

Research Article

DISSOCIATION OF STORAGE AND REHEARSAL IN VERBAL WORKING MEMORY:

Evidence From Positron Emission Tomography

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Abstract—*Current cognitive models of verbal working memory include two components: a phonological store and a rehearsal mechanism that refreshes the contents of this store. We present research using positron emission tomography (PET) to provide further evidence for this functional division. In Experiment 1, subjects performed a variant of Sternberg's (1966) item recognition task. Experiment 2 used a continuous memory task with control conditions designed to separate the brain regions underlying storage and rehearsal. The results show that independent brain regions mediate storage and rehearsal. In Experiment 3, a dual-task procedure supported the assumption that these memory tasks elicited a rehearsal strategy.*

The working memory system for verbal information has been hypothesized to have two components: a phonological store and a rehearsal mechanism that refreshes the contents of this store (Baddeley, 1986, 1992; Sperling, 1967). The phonological store is presumed to hold a limited amount of verbal information in a phonological representation, and the rehearsal mechanism refreshes the contents of this store through a process of articulatory rehearsal.

The functional independence of the phonological store and the rehearsal mechanism has been supported by both behavioral and neuropsychological evidence. For instance, the two processes are influenced by separate behavioral factors. Memory span is worse for items that are phonemically confusable (the *phonological similarity effect*), and for items that take longer to pronounce (the *word-length effect*). Although the phonological similarity effect is taken as an indicator of the phonological store, the most plausible interpretation of the word-length effect is that longer words take more time to rehearse, and hence are more likely to decay before articulatory maintenance has occurred. In line with this interpretation, articulatory suppression eliminates the effects of word length, but not of phonological similarity (Baddeley, Lewis, & Vallar, 1984). Moreover, these behavioral factors have been shown to exert additive and independent effects on verbal working memory performance, suggesting that they influence discrete processing components (Longoni, Richardson, & Aiello, 1993; Schweickert, Guentert, & Hersberger, 1990).

Neuropsychological evidence also supports the storage-rehearsal distinction. Vallar and Baddeley (1984) reported a patient (P.V.) with a selective verbal memory deficit. P.V. was

unable to repeat more than two auditorily presented items, but performed within normal range on a number of visual memory tasks. Her memory performance showed no evidence of a word-length effect, but clear effects of phonological similarity were found with auditory presentation. Thus, P.V.'s performance shows clear evidence of phonological storage (the phonological similarity effect), but no evidence of rehearsal. This single dissociation of storage and rehearsal supports the functional independence of these components of verbal working memory.

Neuroimaging studies are another potential source of data that would be relevant to dissociating storage from rehearsal. Neuroimaging can uncover some of the brain components that mediate specific cognitive processes and therefore offers the possibility of revealing different sets of brain processes that may be responsible for storage of information and the rehearsal of that information. We exploit this rationale in the present article by reporting two experiments that employed positron emission tomography (PET) as a measure while subjects were engaged in verbal working memory tasks. In Experiment 1, subjects performed a variant of the item recognition task introduced by Sternberg (1966). Experiment 2 used a very different continuous task to study verbal working memory, with control conditions designed to separate the brain regions underlying storage and rehearsal. In Experiment 3, a dual-task procedure was used to test the assumption that our memory tasks elicited a rehearsal strategy.

PET METHODS AND ANALYSIS

Computer Control

All tasks were conducted with a Macintosh IIfx computer with a 14-in. monitor, using a program written in C++ to present stimuli and record subjects' responses. The computer rested on a gantry approximately 18 in. from the subject's eyes; the screen was tilted down to face the subject.

PET Procedure

The PET machine used in Experiment 1 was a Siemens/CTI-931/08-12. The camera produced 15 contiguous slices that were 6.75 mm apart (center to center); the reconstructed axial resolution was 10 mm FWHM (full-width-half-maximum). The PET machine used in Experiment 2 was a newer Siemens ECAT EXACT-47. The camera produced contiguous slices that were

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3.375 mm apart (center to center); the reconstructed axial resolution was 10 mm FWHM.

Both PET machines were in suites designed specifically for PET use, and the same background conditions obtained in all testing: The lights were dimmed, and there was no conversation or intrusive noise. Subjects first gave informed consent, then were familiarized with the PET apparatus prior to the experiment proper. Each subject had an intravenous catheter inserted into his or her left arm to receive the injections of radioactive tracer. The subject was then positioned in the scanner with tape applied from the head holder to the forehead to constrain head movement. Practice blocks were administered, and the subject's position was finalized. The experimental protocols for Experiment 1 and Experiment 2 consisted of six and nine scans, respectively, each corresponding to a block of trials.

