

VERBAL AND SPATIAL WORKING MEMORY IN HUMANS

John Jonides
Patricia A. Reuter-Lorenz
Edward E. Smith
Edward Awh
Lisa L. Barnes
Maxwell Drain
Jennifer Glass
Erick J. Lauber
Andrea L. Patalano
Eric H. Schumacher

I. Introduction

Human memory is not unitary. It is composed of a number of systems that are defined by the length of time they store information, the amount of information that can be stored, the form of that storage, and the cognitive functions that the storage serves. This idea of drawing a distinction between long-term and working memory has been honored for over a hundred years (see, e.g., Atkinson & Schiffrin, 1968; Broadbent, 1958; Galton, 1883; Hebb, 1949; James, 1890; Waugh & Norman, 1965). In 1974, Baddeley and Hitch suggested that working memory itself may be composed of a number of subsystems for storing different kinds of information. This is the issue that motivates the present review.

The study of what is now called “working memory” has a long history in psychology. Galton and James described the precursors of this concept

in their discussions of the “presence chamber” (Galton, 1883), and the “specious present” (James, 1890) that constituted what James came to call “primary memory.” Their discussions referred largely to the consciousness that observers had of information to which they attended. Much later, Broadbent (1958) and Sperling (1960) described an active perceptual system whose processing outlasted the presence of the stimulus. Building on this, Atkinson and Shiffrin (1968; 1971) first proposed a model of what they called a “short-term store” that emphasized linguistic coding of material stored for a short interval. More recently, Baddeley and Hitch (1974; Baddeley, 1986, 1992) proposed the concept of working memory to include not only short-term storage of information but also the processing operations that make use of this information. To be sure, there are differences among these many conceptions of what we now call working memory, but they all include a common set of characteristics—a memory system that (a) stores information briefly, (b) stores a limited amount of information, (c) is rapidly accessible, (d) is subject to frequent updating, (e) and is used in the service of higher cognitive processes.

These characteristics are the common hallmarks of working memory throughout its entire history of discussion in psychology, during most of which working memory has been conceptualized as a unitary construct. Recent proposals suggest a revision to this conceptualization, however. There is now reason to believe that working memory is composed of a number of subsystems that differ from one another in the kind of information they process, but that are related to one another by their common characteristics of limited capacity, limited duration, frequent updating, and use in higher mental computations (Baddeley, 1986, 1992). The evidence that underlies this view is mainly concerned with the distinction between verbal and spatial working-memory systems, and it is concentrated on the storage rather than the executive aspects of working memory. In this chapter we review this evidence in detail and draw from it a picture of working memory that includes at least two storage subcomponents.

A. A METHODOLOGICAL NOTE

How does one establish that some psychological processing system is composed of several parts, as we and others would like to argue for working memory? The logic of double dissociation offers a powerful tool for addressing this problem. Originally conceived as an analysis tool for cognitive deficits following brain damage (Kinsbourne, 1972a; Shallice, 1988; Teuber, 1955), the logic of double dissociation has been fruitfully applied to purely behavioral studies as follows:

If there is a behavioral factor that influences performance on Task A but not Task B, and another behavioral factor that influences

performance on Task B but not Task A, then these two tasks are mediated by different processing mechanisms (Smith & Jonides, 1995, p. 1010).

This same logic can be applied to neuropsychological and neuroimaging studies if one allows a rough assumption about localization: that different processing mechanisms will be implemented in different neuroanatomical locations. Note that this additional assumption does not depend on whether a processing mechanism is strictly localized to just one portion of neural tissue or instead is distributed over several locations. What is critical is that the site or sites of implementation of one processing mechanism differ from those of another. When studying the effects of brain damage on behavior, the double-dissociation logic necessitates the study of at least two patients so that the following conditions can be met:

If one patient shows a deficit in performance of Task A associated with loss of function in Brain region a but not Brain region b, whereas another patient shows a deficit in performance of Task B associated with loss of function in region b but not region a, then the two tasks are mediated by different processing mechanisms.

Likewise, the selective activation or deactivation of brain regions evidenced by neuroimaging can use the logic of double dissociation in the following way:

If performance on Task A is associated with changed neural activity in Brain Region a but not Brain Region b, whereas performance on Task B is associated with changed neural activity in Region b but not Region a, then the two tasks are mediated by different processing mechanisms.

When applied in any of these ways, the logic of double dissociation permits one to make strong inferences about the existence of multiple processing systems. It is often the case, however, that the double dissociations one seeks—whether in behavioral data, in neuroimages, or in data from brain injury—are not pure in form. For example, there are behavioral studies in which some experimental manipulation influences performance *more* in Task A than Task B, while another manipulation influences performance *more* in Task B than Task A. In these cases, both factors influence performance in both tasks, and so the strict conditions of a double dissociation are not satisfied. Nevertheless, one may continue to respect this weaker

form of dissociation in that it provides evidence of a separation in processing systems, though it might also indicate some overlap in those systems.

One can obtain impure evidence of a double dissociation from neuroimaging studies as well. This occurs if one finds changed neural activity in response to both Tasks A and B, but more change in the activity of one region in response to Task A than to B, and more change in the activity of another region in response to Task B than to A. Again, this would lead one to conclude that the two tasks recruit some of the same mechanisms in the two regions in common, but it would also indicate that there is some residual specialization of the two regions for the two tasks.

Finally, neuropsychological studies are often cases of somewhat compromised double dissociations (see Shallice, 1988, for discussion). Frequently, one patient may show deficits in both Tasks A and B, with the deficit in Task A being greater, whereas another patient with damage in a different region shows deficits in both Tasks A and B, but with the deficit in B being greater. This sort of finding is possible because tasks recruit more processes than the ones that might be specialized to two areas, and the commonly recruited processes may be the ones that produce common deficits.

While the logic of double dissociation is not without its critics (Caramazza, 1986; Dunn & Kirsner, 1988), it is generally recognized as providing a strong evidential basis for inferring the separability of subsystems (e.g., Coltheart, 1985; Teuber, 1955; Weiskrantz, 1968), which is a fundamental step toward specifying the architecture of any cognitive system. Furthermore, Weiskrantz (1991) has argued that one's confidence in the separability of two systems is solidified if the evidence for double dissociations is derived from multiple populations and multiple techniques. We endorse this argument and extend it to include not only evidence from patient populations and neuroimaging, but also evidence from strictly behavioral studies of the systems in question. Accumulating double-dissociation evidence from all these sources renders quite strong the inference that the dissociated systems are separable, both psychologically and neurally.

In this chapter we review a body of evidence that demonstrates dissociations of both the weak and strong variety to develop the case for multiple processing systems in working memory. Note that the focus of this review is spatial and verbal processing in working memory. Consequently, even though there is a good deal of evidence about working memory in animals other than humans, this evidence does not directly inform us about verbal processing. So, the data we review come exclusively from studies of humans.

II. Dissociating Phonological and Spatial Storage

There are reasons to suspect, even in the absence of empirical evidence, that working memory may dissociate by verbal and spatial qualities. One

of the most time-honored generalizations about specialization in the human brain is that verbal functions are lateralized in the left hemisphere and visuospatial functions in the right. It seems reasonable, then, to suspect that working-memory tasks that recruit these two functions may also show selective specialization. Supporting this possibility are introspections of subjects performing verbal versus spatial tasks, such as mental addition of several numbers versus mental rotation of a visual form. These introspections often suggest the use of different sorts of representations in these tasks.

Indeed, for these and other reasons, Baddeley and his colleagues (e.g., Baddeley, 1986, 1992; Baddeley & Hitch, 1974) proposed a model of working memory that explicitly includes the dissociation of spatial and phonological storage. According to the canonical version of this model, working memory is composed of a central executive processor and slave buffer systems that serve the central executive. The central executive is claimed to be the seat of computing operations that permit one to engage in such tasks as mental arithmetic or mental rotation (see, e.g., Hitch, 1978). To implement these operations in any task, the central executive requires information that is fed to it from the slave buffer systems. There are two such buffers: one responsible for information stored in a phonological form and one for information coded visuospatially. These two buffers are assumed to be separate storage systems that feed independently to the common central executive.

A. BEHAVIORAL EVIDENCE

Two behavioral techniques have been used to distinguish between verbal and spatial buffers using the logic of double dissociation. Perhaps the more popular one is the *selective interference* paradigm. The assumption underlying selective interference is that introducing a secondary activity during the retention interval of a working-memory task will produce interference on that task. The secondary task is made *selectively* interfering by having the mental code used during this task be either similar to or different from the code used during the main task. A secondary task that involves manipulation of a phonological code should be more interfering on a working-memory task that involves a phonological buffer than on one that involves spatial material. Likewise, a secondary task that involves a spatial code should interfere more with a spatial working-memory buffer than with a phonological buffer.

Various experiments have implemented this rationale (see Logie, Zucco, & Baddeley, 1990; Meudell, 1972; Salthouse, 1974). As one example, consider an experiment by den Heyer and Barrett (1971). They had subjects view 4×6 matrices that contained eight letters randomly positioned in eight of the cells of the matrices. After a subject saw a matrix, a 10-second

retention interval ensued, during which subjects either did nothing but remember the matrix or engaged in one of two interfering tasks. Then they recalled the matrix by writing in letters on a blank matrix. Thus, subjects had to remember both the *identities* of the eight letters and their *positions*—that is, a verbal and a spatial task. One of the interfering tasks required them to view three 2×4 matrices in each of which there were three dots. Two of these matrices were identical and subjects had to judge which of them was different. The other interfering task involved aurally presenting subjects five numbers that they had to add mentally. Consistent with the logic of double dissociation, the rationale behind the experiment was this: If subjects stored the identities of the letters using a phonological code, then the mental arithmetic task should interfere with the stored letters because subjects would have to store a phonological code in part to do their arithmetic (see Hitch, 1978, for elaboration of a model of working memory for mental arithmetic). Furthermore, if subjects stored the positions of the letters using a spatial code, then having to make a spatial judgment during the retention interval should interfere with memory of the letter positions because the spatial judgment would also require a spatial code.

The results support these predictions. Relative to the control condition in which there was no interpolated activity during the retention interval, identity responses were 56% worse when the interpolated task was spatial but 68% worse when it was mental arithmetic. By contrast, position responses were 45% worse than the control when mental arithmetic intervened during the retention interval but nearly 90% worse when the spatial judgment task intervened. This pattern of results establishes a double dissociation in that the interfering task involving arithmetic had a greater effect on phonological working memory than on spatial working memory, but the spatial interfering task had a greater effect on spatial than on phonological memory. The dissociation is of the weak variety, as seen by the fact that both tasks suffered from both kinds of interference to some extent compared to the control.

The second technique used to isolate spatial from phonological buffers in working memory makes use of a logic that is related to that of selective interference. In this case, rather than the variable being the kind of interfering task that intrudes on the retention interval, it is the type of response that the subject must produce. Responses that recruit a spatial processing system are predicted to interfere with spatial working memory whereas responses that recruit a verbal system are predicted to interfere with verbal working memory. The basis for these predictions hinges on an often unstated assumption about working-memory processes—namely, that working-memory processes use mechanisms that plan and produce behav-

ioral responses. The consequence is that having to produce a verbal response in a task that uses verbal-output processes to store information will result in interference. In a similar manner, having to produce a response that requires spatial processing will interfere with working memory for spatial information. A classic example of the use of this rationale is an experiment by Brooks (1968; see also Smyth & Scholey, 1994).

