

# The architecture of working memory

*John Jonides & Edward E. Smith*

## 8.1 INTRODUCTION

We begin with a simple observation: cognition requires memory. Every intelligent being has some form of memory play a critical role in its higher cognitive function. This is true of any complex computing device, it is true of any animal that is respected for its cognitive skill, and it is true of humans. In fact, the role played by memory in cognition is sufficiently complex that just a single memory will not do. Rather, computers, humans and other animals have all developed (some by evolution, some by design) multiple memory systems that aid in higher level cognition. Our goal in this chapter is to examine one of these systems, working memory, so as to reveal its architecture and illustrate its role in cognitive functioning. Perhaps the best way to begin is with an example which captures the role of memory systems in cognition and highlights some of the features that working memory must have to support higher cognitive function.

Think about mental arithmetic. One of the products of the extensive training we receive in school is the ability to execute arithmetic operations without the use of external aids. Of course, our ability to do this is limited to the solution of relatively simple problems, but in the solution of even these problems we can see the elements of a complex cognitive skill that requires extensive use of memory. To illustrate, think about the operations required to solve the following addition problem “in your head”:

$$\begin{array}{r} 836 \\ + 429 \\ \hline \end{array}$$

Most people begin by computing the sum of 6 and 9, storing the units digit of this sum (5) and carrying the tens digit (1) over to the next column. Then they add this carried digit to the 3 and 2, to give them the desired tens digit, 6. To this point, they would have to hold in memory the original problem and the partial solution of 65. Next, they would move to the third column of the original problem, add the digits there to arrive at 12, which they would append to the 65 that is already

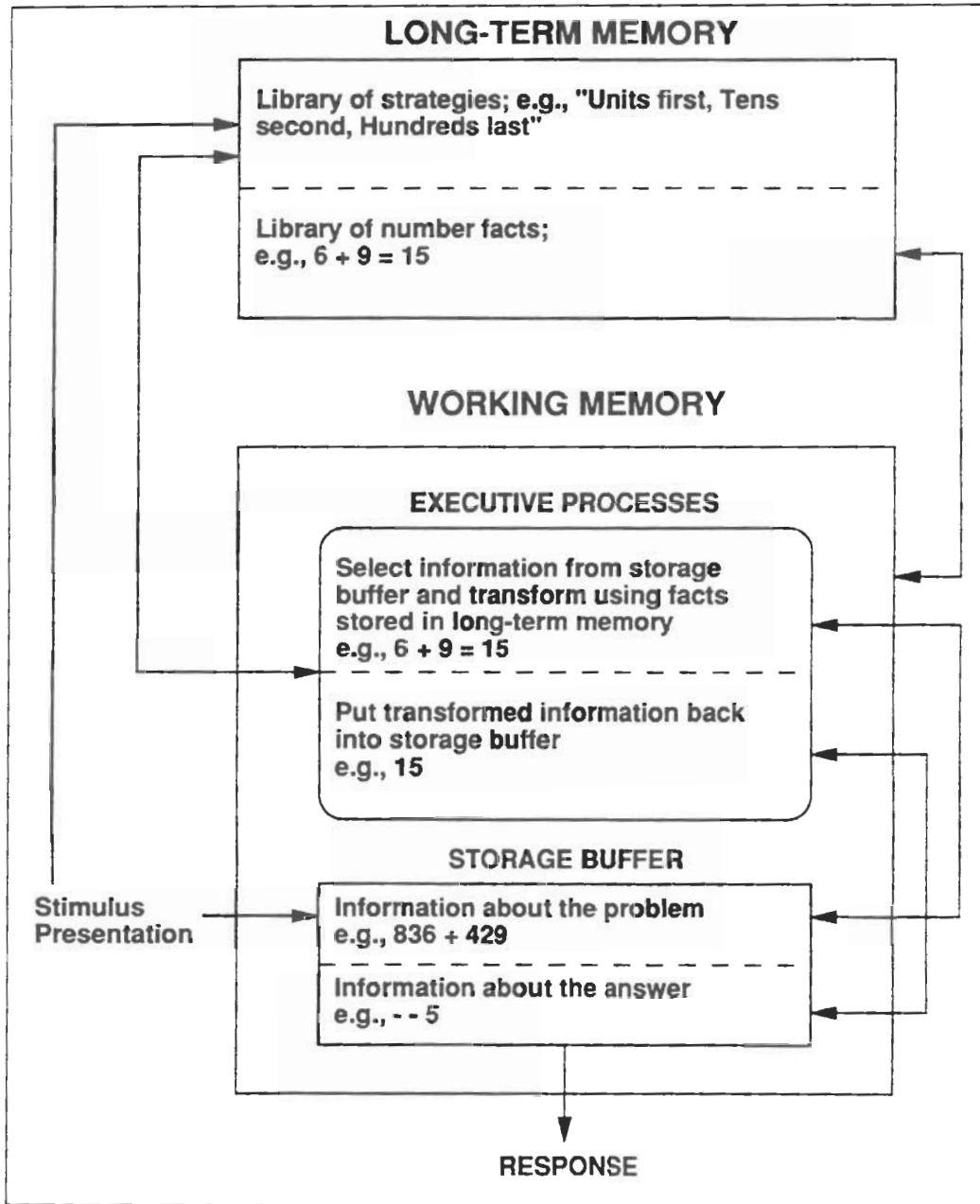


FIG. 8.1. A flow chart after Hitch (1978) showing the processing components necessary to conduct mental arithmetic. Note that long-term and working memory are both required, and that working memory itself is composed of a storage buffer and a set of executive processes.

of executive processes". These processes are presumably responsible for controlling the computations that are performed on the contents of working memory. In performing mental arithmetic, for example, the executive processes would include: shifting attention from the ones column of the problem to the tens column, and then to the hundreds

column as the solution progresses; scheduling the actual numerical operations performed (such as looking up arithmetic rules in long-term memory, applying these rules to the current contents of working memory, adding any carryover from the previous column, and so on); and inhibiting or suppressing the numbers in the problem that have already been taken into consideration. Note that, as the name implies, executive processes control lower-level computational processes. That is, they are not the simple computations such as adding 6 to 9; rather, they are processes such as scheduling the order in which 6 and 9 should be added as compared with 3 and 2. Note further that this characterization of executive processes implies that they are several in number. In our illustration, one is attentional, being able to focus attention on one part of a problem to the temporary exclusion of others. Another process is inhibition, being able to inhibit previous information that was the focus of attention so that new information can be put into the spotlight for current processing. Yet another process is a scheduling operation that allows us, for example, properly to order our work on the units digits before working on the tens digits. Still another process might be setting priorities for different tasks if we are doing something else at the same time that we are trying to solve this arithmetic problem. (For

as the model proposed by Hitch (1978) illustrates, working memory is not an end in itself; it is a system that is designed to serve higher mental processes (Baddeley 1986).

At this point, we have a reasonably clear idea of the psychological functions of working memory and of its major behavioural characteristics. We can turn now to considering the architecture of working memory in more detail, which will lead us to an examination of its neural implementation. Let us begin with working memory for verbal information (such as arithmetic problems), since this is probably the most frequently used part of the working memory system for humans.

## 8.2 VERBAL WORKING MEMORY

### 8.2.1 Behavioural evidence

You can get a reasonably clear idea of the major components of verbal working memory by thinking about a common example, storing a telephone number. Once you have found the number you want in a directory, what is involved in storing it? First, of course, the number must be placed in a storage buffer of the sort we described in connection with our analysis of mental arithmetic. Consistent with our description of that buffer, however, we know that the number will be quickly forgotten if attention is not paid to it constantly. For verbal material such as telephone numbers, our introspections tell us that paying attention is accomplished by covertly speaking the number repeatedly, what psychologists have called "maintenance rehearsal" or "rehearsal". This example suggests, then, that there are two components to verbal working memory, a storage site and a rehearsal process that recirculates the contents of storage for as long as needed.

