

The Search for the Phonological Store: From Loop to Convolution

Bradley R. Buchsbaum and Mark D'Esposito

Abstract

■ The phonological loop system of Baddeley and colleagues' Working Memory model is a major accomplishment of the modern era of cognitive psychology. It was one of the first information processing models to make an explicit attempt to accommodate both traditional behavioral data and the results of neuropsychological case studies in an integrated theoretical framework. In the early and middle 1990s, the purview of the phonological loop was expanded to include the emerging field of functional brain imaging. The modular and componential structure of the phonological loop seemed to disclose a structure that might well be transcribed, intact, onto the convolutions of the brain. It was the phonological store component, however, with its simple and modular quality, that most ap-

pealed to the neuroimaging field as the psychological "box" that might most plausibly be located in the brain. Functional neuroimaging studies initially designated regions in the parietal cortex as constituting the "neural correlate" of the phonological store, whereas later studies pointed to regions in the posterior temporal cortex. In this review, however, we argue the phonological store as a theoretical construct does not precisely correspond to a single, functionally discrete, brain region. Rather, converging evidence from neurology, cognitive psychology, and functional neuroimaging argue for a reconceptualization of phonological short-term memory as emerging from the integrated action of the neural processes that underlie the perception and production of speech. ■

INTRODUCTION

Working memory (WM), as an idea, a concept, and a theoretical model, is in many ways the poster-child of the successful union of cognitive psychology and neuroscience that has taken place in the last 20 years or so. In the mid-1980s, Baddeley and colleagues' conceptualization of short-term memory (Baddeley, 1986, 2003; Baddeley & Hitch, 1974) as a dynamic, multicomponent "blackboard of the mind," with its interactive processes of executive control and mnemonic storage, swept through cognitive psychology, touching as it went almost every corner of the field. Indeed, virtually every cognitive psychology textbook written after 1986 offers the multicomponent model of WM as the best theoretical conceptualization of how humans maintain and manipulate information in the service of higher cognitive processing.

The influence of WM was not limited to cognitive psychology, however. In the years following Goldman-Rakic's (1987) landmark review of the physiology and function of the prefrontal cortex, in which she linked the phenomenon of persistent activity in the principal sulcus of the monkey prefrontal cortex during spatial delayed response tasks to the psychological concept of WM, the term would become an essential part of the vocabulary of the vast field of neuroscience and related disciplines

including psychiatry, neurology, and neurobiology. Nowhere in the brain sciences, however, have the specifics of the WM model itself, as opposed to the more general idea of "working memory," been more energetically pursued than in the emerging field of human functional neuroimaging, where the possibility of uncovering the "neural correlates" of the various components of the WM model has had enormous appeal. Unlike the "pure" neurobiologist or the "pure" cognitive psychologist, the practitioner of functional neuroimaging is positioned somewhat awkwardly in the crevasse that separates the world of psychology and the world of biology. Thus, to the cognitive neuroscientist, the WM model provides a certain structure, set of well-defined relations, and logical framework to which he may look to the brain for a mirror image. When the neural reflection, as it were, discloses a logical and spatial structure that corresponds to the processes of the psychological model, then perhaps the neuroimager has transformed the psychological metaphor into its concrete neural realization. It is, however, the responsibility of the cognitive neuroscientist to determine whether the neural reflection and the psychological projection are, in fact, one and the same object. This is precisely the problem that has faced functional neuroimaging in its quest to uncover the brain correlates of WM, and it is the topic of the present article.

We shall focus our attention on one particular component of the WM model, the "phonological store"—perhaps

University of California, Berkeley

the single most studied “box” in the history of cognitive psychology. The phonological store has always appealed to the cognitive neuroscientist for its relatively simple and circumscribed function, and it has been regarded as the component of WM that might most plausibly be localized to a single location in the brain. Thus, we take the phonological store as a kind of perfect test case for the question of how functional neuroimaging can be used not only to localize but also to *inform* and *challenge* a model initially conceived in pure cognitive psychological terms. Ultimately, we view the scientific record of the “search for the phonological store” as part morality tale and part coming-of-age story, a close reading of which will lead to a better understanding of how cognitive psychology and neuroscience can jointly contribute to theoretical advances on the brain bases of cognition.

