either red or green; the cue goes off and they must then press the one of two other keys that bears the same colour.

On all these 'delayed' tasks the animal must make use of an instruction that they can no longer see. There is no evidence, however, that it is crucial that there be a long delay before the animal is allowed to make its choice. On the standard delayed response task monkeys with lesions in sulcus principalis can fail the task completely even if they are allowed to choose only a second or so after being shown the location of the food (Goldman *et al.* 1971). It is important only that their view of the correct location is interrupted (Kojima *et al.* 1982). Similarly both on the counting task and on the matching task impairments can be demonstrated even if the monkey is allowed to respond immediately after the cue has been withdrawn (figure 9).

Either the monkeys suffer from an impairment of memory or they fail to make use of the information even though they have stored it (Passingham 1985*a*). Consider the monkeys with lesions in sulcus principalis. They can learn a non-delayed spatial conditional (figure 6). Thus they are able to use an external spatial cue to guide their choice; and they can also learn to associate one location (left) with one cue (up) and another location (right) with the other cue (down). Yet they are unable to make sense of the problem if the spatial cue is internal even though it was visible only a second before.

One possibility must be that when they are faced with an external stimulus that demands attention they fail to attend to an internal stimulus. By analogy with visual neglect this would be equivalent to an extinction defect. As a consequence the monkeys would fail to relate internal

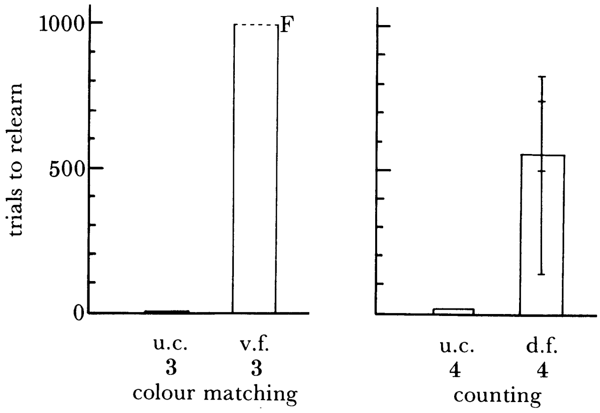

FIGURE 9. Trials for postoperative relearning of a colour matching task (left) and a counting task (right). Monkeys with lesions of the inferior prefrontal convexity (v.f.) were taught the matching task. Monkeys with lesions of the superior prefrontal convexity (d.f.) were taught the counting task. u.c., Unoperated controls.

to external stimuli. On this view prefrontal cortex plays an essential role not in memorizing *per se* but in performing cognitive operations on information stored in memory (Weiskrantz 1982).

In general frontal cortex has the task of relating cues to action. Monkeys with premotor lesions are poor at guiding their action according to visual cues unless those cues are properties of the objects they are using. Monkeys with lesions in the frontal eye-fields neglect cues that are in the periphery of their visual field when they act. Monkeys with lesions in prefrontal cortex fail to act according to internal cues. In all cases the monkeys fail to take account of relevant cues.

The claim that frontal cortex is an associative mechanism is not a new one (French 1964). But it is important to recognize that frontal mechanisms are crucial only where the items to be related are presented apart, whether in space or in time. The monkeys must then appreciate the relevance of cues that are not immediately evident as they act. To assess the current situation they must search for the relevant cues either in their environment or in their head.

2. CONCLUSIONS

Different species

These studies of frontal cortex all presented the animals with conditional tasks on which the correct action was conditional on the cue presented. Tasks of this sort are taxing for animals. Consider the delayed response problem, a spatial conditional task. This task has been given to rhesus monkeys (*Macaca mulatta*) at different stages of development (Harlow & Mears 1979). Monkeys who start training at 60 days old fail to reach a level of 80 % correct trials in 900 trials, whereas adults reach 90% correct in around 150 trials. Yet if monkeys are presented with a black–white discrimination problem at the age of 11 days they can solve it rapidly (Zimmerman & Torrey 1965).

In young monkeys prefrontal cortex is not functionally mature. If prefrontal cortex is removed in a young monkey (*Macaca mulatta*) the animal can still learn the delayed response task at the age of one year (Goldman 1974). Cooling the tissue in sulcus principalis has no effect on the animal's performance at the age of 9–16 months but it has a disruptive effect in mature animals (Goldman & Alexander 1977). The reason that a lesion has no effect in an infant animal is that the prefrontal tissue is not yet making a major contribution.

Similar reasoning will account for data comparing different species, as opposed to the same species at different ages. A rat learns as quickly as a monkey to discriminate black from white (figure 1) or to guide its actions according to the nature of the object being used (figure 2). If neither task makes much demand on cortical associative mechanisms the rat is not penalized, even though these mechanisms are less well developed than in the monkey.

Cortex

On the basis of the evidence reviewed here it is possible to offer a very general account of the nature of these cortical mechanisms. Cortex is well suited to the task of relating information. It is constructed as a layered sheet and the fibres connecting different areas are gathered underneath. There is a great mass of such fibres. In a macaque monkey the neocortex on its own forms 50.2% of the total volume of brain (Harman 1947); but if the underlying white matter is included the figure rises to 72.2% (Stephan *et al.* 1981). Thus in a macaque the white matter, including incoming and outgoing fibres, accounts for around 20% of the volume of the brain. It is easiest to provide for such rich interconnections if the structure is built as a sheet like a printed circuit board. So dense a mass of connections is less easily accommodated within the structure of a nucleus.

With modern neuroanatomical techniques it has proved feasible to trace some of the interconnections between the various cortical areas. It is now known that there is a hierarchical organization: primary sensory areas project to secondary areas, and these in turn to other association areas (Jones & Powell 1970; Pandya & Seltzer 1982). Situated at the top of the hierarchy frontal cortex (premotor and prefrontal) receives information from association areas processing information in all sense modalities. The fact that information is so readily transmitted between cortical areas led Philips *et al.* (1984) to point to a 'distributive' function of cortex.

But it is not simply that information is passed between areas. The hierarchical organization allows for the bringing together of information. If the animal is to relate the elements of a situation, and if the elements are presented in different places or at different times, then the elements will not be analysed initially in exactly the same cortical region. The brain must then correlate the patterns of activity in the different areas or subareas. Philips *et al.* (1984) refer to the role of the cortex in detecting covariation by representing together in the cortex types of event that are related. Because of the hierarchical organization higher-order areas can compare information that was initially analysed in separate regions. The detection of distant relationships is a challenge to cortical mechanisms.

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