The first trials of each experimental task began approximately 15 s prior to the injection of the radionuclide. Immediately following these trials, an intravenous bolus injection of 66 mCi of oxygen-15 labeled water was administered, after which approximately 15 s elapsed before the radionuclide reached the brain. Trials continued to be administered during the interval. PET scan acquisition was begun 5 s after the count rate was observed to increase above the background level and continued for 60 s thereafter. Injections for scans were separated by 14-min intervals, permitting the oxygen-15 to decay to an acceptable background level.

PET Data Analysis

The PET images for each subject were transformed to a stereotaxic coordinate system (Minoshima, Berger, Lee, & Mintun, 1992; Minoshima et al., 1993), and linearly standardized to an atlas brain (Talairach & Tournoux, 1988). After pixel values were normalized for global flow rate differences among scans (Fox, Fox, Raichle, & Burde, 1985), the data were averaged across the subjects in a condition, giving mean and variance values for each condition. The average image for each control condition was subtracted from that of its corresponding memory condition to reveal differences in activation between these conditions.

The difference image was then analyzed for statistical significance on a pixel-by-pixel basis (using a pooled variance estimate) using *t* statistics, followed by a multiple-comparison adjustment based on the Bonferroni method (Friston, Frith, Liddle, & Frackowiak, 1991; Worsley, Evans, Marrett, & Neelin, 1992). A one-tailed adjusted value of *p* < .05 was used as a criterion for reliability.

EXPERIMENT 1: ITEM RECOGNITION TEST

Subjects

Subjects were 4 male and 7 female right-handed, normal volunteers who were paid for their participation.

Conditions

Two conditions were used: a *letter memory* condition and a *control* condition designed to match the perceptual and re-

sponse selection requirements of the memory condition. These conditions are illustrated in Figure 1. The experiment consisted of six scans: three memory blocks and three control blocks.

Throughout each trial of the letter memory condition, subjects fixed their gaze on a centrally located crosshair. Four uppercase target letters were presented around the crosshair for a duration of 200 ms, followed by a 3-s delay, followed in turn by a lowercase probe letter that replaced the crosshair. The subject's task was to indicate by clicking a mouse once or twice (for positive or negative responses, respectively) whether or not the probe letter was identical to one of the target letters (the probability of a match was .5). The difference in case between the probe and target letters precluded the use of a pure visual-matching strategy.

Subjects had similar task requirements for the control condition: They had to decide whether or not the probe letter was identical to one of the four uppercase letters presented. However, in this condition, the presentation of the target letters was delayed by 3 s, and they remained on the screen as the probe letter was presented. Thus, although the perceptual and re-