ARCHITECTURE OF THE WORKING MEMORY MODEL

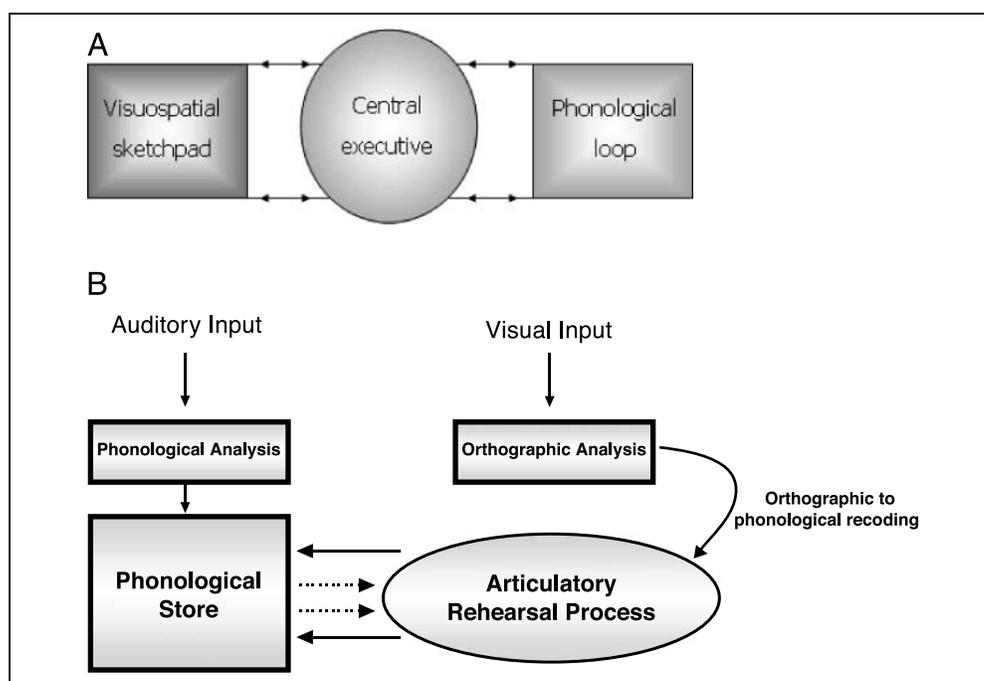
We begin with a brief review of the WM model and its basic architecture before discussing the phonological store in more detail (Figure 1A). The WM model consists of a control process, the central executive, and two slave systems, the phonological loop and the visuospatial sketchpad (Baddeley, 1986). The phonological loop is responsible for maintaining speech-based information, such as an address or telephone number, in readily accessible form, whereas the visuospatial sketchpad is assumed to perform a similar function for the on-line maintenance and manipulation of visuospatial imagery. The central tenets of the WM model are as follows: (1) It is a limited capacity system; at any given moment, there is a finite amount of information directly available for processing in memory. (2) The specialized

subsystems devoted to the representation of information of a particular type, for instance, verbal or visuospatial, are structurally independent of one another, and the integrity of information represented in one domain is protected from the interfering effects of information that may exist in another domain. (3) Storage of information in memory is distinct from the processes that underlie stimulus perception. Rather, there is a two-stage process whereby sensory information is first analyzed by perceptual modules and then transferred into specialized storage buffers that (ostensibly) have no other role but to temporarily “hold” preprocessed units of information. Moreover, the pieces of information that reside in such specialized buffers are subject to passive, time-based decay as well as interitem interference (e.g., similar sounding words like “man, mad, map, cap, mad” can lead to interference within a specialized phonological storage structure). Finally, such storage buffers have no built-in or internal mechanism for maintaining or otherwise refreshing their own contents—rather, this must occur from without, through the process of rehearsal, which is a top-down control mechanism that can sequentially access and refresh the memory traces that remain active within the store.

THE HISTORICAL DEVELOPMENT OF THE PHONOLOGICAL LOOP SYSTEM

The phonological loop system of WM is a descendant of information processing models of short-term memory (STM) that were being developed in the mid-1960s in the emerging field of cognitive psychology (Sternberg, 1969; Sperling, 1967; Waugh & Norman, 1965; Broadbent, 1958). These models attempted to explain the empirical

Figure 1. (A) The Working Memory model of Baddeley and colleagues. The model consists of a central executive and two “slave systems,” the phonological loop and the visuospatial scratchpad. (B) The phonological loop. Verbal information is received from the periphery and then processed in domain-specific perceptual systems before it may be stored and maintained in the phonological loop. Auditory information has obligatory access to the store, whereas visual-verbal information must first be recoded from orthographic to phonological form before entering the phonological store.



results of psychological experiments in terms of the flow of information through a series of processing stages in an abstract computational space. They often took the form of diagrams, consisting of boxes representing a process or a “store” connected by arrows representing the flow of information. For instance, as the distinction between short- and long-term memory gained support from studies of serial and free recall of word lists (Glanzer & Cunitz, 1966; Postman & Phillips, 1965), this dichotomy began to be reflected in contemporary information processing models of STM (e.g., Sperling, 1967). Indeed, the separation between a temporary, limited-capacity fast-access STM store, and an infinite capacity, slow-access and permanent long-term store was entirely compatible with the idea that was then widely espoused, that the human cognitive system might be likened to a digital computer. Thus, STM was analogous to computer random-access memory (RAM), whereas long-term memory was like the crystallized storage structure of a hard-drive, with its large capacity and relatively slow access. When information is needed for on-line processing, it is retrieved from long-term memory and copied into STM.