Brooks had subjects engage in one of two tasks that putatively required spatial or verbal working memory. The verbal task was this: Subjects had to memorize a 10-word sentence such as "Rivers from the hills bring fresh water to the cities." The experimenter then cued the subject to make a linguistic judgment about each word in the sentence, for example, Was it a noun or not? In each case, subjects made a positive or a negative response. The spatial task was quite different. Subjects memorized a block figure, such as a block figure of the uppercase letter F. They were trained to scan mentally around the boundaries of the figure, beginning at an asterisk and going in a clockwise direction as indicated by an arrow. On each trial of the experiment, subjects were cued to make spatial judgments about each vertex in the block figure; for example, Was it at the top or bottom of the figure? If so, they responded positively, and if not they responded negatively.

The critical feature of the experiment was that subjects indicated their responses in one of two manners. In one case, they simply verbalized a response for each Yes or No in the string of decisions they had to make, whether in the sentence or the block-figure task. In the other case, subjects were presented with a response sheet that had rows each containing a Y and an N in a staggered arrangement. In this case, subjects indicated their responses by pointing to a Y or an N in each row corresponding to each decision they had made. This procedure forced subjects to monitor the response sheet visually as they indicated their responses, presumably engaging some spatial processes to do so.

The results of the experiment were clear. Responding vocally hindered performance in the verbal task more than responding by pointing; in a complementary way, pointing resulted in poorer performance for the spatial memory task than did vocalizing. There was a clear double dissociation that suggests two streams of processing for the two working-memory tasks. To produce a vocal response, according to Brooks (1968), requires the engagement of a speech-production system so that the output can be formed and executed. To point, however, requires that subjects spatially select the proper letters on the response sheets to produce their responses, which requires spatial localization. These two response modes, then, engage parts of a verbal or a spatial processing system, respectively. The fact that they produce selective impairment on the working-memory tasks is what suggests

that these working-memory tasks must be engaging verbal or spatial processing systems as well. It is this line of reasoning that invites the hypothesis of two working-memory modules for verbal and spatial information. In fact, subjects in this experiment reported, "that they 'could say the sentence to themselves' while . . . pointing, but not while saying 'yes' or 'no.' The diagrams could be 'pictured' while subjects were . . . saying 'yes' or 'no,' but not while they were trying to point." These introspections are consistent with the operation of two working-memory modules, one for verbal and one for spatial information.

Taken together, the behavioral demonstrations of double dissociations converge on the view that working memory includes separate subsystems for verbal and spatial information. However, this conclusion must be drawn with caution, for several reasons.

First, a careful examination of the tasks used in the behavioral literature reveals that they are often extremely complex, in the sense that they recruit a range of processes. Recall the selective-interference experiment by den Heyer and Barrett (1971), and consider the secondary tasks that they used: mental arithmetic (which was intended to interfere with verbal working memory) and comparing matrices of dots to find the odd one of three (which was intended to interfere with spatial working memory). While the results were consistent with the existence of separate verbal and spatial working-memory systems, the secondary tasks were sufficiently complex to cloud interpretation of the results. Think about the processes that are involved in mental arithmetic. As Hitch (1978) and others have analyzed this task, it involves not only storage of the numbers to be added, but retrieval of rules of addition, table look-up of addition facts, updating of memory with the intermediate solution, computation of sums when they are not available by table look-up, and so forth. Part of the greater interfering effect that mental arithmetic shows on letter versus position memory may well hinge on these other processes that are necessary to accomplish the mental arithmetic task. A similar problem arises with the secondary task of comparing dot matrices. While it is certainly plausible that this task includes a substantial spatial component, it is also plausible that visual memory of the configuration of dots plays some role in the task, and it may be this configural memory that causes the greater interference with memory for position than memory for letters.

We do not intend to focus on only the experiment of den Heyer & Barrett (1971) in leveling this criticism. Indeed, it is common for selective-interference studies to use tasks with multiple possible sites of interference (e.g., Logie, et al., 1990; Salthouse, 1974). While these studies may recruit spatial and verbal working-memory systems, they surely also recruit other processes that could be the source of selective interference.

Another reason for caution in interpreting the results of strictly behavioral studies has to do with uncertainty about the locus of the processing effects. To illustrate the point, recall the study by Brooks (1968) that showed selective interference on spatial and verbal working-memory tasks as a function of the mode of response. The demonstrated interference was substantial and selective, thus offering support for a double dissociation of spatial and verbal processes. However, what sort of dissociation is implicated? One possibility is that the demands of verbal versus spatial responding intrude on the *storage* of verbal versus spatial information respectively. This would lead to the sort of model of working memory that Baddeley (1986, 1992) has proposed. An alternative, however, is that storage of spatial and verbal information is not different, and the source of response interference is lodged in *retrieval* of information from memory. Subjects may have a more difficult time retrieving verbal information from storage when they are activating a verbal response, but a more difficult time retrieving spatial information when activating a spatial response. Thus, while the double dissociations are clear, they do not unambiguously implicate storage functions of working memory. This problem arises in other behavioral experiments as well (e.g., Smyth & Scholey, 1994) although some experiments have managed to isolate interference effects to storage by presenting interfering tasks only during the retention interval of a working-memory task (den Heyer & Barrett, 1971; Meudell, 1972).

What, then, do we make of the behavioral data that have been accumulated about spatial and verbal components of working memory? A minimal interpretation is that they indicate that some portion of the information processing stream for spatial and verbal material differs in working-memory tasks. This difference may be lodged in encoding, storage, or retrieval processes, or in some combination of these.

B. NEUROPSYCHOLOGICAL EVIDENCE

The behavioral evidence reviewed above suggests that there are differences at some point or points in the processing stream for verbal and spatial working memory. One implication of this is that there should be identifiably different brain pathways that are responsible for these processing differences. In turn, this leads to the inference that there may be patients with brain injury or anomalies who will reveal dissociations between spatial and verbal working-memory systems. Indeed, there is growing evidence to support this inference.

Consider a striking dissociation reported by Wang and Bellugi (1994). They studied two groups of subjects, one with Williams Syndrome and one with Down syndrome. Both syndromes are traceable to genetic anomalies

that result in abnormal neurological development and are well known to produce severe cognitive retardation. However, patients with Williams syndrome show remarkably selective preservation of many language functions in contrast to their overall cognitive skills. To study the working-memory capacities of the two kinds of patients, Wang and Bellugi (1994) administered classic tests of verbal and spatial memory. They gave subjects in both groups the Digit-Span subtest from the Wechsler Intelligence Scale for Children-Revised (WISC-R), in which strings of random digits of varying lengths are read to subjects who must repeat them back in order. To test spatial memory span, they administered the Corsi-blocks test, in which the experimenter points to a set of haphazardly arrayed identical blocks in random order, and the subject must then reproduce the order. Scoring the responses either with or without respect to whether the correct order of the strings was preserved, the subjects with Down and Williams syndromes showed a striking dissociation. Subjects with Williams syndrome were superior in their digit span to subjects with Down syndrome, but Down subjects were superior in their Corsi-blocks performance to their Williams counterparts.

While these data are consistent with the involvement of different brain mechanisms in spatial and verbal working memory, they are not specific about either the structural or functional locus of this difference. With regard to neuroanatomical structure, both syndromes are characterized by reduced cerebral volume generally. Relative to this, there is some sparing of the basal ganglia in Down patients and of temporal-limbic structures in Williams syndrome, but this sparing is sufficiently coarse so as not to offer much clue about what structures may be responsible for the dissociations shown in the working-memory tasks.

Moreover, the Down subjects' deficit in verbal working memory and the Williams subjects' deficit in spatial working memory may be secondary to more general difficulties these patients have with verbal and spatial material respectively. That is, these complementary deficits may be material-specific, but not selective for working memory per se. For example, Wang and Bellugi note that Down and Williams' syndromes are associated with distinctive patterns of perceptual abilities. This raises the possibility that these patients differ in their encoding strategies in addition to, or possibly instead of, their short-term storage of verbal or spatial material. Subjects with Williams syndrome also show poorer memory of visual-spatial than verbal materials over longer retention intervals (Udwin & Yule, 1991), again suggesting a material-specific deficit that extends beyond working memory. The problem is the same here as with the behavioral studies reviewed previously: We cannot be sure that the double dissociation that Wang and

Bellugi report reflects a selective dysfunction in separate verbal and spatial working-memory storage buffers.

Large-scale group studies of patients with focal lesions have the potential to be more revealing about the neural substrates of spatial and verbal working memory. However, the few studies of this kind that exist are also limited in the conclusions that can be drawn about the functional locus of the deficit. De Renzi and Nichelli (1975) examined working memory in patients with left- or right-hemisphere damage using four tests of working memory, three verbal ones and a spatial one. The verbal tests included (a) digit span, with subjects verbalizing their responses; (b) digit span, with subjects pointing to the digits as a response rather than verbalizing them; and (c) a picture-word memory test, in which subjects were given names to store and had to point to the referents of the names in an array of pictures. All three tests revealed the same pattern of results for verbal working memory: Patients with left-hemisphere lesions were impaired more than controls with no brain damage, and also more than patients with right-hemisphere damage. In addition, patients with right-hemisphere damage did not differ in their performance from controls. These results are consistent with the hypothesis that important mechanisms of verbal working memory are lodged in the left hemisphere.

The results for spatial working memory are not so clear from this study, however. To assess spatial working memory, De Renzi and Nichelli (1975) used a version of the Corsi-blocks test described earlier. Overall, the right-hemisphere patients scored lower than the left-hemisphere patients, but not reliably so. In fact, the only statistically significant effect to arise from this test had to do with whether the lesion site was anterior or posterior in either hemisphere. Patients with posterior lesions fared worse on the Corsi-blocks test than patients with anterior lesions. In a follow-up experiment that focused specifically on spatial working memory and that used more taxing variations of the spatial span task (8- or 16- s delays that were filled and unfilled), De Renzi and his colleagues (De Renzi, Faglioni, & Previdi, 1977) did find evidence that only patients with right posterior lesions were significantly impaired relative to neurologically intact controls.

Taken together, these studies suggest a picture of working memory that is consistent with a wealth of information indicating left hemispheric specialization for verbal material and right hemisphere specialization for spatial material. Moreover, a posterior locus is suggested for both types of working memory. Yet, can we be any more certain about the functional locus disrupted in these patients than we were in considering the behavioral and neuropsychological evidence reviewed earlier? Unfortunately, these group studies lack the critical information needed to establish a selective deficit of verbal or spatial working-memory buffers, just as the earlier behavioral

and neuropsychological studies did. In particular, we do not know enough about the perceptual abilities of these patient-groups to rule out an encoding problem as the source of the apparent working-memory impairment. There is also the possibility that the deficits reflect generalized memory impairments rather than specific deficits in short-term retention. Indeed, De Renzi et al. (1977) report that their right-hemisphere patients required significantly more trials to learn a spatial sequence to criterion, suggesting that at least the spatial impairment may be more general.

There are several neuropsychological case studies that provide just the sort of information needed to address the question of functional selectivity in addition to providing some indication of structural locus. A classic case, K.F., first reported by Warrington and Shallice in 1969, had mild speech and comprehension difficulties following a head injury affecting primarily the left parietal-occipital area. K.F. had disproportionate difficulty with repetition, as manifested by a dramatically reduced digit span of 2. His limited span could not be attributed simply to speech difficulties since a nonverbal probe-recognition test also indicated a working memory span of 2. Moreover, general comprehension or phonological encoding difficulties could not account for K.F.'s poor working memory since he showed normal long-term memory for verbal material (Shallice & Warrington, 1970). Results from several similar patients, including one patient, J.B., who had minimal comprehension difficulties and fluent nonaphasic speech (Shallice & Butterworth, 1977), offer the same general picture of a deficit that specifically affects short-term retention (Warrington, Logue, & Pratt, 1971; Warrington & Shallice, 1969). There is also some evidence for material specificity of the working-memory deficit, in that K.F. and J.B. were both found to have normal spans when the memory list was composed of nonverbal sounds (Shallice & Warrington, 1974). For these patients, however, information about their spatial working memory is lacking.