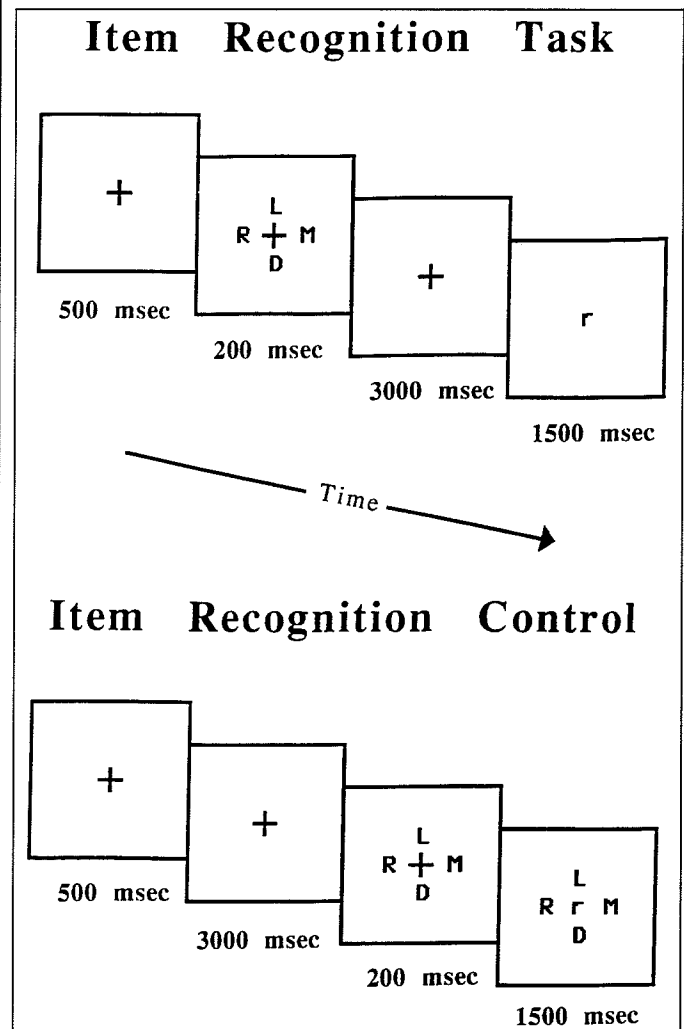


Fig. 1. Sequence of events in a single trial of the letter memory condition and the control condition in Experiment 1.

sponse requirements of this task were similar to those of the memory task, working memory was not required to perform this task accurately.

Results and Discussion

The memory and control tasks were designed to differ only in that memory for verbal information was required in the memory task, but not in the control task. Thus, a subtraction of the brain activation in the control condition from that in the memory condition should inform us about the anatomical loci of verbal working memory mechanisms (using the subtraction logic of Posner, Petersen, Fox, & Raichle, 1988). Table 1 shows the significant sites of activation derived from this subtraction.

The regions activated in the anterior part of the left hemisphere include Broca's area, premotor cortex, and supplementary motor area (SMA). These three regions have all been implicated in the motor output and articulatory coding associated with language production (Petersen, Fox, Posner, Mintun, & Raichle, 1988). Also, Paulesu, Frith, and Frackowiak (1993) have proposed that the site of activation in the right cerebellum is likewise engaged by speech output processes. Given that subjects in our task were not actually speaking during the memory condition, we interpret the constellation of activation in these four sites to indicate the use of subvocal rehearsal processes.

The activated regions in posterior parietal cortex, most notably the left inferior parietal lobule, have been directly implicated in phonological storage. For example, the left posterior parietal region is the most common lesion site in patients who show impairments in verbal short-term memory (McCarthy & Warrington, 1990; Vallar & Shallice, 1990). The activation in the anterior cingulate cortex cannot be interpreted with confidence. This area has been hypothesized to be part of an anterior attentional system (Petersen et al., 1988). Such a system may have been recruited by the relatively higher attentional de-

mands of the memory condition. Table 1 also shows significant activation in thalamus and insular cortex, for which we have no clear explanation.

EXPERIMENT 2: CONTINUOUS WORKING MEMORY TEST

The purpose of Experiment 2 was to replicate the results of Experiment 1 using a different verbal memory task. The task we used requires continuous maintenance of a memory load, unlike the discrete-trial method of Experiment 1. The use of this task accomplished two important goals: First, converging evidence from two distinct memory tasks allows more confident assessment of the brain regions that are essential for verbal working memory. One reason for the need for converging evidence in the present case is that the control and letter memory conditions of Experiment 1 were not identical in their perceptual requirements. Therefore, some of the pattern of activation in the subtraction of these two conditions may be indicative of different encoding demands of the tasks. Second, the discrete trials in Experiment 1 required verbal memory maintenance for only 50% of the total PET recording interval. To saturate the recording interval more completely with verbal storage processes, we designed a task that requires storage 100% of the time.

Subjects

Subjects were 9 right-handed, normal female volunteers who were paid for their participation.

Tasks

Figure 2 illustrates the three conditions employed in this experiment (adapted from Gevins & Cutillo, 1993). The memory task (*2-back*) involved continuous maintenance of a verbal working memory load. The subject saw a series of uppercase

Table 1. Significant activation foci for memory minus control in the item recognition task

Stereotaxic coordinate				
<i>x</i>	<i>y</i>	<i>z</i>	Z score	Brain area
Left hemisphere				
24	-55	43	5.3	Posterior and superior parietal (areas 40 and 7)
55	3	20	5.7	Broca's area (area 44)
44	12	22	5.0	Broca's area (area 44)
1	5	52	4.4	Supplementary motor area (area 6)
48	-6	40	5.8	Premotor (area 6)
28	14	4	5.3	Insular cortex
17	-4	9	4.3	Thalamus
Right hemisphere				
-33	-60	-25	5.4	Cerebellum
Midline				
-6	19	38	4.6	Anterior cingulate (area 32)