Another clear similarity between these information processing models and the computer is the manner in which sensory input is analyzed and then stored in memory. In the computer, for instance, an input device such as the keyboard is responsible for registering the order and identity of a sequence of typed letters, but further processing on this information is carried out elsewhere, for instance, in RAM. Thus, many models of STM, including the phonological loop, distinguished between sensory and perceptual signal analysis, and the sort of temporary storage that underlies STM. Important to this view of signal analysis is the idea of informational redundancy: An acoustic signal that is processed by some sensory-perceptual component may be analyzed, coded, and then *transmitted* (and possibly transformed) to another component in the system, such as a short- or long-term store, for further processing. Likewise, in the computer, the letter “a” that is registered by the keyboard is the same “a” that is subsequently stored in memory, but the physical devices handling registration and storage, respectively, are both structurally and functionally separate. Of course, there is no special reason why the human cognitive system ought to behave at all like a computer—perhaps in the brain the same processor that registers a piece of sensory datum also *stores* that datum. As it turned out, however, the single most compelling argument in favor of the temporary storage buffer would come from neuropsychological investigations of patients with focal brain damage.

NEUROPSYCHOLOGY AND THE PHONOLOGICAL LOOP

Unlike other early models of STM, the logical architecture of the phonological loop was not based solely on infer-

ences derived from psychological inquiries of groups of healthy control subjects. Rather, evidence from cognitive neuropsychology provided some of the key pieces of evidence leading to the formulation of the phonological loop. Indeed, it is often noted that the strongest evidence for the existence of two memory systems comes from case studies of persons with focal brain lesions (Vallar, 2006).

In the early 1950s, an astonishing, if tragic, discovery was made. A surgical procedure for the treatment of intractable epilepsy that involved bilateral removal of the medial-temporal lobe in patient H.M. resulted in a catastrophic impairment in his ability to form new long-term memories, although, remarkably, his short-term memory was left intact (Scoville & Milner, 1957). Thus, H.M. was perfectly capable of repeating back a string of digits—the classic test of STM—but unable to form permanent memories for new facts and events. In the years following that report, Warrington and Shallice (Shallice & Warrington, 1970; Warrington & Shallice, 1969) and others (Vallar & Baddeley, 1984; Caramazza, Basili, Koller, & Berndt, 1981; Saffran & Marin, 1975) described a number of case studies of patients with damage to the left temporo-parietal cortex who had dramatically impaired STM for numbers and words coupled with a preserved ability to learn supraspan (e.g., greater than 10 items) word lists with repeated study. This constituted striking evidence for a double dissociation between short- and long-term memory. Remarkably, the purest examples of such “short-term memory patients” did not evince any major deficits in their on-line language abilities—that is to say, they were not *aphasic*. Thus, famously, patient J.B. was able to carry on conversations normally and to speak fluently without abnormal pauses, errors, or other symptoms of aphasia, and also to perceive and comprehend speech without difficulty. In short, the “language faculty,” considered in a narrow sense to encompass the processes necessary for the on-line comprehension and production of meaningful speech, need not be disturbed even in the presence of a nearly complete eradication of verbal STM (Shallice & Butterworth, 1977). Thus, Warrington and Shallice (1969) characterized the deficit as a selective disruption to an auditory-verbal short-term store, a component whose purpose was to temporarily buffer the flow of information arriving from a peripheral speech perception system. This idea was, of course, consistent with the separation between sensory analysis (e.g., the keyboard) and temporary storage (e.g., RAM) embodied by the information processing models of memory discussed earlier. Finally, it should be emphasized that the memory deficit was entirely limited to a particular informational domain—in this case, verbal (though memory for *auditory*-verbal material in particular was most severely disrupted). J.B. was unimpaired on short-term memory tests that used visuospatial, or even nonlinguistic auditory materials, and therefore the memory impairment could not be explained by some general deficit in retrieving just-presented information.