This was not so with patient P.V., a more recent case whose verbal working-memory impairment has been studied thoroughly and found to occur in the presence of normal spatial working memory (Basso, Spinnler, Vallar, & Zanobio, 1982; Vallar & Baddeley, 1984a, 1984b). In Basso et al.'s initial report (1982), P.V. was a 28-year-old, right-handed woman who had suffered a stroke 5 years earlier. Her lesion was quite large, extending the full anterior-posterior extent of language areas in the left hemisphere. Given the size of her lesion, her language functions were remarkably intact. Her most notable deficit was an inability to repeat auditorially presented sentences. This observation was amplified by Basso et al. (1982), who showed that on memory-span tests with digits, letters, or words, P.V.'s memory span was noticeably worse than normals'. For example, when she was presented 10 strings of 5 digits each, she was able to recall only 1 string

completely correctly (which is far worse than normal). By contrast, her span on the Corsi-block test was 6, which is slightly better than the normal span of 5.7.

We can establish a double dissociation between verbal and spatial working memory by comparing the performance of patient P.V. with that of patient E.L.D., who is the one well-documented case of a spatial working-memory deficit (Hanley, Young, & Pearson, 1991).¹ At the time of the study by Hanley et al. (1991), 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 led to a hematoma in the Sylvian Fissure some 6 years previously. Her major cognitive deficit was an anterograde amnesia for spatial and visual information. When tested on Corsi blocks, 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 to 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 to normal controls. When given three sequences of six phonologically different letters to recall, E.L.D. recalled all sequences perfectly, in comparison to controls who recalled only 1.4 of the six sequences on average.

Thus, a comparison of patients P.V. and E.L.D. establishes a double dissociation between verbal and spatial working memory. In addition, for both patients there is evidence to indicate that the working-memory deficits are not secondary to more general difficulties with the perceptual encoding of verbal or spatial material. For P.V., her strong performance on tests of phoneme discrimination, rhyme judgments, and single-word comprehension all converge on the conclusion that her deficit is not due to impaired phonological processing. Her normal verbal long-term memory for items already in her lexicon also strengthens this conclusion and indicates the selectivity of her deficit (Basso et al., 1982). Likewise, E.L.D. performs normally on quite challenging visual tasks. She is able to identify pictures of objects from unusual views, match unfamiliar faces presented in full and

¹ Note that many temporal-lobe patients have been described who have deficits in spatial memory. However, the preponderance of evidence leads to the conclusion that their deficit is not of spatial *working* memory. Smith and Milner and their colleagues (Smith, Leonard, Crane, & Milner, 1995; Smith & Milner, 1981, 1984, 1989), for example, have described groups of patients with temporal-lobe lesions, especially lesions of the right temporal lobe and hippocampal area, who have difficulty with spatial memory tasks. However, Smith and Milner (1989) showed that these deficits did not appear in tasks in which the spatial material in question had to be recalled shortly after presentation, the kind of task that is typically associated with working memory. Rather, they seem to appear only after a significant delay is required before recall, suggesting that the deficit is one that reflects a longer-term representation of spatial material.

profile poses, and judge facial expressions. She also reads normally and shows no signs of visual neglect. Unlike P.V., E.L.D.'s memory deficit does affect long-term memory and the learning of new visual materials (e.g., faces and routes; Hanley et al., 1991). So, while the material-specific deficit is unlikely due to a perceptual problem, E.L.D.'s difficulties extend beyond the short-term storage of visual-spatial material.

These two cases offer the strongest evidence considered thus far for separable verbal and spatial working-memory systems. Beyond that, what do these patients tell us about the brain pathways involved in working memory? The most salient difference in lesion sites between the two patients is hemispheric: P.V.'s lesion is in the left hemisphere while E.L.D.'s is in the right. Both patients show damage in the region of the Sylvian fissure although the damage reported for patient P.V. seems to extend well beyond this site. Elaborating on the nature of this circuitry from an examination of these patients alone is not possible, however. Partly this is a function of the size of the lesions that produced their deficits. Partly it is due to the possibility that even local damage can have global effects (e.g., Farah, 1994). Once a patient has lost a part of a processing circuit, later functions of that same circuit will appear to be damaged as well, a result of upstream processes affecting downstream ones. Based on this type of argument, Allport (1984) has challenged the claim that the problem in patients like K.F. and P.V. is due to a working-memory deficit rather than damage to an earlier processing system for phonological information (see Vallar, Basso, & Bottini, 1990; Vallar, Corno, & Basso, 1992). Similar objections can undoubtedly be raised in the case of visual-spatial working-memory impairments as well. In short, additional information is needed in order to define the functional architecture and localize the circuitry responsible for working memory, and for this reason we turn to neuroimaging data from subjects with intact brains.

C. NEUROIMAGING EVIDENCE

Two neuroimaging techniques have been used to isolate storage processes of working memory for spatial and verbal material. One technique makes use of event-related potentials (ERPs) that can be recorded with temporal precision during just the epochs when storage occurs, isolating it from encoding and retrieval processes. The other technique uses positron emission tomography (PET) to measure areas of activation in the brain during working-memory tasks. To isolate storage processes in PET studies, experimenters have compared activation during a working-memory task with activation in a task that is similar except for storage. In this way, the difference in activation can be attributed to storage processes alone, follow-

ing the assumptions of subtractive logic (see Posner, Petersen, Fox, & Raichle, 1988).

1. Event-Related Potentials

One ERP study by Ruchkin, Johnson, Grafman, Canoune, and Ritter (1992) documents a double dissociation in storage processes in spatial and verbal working-memory tasks. They had subjects engage in two different working-memory tasks on different trials. In one task, subjects saw a target string of consonants and vowels of three, four, or five syllables in length and had to store the string for 5 s, after which a probe string was presented and subjects had to indicate whether it differed from the target string. In the other task, subjects saw a target pattern of letter pairs arranged at three-, four-, or five locations in a visual display, and had to store this pattern for 5 s. After the retention interval, a probe pattern of asterisks appeared, and subjects had to indicate whether this pattern occupied the same locations as the target stimuli. During the stimulus presentation and retention intervals, ERPs were recorded from 13 scalp locations covering posterior and anterior locations.

Globally, the pattern of obtained ERPs showed an increasing slow-wave negativity during the retention interval that was sensitive to the memory load of each task. Importantly, this pattern differed in scalp distribution between the spatial and verbal tasks, implying the involvement of different neural sources for the two tasks. For the spatial task, the major effect was a negative slow wave that was maximal over parietal areas and that was sensitive to the memory load of the task. This negativity began during the presentation of the stimulus and continued during the retention interval. It was lateralized during the early portions of the recording interval in that it was maximal over scalp locations on the right. During the retention interval, the slow wave increased in amplitude and became less lateralized and somewhat more sensitive to memory load. This effect may be a signature of several processes related to the memory task. Its initiation during stimulus presentation could be an indicator of its relation to encoding processes. Its increased amplitude during the retention interval and its increased sensitivity to memory load during this interval may be an indicator of its relation to storage processes as well.

The pattern of ERPs in the verbal task was more complex, but only some of the effects persisted during the retention interval, and only these are likely to be related to storage of information in a verbal buffer. One effect was a negativity that was present only early during the retention interval and that was not sensitive to memory load. Presumably, this effect was not related to the storage requirements of the task. A second effect

was a positivity that was also present early during the retention interval but not later, but *was* sensitive to memory load. This effect may be related to storage, but the fact that it was nascent during the interval when the stimuli were presented suggests that it may have more to do with encoding of information into memory. Perhaps the most interesting effect for the verbal task was a frontal negativity that was present during stimulus presentation and during the entire retention interval. This effect was definitely sensitive to memory load during its later portions and may have shown some sensitivity to load early on as well. The fact that this effect began during stimulus presentation may lead one to believe that it had something to do with stimulus encoding. However, the fact that it increased in amplitude and that its sensitivity to memory load became more pronounced during the retention interval suggests that it may be a result of storage processes as well. Of clear interest is that this negativity was most pronounced over left and central frontal sites.

To summarize, the effects that seem most related to the memory requirements of the task are these: a largely right-hemisphere posterior negativity in the spatial task and a largely left-hemisphere anterior negativity in the verbal task. These effects clearly differentiate the two conditions of the task, and so they confirm the pattern of double dissociations that the behavioral and neuropsychological evidence has demonstrated. In support of the neuropsychological evidence, these findings confirm the role of lateralized processes in verbal and spatial working-memory tasks. In addition, they suggest that there may be different contributions of posterior and anterior mechanisms to the two tasks. Of course, it is well known that ERP data with as few recording sites as there were in this study may not be unambiguously revealing about the localization of neural generators (see, e.g., Gevins, 1990; Tucker, 1993). In light of this, we turn to data from PET, which are more revealing about the localization of storage processes in working memory.

2. *Positron Emission Tomography*

Consider first a pair of experiments reported by Jonides et al. (1993) and Smith, Jonides, and Koeppel (1996; also reported by Awh et al., 1996). One of these experiments involved spatial and the other verbal working memory. The Spatial Memory Task is schematized at the top of Fig. 1. Each trial began with a fixation cross for 500 ms which was followed by the presentation of three dots for 200 ms at essentially random locations around the circumference of an imaginary circle. These dots were followed by a 3000-ms retention interval during which the fixation cross reappeared. Following this, a probe stimulus was presented for 1,500 ms; it consisted of an outline

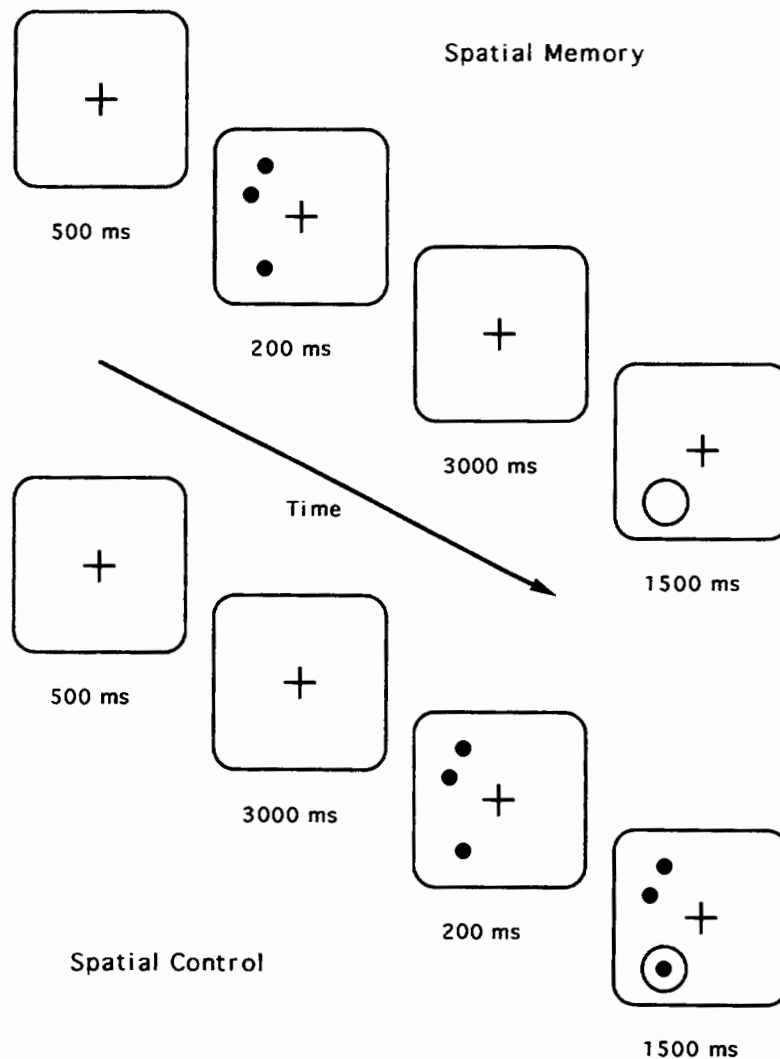


Fig. 1. A schematic of the Spatial Memory and Spatial Control conditions from the experiment by Jonides et al. (1993).

circle. The subjects' task was to determine whether this probe encircled the location of one of the dots presented previously; if so, the subject pushed a response button once and if not, twice. Subjects engaged in a series of such trials during which they were scanned using positron emission tomography (PET).