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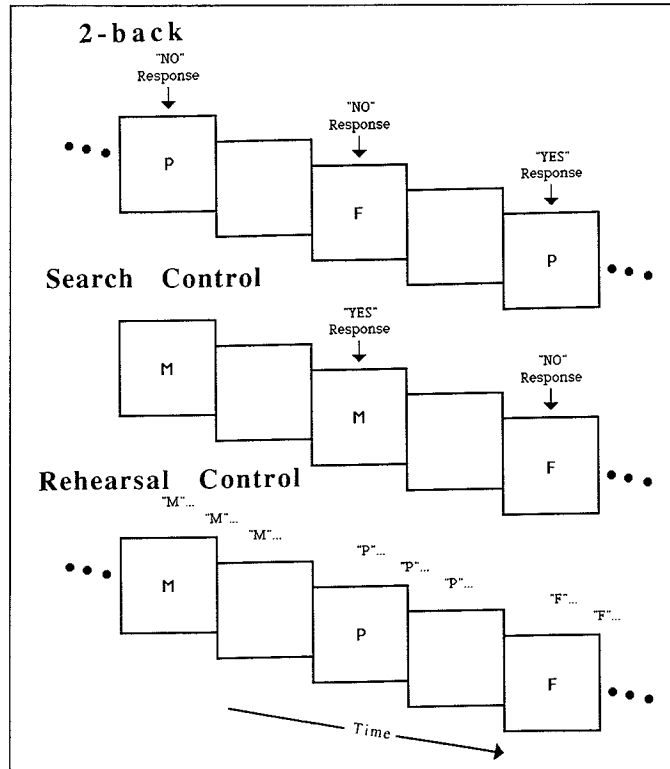


Fig. 2. Sequence of events and appropriate response for each item in sample series from the 2-back condition, search control condition, and rehearsal control condition in Experiment 2.

letters on the screen of a computer. Each letter appeared on the screen for 500 ms, with a 2,500-ms interstimulus interval. The subject's task was to indicate (by clicking a mouse once or twice, respectively) whether or not each letter presented was identical to the one presented two letters previously in the sequence. Notice that at any given point in the block, the subject must maintain at least two letters in working memory, because the last two letters always determine the next two responses.

The second condition (*search control*) was designed to match the perceptual and response requirements of the 2-back condition. Once again, the subject saw a sequence of uppercase letters presented in the center of a computer screen (presentation parameters were identical to those used in the 2-back task). The subject's task in this condition was to indicate (by clicking a mouse once or twice, respectively) whether or not each letter was the same as the first letter presented in the series. Thus, perceptual and response requirements were closely matched to those of the 2-back task, but the working memory load was substantially lower.

In the third condition (*rehearsal control*), subjects were instructed to engage in silent rehearsal. Once again, subjects saw a series of uppercase letters presented on the computer screen (again, the presentation parameters were identical to those used in the 2-back task). The task was to click the mouse once when each letter appeared and to repeat this letter silently until the next letter appeared. This condition was designed to isolate brain mechanisms associated with subvocal rehearsal and response execution.

Results and Discussion

Two subtractions are of direct interest in this experiment: Subtraction of the activation in the search control from that in the 2-back task should provide information about the brain regions involved in verbal working memory, including both phonological storage and rehearsal, and subtraction of activation in the rehearsal control from that in the 2-back task should provide an indication of which brain regions are involved in phonological storage (and, by inference from comparison to the first subtraction, which regions are involved in subvocal rehearsal). Tables 2 and 3, respectively, show the significant sites of activation revealed by these subtractions.

Note first that all areas of reliable activation in Experiment 1 (with the exception of the two regions for which interpretation was unclear—thalamas and insular cortex) show significant activation in the subtraction of the search control from the 2-back task, shown in Table 2. These common areas suggest a neurological substrate for verbal working memory that is consistent with previous neuroimaging research (Paulesu et al., 1993; Petrides, Alivisatos, Meyer, & Evans, 1993), and with studies of verbal short-term memory deficits in brain-injured patients (Vallar & Shallice, 1990). In addition to these common areas of activation, three new areas reveal significant activation in this subtraction. These additional sites are right-hemisphere regions homologous to those activated in the left hemisphere, and include superior parietal cortex, premotor cortex, and SMA. (Note that the level of significance for these areas in the right hemisphere is lower than for those found in the left hemisphere.)