In the earliest version of the phonological loop (known then as the “articulatory loop”), Baddeley and Hitch (1974) proposed that the maintenance of verbal information was achieved through the repeated circulation of articulatory codes in a process resembling a “closed tape-loop.” The ability to keep a sequence of digits in mind involved a motor–speech processor that could repeatedly loop through its own contents and, through this iterative process, keep the verbal information “on-line.” The articulatory loop was thought to depend on the same central articulatory mechanisms that underlie speech production. However, as the case of J.B. would illustrate, and subsequent investigations of patient P.V. by Vallar and Baddeley (1984) would confirm, the nearly complete loss of verbal short-term memory capacity need not be accompanied by any deficit to the speech-production system. To account for the neuropsychological data, then, Vallar and Baddeley (1984) and Salame and Baddeley (1982) proposed a fractionation of the articulatory loop into a phonological store and an articulatory rehearsal process, and renamed the circuit the “phonological loop.”

Within the phonological loop, it is the interplay of its two components—the phonological store and the articulatory rehearsal process—that enables representations of verbal material to be kept in an active state (Figure 1B). The phonological store is a passive buffer in which speech-based information can be stored for brief (approximately 2 sec) periods (Baddeley, Thomson, & Buchanan, 1975). The articulatory control process serves to refresh and revivify the contents of the store, thus allowing the system to maintain short sequences (or about as much information that can be spoken in 2 sec) of verbal items in memory for an extended interval. This division of labor between two interlocking components, one an *active process* and the other a *passive store*, is crucial to the model’s ability to account for a wide range of experimental data. For instance, when the articulatory control process is interfered with through the method of articulatory suppression (e.g., by requiring subjects to say “hiya” over and over again), items in the store rapidly decay, and recall performance suffers greatly. The store, then, lacks a mechanism of reactivating its own contents but possesses memory capacity while, conversely, the articulatory rehearsal process lacks an intrinsic memory capacity of its own, but can exert its effect indirectly by refreshing the contents of the store.

THE LOGICAL STRUCTURE OF THE PHONOLOGICAL LOOP

The success of the phonological loop as a model of the operation of verbal working memory must be attributed to the simplicity and elegance of its componential structure coupled with the ease with which it is able to capture and cleanly explain almost all of the classic behavioral effects that have been consistently reported over the years in tasks that test verbal short-term

memory. The phonological loop model may be thought of as consisting of a number of rules or axioms that govern how the mechanism of the loop gives rise to the four basic behavioral phenomena that the model was primarily devised to explain. The appeal of the model comes partly from its extreme parsimony—with only a very minimal set of axioms, it is able to account for a large number of behavioral findings. It is important for our purposes to review how the phonological loop explains these canonical behavioral effects, namely: the *phonological similarity effect*, the *word-length effect*, the *effect of articulatory suppression*, and the *irrelevant sound effect* (see, e.g., Repovs & Baddeley, 2006, for a more extensive description of the model).

The *phonological similarity effect* refers to the finding that similar sounding sets of words (e.g., “man, mad, cap, tan”) are more difficult to retain in memory than sets of phonologically dissimilar words (Conrad & Hull, 1964). The locus of this effect is the phonological store, and it results from the increased amount of interference that occurs between memory traces that share overlapping representational (e.g., phonemic) features, relative to those that do not.

The *word-length effect* simply refers to the fact that lists of words that take more time to articulate—longer words—are more poorly remembered than words that take less time to articulate (Baddeley et al., 1975). This occurs not only between sets of words that have different numbers of syllables but also for sets of words that are equated for number of syllables but are, nevertheless, unequal in absolute articulatory duration. The effect is explained by assuming that items in the phonological store suffer *time-based decay* that can only be reversed by way of articulation. Thus, as the articulatory loop cycles through a set of long words, the overall time elapsed between successive iterations will be greater, and, therefore, the probability that one of the several items in the store may have (irretrievably) decayed will be consequently increased. This effect, then, is jointly determined by the properties of the rehearsal process (rate of articulation) and that of the phonological store (rate of decay).

The negative effect of *articulatory suppression* on recall performance is observed when subjects are prevented from using inner speech either during presentation or during a delay inserted before recall. Thus, as articulatory suppression interferes with the articulatory rehearsal process, the mechanism that is ordinarily used to refresh the items in the phonological store is occupied, and the system is therefore unable to counteract trace decay, leading to a decline in recall performance.

The irrelevant sound effect occurs when the to-be-remembered verbal stimuli are accompanied by a stream of unattended auditory information (Salame & Baddeley, 1982). These “irrelevant sounds” need not be in the speaker’s native language or even phonemic to be disruptive, provided there is some degree of variation in the

sound stream. For instance, a single tone or even white noise does not have an effect, although a changing sequence of tones does cause impairment (Jones & Morris, 1992). The locus of the irrelevant sound effect is in the phonological store, where the incoming acoustic information interferes with the to-be-remembered items in the store. Because the presentation of irrelevant visual-verbal information does not have an effect on recall, it is assumed that auditory information has *obligatory access* to the store, whereas visual-verbal information does not.