It is plausible to assume that this task requires the storage of spatial information for a short period of time, thus recruiting spatial working memory. However, the task also clearly requires other processes, such as those needed to: encode the dots, encode the probe circle, attend to the location of the dots, select a response, execute the response, and so forth. These processes were also captured in the PET images of this task because

the images were accumulated over a 60-s window of time during which subjects engaged in a number of spatial-memory trials. In order to isolate the storage processes of the task from these additional processes, Jonides et al. (1993) had the same subjects engage in a Spatial Control Task that is shown at the bottom of Fig. 1. In this task, a fixation cross initiated each trial and persisted for 3,500 ms, the duration of the fixation-plus-retention intervals in the Spatial Memory Condition. The cross was succeeded by the presentation of three target dots for 200 ms, which were immediately succeeded by a probe display for 1,500 ms. The probe consisted of the three target dots that had just been presented plus an outline circle. Subjects' task was the same: to indicate whether the circle was superimposed on the location of one of the dots. In this condition, of course, no memory of the dots' locations was required because they were present at the same time as the outline circle. Yet, the condition includes many of the nonstorage processes that were also included in the Spatial Memory Condition. By subtracting the activation images acquired for this Control Condition from the images acquired from the Spatial Memory Condition, then, a relatively pure estimate of activation due to spatial storage could be obtained.

This subtraction revealed four reliable sites of activation, all in the right hemisphere: one in extrastriate occipital cortex, one in posterior parietal cortex, one in premotor cortex, and one in inferior prefrontal cortex. Jonides et al. (1993) attributed these activations to a combination of storage and related processes necessary to create an internal representation of the stimulus to store. It is quite noteworthy that all the reliable activations were present in the right hemisphere. This result is consistent with the data of Ruchkin et al. (1992), Hanley et al. (1991), and De Renzi and Nichelli (1975), who also concluded that right-hemisphere mechanisms were critical to spatial working memory.

Compare this spatial working-memory task to a verbal working-memory experiment that used Sternberg's (1966) item-recognition task (Awh et al., 1996; Smith et al., 1996). The Verbal Memory Condition of this experiment had a structure quite similar to that of the Spatial Memory Condition just discussed. The task is schematized at the top of Fig. 2. Each trial began with a fixation cross for 500 ms that was followed by four uppercase letters arrayed around fixation and presented for 200 msec. These letters were followed by a retention interval of 3,000 ms, after which a probe display appeared for 1,500 ms. The probe consisted of a single lowercase letter presented in the center of the screen. Subjects were to decide if this probe matched in identity any of the letters on that trial. If so, they responded with a single button-push; if not, with a double button-push. Note that the use of a lowercase probe in comparison with uppercase target letters prevented subjects from making a decision on the basis of the shape of the

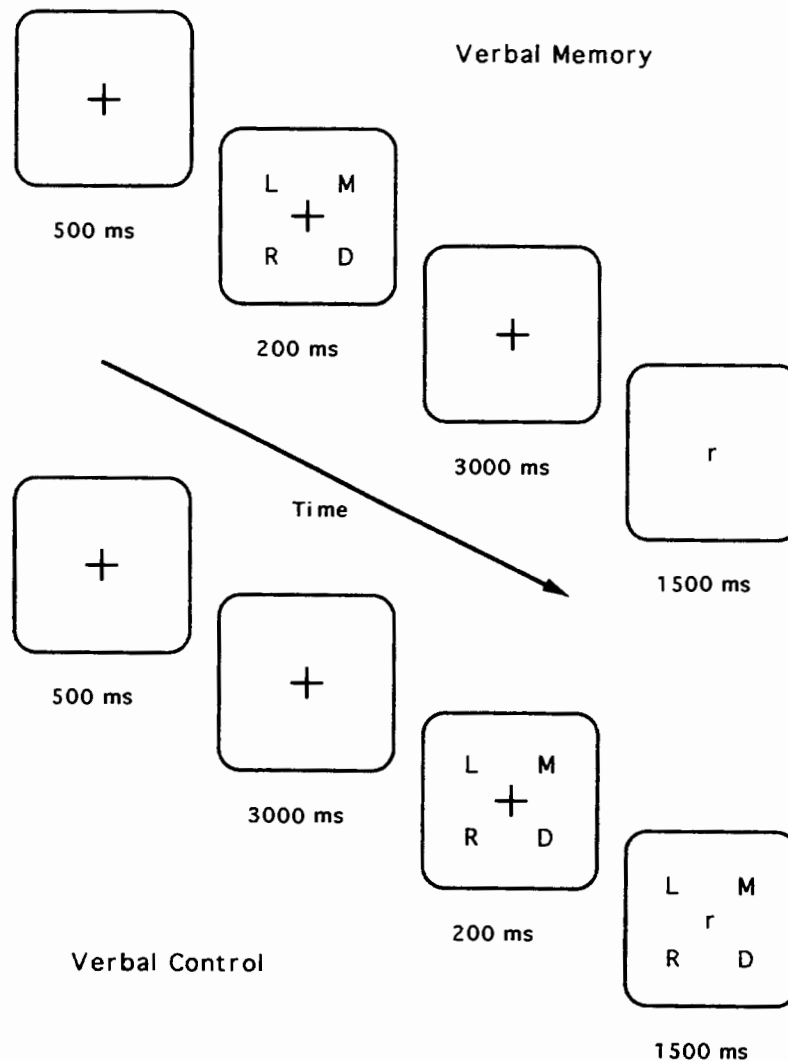


Fig. 2. A schematic of the Verbal Memory and Verbal Control conditions from an experiment reported by Smith et al. (1996) and Awh et al. (1996).

letter; instead, they had to construct a phonological representation of the letters as the basis of their judgment.

This Verbal Memory Condition requires not only storage of letter identities, but additional processes related to encoding of the displays, responding, and so forth. These processes were controlled by collecting activations from a Verbal Control Condition, schematized at the bottom of Fig. 2, and subtracting these from the activations in the Verbal Memory Condition. The Verbal Control is similar in structure to the Spatial Control Condition discussed earlier. The Verbal Control began with a fixation cross for 3,500 ms (the duration of fixation plus retention intervals in the Verbal Memory Condition), followed by the presentation of four uppercase letters

for 200 ms. These were followed by the same four letters plus a single lowercase letter in the center of the screen for 1500 ms. As in the Verbal Memory Condition, subjects were to decide whether the lowercase letter matched any of the uppercase letters. In this condition, of course, the judgment did not depend on memory of the uppercase letters because they were present on the screen simultaneously with the lowercase letter. Activations from this Verbal Control Condition were subtracted from those of the Verbal Memory Condition to isolate storage processes.

The PET activations that resulted from this Verbal Memory–Verbal Control subtraction were quite different from those of the Spatial Memory–Spatial Control subtraction. One global difference is that the reliable verbal activations in cortical structures appeared largely in the left hemisphere. These include two sites in posterior parietal cortex (one superior to the other), and three sites in prefrontal cortex: inferior prefrontal, premotor, and supplementary motor. In addition to these, there were also reliable activations in anterior cingulate, right cerebellum, left-hemisphere thalamus, and left-hemisphere insular cortex.

Taken together, the results of the spatial and verbal memory experiments reported by Jonides et al. (1993) and Smith et al. (1996) provide evidence of a double dissociation of spatial and verbal working-memory systems that supplements the evidence reviewed earlier. The reliable activations that resulted from these two experiments did not overlap at all, suggesting two separable pathways for processing information in the two tasks. The spatial task recruited brain mechanisms in the right hemisphere predominantly for the creation and storage of a mental representation of spatial information, while the verbal task recruited largely left-hemisphere mechanisms. Even with this noticeable difference in activation patterns, there were similarities as well. Both tasks resulted in activation of posterior and anterior cortical areas in parietal and premotor cortex respectively, albeit in different hemispheres.

Smith et al. (1996) proposed a pair of hypotheses to account for this pattern of results. One hypothesis is that the activation in posterior parietal cortex was due to the storage of information in the two tasks, with spatial information stored in the right hemisphere and verbal in the left. (The additional occipital activation in the right hemisphere of the spatial task was attributed to the creation of a visual representation of the target locations that was subsequently stored by parietal mechanisms).

The second hypothesis was that the anterior activation was attributed to rehearsal processes in the two tasks, with verbal rehearsal using left-hemisphere anterior structures, and spatial rehearsal using right-hemisphere structures. Rehearsal of verbal information was proposed by Baddeley and Hitch (1974), and Baddeley, (1986, 1992) as an integral

component of the phonological portion of working memory. In the case of the verbal task described by Smith et al. (1996), it is plausible to suppose that the anterior structures that were activated (Broca's area, premotor and supplementary motor cortex) participated in rehearsal because these structures are ones that are typically implicated in explicit speech. Indeed, as reviewed later, there is evidence from other PET studies that these structures are involved in implicit speech with little involvement in storage per se. Smith et al. (1996) went on to propose that the right-hemisphere frontal structures activated in the spatial task (premotor and inferior-posterior-frontal areas) accomplished the same sort of rehearsal function for spatial storage. In this case, rehearsal might be, as Baddeley (1986) has proposed, a result of an internal attentional mechanism that reviews each of the spatial locations in turn by directing attention to each. This proposal has anatomical plausibility by virtue of the homology of the premotor and inferior frontal activations in the right hemisphere for the spatial task to the premotor and Broca's area activations in the left hemisphere for the verbal task. There is, however, no additional research that can add to this anatomical case for a right-hemisphere rehearsal function at this time.