Going beyond introspection, we can document the functional separability of verbal storage and verbal rehearsal by examining some behavioural experiments. The logic of these studies is this: if there are two components of working memory that are separable, then one ought to be able to identify two experimental variables, where one variable influences the operation of the first component of working memory but not the second, and the other variable influences the operation of the second component of working memory but not the first. This pattern of results is called a "double dissociation". If one could not find a double dissociation for two putative components of working memory, then it would not be clear what is meant by the claim that they are "functionally separable". Of course, it may not be easy to identify two variables that have the predicted effects. Happily, however, there have been some successful behavioural studies of storage and rehearsal in verbal working memory

that provide compelling evidence for the notion that there are two components, i.e. that provide a double dissociation.

The experiments are based on a view of rehearsal that characterizes it as a kind of internal tape-recorder loop that recycles the contents of a verbal storage buffer. Baddeley et al. (1975) reasoned that if rehearsal is like a tape loop of limited length, then the number of items one should be able to rehearse and keep refreshed should be limited by the length of the items themselves. They confirmed this prediction in a series of experiments showing that longer words are more poorly remembered than shorter words, even when the words have the same number of syllables. For example, compare the words "bishop" and "voodoo"; it takes longer to articulate the second of these than the first, even though they are both two-syllable words. Baddeley et al. (1975) demonstrated that the immediate recall of lists composed of words that take longer to articulate was poorer than the immediate recall of lists of shorter words. This result has been interpreted as evidence that word length affects the success of rehearsal without affecting the storage of words *per se*.

Another variable that affects verbal working memory is phonemic similarity (e.g. Conrad 1964, 1970). Words that all sound alike are more difficult to remember than are words that sound different from one another. The effect of phonemic similarity has been attributed to the storage component of working memory, specifically to confusion that occurs among items stored in a verbal buffer. Presumably, the features of the items become interposed with one another, resulting in a loss of item information, which, in turn, results in poorer recall (Baddeley et al. 1984, Baddeley 1986).

Now we have evidence of two variables that affect verbal working memory: word length and phonemic similarity. If these two variables have their effects by influencing the operation of rehearsal and storage

it might be possible to isolate a component of the circuitry that represents storage and a component that represents rehearsal. Of course, this need not be so. It could be that the representations of storage and rehearsal are so distributed in the brain, with substantial overlap, that it would not be practically possible to isolate one from the other anatomically.

It turns out, however, that it is possible to separate storage and rehearsal components. Several studies using positron emission tomography (PET) (see Ch. 6) have now led to a reasonably clear view of which parts of the verbal working memory circuitry are devoted to storage, and which parts are devoted to rehearsal. Consider one experiment from our laboratory (Smith et al. 1996; see also Paulesu et al. 1993, Awh et al. 1996). The task required subjects to maintain verbal information in working memory continuously, thereby forcing them to use storage and rehearsal strenuously. Subjects saw a stream of single letters appear on a screen, each for 0.5s, with 2.5s intervening between letters. As each letter appeared, subjects had to decide whether or not it matched the letter that had appeared two items back in the sequence (hence this is called a "two-back" task). Note that, in order to be successful in this condition, subjects must always maintain in memory representations of the two most recent letters to compare with the current one, and constantly update their representations as new letters appear.

Two control conditions were also tested. One control required subjects to search for a single target letter in a sequence similar to that presented in the two-back condition. The visual and response events in this "search" task were quite similar to those in the two-back task, but the working memory requirements were minimal. When brain activations in this search task were subtracted from those in the two-back task, two major sites of activation were revealed. One was in posterior parietal cortex in the left hemisphere. What is its function? An answer comes from noting that the most frequent site of damage in patients who have deficits in verbal working memory is posterior parietal cortex (see e.g. McCarthy & Warrington 1990). Thus, it seems reasonable to conclude that the activation in this region reflects the storage of verbal material.

The other major site of activation found in this experiment included a trio of locations in left prefrontal cortex: one in the inferior frontal gyrus (in the area called Broca's region, after the neurophysiologist who is famous for documenting its function in language), one posterior to this in premotor cortex, and one more superior in the supplementary motor area (SMA). These sites have been implicated in the production of speech (see e.g. Hinke et al. 1993, Paulesu et al. 1993). Thus, it seems

reasonable to infer that their function in this task is the production of an internal speech code of the sort required for rehearsal.

The other control condition included in this experiment confirms that rehearsal in the form of internal speech is involved in the two-back task. In this control condition, subjects were presented with a stream of letters, just as in the two-back task, but they were required only to emit a manual response upon presentation of each letter and then silently rehearse the letter to themselves until the next one appeared. Thus, this condition duplicated the perceptual and response requirements of the two-back condition, but required only rehearsal with virtually no memory load compared with the two-back task. So, subtraction of the activations in this "rehearsal" control from those in the two-back task should have yielded left-hemisphere posterior activations if these activations represent storage, but it should have eliminated left-hemisphere anterior activations if these represent rehearsal. We did find that the posterior parietal activation was still reliable in this subtraction. We also found that the anterior activations in Broca's area and premotor cortex were no longer statistically significant, also consistent with predictions. All in all, the results of our experiment confirm nicely the involvement of left posterior parietal cortex in storage and left prefrontal cortex in rehearsal processes.

Finding that storage and rehearsal are dissociable in terms of the neural circuitry suggests that there may be patients with damage to one mechanism with the other mechanism spared. Indeed, this is so. We have already alluded to the fact that there are many cases of patients with left-hemisphere posterior brain damage who show deficits in verbal working memory tasks (Shallice 1988). One such patient, for example, cannot recall more than a single item when presented with a string of letters in random order and asked to repeat them back. There is also evidence that patients with damage to their speech production centres in anterior parts of the brain show impaired working memory performance (Swinney & Taylor 1971). Their retrieval of verbal information is markedly slowed compared with control subjects. These patients presumably have damage to the structures that are involved in rehearsal.<sup>1</sup>

All in all, the case is compelling that verbal working memory consists of two components. One component is responsible for storing information and the evidence points to a posterior brain location for this com-



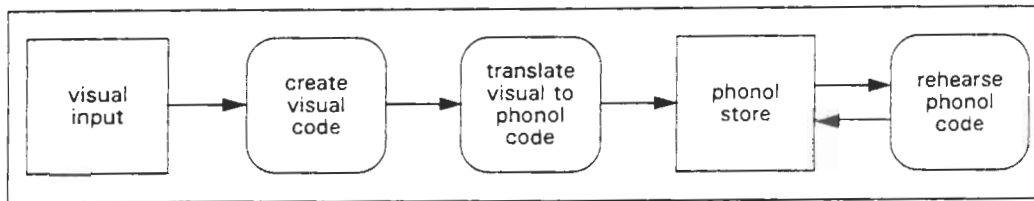


FIG. 8.2. A schematic flow diagram of processes involved in verbal working memory when the input to memory is visual. Note that the diagram includes different sorts of internal representational codes that need to be created, as well as storage and rehearsal processes.

stored in working memory is given in Figure 8.2. First, this information would be encoded visually, using mechanisms of the inferior temporal lobe that are beyond the scope of this chapter. This visual code would then be translated into a phonological one. The brain areas responsible for this translation are not well understood; however, various investigators attribute this step to posterior mechanisms (see e.g. Posner & Raichle 1994). This code would then be entered into a verbal storage buffer, which is presumably housed in parietal cortex, and recirculated by rehearsal mechanisms of the frontal cortex.

### 8.3 MULTIPLE WORKING MEMORIES

#### 8.3.1 Neuropsychological studies of spatial working memory

The foregoing discussion is clearly incomplete. If working memory is to play a central role in cognition, it must be capable of storing and manipulating information in a variety of codes, not just a linguistic one (e.g. Kosslyn 1980, 1981, Byrne and Johnson-Laird 1989). Think about the mental processes involved when you try to comprehend a set of directions for getting from your present location to an unfamiliar destination. For many people, this task involves translating a linguistic representation (the verbal utterance that corresponds to the directions) into a spatial one. Then the spatial representations for various parts of the route are combined to give an overall plan for the itinerary in question. Storing the parts of the route, adding new parts to it, and manipulating the representation mentally constitute a working memory task, one that relies on a spatial representation quite different from the verbal representations we have discussed thus far.