How, then, does visual-verbal information enter the phonological store? The answer, supported by several lines of evidence (Baddeley, Lewis, & Vallar, 1984; Levy, 1971), is that textual information must first be recoded phonologically before it can enter the store (see Figure 1B). This recoding process, moreover, requires the involvement of the articulatory rehearsal process, as subvocalization is necessary to reroute visually derived verbal information into the phonological store. In support of this contention is the finding that articulatory suppression abolishes the phonological similarity effect for visual, but not auditory, presentation. Because auditory information has obligatory access to the store, articulatory suppression has no effect on its deposition within the store. For visual presentation, however, articulatory suppression ties up the rehearsal system, preventing phonological recoding of visual-verbal material and, consequently, blocking subvocally mediated access to the store.

In the preceding sections, we have briefly outlined the main components of the phonological loop, as well as the manner in which its architecture and functional characteristics account for certain reliable effects observed in studies of verbal STM. We should make clear that it is not universally accepted that every detail of the phonological loop is perfectly supported by available evidence. For instance, there is a great deal of debate about whether the word-length effect is actually caused by an increase in the absolute spoken duration of the items, or whether it is better explained by, for instance, the phonological complexity of the items (Mueller, Seymour, Kieras, & Meyer, 2003; Caplan, Rochon, & Waters, 1992). The purpose of this section has been merely to provide a reasonably complete picture of the model as it stands, rather than to discuss the various challenges (in the psychological literature) that exist to its correctness. In general, however, it can be asserted as a matter of fact that there is currently no other model of verbal working memory that is as complete and well accepted as the phonological loop model.

FUNCTIONAL NEUROIMAGING AND THE SEARCH FOR THE PHONOLOGICAL STORE

In the mid-to-late 1980s, technological advances in positron emission tomography (PET) using the O-15 radioactive tracer, with its relatively high spatial resolution (approximately 1 cm³), were accompanied by a critical

conceptual innovation—that adaptation of as “cognitive subtraction” to neuroimaging—provided the inferential machinery necessary to link regional variation in brain activity to experimental manipulations at the task or psychological level (Posner, Petersen, Fox, & Raichle, 1988). The earliest effort to identify the “neural correlates” of the phonological loop using the method of cognitive subtraction was carried out by Paulesu, Frith, and Frackowiak (1993) in a landmark PET study. It was one of the first functional neuroimaging studies in which the inferential objectives of the study were specified entirely at the level of the cognitive model, rather than at the task or stimulus level. In other words, the aim of the experiment was not to distinguish differences in brain activation due to task manipulation or a contrast in stimulus properties per se, but rather to exploit the internal logic of the phonological loop model to reveal a correspondence between a set of hypothetical cognitive processes and regional brain activity. The results were striking, with the authors concluding that the left supramarginal gyrus (BA 40) is the “primary neural correlate of the phonological store.” The study of Paulesu et al. (1993) remains the canonical neuroimaging study of the phonological loop and is still the most widely known and most frequently cited (954 citations at time of writing) imaging study on the topic. Because of its historical importance and because the study illuminates many of the key aspects and dilemmas involved in the search for the phonological store, we will examine the study in some detail.

The strategy used by Paulesu et al. (1993) was to isolate components of the phonological loop by means of a hierarchically arranged sequence of cognitive subtractions. First, a task requiring a contribution of all components of the phonological loop was contrasted to a formally identical nonverbal visual memory task with no demand on phonological memory. Thus, in one task, a short-term item-recognition task, six visually presented letters were presented followed by a 2-sec rehearsal period and a probe letter requiring a yes/no recognition judgment. In the baseline task, the format was the same except that Korean letters (ostensibly not capable of being phonologically coded) were used in place of the English letters. This first task comparison was designed to reveal the regional activity associated with the operation of the phonological loop, but not to isolate specific subcomponents of the system. A second task was used to dissociate the brain regions associated with articulatory rehearsal from those associated with phonological storage. A rhyme-judgment task was used to achieve the latter goal because, as the authors argued, when letters are presented visually, rhyming decisions engage the subvocal rehearsal system but not the phonological store (Burani, Vallar, & Bottini, 1991; Besner, 1987; Vallar & Cappa, 1987). Thus, subtracting the activity elicited by the second task from that of the first task should reveal the phonological store.