Smith et al. (1996) also report an experiment that compares verbal and spatial working memory in more nearly comparable tasks, tasks that load heavily on the storage of information so as to increase the brain activation due to storage. In both the verbal and spatial tasks, subjects were presented a stream of letters during each PET scan, as illustrated in Fig. 3. Each letter was displayed for 0.5 s, with 2.5 s intervening between successive letters. As shown in Fig. 3, the letters were displayed at seemingly random locations around the perimeter of an imaginary circle and they varied in whether they were upper- or lowercase. The presentation conditions for the verbal and spatial tasks were essentially identical. The only difference between the tasks was whether subjects were instructed to remember verbal or spatial information. In the Verbal Memory Condition, shown at the bottom of Fig. 3, for each letter subjects had to decide whether it matched in identity the letter that appeared three previously in the series, regardless of spatial position. Because letter-case was varied, this decision had to be made on the basis of letter identities, not visual shapes. In the Spatial Memory Task, shown at the top of Fig. 3, subjects had to decide whether each letter occupied the same spatial position as the one that appeared three previously in the series, regardless of letter identity. Note that the requirement to consult one's memory of the stimulus "3-back" (the name given to this task) in the series imposes an essentially constant memory load because subjects must store at least the previous three stimuli, constantly updating this representation. Thus, the storage requirements during an entire scan are substantially enhanced over discrete-trial tasks, such as the

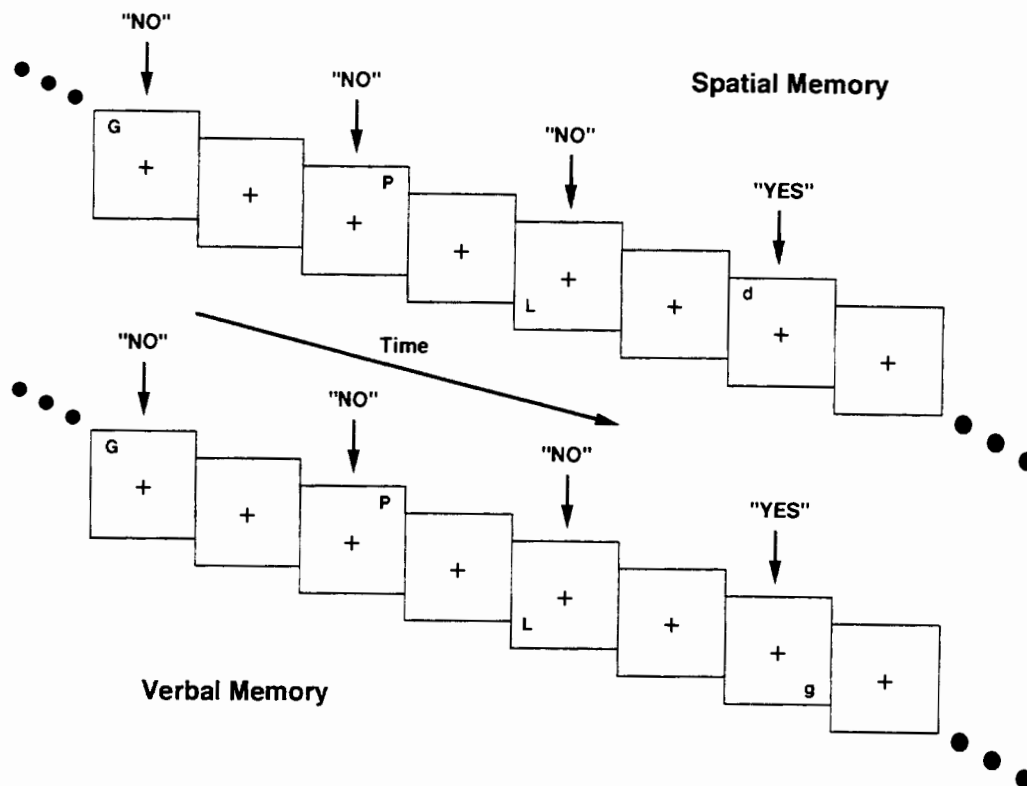


Fig. 3. A schematic of the Spatial Memory and Verbal Memory conditions from an experiment reported by Smith et al. (1996).

spatial task of Jonides et al. (1993) and the item-recognition task reported by Smith et al. (1996).

In order to remove unwanted processes not directly related to storage, Smith et al. (1996) reported two control conditions, one for the Verbal Memory Task and one for the Spatial Memory Task. In the Verbal Control Condition, subjects were given three target letters at the beginning of a stimulus sequence that was essentially identical to the sequences shown at the top of Fig. 3. They were then to decide whether each letter in the sequence matched one of the three target letters. In a similar way, in the Spatial Control Condition, subjects were shown three target spatial positions at the beginning of each sequence similar to the sequence shown at the bottom of Fig. 3. They then had to decide whether each letter in the sequence occupied one of the three target positions. The activations from these control conditions were subtracted from those of their respective memory conditions.

The storage requirements of these tasks are high, and this led to substantial activations in the PET images. The patterns of activations were similar in many respects to those described earlier in this section. Globally, although

there was clear evidence of bilateral activation in both tasks, there was more activation in posterior and anterior areas in the left hemisphere of the verbal task than in the right hemisphere; in a complementary way, the activation in the right hemisphere of the spatial task was higher than that in the left hemisphere. Thus, we have the further evidence of a double dissociation between spatial and verbal working-memory tasks.

At a finer level of analysis, the verbal task resulted in activation in several regions. As in the item-recognition task described previously, there was activation in two regions of the posterior parietal cortex in the left hemisphere. One of these, in the supramarginal gyrus, overlapped almost completely the activation site found in posterior parietal cortex in the item-recognition task of Smith et al. (1996). The other left-hemisphere, posterior activation was in the superior parietal lobule; it may also have been present in the item-recognition task except that that task was conducted on a scanner with a more limited field of view, preventing the collection of data in this portion of the brain. The site in the superior parietal lobule has also been reported in other verbal working memory tasks (see Petrides, Alivisatos, Evans, & Meyer, 1993b). These data contribute to the case that posterior parietal mechanisms are involved in the storage of information in verbal working memory.

Continuing with the verbal task, in addition to the posterior sites, Broca's area in prefrontal cortex showed reliable activation, as in the item-recognition task. By contrast, the other two anterior regions that also showed reliable activation in the item-recognition task, left premotor and supplementary motor areas, did not show reliable activation in the 3-back verbal task. Smith et al. (1996) argue that this may be because the control task in this 3-back experiment was itself somewhat demanding of rehearsal processes, and consequently some of the activation due to rehearsal may have been subtracted out of the Verbal Memory Condition. Alternatively, these other areas may not be integral to rehearsal, and may be involved in some other aspect of processing not yet specified. We shall return to this issue when we later review studies that discriminate between rehearsal and storage functions in verbal working memory.

This verbal task also produced activation in dorsolateral prefrontal cortex in the left hemisphere, an area that has been found by others to play a role in working memory (Cohen, Forman, Braver, Casey, Servan-Schreiber, & Noll, 1994; Petrides et al., 1993b). While studies of working memory in animals have implicated dorsolateral prefrontal cortex in storage functions (e.g., Goldman-Rakic, 1987; Wilson, O'Scalaidhe, & Goldman-Rakic, 1993), this area of the brain is also important in various other cognitive functions, such as temporal coding of stimuli (see Fuster, 1995). The 3-back task of Smith et al. (1996) requires subjects to code the input for the temporal

order of the letters that are presented so that subjects can make their memory comparisons to the item that was 3-back. Likewise, the task of Cohen et al. (1994) required a temporal coding operation in that they had subjects determine whether each was identical to the one 2-back in the sequence. Although the task of Petrides et al. (1993b) did not require temporal coding, it did require subjects to manipulate the information in working memory in a way that may also have recruited mechanisms in dorsolateral prefrontal cortex. Thus, the dorsolateral prefrontal activation found by Smith et al. (1996) and others may not reflect storage functions of working memory as much as it reflects "executive functions," as Baddeley (1986) has termed them. If this is the case, there may not be a close analogy between the neural processes of working memory in humans and those in other animals. Although one can make a quite compelling case that the prefrontal neural activity found in animals has something to do with the short-term storage of information (see Funahashi, Bruce, & Goldman-Rakic, 1989), in humans one can find successful performance in a working-memory task with little evidence of dorsolateral prefrontal activity if the task does not recruit executive processes (see Jonides et al., 1993; Paulesu, Frith, and Frackowiak, 1993). This issue remains to be more thoroughly investigated.

The pattern of activations found in the Spatial Memory Condition minus its control replicated and expanded on the results of Jonides et al. (1993). First, there was activation in two posterior sites in the right hemisphere, one in the supramarginal gyrus and one in the superior parietal lobule. The site in the supramarginal gyrus agrees well with the site reported by Jonides et al. (1993). The site in the superior parietal lobule is new; however, as in the item-recognition task, the field of view of the PET camera used by Jonides et al. (1993) was not sufficiently large to capture a site this superior in parietal cortex.

The Spatial Memory–Spatial Control subtraction of the 3-back task also revealed activation in dorsolateral prefrontal cortex of the right hemisphere, in an area homologous to that found in the left hemisphere for the verbal task. Once again, we raise the possibility that this area may be involved either in the storage of information or the manipulation of this information by executive processes of various sorts. Activation in this region has also been documented by Petrides, Alivisatos, Evans, and Meyer (1993a) and by McCarthy et al. (1994). Their tasks as well demand not only storage of spatial information, but also its manipulation in various ways that might be characteristic of frontal mechanisms.

While the 3-back spatial task did not show evidence of reliable activation in the right inferior frontal gyrus, as in the study of Jonides et al. (1993), there was activation in a right-hemisphere premotor area that is consistent

with the earlier study. Smith et al. (in press) speculate that this activation plus the activation in inferior frontal gyrus may be indicative of a spatial rehearsal mechanism, comparable to the rehearsal of verbal information that has been attributed to similar sites of the left hemisphere. Why the same sites in frontal cortex have not been activated consistently in the spatial tasks we have discussed remains something of a mystery. One possibility (as in the results of the 3-back verbal task) is that some of the putative rehearsal processes in the spatial memory task were subtracted out by the subtraction of the Spatial Control, which itself may have required a modest amount of rehearsal to maintain the three target locations. This explanation, although plausible, remains to be tested.

The results of these various experiments from our laboratory lead to the following conclusions about working memory:

1. Spatial and verbal working memory are mediated by different and separable processing mechanisms.
2. These processing mechanisms are instantiated in different brain circuits.
3. Verbal working memory recruits mechanisms principally of the left hemisphere, including posterior and anterior structures.
4. Spatial working memory recruits mechanisms principally of the right hemisphere, including posterior and anterior structures.

These conclusions are well supported by the neuroimaging data, and they are amplifications of the conclusions that can be drawn from the behavioral and neuropsychological data as well. Thus, we have confidence in the claim that there are different modular systems within working memory for spatial and verbal information.

The neuroimaging studies also support a further claim about working memory, one that was originally proposed by Baddeley and Hitch (1974) and that we shall pursue in detail in the next section. The claim is that the storage functions of verbal and spatial working memory are each mediated by two processes acting in concert: a buffer and a rehearsal process, each of which is specialized for verbal or spatial information. The most compelling basis for this claim is the documentation that verbal working-memory tasks result in activation in posterior parietal and inferior prefrontal cortex in the left hemisphere. The posterior activation is consistent with the site of damage in patients who display deficits in verbal memory span (e.g., Basso et al., 1982; Shallice & Warrington, 1970; Vallar & Baddeley, 1984a; Warrington, Logue, & Pratt, 1971; Warrington & Shallice, 1969), and, thus, this site of activation may underlie the short-term storage of verbal information. The inferior prefrontal site is centered in structures typically associated with Broca's area, structures that neuropsychological evidence suggests are

associated with articulation skills (e.g., Goodglass & Kaplan, 1972); this site may underlie the rehearsal of verbal information, using some of the same set of neural mechanisms that mediate explicit speech.