The subtraction of the rehearsal control from the 2-back task should reveal activations in brain areas that mediate phonological storage, with areas related to subvocal rehearsal subtracted away. As expected, this subtraction reveals a loss of significant activation in Broca's area and premotor cortex, both of which were hypothesized to underlie subvocal rehearsal. Furthermore, the activation in posterior parietal cortex remains significant, supporting the hypothesis that this area participates in phonological storage. However, there are complications. There is still activation in SMA and right cerebellar cortex after rehearsal activation is subtracted, despite the fact that these areas have also been associated with rehearsal (Petersen et al., 1988). One possibility is that the rehearsal control was not sufficiently demanding to engage a full complement of rehearsal processes. Alternatively, these areas may mediate processes unrelated to rehearsal. For example, a case study of a patient with right cerebellar damage (Fiez, Petersen, Cheney, & Raichle, 1992) suggests that the cerebellum may play a role in error detection and practice-related learning, not just motor programming.

The 2-back-minus-rehearsal-control subtraction also reveals activation in the thalamas, for which we have no interpretation. Finally, the activation in anterior cingulate cortex that appeared in the 2-back-minus-search-control subtraction drops out in this subtraction, though there is no evidence that this area is part of the brain circuitry involved in speech planning and execution. The lack of significant anterior cingulate activation in this subtraction may also cast doubt on interpretations that center on an attentional role for this brain region, because the attentional imbalance between the 2-back task and the rehearsal control

Table 2. Significant activation foci for the 2-back task minus the search control

Stereotaxic coordinate			Z score	Brain area
x	y	z		
Left hemisphere				
33	-46	38	5.4	Posterior parietal (area 40)
17	-60	45	5.7	Superior parietal (area 7)
42	17	22	4.4	Broca's area (area 44)
28	1	52	6.0	Supplementary motor area, premotor (area 6)
26	-67	-50	5.1	Cerebellum
6	3	54	5.2	Supplementary motor area
Right hemisphere				
-12	-64	47	5.3	Superior parietal (area 7)
-26	-55	50	4.6	Superior parietal (area 7)
-24	3	52	5.5	Supplementary motor area, premotor (area 6)
-1	-64	-25	4.8	Cerebellar vermis
-33	-60	-25	5.4	Cerebellum
Midline				
3	12	40	5.0	Anterior cingulate (area 32)

can be assumed to be similar to that between the 2-back task and the search control.

EXPERIMENT 3: VERIFICATION OF REHEARSAL STRATEGIES

Our interpretation of the PET data in Experiments 1 and 2 presumes the use of a rehearsal strategy. To obtain converging evidence for this strategy, we conducted a behavioral study using a concurrent task technique. This study demonstrates that subjects' performance on these verbal working memory tasks declines significantly under conditions of articulatory suppression, but remains unchanged during a concurrent-tapping task.

Subjects

Two separate groups of 9 right-handed undergraduate students participated in this experiment for pay.

Method

Aside from the addition of concurrent tasks, the memory tasks and presentation parameters were identical to those in Experiments 1 and 2. Each group was tested in three separate conditions: verbal memory alone, verbal memory with articulatory suppression, and verbal memory with concurrent tapping. One group of subjects was tested using the item recognition memory task, and the other group with the 2-back task.

When subjects were required to suppress articulation, they were instructed to repeat aloud the words "one, two, three,

Table 3. Significant activation foci for the 2-back task minus the rehearsal control

Stereotaxic coordinate			Z score	Brain area
x	y	z		
Left hemisphere				
17	-60	43	5.8	Posterior and superior parietal (areas 40 and 7)
28	1	50	5.5	Supplementary motor area
3	14	43	4.8	Supplementary motor area
Right hemisphere				
-26	-58	45	5.3	Superior parietal (area 7)
-12	-64	47	5.7	Superior parietal (area 7)
-26	3	50	4.5	Supplementary motor area (area 6)
-3	-17	2	4.7	Thalamas
-3	-62	-25	4.8	Cerebellar vermis
-28	-60	-38	4.6	Cerebellum

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four" at a rate of approximately three items per second. Their rate of articulation was monitored by the experimenter, and they were prompted if their rate faltered in any way. When subjects engaged in concurrent tapping, they tapped all fingers of their left hands at approximately three taps per second. Again, the experimenter monitored their rate of tapping and prompted them if they failed to maintain a consistent rate.