There is compelling evidence that the circuitry for spatial working memory differs from that for verbal working memory. An experiment from our laboratory using positron emission tomography (PET) measurement demonstrates this (Smith et al. 1996). Subjects were presented with a stream of letters during each PET scan, as illustrated in Figure

8.3. Each letter was displayed for 0.5s, with 2.5s intervening between successive letters. As shown in the figure, the letters were displayed at seemingly random locations around the perimeter of an imaginary circle, and the letters varied in whether they were upper or lower case. These presentation parameters were used for two separate experimental conditions. In one, subjects were responsible for storing spatial information, and in the other they were responsible for storing verbal information. In the spatial memory condition (shown at the top of Fig. 8.3), for each letter subjects had to decide whether it matched in position the letter that appeared three previously in the series, regardless of identity (this is a "three-back" task, analogous to the two-back task described above). In the verbal memory condition (shown at the bottom of Figure 8.3) subjects had to decide whether each letter matched in identity the one that appeared three previously in the series, regardless of its spatial position. Because the case of the letters was varied, the matching decision had to be made on the basis of letter identities, not visual shapes.

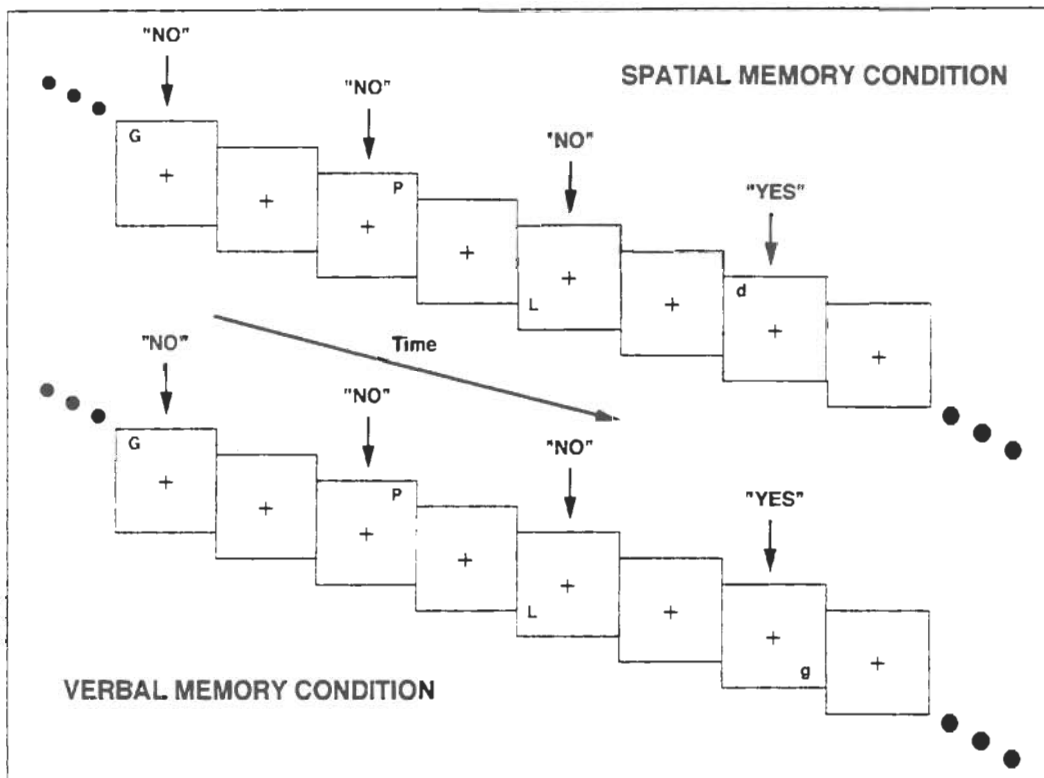


FIG. 8.3. Schematic diagrams illustrating the procedures in two three-back tasks. The upper panel shows the sequence on a trial in which the subject would have to match each letter-position to the position of the letter that appeared three back. The lower panel illustrates the sequence of letters that would be shown in a trial in which the subject would be responsible for matching each letter to the letter that was shown three back.

In order to remove unwanted processes not directly related to storage, Smith et al. (1996) used two control conditions, one for the verbal memory task and one for the spatial memory task. In the spatial control condition, subjects were shown three target positions (marked by dots) at the beginning of a stimulus sequence that was largely identical to the sequence shown at the top of Figure 8.3. Subjects then had to decide whether each position in the sequence matched one of these three target positions. In a similar way, in the verbal control condition, subjects were shown three target letters at the beginning of each sequence, similar to the sequence shown at the bottom of Figure 8.3. Subjects then had to decide whether each letter in the sequence matched one of these three target letters. The activations from these control conditions were then subtracted from those of their respective memory conditions.

Figure 8.4, which has been reproduced on page 152, displays right, left and superior renderings of brains on which have been superimposed the PET activations from the three-back tasks, separately for the spatial and verbal conditions. The activations are shown as coloured splotches that code increasing activation as yellow and red areas superimposed on the magnetic resonance images of the brains. Although there was clear evidence of bilateral activation in both tasks, in the spatial task there was more activation in posterior and anterior areas in the right than those in the left hemisphere. Conversely, in the verbal task, the activations in the left hemisphere were higher than those in the right hemisphere. This presents us with a double dissociation between spatial and verbal working memory at a global level of analysis.

At a finer level, the verbal task resulted in activation in several regions. As in the two-back verbal task described above, there was activation in posterior parietal cortex in the left hemisphere. As we have argued, this region seems to be associated with the storage of verbal information in working memory (Paulesu et al. 1993, Petrides et al. 1993b, Awh et al. 1996).

In addition to the posterior activation, Broca's area in prefrontal cortex showed reliable activation, as in the two-back task. However, the three-back verbal task did not show evidence of activation in premotor or supplementary motor areas; but this may be because the verbal control task itself may have involved some rehearsal, and some of the activation due to rehearsal may have been subtracted from the verbal memory condition (as argued by Smith et al. 1996). The verbal memory condition also shows evidence of activation in dorsolateral prefrontal cortex in the left hemisphere, an area that has been found in other complex verbal working memory tasks and that may be a signature of the operation of executive processes rather than storage or rehearsal

processes (Petrides et al. 1993b, Cohen et al. 1995). We shall return to this point later.

Figure 8.4 shows that the spatial memory condition minus its control also showed activation in posterior parietal cortex, but the activation was largely in the right hemisphere. This is consistent with other PET studies of spatial working memory that have repeatedly found activation in right parietal cortex (Jonides et al. 1993, Petrides et al. 1993b). By analogy to the posterior activation in the verbal task, we attribute this site of activation to spatial storage processes.

Note that the spatial memory subtraction also shows substantial evidence of frontal activation, also concentrated in the right hemisphere. One site of this activation is in premotor cortex. Recall that this is one of the sites which, when activated in the left hemisphere in a verbal memory task, we attributed to part of a verbal rehearsal mechanism. It is tempting to draw an analogy between these two results, and suggest that subjects have the capability of engaging a spatial rehearsal mechanism when they are storing spatial information, just as they can engage verbal rehearsal when storing verbal material. It remains to be seen whether this case can be made empirically (but for some evidence concerning this case see Awh et al. 1995).