The dramatic result was that the comparison revealed differential activity in a single brain area—the left supramarginal gyrus. Of course, the contrast *might* have revealed two areas or three areas or a whole network of brain regions associated with phonological storage. The phonological store, however, as an abstraction, *suggests* something self-contained and unitary, and thus, to have discovered that in the brain the store is spatially distributed across a jumble of far-flung cortical fiefdoms would have been, at best, inelegant. The discovery of a one-to-one correspondence between the cognitive concept and its neural implementation, therefore, seemed to fit quite well with the intuitive expectation.¹

It is important to emphasize that the subtraction logic of the Paulesu et al. (1993) study requires that rhyming judgments *engage* the subvocal rehearsal system, but not the phonological store. The basis for this assumption may be found in two lines of evidence. First, with respect to articulatory rehearsal, it has been observed that subjects are slightly slower and less accurate at performing rhyme judgments (e.g., does “fraught” rhyme with “bought”?) when they must simultaneously carry out a concurrent articulation task. This effect cannot be attributed to a general disruption of information processing incurred by articulatory suppression because the effect is not observed in tasks requiring graphemic or synonymy decisions (Kleiman, 1975). The explanation of the deleterious effect of articulatory suppression on rhyme judgments put forth by Burani et al. (1991) and Besner (1987), and cited by Paulesu et al., maintains that certain types of phonological operations (such as postassembly and deletion) require access to a code that cannot be produced without recourse to subvocal articulatory processes. Thus, rhyming judgments are aided by subvocal speech. The second requirement, that rhyming judgments *do not* engage the phonological store, however, is not so clear. The critical piece of evidence cited by Paulesu et al. for the assertion is that the patient J.B., who Vallar and Baddeley (1984) have posited to have a severe impairment of the phonological store, can perform rhyme judgments with little difficulty. There are two difficulties with this particular line of argument. First, with respect to the PET imaging study, the assumption that rhyme judgments do not *engage* the phonological store rests on the assumption that a particular patient, J.B., has a defective phonological store. Using rhyme judgments, then, as a probe to discover the location of the phonological store in a PET study is contingent on having correctly linked phonological store (or, rather, its *absence*) with a particular lesion in the first place—which is circular.

A less abstruse problem with the use of rhyme judgments in localizing the phonological store follows straightforwardly from the architecture of the phonological loop. Visual-verbal information enters the store via the articulatory rehearsal process, and rhyme judgments (according to the logic) require subvocalization.

Thus, rhyme judgments will result in phonological information entering the phonological store obligatorily by way of articulatory recoding. In this sense, rhyme judgments, although they may not *necessitate* a functional contribution from the phonological store, may indeed *engage* the store in the context of a PET activation study. This illustrates the distinction between the *necessary* contribution of a component to the performance of a task (i.e., phonological store may not be necessary for rhyme judgments) and what might be called the *metabolic side effects* of a necessary operation (i.e., subvocalization transmits phonological information to the store). It may be argued, of course, that there are, nevertheless, differences in neural activity that should be expected to occur between one condition, in which information in the phonological store is explicitly accessed in order to perform the task, and in the “side effect” case where the store is engaged, but the information within it is never accessed. This is a reasonable hypothesis, but one for which the phonological loop model is silent: for it makes no prediction as to the *metabolic cost* of accessing versus merely depositing (and never withdrawing) phonological material in the store. Finally, a number of recent functional magnetic resonance imaging (fMRI) studies (Seghier et al., 2004; Billingsley, McAndrews, Crawley, & Mikulis, 2001; Pugh et al., 1996) have shown that visual rhyme judgments, compared with a suitable control, are associated with enhanced activation in the posterior temporo-parietal area, a finding that was not reported in the study of Paulesu et al. (1993).

In summary, the report of Paulesu et al. (1993) was one of the earliest examples of a functional neuroimaging study that exploited the structure and logic of a cognitive model for the purpose of localizing one of its components. The experimental design of this study, although innovative and empirically supportable, does not conclusively demonstrate that the primary neural correlate of the phonological store is BA 40, or the supramarginal gyrus.

In the years following the study of Paulesu et al. (1993), a number of PET activation studies, using a variety of verbal memory paradigms, were undertaken to localize the components of Baddeley’s phonological loop model (Jonides et al., 1998; Awh et al., 1996; Fiez et al., 1996; Salmon et al., 1996; Schumacher et al., 1996). These studies have been exhaustively reviewed elsewhere (Baddeley, 2003; Chein & Fiez, 2001; Becker, MacAndrew, & Fiez, 1999), so we will not examine them in detail. As a general matter, though, the PET studies of the middle and late 1990s concluded that the neural correlate of the phonological store was in the posterior parietal lobe (Baddeley, 2003; Smith, Jonides, Marshuetz, & Koeppel, 1998). In such studies, especially those employing the “*n*-back” paradigm, increases in mnemonic load (e.g., the number of items maintained in memory) were assumed to index storage processes (Awh et al., 1996).