There is tantalizing evidence that this same sort of architecture can be applied to the storage and rehearsal of spatial information as well. Spatial working-memory tasks also produce activation in posterior parietal cortex, in the right hemisphere in an area homologous to the left-hemisphere area activated in verbal working-memory tasks. The symmetry in these two areas leads to the claim that the right posterior activation is reflective of spatial storage processes, just as the left seems to be reflective of verbal storage processes. Also, there is evidence that spatial working-memory tasks at least sometimes produce activation in inferior prefrontal cortex and premotor cortex in the right hemisphere; again, there is a striking parallel here to the left-hemisphere activation produced by verbal working-memory tasks. In the case of verbal working memory, it is plausible to argue that this prefrontal activation reflects rehearsal, given the well-documented functions of Broca's area. In the case of spatial working memory, no such argument can be made at present because too little is known about the function of the inferior prefrontal and premotor structures of human right hemisphere. However, their close homology to the structures activated in the verbal tasks certainly raises the possibility that they may also be mediating rehearsal of some sort (see Awh, Smith, & Jonides, 1995).

Just what this rehearsal may be is not entirely clear. Baddeley (1986) proposed that it may involve an internal allocation of attention to different locations in space, in a kind of parallel to the internal reallocation of attention to different verbal codes in verbal rehearsal. The most straightforward prediction from this sort of account, however, is that brain structures involved in attention or eye-movement control should be involved, and yet we see no evidence of the activation of such structures as the frontal eye fields, the pulvinar nucleus, or the superior colliculus. Of course, absence of evidence is not good reason to conclude that there is evidence of absence, so we must leave it for now that there is simply insufficient basis to say much about the nature of rehearsal of spatial material in working memory.

Let us return to the better justified claim that verbal working memory itself consists of storage and rehearsal processes. This claim has a quite good evidential base in behavioral, neuropsychological, and neuroimaging data, as we will review later in this chapter.

III. Dissociation of Verbal Storage from Rehearsal

A. BEHAVIORAL EVIDENCE

Consider the classic proposal about the architecture of verbal working memory, attributed to Baddeley, Thomson, and Buchanan (1975) originally,

and elaborated by Baddeley (1986), among others. The central claim is that verbal working memory is mediated by two subsystems. One is a storage buffer of limited capacity and short duration that is specialized for the storage of information in a phonological code (as opposed to a visuospatial code). The other is a mechanism that is responsible for recirculating the stored information to refresh it. The idea is that recirculation of this information causes its activation to increase, thereby offsetting the decay that afflicts information in the storage buffer. A common example used to motivate this proposal is looking up a number in a telephone book. One finds the number, stores it in the buffer, and then repeats it either aloud or silently until it is dialed. The repetition is identified with this recirculation process, a process sometimes called "rehearsal," "maintenance rehearsal," or "articulatory control." Whatever name is applied to it, this process is typically assumed to be like a tape-recorder loop that runs repeatedly on the material stored in the buffer.

The analogy to a tape loop raises a prediction about rehearsal that was tested by Baddeley et al. (1975): They reasoned that if rehearsal is like a tape loop of limited length, then the number of items one should be able to rehearse should be limited by the length of the items (see also Craik [1968] and Glanzer & Razel [1974] for previous tests of this prediction; Baddeley et al. [1975] for a discussion of these previous tests.). Baddeley et al. (1975) confirmed this prediction in an extensive series of experiments whose composite result was that lists of longer words were more poorly remembered than lists of shorter words (with the same number of words each), where length was measured in either number of syllables or time of articulation by speakers. Quantitative analysis of their results led Baddeley et al. (1975) to conclude that the duration of the tape loop that corresponds to rehearsal is between 1.5 and 2 s.

In addition to the effect of word length, it has been known for some time that the phonemic similarity among verbal items also affects memory-span performance (e.g., Conrad, 1964, 1970, 1972). The effect of phonemic similarity has been attributed to confusion that occurs among items stored in a phonological buffer, such that features of the items become interposed with one another, resulting in a loss of item information, and hence less success in recall (Baddeley, 1986; Baddeley, Lewis, & Vallar, 1984). If word-length and phonemic similarity affect rehearsal and storage, respectively, then one ought to find independent effects of these two variables if they are simultaneously applied in a single experiment (cf. Garner, Hake, & Eriksen, 1956). Longoni, Richardson, and Aiello (1993) tested this prediction and confirmed it. This provides evidence of some functional independence of these two stages in working memory.

Further evidence of the independence of these stages comes from a second experiment by Longoni et al. (1993) that examined the relationship

between word length and another variable that has been assumed to affect storage, irrelevant speech. Memory for a string of items is hampered by introducing irrelevant speech that is to be ignored during the presentation and retention of those items (e.g., Colle & Welsh, 1976; Jones & Macken, 1993), and this interference effect has been attributed to a mutual interference between the irrelevant speech and items in the phonological buffer, with little effect of irrelevant speech on rehearsal (Salame & Baddeley, 1982). Two predictions follow from this. One is that the effects of irrelevant speech and phonemic similarity should interact if varied together. They do (Colle & Welsh, 1976; Salame & Baddeley, 1982). A second prediction is that there should be independent effects of irrelevant speech and word length on recall just as there are independent effects of phonemic similarity and word-length. Indeed, there are, as demonstrated by Longoni et al. (1993).

Beyond these tests of the independence of various behavioral manipulations, there is another research strategy that has been explored as a test of the separability of rehearsal and storage in verbal working memory. If rehearsal is a sort of internal articulation, then it should be subject to interference if the mechanism responsible for articulation is also engaged in a secondary, interfering task. This prediction has been tested repeatedly by having subjects articulate something externally, such as “the, the, the . . .” or “one, two, three, four, one, two, . . .” during a memory-span task, thereby suppressing their ability to articulate internally. Of course, doing *any of several* interfering tasks could result in degradation of memory performance. The point of studying the effects of articulatory suppression goes beyond this, however. If articulatory suppression has a selective effect on rehearsal, and if rehearsal is separable from the storage of verbal information, then one should show that articulatory suppression will modulate the effect of a variable affecting rehearsal but it will not modulate the effect of a variable affecting storage. As we have discussed, word length has been implicated as a variable that affects rehearsal, while phonemic similarity has been shown to affect storage. So, articulatory suppression should modulate or interact with the word-length effect but not the phonemic-similarity effect.

Before examining the results of experiments that have tested this prediction, a caution is in order about the mode of stimulus presentation in such a study. Consider an experiment in which material is presented visually and subjects engage in articulatory suppression during the presentation of this material and during the subsequent retention interval. Several studies have found that under such conditions, contrary to the prediction of interest, articulatory suppression diminishes the effects of *both* word length and phonemic similarity on recall (Murray, 1967; Peterson & Johnson, 1971;

see also Richardson, Greaves, & Smith, 1980). With visual presentation, however, suppression may have a pronounced effect on memory not because it exerts its effect on rehearsal, but rather because it interferes with the process of translating visual material into a phonological code before that material is stored. If so, then subjects will not be able to create a phonological code effectively, and any variable that is a sign of this code, such as word length or phonemic similarity, will have its effects diminished.

To meet this caution, investigators have examined the effect of articulatory suppression under conditions in which the material to be remembered was presented by ear. Although a translation process is still required during encoding even with auditory presentation (to turn an auditory input into a phonological code), this translation process is tacitly assumed to be more automatic in character in that it is the staple of natural language processing. In such an experiment, Baddeley et al. (1984) and Longoni et al. (1993) confirmed the prediction of interest: Articulatory suppression eliminated the word-length effect on recall, but it did not affect the influence of phonemic similarity. This points once again to an independence of storage and rehearsal in verbal working memory. (Some earlier studies with auditory presentation failed to find support for the critical prediction, but in these cases rehearsal was not prevented during the entire testing interval: Levy, 1971; Murray, 1968; Peterson & Johnson, 1971.)

B. NEUROPSYCHOLOGICAL EVIDENCE

Because the selective effects of phonemic similarity and word length are relatively clear, the predicted effects of these variables on patients with verbal working-memory deficits should be rather straightforward. If a memory deficit is due to just impaired rehearsal, then:

1. An effect of word length should be minimal.
2. Articulatory suppression should not influence performance (because presumably there would be no rehearsal to interfere with).
3. Phonemic similarity would be expected to reduce memory for auditory material, as in normals.
4. Phonemic similarity should not influence visual items (since rehearsal is needed to translate these items into a phonological code).

A deficit in the phonological-storage component, on the other hand, should (a) selectively influence the phonemic similarity effect in both the visual and auditory modality, while (b) leaving the effects of word length and articulatory suppression intact.

As straightforward as these predictions may be, the interpretation of verbal working-memory deficits has been less than clear (see Shallice &

Vallar, 1990). For example, the patient P.V. (considered earlier) would appear to display the pattern indicative of a rehearsal deficit—e.g., an absence of word-length and articulatory suppression effects—yet, for a variety of reasons, her deficit has been interpreted as one due to the phonological store (Vallar & Baddeley, 1984b). There are two aspects of her performance profile that pose a particular challenge to a rehearsal-deficit interpretation. First, her overt articulation rate is normal (Vallar & Baddeley, 1984a). Such a sparing of function is inconsistent with a rehearsal deficit because overt and covert speech are generally claimed to depend on common mechanisms; this claim is supported not only by the interference of overt articulation on covert rehearsal (discussed earlier), but also by the high correlation between reading rate and verbal memory span in normal subjects (Baddeley et al., 1975; Mackworth, 1963). Second, there are indications that P.V.'s phonological store is not functioning normally in spite of the normal effect of phonemic similarity with auditory presentation. P.V. shows very rapid forgetting on the Brown–Peterson task which is generally thought to measure the duration of a phonological memory trace (Basso et al., 1982). This task requires a subject to retain a short list of items that is typically well below span (about 2–3), while engaging in counting backward or in simple arithmetic during a retention interval. Because rehearsal is prevented by the secondary task, performance can be used to measure the rate of decay of auditory memory from the phonological store. P.V. forgets everything in 3 s, which is faster than normal. So what are we to make of the absence of word-length and articulatory suppression effects for P.V., which suggest a problem in rehearsal? Vallar and Baddeley (1984b) suggest that though rehearsal is available, P.V. chooses not to use it because of the general ineffectiveness of her verbal working memory.

Other patients, such as C.M. (Nichelli & Cubelli cited in Logie et al., 1989) and G.F. (Vallar & Cappa, 1987), have deficits in articulation (or dysarthria) and do not show word-length effects on span tasks but do show phonemic similarity effects. Although additional information (from the Brown–Peterson test, for example) is lacking, on the surface these cases offer some indication that rehearsal can be selectively impaired. A problem with such cases however, is that they may not have much of a verbal memory deficit; C.M.'s span of 5 is certainly within normal limits.

Belleville, Peretz, and Arguin (1992) reported evidence of case Ro.L., which may offer the clearest indication thus far for a rehearsal component of working memory that can be impaired independently of the phonological store. Ro.L., a right-handed male, sustained a left cerebrovascular accident at the age of 57 which resulted in a lesion of the temporoparietal region. This left him with sensory and motor deficits affecting the right limbs, in addition to aphasia. These deficits showed marked improvement over the

subsequent 12-month period. Ro.L.'s language comprehension was relatively intact and his speech was fluent. However, his repetition of single words and sentences was impaired even though his ability to compare auditorily presented phoneme pairs (e.g., "bo" vs. "ro") was normal. His language profile is typical of conduction aphasia, a disturbance that is closely linked with deficits in verbal working memory (see Allport, 1984; Caramazza, Basili, Koller, & Berndt, 1981; Kinsbourne, 1972b; Shallice & Vallar, 1990; Shallice & Warrington, 1977; Strub & Gardner, 1974). Accordingly, Ro.L. has a verbal span of 3 in conjunction with a normal spatial span of 5.