The neuroimaging data from our laboratory confirm a division between verbal and spatial working memory that has also been suggested by comparison of the working memory deficits of two patients. Consider first patient P.V. At the time of the report by Basso et al. (1982), P.V. was a 28-year-old, right-handed woman who had had a stroke, with subsequent commissurotomy. Her lesion was quite large, extending over the full anterior-posterior extent of language areas in the left hemisphere. Given the size of her lesion, her language functions were remarkably intact. However, she had a noticeable inability to comprehend auditorally presented sequences of digits. This observation was documented by Basso et al. (1982), who showed that on memory-span tests with digits, letters or words, P.V.'s memory span was worse than would be shown by normals. For example, when tested on ten digit strings each string being 5 digits long, she was able to recall only one string completely correctly; normal subjects typically get all ten strings completely correct. This performance is to be contrasted to P.V.'s perfectly normal spatial working memory. This was tested using a standard neuropsychological task called the "Corsi blocks" test. In this task, the experimenter touches a set of randomly arrayed blocks one at a time, and then the patient repeats the order by touching the blocks one at a time. For this test, P.V. was given strings of span-plus-two in length with repeated presentations of each string until she was able to repeat each string three times perfectly. She needed 11 attempts to

reach this criterion, compared with a group of normal controls who needed 11.8 attempts on average. These results indicate that P.V.'s verbal working memory span is considerably worse than her spatial span, which appears normal.

Contrast P.V.'s performance on these tasks with that of patient E.L.D., studied by Hanley et al. (1991). At the time of their study, E. L. D. was a 55-year-old, right-handed woman who had suffered an aneurysm of the middle cerebral artery in the right hemisphere which had led to a haematoma in the area of the Sylvian fissure some 6 years previously. Her major cognitive deficit was an anterograde amnesia for spatial and visual information with which she was unfamiliar prior to her trauma. When tested on the Corsi blocks task, she was noticeably worse than normals, indicating a deficit in spatial working memory. For example, E.L.D. correctly recalled no sequences of length 5, compared with a group of normals who recalled 70% of sequences of this length perfectly. E. L. D. showed no deficit in verbal working memory, however, performing comparably with normal controls. When given three sequences of six phonologically different letters to recall, E.L.D. recalled all sequences perfectly, in contrast to controls who recalled only 1.4 sequences on average.

It thus appears that the circuitry for verbal and spatial working memory are differentiable. This accords well with behavioural evidence, indicating that one can identify experimental variables that selectively affect verbal or spatial working memory differently (Brooks 1968, Logie et al. 1990). The model shown in Figure 8.2 needs to be amended to recognize this evidence. If we assume, as the evidence

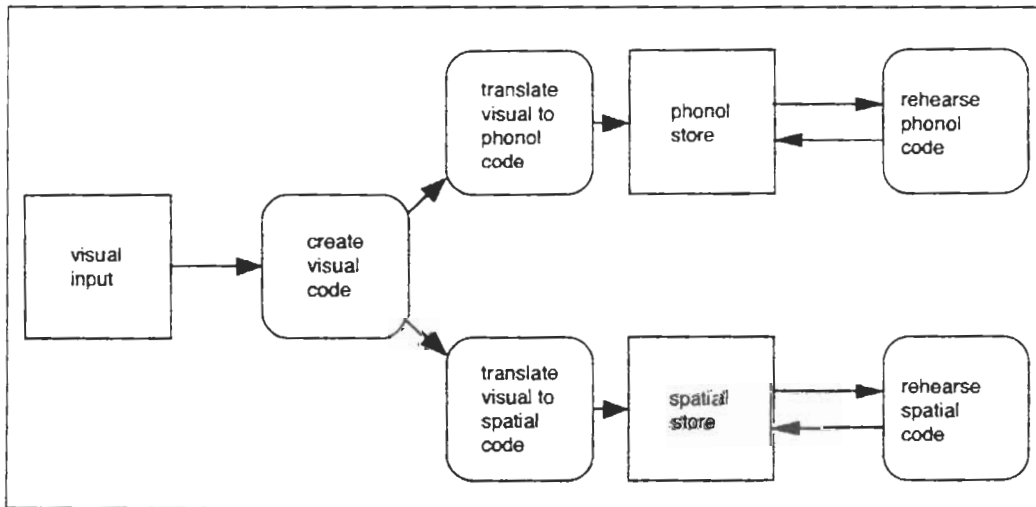


FIG. 8.5. An elaboration of the model shown in Figure 8.2 to include processes responsible for creating a spatial code and for storing and rehearsing that code in working memory.

indicates, that spatial storage may be accompanied by spatial rehearsal, then we can summarize our model as shown in Figure 8.5. This figure shows that, when visual information is presented to a subject, depending on the kind of information and task demands, the subject can create a visual code to be translated into a phonological or a spatial code for storage and manipulation in working memory.

### 8.3.2 Spatial working memory in monkeys

Verbal working memory must be a uniquely human capacity, humans being the only animals with a fully developed language system. However, the same need not be true of spatial working memory. In fact, some of the most detailed evidence about spatial working memory comes from experiments that have used monkeys as subjects.

For some time, it has been known that lesions to the dorsolateral prefrontal cortex cause deficits in monkeys' spatial working memory. For example, examine the pair of tasks illustrated in Figure 8.6, taken from Goldman-Rakic (1993). In the left panel, the animal is engaged in a working memory task called the "delayed response" task. The monkey is shown two locations in one of which food is placed. It cannot reach for the food immediately, however; rather, an enforced delay of several seconds is introduced so that the animal must rely on its memory of the baited location, as shown in the second row of the left panel in the figure. Then, in the third row, the monkey is allowed to reach for the food. In this task, the location of the food is changed from trial to trial, and so the animal must remember the relevant location in each particular trial in order to be rewarded. Performance in this delayed response task is dramatically degraded if an animal has lesions in the dorsolateral area of prefrontal cortex. By contrast, if the same lesioned animal is given another delayed response task, but one that does not require working memory, it performs normally. This is shown on the right in Figure 8.6, which illustrates what is sometimes called an "associative memory" task. Again, one of two locations in the stimulus array is baited, but this time the location is marked by a unique stimulus, as shown by the "plus" sign in the figure. Then the animal has a forced delay, following which it can reach for the food. The food is marked by the "plus" sign, regardless of the side on which it appears, and the animal, even though lesioned, can learn to use this associative cue to find the reward. This experiment illustrates that, in monkeys, dorsolateral prefrontal cortex is critical to the maintenance of spatial information in working memory, but it is not necessary for all memory, as the associative memory task shows.

Further studies of spatial working memory in monkeys reveal a remarkable finding. Not only can one identify working memory with a