For instance, a task requiring one to match the current letter with the letter “2-back” places a greater demand on storage than a 1-back or 0-back (e.g., match the currently presented letter) condition. This assumption, however, can be called into question. In each of these cases, because the rate of presentation is constant, the amount of information entering and exiting the phonological store is also relatively stable, and therefore, it is not clear, from the standpoint of phonological throughput, that increasing load in such tasks should place increasing metabolic demands on the phonological store. Thus, in a 1-back condition, subjects may rely on a rapid rehearsal strategy (high phonological throughput) whereas in a 2-back condition, subjects may draw on other strategies or at any rate fail to increase the amount (per unit time) of phonological throughput generated from subvocal rehearsal. Although phonological processing demand need not increase with putative mnemonic load, other executive, attentional, and processes associated with memory search would be expected to scale with load (see Chein, Ravizza, & Fiez, 2003), and therefore, the *n*-back task is not well suited for isolating the phonological store.

It should be emphasized that these early functional neuroimaging studies of WM were primarily concerned with the problem of localization—of discovering *where* the components of the phonological loop may be found in the brain. This enterprise is, of course, orthogonal to the question of whether the concept of phonological loop is *true*. One cannot find the “neural correlates” of the phonological loop if the theory itself does not accurately depict reality. Such studies, however, were enormously important insofar as they allowed for a provisional and tentative link to be drawn between specific brain regions and particular components of the phonological loop.

THE PHONOLOGICAL LOOP AS A COGNITIVE BRAIN MODEL

As the evidence accumulated in favor of a certain set of relations between the components of the loop and particular regions of the brain, cognitive neuroscience began as a field to view the phonological loop model as a kind of hybrid cognitive brain model. Indeed, in a recent review of the WM model, Baddeley (2003), the primary architect and theoretical guardian of the phonological loop, provided a new information processing diagram of the model. In this “new” version, below each cognitive box representing a component of the model was a label designating the brain area for which that component had been found to correspond. Beneath the “phonological store” box, for instance, could be read: “inferior parietal lobe.” In addition, the standard box rendering of the model was supplemented by a lateral view of the cerebral cortex with circles drawn in various locations indicating where the components of the WM

model are thought to be located in the brain (see Figure 2). In this brain rendering of the WM model, sitting approximately 2 cm above the posterior end of the Sylvian fissure, at the border of the inferior and posterior parietal cortex, was a circle surrounding the letters “PS”—or phonological store (Baddeley, 2003, p. 836). To be clear, although Baddeley’s intent with these figures was not to transform his information processing model into a fully specified neural circuit diagram, the endorsement of the functional neuroimaging research tends to validate the viewpoint that the model itself had been resituated into the brain. To the extent that the phonological loop may be identified with specific neural systems, it exposes itself (or its neural incarnation) to challenge and disproof from evidence derived from biological measures. This is, indeed, a valuable property of a model from the standpoint of cognitive neuroscience, as it allows the researcher to go beyond “where” questions (e.g., where is component *X* located?) and begin to ask questions that speak to the *validity* of the theory in question. Precisely how this may be achieved is the topic to which we now turn.

THE PHONOLOGICAL STORE AND THE PARIETAL LOBE

In the preceding sections, it was established that the vast majority of functional neuroimaging studies carried out in the 1990s were in agreement with respect to the neural localization of the phonological store in Brodmann’s area (BA) 40 in the posterior/inferior parietal lobe. However, in a review and meta-analysis of studies that had investigated the neural correlates of the phonological loop, Becker et al. (1999) observed that there was a great deal of variability in the location of the reported Talairach coordinates (Table 1). For instance, whereas Paulesu et al. (1993) had reported phonological store activity at a more inferior location ($x = -44, y = -32, z = 24$), a number of other studies, for example, that of Awh et al. (1996), identified a locus at a more

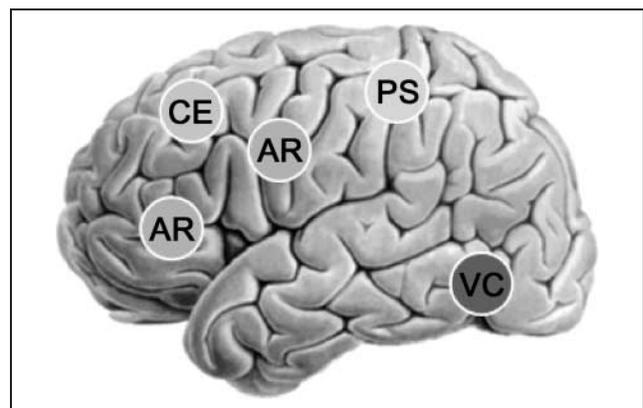


Figure 2. The brain basis of working memory. Adapted from Baddeley (2003).

superior location (see Figure 3). Indeed, the full array of Talairach coordinates associated with the phonological store extends from the most lateral and inferior portion of the supramarginal gyrus (e.g., Salmon et al., 1996) all the way to the superior parietal cortex (e.g., Awh et al., 1996), with stops scattered in between (e.g., the intraparietal sulcus; Smith et al., 1998). It should also be noted that the study of Fiez et al. (1996) did not observe activity associated with phonological storage in any region in the parietal cortex (but see Jonides et al., 1998).