Results

Subjects in both groups showed significantly poorer performance under conditions of articulatory suppression than when the memory task was performed alone. Accuracy in the item recognition task was 93.6% when performed alone and 84.4% under articulatory suppression, $t(8) = 3.02, p < .05$, one-tailed. Accuracy in the 2-back task dropped from 93.2% to 89.7% during articulatory suppression, $t(8) = 2.16, p < .05$, one-tailed. Concurrent tapping, however, did not affect memory performance significantly. When subjects performed the concurrent-tapping task, accuracy in the item recognition task showed a nonsignificant decrease from 93.6% to 90.6%, $t(8) = 1.74, p > .05$, one-tailed. Likewise, concurrent tapping in the 2-back task caused a nonsignificant decrease in accuracy from 93.2% to 90.2%, $t(8) = 1.29, p > .05$, one-tailed.

Note that accuracy in the 2-back task with suppression (89.7%) is very similar to accuracy with tapping (90.2%). That the former is reliably less than accuracy in the 2-back task alone while the latter is not is due to the fact that the variance was much higher in the tapping condition. (In fact, 3 of 9 subjects showed higher accuracy on the 2-back task during tapping than alone.) We were concerned that the lack of significant performance decrements during tapping might have been due to a lack of experimental power. Accordingly, we performed a second analysis that considered accuracies only for positive decisions. (Positive decisions should be more revealing than negative ones because there could have been an overall bias to respond "no," given that two thirds of the items required negative decisions.) Accuracies for positive decisions on the 2-back task showed much larger effects than the overall accuracies suggested. Accuracy on target trials fell significantly from 92.7% to 82.1% under articulatory suppression ($t[8] = 2.79, p < .05$, one-tailed), but showed a nonsignificant drop to 89.3% ($t[8] = 1.06, p > .05$, one-tailed) during concurrent tapping.

CONCLUSIONS

Converging evidence from two different tasks revealed a pattern of brain activations that implicates separable rehearsal and storage components of verbal working memory. Both tasks activated speech planning and execution areas in anterior brain regions, as well as posterior parietal regions associated with the storage of verbal information. Furthermore, when rehearsal-based activation was subtracted from the activation due to storage and rehearsal together, the bulk of the anterior brain activation was subtracted out, while the posterior parietal regions remained active. From this result we are drawn to the conclusion that rehearsal is a process drawing on a frontal mechanism similar to the one used for overt speech. This conclusion is

based in part on the activation of this same anterior region in overt speech tasks (e.g., Petersen et al., 1988). Furthermore, studies showing that articulatory suppression interferes with verbal working memory and dramatically reduces the word-length effect also suggest that overt and covert speech engage the same mechanism (Baddeley et al., 1984). Also, recall that although the rehearsal task in our Experiment 2 did not involve overt speech, it nonetheless activated the same areas associated with speech production.

The conclusion that overt and covert speech may be mediated by the same mechanism leads to an obvious prediction: that subjects who are incapable of overt speech should show no evidence of rehearsal and, consequently, impaired verbal working memory. This prediction has been tested by various investigators. For example, Bishop and Robson (1989) conducted studies of the verbal working memory performance of congenitally anarthric children. Although these children had never produced overt speech, they showed relatively normal memory spans, and clear phonological similarity and word-length effects. How could this be so if overt and covert speech are mediated by the same mechanism? One resolution is that anarthric subjects have damage restricted to relatively peripheral speech mechanisms. For example, Vallar and Cappa (1987) demonstrated intact rehearsal processing in an anarthric patient whose damage was restricted to the brain stem, sparing the cerebral cortex. In such cases, although the same cortical mechanisms might mediate overt speech and rehearsal, peripheral damage could lead to unimpaired rehearsal in the absence of overt speech. Thus, successful rehearsal may depend not on peripheral speech mechanisms, but only on use of the same cortical structures.

These findings converge with previous behavioral and neuropsychological evidence in two important ways: First, clear support for the functional dissociation of storage and rehearsal has been generated: Separate anatomical areas mediate these processes. Second, the specific brain regions activated by storage and rehearsal are consistent with the clinical and neuroimaging evidence implicating posterior parietal regions in storage and anterior speech mechanisms in rehearsal. These results provide support for a model of verbal working memory in which verbal information is stored in a phonological buffer with periodic rehearsal of that information by a covert articulatory mechanism (Baddeley, 1992).

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