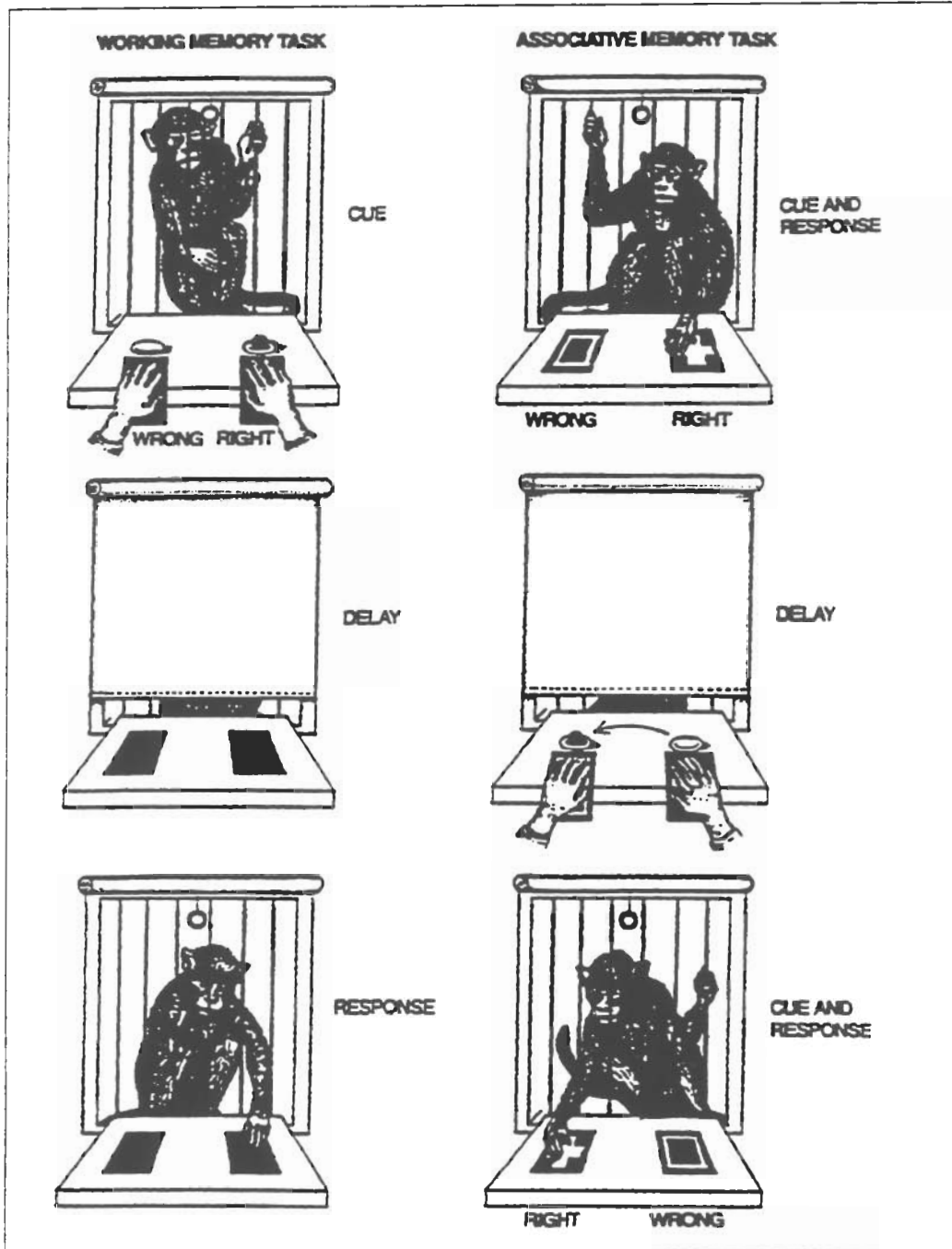


FIG. 8.6. Illustrations of a delayed response task and an associative memory task that have been used to test memory in monkeys. Adapted from Goldman-Rakic (1993).

particular region of prefrontal cortex, but one can also show that individual nerve cells in this region behave as if they themselves are the mechanism of the memory storage. This is most impressively illustrated by considering an experiment by Funahashi et al. (1989). Three

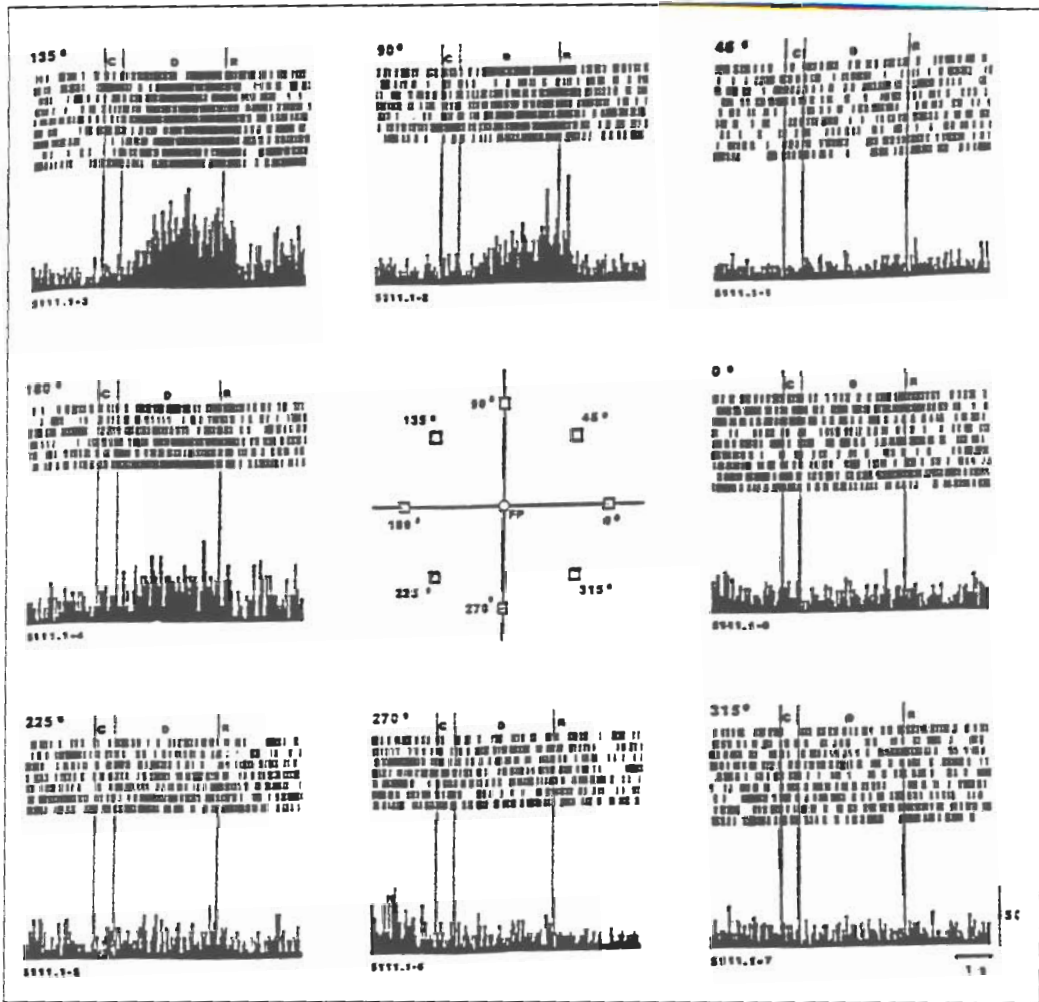


FIG. 8.7. Illustration of a task used to test spatial working memory in monkeys together with illustrative recordings from a single neuron from which recordings were taken on this task. From Funahashi et al. (1989).

monkeys were taught the working memory task shown schematically in Figure 8.7. The monkeys learned to fixate a spot in the centre of a screen to begin a trial. This is marked by “FP” (“fixation point”) in the figure, in the centre of the schematized display. After fixation was achieved, a monkey would be shown a small square that could appear unpredictably at one of eight locations surrounding the fixation point. The animals were trained to maintain their fixation while this square was presented and to continue fixation during a 3-s retention interval that followed presentation of the square. Following this period, the fixation point disappeared, which served as a signal to the subject to shift its gaze to the location that had contained the square on that trial. The design of this procedure requires the animals to maintain a



memory of the location of the stimulus on each trial. Since the relevant location changed from trial to trial, presumably the spatial information was being stored in working memory. The experimenters recorded the responses of individual neurons in the region of the principal sulcus in dorsolateral prefrontal cortex while the monkeys performed the task.

The experimenters found a number of neurons with responses similar to the ones shown in Figure 8.7. The figure includes data from a single neuron when the animal was shown stimuli at each of the eight locations used in the task. Each of the graphs plots the responsiveness of the neuron as the number of spikes per second during each of the epochs of a trial: before a stimulus cue was presented (the first period in each graph); during presentation of the cue (denoted by "C"); during the delay interval, while the animal presumably retained the location of the cue (denoted by "D"); and during the response interval, when the animal shifted its gaze to the cued location (denoted by "R"). Focus on the responsiveness of the neuron when the cue was presented at the location labelled "315°". You can see that the cell did not change its basal level of responsiveness during the entire trial, indicating that it was not sensitive to the presentation of this cue. By contrast, consider the responsiveness when the cue was presented at the 135° position. While the cell did not discharge with any greater frequency than during the pre-trial baseline, during the delay interval the responsiveness increased dramatically, and then it dropped off again during the interval when a response was required. This pattern is quite different from that when the cue was presented at the 315° position. Note also, that the responsiveness of the cell when a cue was presented at either 90° or 180° was quite similar to that when the cue was presented at the 135-degree position, although with a somewhat lower spike frequency.