Like P.V., Ro.L.'s span is reduced by phonemic similarity and by using longer words, but is unaffected by articulatory suppression. Unlike P.V., however, Ro.L. has a reduced rate of articulation and appears to perform normally on a Brown–Peterson test of trace decay (though there is some question about the sensitivity of this test). Thus, Ro.L. seems to provide the best neuropsychological evidence thus far for a selective rehearsal deficit as the basis for verbal working-memory impairment.

The study of impaired rehearsal in these and other patients has revealed another potential dissociation that should not go unnoticed. Many have assumed that in addition to recycling information from the phonological buffer to keep it fresh, rehearsal translates information that comes into memory via vision into a phonological code for storage in the buffer. One can now make a case that these two alleged functions of rehearsal themselves may be dissociable. In support of this argument, Nichelli and Cubelli (in Logie, Cubelli, Della Sala, Alberoni, & Nichelli, 1989; see also Della Sala, Logie, Marchetti, & Wynn, 1991) cite the pattern of deficits exhibited by three patients. One, M.D.C., is argued to have damage to the visual-phonological translation process. This patient shows a phonological similarity effect and a word-length effect with auditory presentation, as would be expected if her ability to use phonological storage and rehearsal were intact. However, she does not show either of these effects with visual presentation (Vallar & Cappa, 1987). Nichelli and Cubelli argue that this is because she may have damage to the process that translates visual information into a phonological code. With this damage, she cannot gain access to a phonological buffer from visual input and therefore cannot show effects of variables that affect either the buffer or rehearsal. In comparison to M.D.C., Nichelli and Cubelli cite patients G.F. (Vallar & Cappa, 1987) and C.M. (Nichelli & Cubelli in Logie et al., 1989). These patients are argued to have deficits in rehearsal *per se*, but a normal coding process to translate visual input into a phonological form. According to this argument, both patients should show a phonological similarity effect for both visual and auditory presentation because they can gain access to the phonological store via either input

pathway if their coding processes are intact. However, they should show no effect of word length with auditory presentation if rehearsal is damaged, though they might show some effect of word length with visual presentation if word length affects the ease of creating a phonological code from visual input. All these predicted effects have been documented. To place this argument on a completely firm footing will require the identification of two variables that show clear and independent effects on rehearsal and phonological coding respectively. This remains to be documented.

All in all, a compelling case has been developed on the basis of behavioral and neuropsychological studies that rehearsal and storage of verbal information in working memory are mediated by separable processes. In particular, if the published interpretations of P.V. and Ro.L. are correct, these cases represent evidence for the double dissociability of rehearsal and phonological storage. In addition, as we have just summarized, there is suggestive evidence that the creation of a phonological code for visual input is separable from the process that recycles this code once created. What is not clear from the neuropsychological evidence, however, is the anatomical loci of any of these processes. The anarthric patients discussed have widely different brain regions associated with their deficits. P.V.'s lesion apparently affects the entire language region of the left hemisphere. Ro.L.'s relatively circumscribed lesion affects the posterior language areas—which is very surprising given that its impact is seemingly on the articulatory processes underlying rehearsal. For more evidence about the different brain structures that mediate the processes of interest, we need to consider evidence from neuroimaging studies.

C. NEUROIMAGING EVIDENCE

A classic paradigm for studying the mechanisms of verbal working memory is the item-recognition task that we discussed at length in Section IIC2. Recall that in this task, subjects are presented a short series of items to remember, then a probe item, and they must judge whether the probe is a member of the set they are holding in memory. Paulesu et al. (1993) were the first to search for brain activations that accompanied performance in this task. In their main experimental task, subjects saw a memory set of six consonants, presented sequentially, which they were instructed to rehearse and memorize. These were followed by a probe consonant, and subjects were required to judge whether the probe was a member of the memory set. Trials of this sort were strung together during which PET measurements were taken. Note that this procedure emphasizes the role of storage and rehearsal in that the major portion of each PET recording interval is occupied with storing and maintaining the sequentially presented

letters. In order to subtract out task components that were not related to verbal storage and rehearsal, a control condition was included, and activation from it was subtracted from activation in the item-recognition task. The control was identical to the item-recognition task except that the items were Korean letters with which the subjects were not familiar. In this task, subjects were instructed to use a visual code as the basis of their memory. Subtraction of activation in the control task from activation in the experimental task revealed reliably increased blood flow in the left supramarginal gyrus and in Broca's area. Activation of supramarginal gyrus, as reviewed earlier, is consistent with neuropsychological evidence from patients who have deficits in verbal working memory, and again we conclude that activation of this site represents verbal-storage processes in the item-recognition task. The second site, Broca's area, is routinely identified with external speech, and so it is plausible that this is the site of rehearsal processes.

To confirm that the supramarginal gyrus is involved in storage and Broca's area in rehearsal, Paulesu et al. (1993) had subjects engage in a second experimental task. In this task, subjects were presented a sequence of letters and had to judge whether each one rhymed with the letter "B," which was always present on the screen. The control condition for this task was one in which a string of Korean letters was presented on the screen, and subjects had to judge whether each was visually similar to a target Korean letter that was always present on the screen. Paulesu et al. (1993) reasoned that the rhyming task involves some internal articulation compared to its control, and so it should activate Broca's area. However, the rhyming task compared to its control does not involve any verbal storage, and so if the supramarginal gyrus is the structure recruited for storage, it should not be activated in the rhyming task. As predicted, Paulesu et al. (1993) found that the rhyming-minus-control subtraction revealed reliable activation of Broca's area but not of the supramarginal gyrus.

It is also interesting to note another pattern of activations that resulted from the study by Paulesu et al. (1993). They combined activations from the verbal item-recognition task with those from the rhyming task and subtracted from this the combined activations from the two control conditions. Of course, this grand subtraction revealed activation in the supramarginal gyrus and in Broca's area, as reviewed above. It also revealed activation in the supplementary motor area and cerebellum as well, areas that are thought to be involved in the planning and production of overt speech. Paulesu et al. (1993) reasoned that these areas may have been activated as part of a speech-production circuit although no overt speech was required in the tasks. This result leads to the inference that silent rehearsal may engage a circuit of frontal sites just as overt speech does. In this sense, rehearsal may be quite well characterized as "internal speech."

Though the evidence reported by Paulesu et al. (1993) is compelling about the sites of storage and rehearsal, one would like to have additional evidence about these sites for two reasons. First, the data reported by Paulesu et al. (1993) constitute a single, not a double, dissociation. The single dissociation is a result of their showing activation in supramarginal gyrus in the item recognition task but not the rhyming task, while the activation in Broca's area was present in both tasks. Their interpretation of this single dissociation is plausible, though other interpretations may do as well. Suppose, for example, that the item-recognition task was simply more difficult than the rhyming task and so resulted in more activation overall. Indeed, not only did this task show reliable activation in supramarginal gyrus while the rhyming task did not, it also showed a higher level of activation in Broca's area as well, even though the rhyming task produced significant activation in this area. A second difficulty in interpreting the Paulesu et al. (1993) data is that the function of Broca's area in the two tasks may have been quite different. In the item-recognition task it may have been required for internal speech, but in the rhyming task it may have been required for phonological analysis of each letter sound to determine whether there was sufficient similarity to constitute a rhyme with the target.

In light of these concerns, it is comforting that there are two additional reports of PET measurements of storage and rehearsal processes in verbal working memory. One of these is the item-recognition experiment described by Smith et al. (1996) and Awh et al. (1996), which we discussed in the context of spatial-verbal dissociations. Recall that the experiment included an item-recognition task similar to the one presented by Paulesu et al. (1993), plus a control condition in which subjects saw quite similar perceptual events and made responses similar to those in the main condition so that these processing components could be subtracted from the activation images of the item-recognition task. The results showed reliable activation in the anterior part of the brain, including Broca's area, supplementary motor cortex (SMA), and premotor cortex in the left hemisphere. Recall that Paulesu et al. (1993) also reported activation in Broca's area and SMA when they combined activations from their item-recognition and rhyming tasks relative to the controls. Given that Smith et al. (1996) obtained these activations for the item-recognition task alone, they extend the results of Paulesu et al. (1993). The three anterior frontal regions of interest have been implicated in explicit speech production by Petersen et al. (1988). Together with the evidence from Paulesu et al. (1993) about the involvement of these areas in item-recognition plus rhyming, and the evidence from Smith et al. (1996) about their involvement in item-recognition alone, it is becoming quite convincing that these areas are engaged in the processes necessary for silent rehearsal. Together with the activation in right cerebel-

lum that has been associated with these three cortical regions (reported by Paulesu et al., 1993, and Smith et al., 1996), a circuit mediating the production of inner speech is emerging.

As described earlier, Smith et al. (1996) also reported activations in the superior parietal lobule and the supramarginal gyrus. One of these sites of activation is similar to the parietal site reported by Paulesu et al. (1993) for their item-recognition task, which they too associated with storage processes in that task. Indeed, the most common site of damage in patients with deficits in verbal memory span is a posterior site (e.g., McCarthy & Warrington, 1990) that is consistent with the posterior sites discovered by Paulesu et al. (1993) and Smith et al. (1996). Thus, a compelling case is developing that this posterior region is involved in the storage of verbal information in working memory.

A second PET experiment that confirms and extends these results has been detailed by Awh et al. (1996). The main task used in this experiment was one in which subjects had to maintain verbal information in working memory continuously, much as in the 3-back task described in Section IIC2. As such, this experiment emphasized the storage and rehearsal components of working memory more than the item-recognition tasks already described. The paradigm is shown in Fig. 4. The top of the figure illustrates the Verbal Memory condition: Subjects saw a stream of single letters appear centered on a screen, each for .5 s, with 2.5 s intervening between successive letters. As each letter appeared, the subject's task was to decide whether it matched the letter that had appeared two items back in the sequence (hence this is a 2-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, constantly updating their representations as new letters appear.

Awh et al. (1996) report two control conditions, one intended to isolate storage and rehearsal processes in the 2-back task, and one intended to isolate storage alone. The Search Control Condition, shown in the middle of Fig. 4, required subjects to search for a single target letter in a sequence similar to that presented in the 2-back condition. The visual and response events in this Search Task were quite similar to those in the 2-back task, but the working memory requirements were minimal. When brain activations in the Search Task were subtracted from those in the 2-back task, there was clear evidence supporting the circuit for working memory that emerges from the item-recognition experiments. In particular, there was activation in left-hemisphere posterior parietal sites as well as in left-hemisphere prefrontal sites, including Broca's area, SMA, and premotor cortex. This constellation of results confirms the involvement of these sites in storage and rehearsal processes, respectively.