What can we make of this pattern of activity by this neuron? One thing to note is that this cell (and others recorded in this region of prefrontal cortex) was selectively responsive during the retention interval of the task; this suggests that these cells have a memory function. Secondly, the activity of the cell was in response to only some of the locations that could be shown, and not to others. These two facts lead to the conclusion that the cell in question encoded and retained the location of the stimulus for a brief period of time, just what would be required of a working memory system. Goldman-Rakic and her colleagues have also shown that cells in this region are connected closely with cells in posterior parietal cortex (Chafee & Goldman-Rakic 1994, Goldman-Rakic & Chafee 1994), in a region similar to the one that is activated in human studies of working memory for spatial information. Furthermore, cells in parietal cortex show the same kind of location-specific and

delay-specific responsiveness as cells in prefrontal cortex. In short, it appears that there is a circuitry including parietal and prefrontal cortex that is specialized for briefly storing information about spatial location in monkeys.

One question that arises from these studies is: What is the nature of the memory that is stored by these cells? Two possibilities present themselves. One is a straightforward conclusion from the obvious details of the experiment: The cells store a representation of the spatial locations themselves. Another possibility is that the cells store not spatial location *per se*, but rather a representation of the eye movement that the animal must make in order to respond properly after the delay interval has passed. According to the first interpretation, the working memory is for spatial location; according to the second, it is for a motor programme that is executed shortly afterwards.

A direct test of these two alternatives comes from an experiment by Funahashi et al. (1993). They trained monkeys on a delayed response task that was a bit more complex than the oculomotor task described above. In this case, the stimuli appeared only to the left or right of fixation point (as opposed to appearing at one of eight locations), but again there was a 3-s delay before the animal could respond with an eye movement. The eye movement varied as a function of the kind of fixation point the animal was given. If the fixation point was a spot, this was a signal to the animal that it should move its eyes to the stimulus cue after the delay period terminated. If the fixation point was a plus sign, however, this was a signal that the animal should move its eyes diametrically away from the stimulus cue after the delay interval. Again, the investigators recorded the responses of neurons in the region of the principal sulcus of dorsolateral prefrontal cortex. Interestingly, they found cells of two types. Some responded during the delay interval to stimuli in a particular location, regardless of whether the animal had to move its eyes to the target or away from it. Other cells responded specifically to the direction of the eye movement, regardless of whether the stimulus cue appeared in one location or another. This pattern of results indicates that there may be at least two different representations stored in the prefrontal cortex of monkeys during a working memory task. One is for spatial position and the other is for a motor programme of an oculomotor response (for a related description, see also Fuster 1995). These results raise the possibility that the representation of spatial location that may be stored in working memory may be a complex mixture of a representation of space *per se* and a representation of motor actions that accompany responding to stimuli in space. Further research is needed to uncover more details of this representation.

### 8.3.3 Working memory for objects

The evidence we have reviewed presents a case that the working memory system is composed of more than one module. A combination of behavioural, neuropsychological, neuroimaging and electrophysiological data convince us that working memory for verbal information is mediated by a different set of brain circuits than for spatial information. This is the case presented by Baddeley and his colleagues in first proposing the idea of a working memory (Baddeley & Hitch 1974, Baddeley 1986, 1992). However, the architecture of working memory storage buffers is still more complex. There is neuropsychological and neuroimaging evidence that a pathway exists in humans and in other animals for the short-term storage of visual information about objects and their characteristics that is different from the pathways for verbal and spatial information. As such, a case can be made for a visual storage buffer in addition to a spatial and a phonological buffer.

Early evidence for an object memory pathway comes from studies of animals with lesions in the prefrontal cortex (e.g. Passingham 1975, Mishkin & Manning 1978). Mishkin & Manning (1978), for example, trained three groups of monkeys on one of three non-spatial memory problems: (a) delayed object alternation, in which an animal was rewarded if, after a delay, it chose an object that it had not chosen on the previous trial; (b) delayed colour matching, in which a sample colour patch had to be matched by the monkey after a delay by choosing one of two choice stimuli; or (c) delayed object matching, in which a sample object had to be matched after a delay by selecting one of two choice stimuli. Lesions in the area of the principal sulcus produced few deficits on any of these tasks. However, lesions in an area just inferior to the principal sulcus (called the "inferior convexity" of dorsolateral prefrontal cortex) produced marked deficits in performance in all the tasks. Note that all the tasks share the feature that animals were tested on memory for objects or for features of objects.

These results, taken together with those on spatial working memory in monkeys, suggest the following hypothesis: the region of the principal sulcus is responsible for storing representations of spatial locations, and the inferior convexity of prefrontal cortex is responsible for storing information about object identities. This hypothesis was tested directly in a later experiment by Wilson et al. (1993), in which they recorded from single neurons in either principal sulcus or inferior convexity regions during spatial or object working memory tasks. The spatial task involved stimuli that were presented briefly to the left or right of fixation while the monkeys fixated the centre of a display. As in the experiment by Funahashi et al. (1989), the monkeys learned to shift their gaze to the location of the stimulus after it disappeared and after

a delay had ensued. The object memory task involved a brief presentation of one of two patterns in the centre of the display screen, after which a delay followed. The monkeys were trained to shift their gaze to the left or right after the delay, depending on which of the two patterns they had seen. Thus, in the spatial task the animals produced one of two oculomotor responses depending on which of two spatial locations they stored in memory, and in the object task they produced one of two responses depending on which of two objects they held in memory.

The results of this experiment revealed that working memory for spatial position and for object shape are the responsibility of different frontal areas in monkeys. Neurons in the principal sulcus were responsive during the delay interval in the spatial memory task but not in the object memory task; conversely, neurons in the inferior convexity were responsive only in the object memory task and not in the spatial memory task. These results are consistent with the neuroanatomical connections to each of these regions. The area of the principal sulcus receives substantial projections from the posterior parietal cortex, a region that is known to subservise spatial vision among other things (Ungerleider & Mishkin 1982). The inferior convexity, however, receives many of its projections from the inferior temporal cortex, which has been implicated in object processing and object memory (e.g. Fuster & Jervey 1981, Miyashita & Chang 1988, Miller & Desimone 1991). Based on this pattern of projections and on the selective responsiveness of the two regions of prefrontal cortex, it seems plausible to hypothesize that there are two pathways for working memory, one for spatial and one for object information. The spatial pathway begins with visual input in occipital cortex, then makes use of a spatial processing apparatus in parietal cortex, with the resulting spatial code being stored in some combination of parietal cortex and dorsolateral prefrontal cortex in the region of the principal sulcus. The object pathway also begins with occipital processing, progresses with object coding and recognition processes in inferotemporal cortex, and continues with storage involving some combination of inferotemporal and inferior prefrontal cortex.

Thus far our inferences about the circuitry of spatial and object working memory derive from studies of monkeys. The data on human working memory for these two types of information also suggest two systems; however, their architecture seems to be somewhat different, making use of the lateralized specialization of the two hemispheres in the human brain and, perhaps, relying more on parietal mechanisms for the storage of information than seems to be the case in monkeys. The data that support this position come from neuroimaging studies described by Smith and co-workers (Smith & Jonides 1994, Smith et al. 1995). Subjects engaged in one of two tasks while PET measurements

were made. In one, they had to retain the locations of three dots for a retention interval of 3s, after which they were probed for their memory of one of the dot positions. In the other condition, they had to retain the identity of two unfamiliar, line-drawn objects for 3s after which a probe object was shown and they had to decide whether or not it matched one of the two objects they held in memory. Each of these conditions had appropriate control conditions associated with it to subtract out processes that were not directly related to storage. When these were subtracted, the resulting brain activations revealed different pathways for spatial and object memory. The spatial pathway included largely right-hemisphere processes, including occipital, parietal and prefrontal sites. The object pathway included largely left-hemisphere processes, mainly in the parietal and inferotemporal areas.

These results are consistent with the general view of spatial and object working memory that derives from the data on monkeys, data that implicate a dorsal stream of processing for spatial information and a ventral stream for object information. However, the PET findings lead to the view that parietal mechanisms may play a more prominent role in storage processes in humans than they do in monkeys. These findings also show that the pathways in humans are consistent with the general fact that spatial processing is a skill for which the right hemisphere seems to be specialized.

The human studies of working memory for objects also suggest a parallel to the rehearsal processes that we have proposed for verbal and spatial working memory. In at least one of the object working memory experiments, there was activation in prefrontal cortex, specifically in the premotor area – an area that has consistently shown activation in spatial and verbal working memory studies. This area, as discussed above, may mediate processes that are involved in generating and refreshing an internal representation of stored material so that it can be protected from interference and decay. At this point, it is premature to conclude that rehearsal is an integrated part of the working memory system for objects, but it is certainly a hypothesis that deserves further scrutiny. If we assume for the moment that this hypothesis has some currency, then we can expand our model of working memory for visual input as shown in Figure 8.8. This figure takes what we had determined previously about the circuitry for spatial and verbal working memory and adds to it circuitry for working memory for object representations, including a rehearsal process.

#### 8.3.4 Other working memory modules

While we have focused on verbal, spatial and visual-object working memories, there is reason to believe that there are other memory

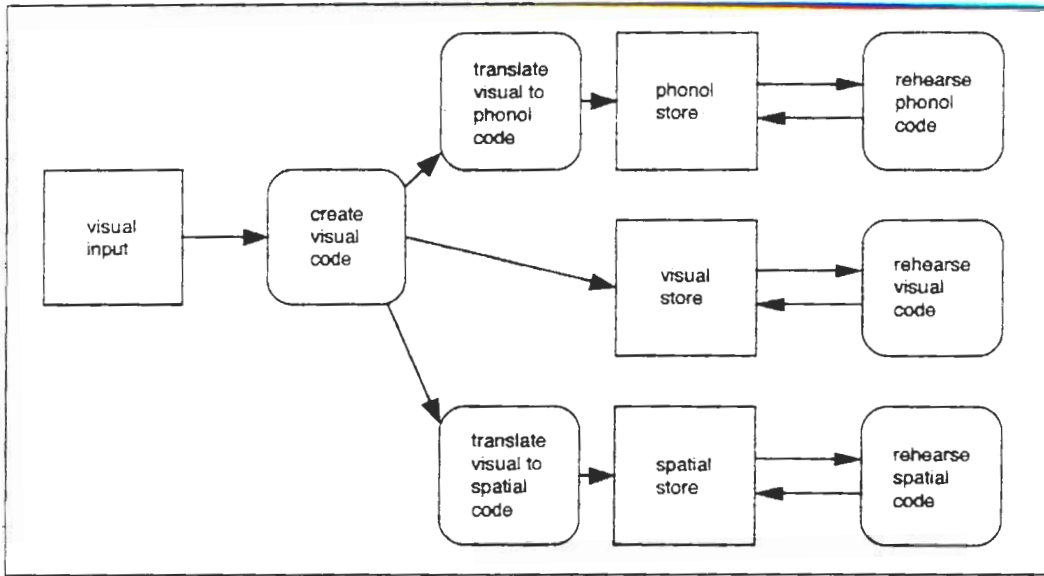


FIG. 8.8. An elaboration of the model shown in Figure 8.5, recognizing a circuit for the processing and storage of information about visual objects.

modules as well. For one thing, there may be a separate working memory module for each major sensory system, perhaps for use in processing the identities of the inputs to these systems. The visual-object module just discussed may be the working memory buffer for the visual system; similarly, there is some evidence for a comparable short-term buffer for auditory information (e.g. Colombo et al. 1990, Zatorre & Samson 1991). In addition, there may be a working memory system that is specialized for storing motoric representations, as indicated by evidence from studies of monkeys (for some relevant evidence see e.g. Gnadt & Andersen 1988, Georgopoulos et al. 1989). However, the case for these further modules has not yet been established with the variety of evidence in both humans and other animals that characterizes the case for verbal, spatial and object representations. Still, as further studies of working memory continue, there may be reason to elaborate the model shown in Figure 8.8, with further modules for yet other kinds of representation.

Assuming that all the above-mentioned buffers exist, note that there is an important difference between those buffers that are tied to a sensory system and the spatial or verbal buffers. Sensory buffers, by definition, store information only from their own input modality, whereas the spatial and verbal modules can, in principle, accept information from multiple input modalities. In this sense, spatial and verbal working memory are relatively abstract; they are not tied to sensory modality, as a recent experiment from our laboratory demonstrates

(Schumacher et al. 1995). In this experiment, the very same verbal information was presented either auditorally or visually in a working memory task; regardless of input modality, the identical working memory circuit was activated.

Another issue that certainly requires further study is this. The prevailing view of working memory is that it stores verbal, spatial and visual codes. These codes, by assumption, are stored in the service of cognitive processes that are engaged in various tasks that require working memory. For example, one could draw on a spatial code of locational information in building up a representation of a familiar environment while comprehending directions. Or one could draw on a visual code as the basis for making similar judgments from memory about two objects that one has stored. Yet again, one could draw on a phonological code of a set of digits in the service of mental arithmetic processes of the sort we illustrated at the beginning of this chapter. What is lacking, however, is any statement about an even more abstract representation, the sort one would need to use working memory productively in the comprehension of language, in problem-solving, in inductive or deductive reasoning, and so on. The critical point is that there must be some sort, or sorts, of more conceptual or propositional representations that are involved in cognition which have not been captured by current conceptions about working memory.

It is worth noting that there is some behavioural evidence that a conceptual code may be stored in working memory (for a partial review see Shulman 1971). Hintzman (1965) found, for example, that recall of letters and digits was influenced not only by acoustic confusions (as reviewed above), but also by confusions in semantic category, suggesting that the category of the items had been coded in memory in addition to the phonological code. Also, Dale & Gregory (1966) and Wickens et al. (1963), among others, have shown that interference in recall in working memory tasks can be traced to semantic factors in addition to phonological ones. This finding allows one to infer that there is a semantic code used for storage. These bits of evidence lead one to suspect that there may be a working memory code for semantic or conceptual information as well as phonological, spatial, and visual codes. However, this issue remains unsatisfactorily resolved at present and requires further investigation.

#### 8.4 EXECUTIVE PROCESSES

The architecture of working memory proposed thus far is incomplete. It lacks any discussion of the processes that make use of information that

is stored in working memory. There are, of course, many such processes. Consider the mental arithmetic task with which we began the chapter. Successful solution of this problem requires ordering of the addition of the three columns in the problem, attending to the number that is carried from one column to another, inhibiting the numbers of a column that has been added when one moves on to the next one, and so forth. The original conception of working memory classed these and other processes under the general heading of a "central executive", but listing them in this way makes clear that there is little reason to view them as a single entity. Rather, it is probably more appropriate to classify these as "executive processes", as we mentioned above, to highlight the fact that there are various such processes used in different task contexts.

Even seemingly simple tasks include some role for executive processes. We introduced one such task above, the " $n$ -back" task, in which a subject is shown a sequence of letters and for each must decide whether it matches the one that appeared  $n$ -back in the series ( $n$  can vary, and was 2 and 3 in the examples discussed). As emphasized earlier, this task loads heavily on storage processes because subjects must constantly have information stored in working memory in order to perform successfully. Note, though, that the task requires other processes too. One such process is a constant updating of the contents of working memory as each new letter is presented in the sequence. Older letters must be dropped or inhibited and new ones added. The requirement to drop and add letters also introduces a need to keep track of the temporal order in which each letter occurred because it is the " $n + 1$ " letter back in the sequence that must be dropped and the newest one that must be added. To accomplish this, there must be a time-tagging of which letter occurred when. Also, a response inhibition process plays a role in the typical version of this task. If the task is a three-back task, for example, there will occasionally be matches to the current letter that appear one-back or two-back, and it would be incorrect to respond to these as matches. So the subject must guard against a positive response in these cases, inhibiting what may be a natural tendency to respond because a match has occurred.