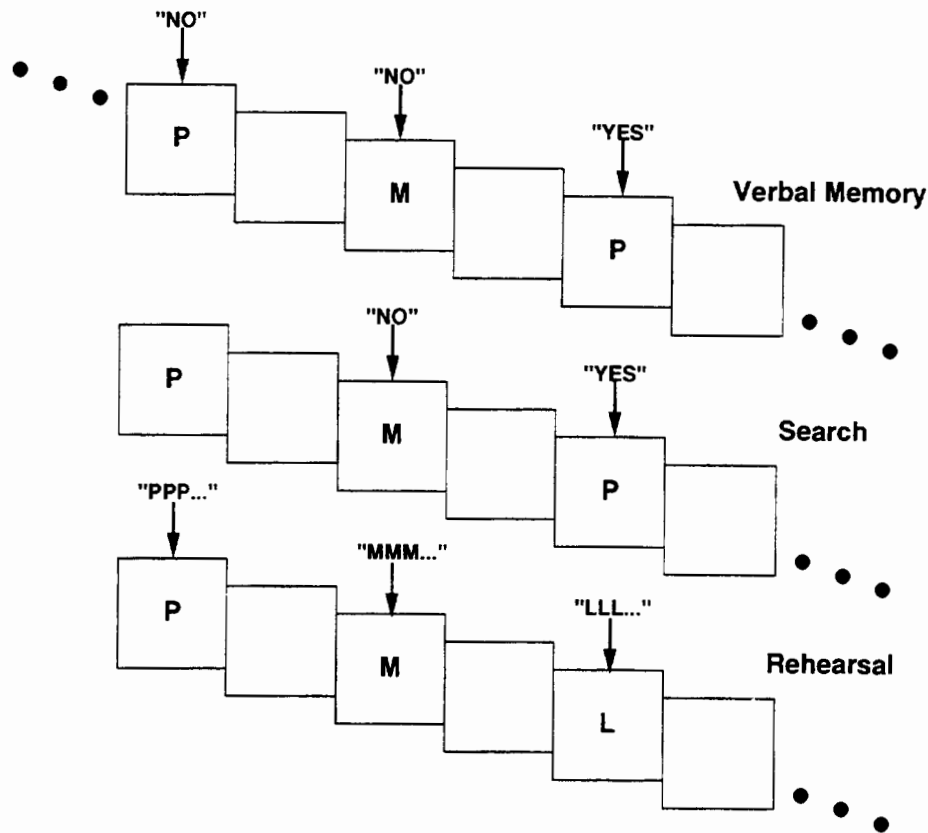


Fig. 4. A schematic of the Verbal Memory, Search, and Rehearsal conditions from an experiment reported by Awh et al. (1996).

The Rehearsal Control Condition from the experiment of Awh et al. (1996) adds more evidence about the circuitry of verbal working memory. In this condition, shown at the bottom of Fig. 4, subjects were presented with a stream of letters, just as in the 2-back task; they had 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 2-back condition, but subjects engaged only in rehearsal, with much less memory load than in the 2-back task. Thus, subtraction of the activations in this Rehearsal control from those in the 2-back task should have yielded left-hemisphere posterior activations if these represent storage, but it should have eliminated left-hemisphere anterior activations if they represent rehearsal. Awh et al. (1996) did find that the posterior parietal activation was still reliable in this subtraction. They also found that the anterior activations in Broca's area and premotor cortex in the left hemisphere were no longer statistically significant, also consistent with their predictions. There was, however, still

remnant activation in left SMA and in right cerebellum, both also associated with language production (Paulesu et al., 1993). This remnant activation may well be a result of the heavier rehearsal demands of the 2-back condition than of the Rehearsal condition in that the former demanded constant rehearsal for subjects to be successful in the memory task whereas the latter merely required rehearsal for each letter presented. All in all, the results of Awh et al.'s (1996) experiment confirm nicely the involvement of left posterior parietal cortex in storage, and left prefrontal cortex in verbal rehearsal processes.

IV. Summary and Conclusions

Let us take stock of the large body of evidence presented in this chapter. The central point of our review has been to argue, largely via evidence of double dissociations, that there are at least two storage systems in working memory—one responsible for verbal and one responsible for spatial information. This conclusion seems inescapable in that:

1. One can identify different experimental factors in behavioral studies that separately influence each type of storage.
2. There is at least one pair of patients such that one of them shows a deficit in verbal storage with no deficit in spatial storage and the other shows the complimentary pattern of deficit.
3. Neuroimaging studies find different circuitries for verbal and spatial storage when these storage systems are isolated using subtraction techniques.

We also reviewed evidence that bears on another aspect of working memory, the involvement of rehearsal in addition to storage processes for verbal material. Behavioral studies of normal subjects have yielded a set of variables that seem to exert separable effects on verbal storage and rehearsal. The hypothesis that these two processes are distinct is strengthened by neuropsychological evidence that one or the other process can be selectively damaged. Finally, data from PET studies indicate that rehearsal processes may be mediated by left-hemisphere anterior cortical mechanisms while storage is mediated by left-hemisphere posterior structures.

The PET evidence about dissociations of storage and rehearsal processes for verbal material has implications beyond its value in establishing that these two aspects of processing may be separable. One such implication has to do with the processes of rehearsal. We take it as quite significant that the structures that are associated with verbal rehearsal (Broca's area, premotor cortex, and SMA) are also structures that have been associated with the planning and production of explicit speech. Furthermore, Hinke

et al. (1993) have shown that Broca's area is active during internal speech, and McGuire, Shah, and Murray (1993) have shown that this same area is active in schizophrenics during episodes when they report auditory hallucinations (i.e., internal speech). All these lines of evidence converge on the conclusion that some or all of the very same structures that are at the heart of our skill at producing speech are harnessed in the service of internal processes that make use of a speechlike code in other cognitive tasks as well. In particular, it seems as if these structures are involved at least in the internal recycling of verbal information that occurs during the retention interval of a working-memory task. Although we have been assuming that this recycling is done for the purpose of keeping information alive and resistant to forgetting, this issue is not yet settled (see, e.g., Longoni et al., 1993). Whatever the functions of rehearsal, however, it is clearly an integral part of verbal working memory, and separable from the storage of information *per se*.

There are, however, two caveats to the conclusion that the neural loci involved in covert speech and rehearsal are the same as those involved in overt language production. The first has to do with the uncertain evidence concerning the relationship between damage to anterior regions of the left hemisphere and impaired verbal working memory. To the extent that Broca's area, for instance, participates in rehearsal, damage to it would be predicted to impair short-term verbal memory that relies on rehearsal. The evidence on this point is equivocal. Contrary to the prediction, two large-scale studies examining the relative impact of anterior versus posterior left-hemisphere damage on span tasks found that posterior damage produced significant impairment whereas anterior damage did not (De Renzi & Nichelli, 1975; Risse, Rubens, & Jordan, 1984). On the other hand, more in line with the prediction of interest, Swinney and Taylor (1971) and Vallar et al. (1992) included both anterior and posterior aphasics in their populations and found no differences between them in short-term memory tasks, although neither study mentions any specific comparisons as a function of lesion site. Along these same lines, to the extent that the profile of patient Ro.L. can be taken to reflect a rehearsal deficit, the posterior locus of his lesion is particularly puzzling (though it is possible that the computerized tomography [CT] imaging study of this patient did not reveal the full extent of the lesion). One way to reconcile these findings with the claim that rehearsal is implemented by left anterior regions is to assume that the rehearsal loop cannot function properly if the phonological store is impaired. That is, a deficit in the phonological store may compromise the functioning of rehearsal so that it too is no longer effective. If so, it may *not* be possible to have a pure deficit of storage without an associated, albeit secondary, deficit of rehearsal. By this hypothesis, Ro.L. would be

expected to have some (as yet undetected) deficit of the phonological storage system resulting from his posterior left-hemisphere damage.

The second caveat about our localization of rehearsal to anterior regions has to do with the resolution of PET. It is conceivable that the loci identified by Awh et al. (1996) and by Paulesu et al. (1993) are merely in close proximity to areas responsible for overt articulation, but are not these areas themselves. Given that the resolution of PET is no better than approximately 7–10 mm and that the technique requires averaging across individuals, this is certainly a possibility. Indeed, based on the effects of intracranial stimulation during verbal working-memory tasks, Ojemann (1978) concluded that the anterior and posterior loci that participate in such tasks are very close but not identical with the areas involved in naming.

The dissociation of storage and rehearsal for verbal material evident through PET also has implications for the site of storage. Just as anterior structures have been associated with rehearsal, posterior structures, in parietal cortex, have been associated with storage. There are at least two interesting observations to make about this. One is that the many findings in nonhuman animals of storage sites for working memory in frontal lobes (e.g., Funahashi et al., 1989) may not be very telling about verbal working-memory storage in humans. Indeed, this conclusion may apply to the storage of spatial material as well. Given the homology between the right-hemisphere parietal activations in PET studies of spatial working memory and the left-hemisphere parietal activations in verbal studies, it is reasonable to suppose that a key site of short-term spatial storage is the right parietal lobe. While there has been some evidence that monkeys also have parietal sites with spatial storage functions (Chafee & Goldman-Rakic, 1994; Quintana & Fuster, 1993), the dominant conclusion that can be drawn from animal studies is that the frontal lobes are more central to storage. So, here also, there may be an important difference in the anatomical structure of working memory between humans and other animals.

A second observation about the apparently posterior site of storage is more speculative. We consider it interesting that storage mechanisms for working memory are near the anatomical sites at which perceptual processing occurs. For the visual and auditory modalities, the sites of perceptual processing (both very early processes and those responsible for pattern recognition) are all in the posterior parts of neocortex. That working-memory storage also seems to be housed in this same general locale raises the possibility that working-memory mechanisms make use of some of the machinery that is involved in perception of stimuli. This may be true not only of verbal and spatial working memory, as already reviewed, but also of working memory for form (Smith, Jonides, Koeppel, et al., 1995). For example, the spatial-analysis mechanisms that have been identified in pari-

etal cortex (the so-called “dorsal pathway of vision”: Ungerleider & Mishkin, 1982) may be among those used in the storage of spatial information as well. Of course, at present it is premature to make much of what may be a coincidence in localization, but the existing data do raise a hypothesis that merits further investigation.

Yet another implication arises from the neuroimaging evidence that shows a dissociation of verbal storage and rehearsal. If there is a homology between verbal and spatial storage in parietal cortex of the left and right hemispheres respectively, perhaps it is worth entertaining the hypothesis that there is also a homology between verbal and spatial rehearsal in frontal cortex of the left and right hemispheres. Several neuroimaging studies of spatial working memory have revealed activations in right inferior prefrontal cortex (Jonides et al., 1993; Smith et al., 1996), in areas that are quite similar to the sites of verbal rehearsal in the left hemisphere. These activations lead one to the hypothesis that there are spatial rehearsal processes as well as verbal ones. At present, this is a hypothesis with little support; however, it is one that merits attention (see Awh, Smith, & Jonides, 1995).

We close with one final comment. The data we have reviewed provide strong support for the architecture of working memory first proposed by Baddeley and Hitch (1974) and since elaborated by others. According to this architecture, the storage of information in working memory is not unitary, but is composed of multiple storage buffers that vary in the type of information they store. The evidence we have reviewed summarizes the case that there are at least two such buffers, one for verbal and one for spatial information. We note, however, that there is growing evidence of more than just two working-memory buffers in humans as well as in other animals. Smith and Jonides (1995), for example, offer evidence of a dissociation between the storage of spatial and visual-object information in working memory. Others offer evidence of the involvement of a motoric working memory as well (see, e.g., Georgopolous, Crutcher, & Schwartz, 1989; Reisberg, Rappaport & O’Shaughnessy, 1984; Saltz & Donnenwerth-Nolan, 1981; Smyrnis, Masato, Ashe, & Georgopoulos, 1992; Smyth & Pendleton, 1989). There is also evidence of an auditory memory that does not store a phonological code (e.g., Colombo, D’Amato, Rodman & Gross, 1990; Zatorre, Evans, Meyer, & Gjedde, 1992; Zatorre & Samson, 1991). In that working memory plays a critical role in various higher cognitive functions, there may well be need to investigate a more abstract working memory as well, one that stores a semantic or propositional code (e.g., Martin, Shelton, & Yaffee, 1994; Shulman, 1971). In all these ways, the architecture of working memory is more complex than our discussion in the bulk of this paper implies. Nevertheless, in that it often has been documented that the human brain is organized around the processing of verbal and spatial

information by its hemispheric lateralization, we suspect that the verbal and spatial buffers that we have discussed play a central role in human cognitive functioning.

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