This analysis of the  $n$ -back task suggests that an examination of brain activations in  $n$ -back experiments may provide hints about the locus of executive processes. Indeed it does. Various results from our laboratory, for example, indicate that there is substantial activation in dorsolateral prefrontal cortex; this has also been reported by others for  $n$ -back tasks (Cohen et al., in press) as well as for other working memory tasks that extensively involve executive processes (Petrides et al. 1993a,b). Interestingly, we find that the hemispheric site of this dorsolateral prefrontal activation varies depending on whether the



task requires the processing of spatial or verbal information. For the former, the predominant site is a right-hemisphere dorsolateral prefrontal one, whereas for the latter it is a homologous area in the left hemisphere (for a similar contrast between right- and left-hemisphere prefrontal activation due to executive processes see also Petrides et al. 1993a,b).

The preceding data suggest that at least some executive processes may be the responsibility of prefrontal cortex. If so, then damage to this area should produce deficits on tasks in which the executive processes of working memory play an important role. A classic example of this comes from study of the Wisconsin card-sorting task (Berg 1948). In this task subjects are first given four target cards, each bearing a design in which shape is one dimension of variation (e.g. cross or triangle), colour is another (e.g. red or blue), and the number of figures on the card is the third (e.g. one or two). Subjects are then given a stack of cards to sort, placing each card in front of one of the four target cards depending on what they think the proper criterion is on which to sort the cards. The experimenter has a sorting criterion in mind (say, colour), but the subject does not know this and is simply given feedback about whether or not the placement of each card is correct, according to the criterion. When the subject begins sorting correctly according to the chosen criterion, the criterion is abruptly changed to another dimension (e.g. shape) without informing the subject. Sorting must then continue until the subject has satisfied this new dimension, at which point the criterion is changed again.

This task has an obvious working memory component. Subjects must keep in mind the current sorting criterion, using it as a guide to place each card. The main executive processes that are engaged by the task come into play at the time of a switch of criterion, at which point subjects use the feedback to determine that the current criterion is no longer correct, suppress or inhibit this criterion, generate a new criterion that is consistent with the current feedback (and with that on any previous trials the subject can remember), hold this new criterion in mind, and assess the feedback that comes when it is used as the basis of sorting. Normal subjects have little difficulty with this task, finding the correct criterion within a few trials, and switching to a new one when it is called for within a few trials. Patients with damage to the prefrontal cortex, however, find this task most difficult (Milner 1964). They can find the first dimension relatively quickly, but they then persevere with it when they are required to switch to another dimension. This pattern of behaviour suggests that the patients have little difficulty storing information about a dimension, but they cannot engage the executive processes necessary to accomplish a switch, including the

processing that recognizes various kinds of code for numbers that are necessary to account for our skill in mentally manipulating them.

Given that multiple processes and representations are required to account for our mental skill with numbers, it would not be surprising to discover that there are multiple brain centres involved with number processing. Dehaene & Cohen (1995) have proposed a model of the anatomical representation of number processes that includes structures in occipital, temporal and parietal cortices of the right hemisphere, as well as structures in occipital, temporal, parietal and prefrontal cortices of the left hemisphere. This model makes clear that there is no one centre of numerical representation in the brain, and that elegant co-ordination of processes in multiple brain locations is needed to perform mental arithmetic.

What kinds of numerical representation are created and used by these various anatomical sites? Several possibilities suggest themselves. One is that visual representations of the numbers presented on a page may be created and stored by inferotemporal mechanisms. A second possibility is that these visual representations may be translated into a phonological representation of the problem elements, with this stored by the parietal–prefrontal circuit that we discussed in the context of studies of verbal working memory. A third possibility is that the visual and verbal representations of numbers need to be translated into magnitude representations that can be used for calculation purposes, which may be a function of parietal mechanisms in both hemispheres (Dehaene & Cohen 1995).

The operations involved in mental arithmetic – retrieving number facts, deciding what to carry, sequencing which operations to perform before others, using short-cut strategies that may help with certain problems, etc. – may involve a complex interplay among the neural systems housed in the above-mentioned areas. This seems likely given that the mental operations involve a combination of long-term memory retrieval, short-term storage, sequencing of operations, strategies, and so forth. That multiple mechanisms are involved is suggested by a behavioural study by Logie et al. (1994). Subjects had to keep a running total of a series of two-digit numbers while they engaged in various secondary tasks. The secondary task that caused the most interference on performance was one in which subjects had to produce a series of random letters while doing their arithmetic. Random generation has been shown to require extensive use of dorsolateral prefrontal mechanisms in humans and in other animals (Petrides et al. 1993b, Petrides 1995). Consequently, it is reasonable to suppose that some components of mental arithmetic involve these same mechanisms. In addition, Logie et al. (1994) also found that articulatory suppression also produced interference, although to a lesser extent. As argued above, articulatory suppression has an effect on disrupting verbal rehearsal, thus suggest-

ing that this is another component process in mental arithmetic.

In light of the above, it is natural to predict that lesions in a number of brain sites should affect the ability to perform arithmetic calculations. Indeed, this is the case (Dehaene & Cohen 1995). Lesions in inferior parietal, subcortical, and frontal sites have all been implicated in deficits in arithmetic skill, a syndrome called "anarithmetia" (see e.g. Warrington 1982, Corbett et al. 1988, Lucchelli & De Renzi 1993). Further evidence that multiple regions involving storage and executive processes are involved in mental arithmetic comes from neuroimaging studies (Roland & Friberg 1985, Appolonio et al. 1994). In these studies, subjects had iteratively to subtract 3 from a starting number (e.g. 50, 47, 44, 41). Contrasting the activation from this task with either a rest control condition or a forward-counting control revealed several areas of activation: inferior parietal, prefrontal, premotor and motor cortices. These activations were largely bilateral in locus, but with somewhat higher activation in the left hemisphere. Note that this pattern of activation follows nicely from the activations we have previously identified with storage and executive components of working memory. The parietal and premotor areas are ones that have shown themselves to be prominent in verbal storage tasks, and the prefrontal activation could represent a combination of rehearsal processes and the scheduling and control processes required to conduct the arithmetic operations themselves. Mental arithmetic, in short, is a complex task that seems to recruit fully the storage and executive processes of working memory.

## 8.5 SUMMARY

As we have shown, current conceptions of working memory identify two general classes of component. One class is devoted to the temporary storage of information. This component is itself not singular in form: evidence leads to the view that different forms of information (verbal, spatial, visual and possibly others) are stored using different mechanisms. The evidence that leads to this view comes from a combination of studies of behaviour in normal individuals, behaviour in brain-injured patients, lesion and single-cell studies of animals performing working memory tasks, and neuroimaging studies of human performance. This evidence converges on a model of storage processes such as that illustrated in Figure 8.8, in which there are processes for creating representations, for transforming these into other codes, for storing information and for rehearsing information in various storage buffers.

The second class of working memory components is devoted to various processes that manipulate and transform information in the

storage buffers. Again, this component is not unitary in nature. Rather, it seems best characterized as a set of processes capable of controlling various aspects of processing, such as temporally tagging information, sequencing operations, inhibiting some processes in favour of others, and so on. Again, our knowledge of the workings of executive processes comes from a combination of sources studying behaviour and brain mechanisms in humans and other animals. While our understanding of executive processes lags behind that of our understanding of storage mechanisms in working memory, the available evidence is beginning to reveal the complex architecture of executive processes and their representation in the brain.

No doubt, further understanding of working memory will elaborate on, and possibly change, our current view. Whatever the future development of theory about this fundamental set of psychological mechanisms, our understanding of working memory will continue to be guided by a combination of behavioural and brain evidence. Only by gathering converging evidence from several sources are we likely to unravel the complexities of this critical component in cognition.

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### NOTE

1. It is not inevitable that lack of speech produces a working memory deficit, however. It has been shown that some patients who are anarthric (see e.g. Vallar & Cappa 1987) – that is, cannot produce speech – nonetheless have reasonably normal verbal working memories. Such patients may not have damage to their cortical circuits for producing speech (such as those described above) so much as damage to more peripheral structures necessary for speech production. Alternatively, they may represent evidence that internal speech is not the result of precisely the same mechanism that results in explicit speech.

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