Becker et al. (1999) made some further observations on the topic of the neural localization of the phonological store that were particularly insightful. First, they noted that the foci located more superiorly, around BA 7, were quite close to areas associated with visual attention; and some speculation was offered as to why “shifting of visual attention” might be associated with verbal WM tasks that employ rapidly changing visual-verbal stimuli. Indeed, from our current vantage point, we can make the more general statement that activation in BA 7 and the area around the intraparietal sulcus is implicated in a large number of cognitive tasks, especially those that might be classified as attention-demanding, executive, mnemonic, and so on (Cabeza & Nyberg, 2000; Duncan & Owen, 2000). Moreover, attempts to find isolated areas along the intraparietal sulcus that show a stimulus- or modality-specific storage function have been inconclusive (Majerus et al., 2007; Ravizza, Delgado, Chein, Becker, & Fiez, 2004; Zurowski et al., 2002; Nystrom et al., 2000).

Becker et al. (1999) also reasoned that because auditory material has, by definition, obligatory access to the phonological store, *passive listening* to auditory stimuli ought to activate the “neural correlate” of the phonological store. Activation in the posterior parietal cortex, however, is not typically observed during functional neuroimaging studies of passive listening; indeed, studies that have examined passive listening with a variety of auditory stimuli usually observe a pattern of activation

Table 1. Talairach Coordinates of Parietal Lobe Activations in the Five PET Studies Shown in Figure 3

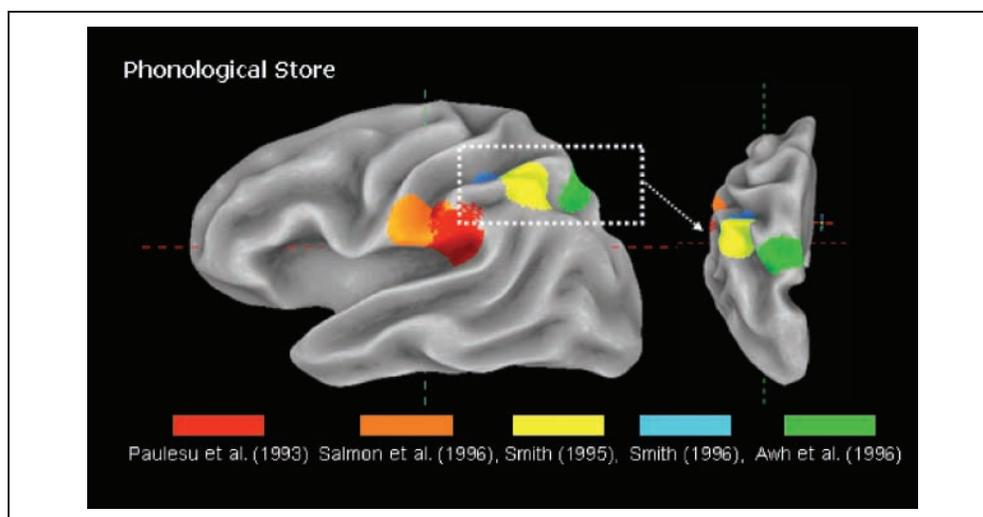
Study	<i>x</i>	<i>y</i>	<i>z</i>
Paulesu et al. (1993)	−44	−32	24
Salmon et al. (1996)	−56	−22	24
Smith, Jonides, and Koeppel (1996)	−37	−49	40
Smith et al. (1995)	−35	−42	34
Awh et al. (1996)	−17	−60	43

that is largely confined to the superior temporal cortex (e.g., Binder et al., 2000). Thus, according to the rationale of Becker et al. (i.e., that the phonological store should be responsive to passive auditory stimulation), it follows that the parietal lobe (BA 40 and superior) is a poor candidate for the neural locus of the store. This is not to say that the parietal lobe does not *in one way or another*—for instance, as a node in the executive attention network—play an important role in “phonological working memory,” but only that it appears to lack the special functional properties that have been attributed to the phonological storage component of the WM model. Finally, it is important to note that, as can be seen in Figure 3, the foci reported in Salmon et al. (1996) and Paulesu et al. (1993) are located at a relatively more inferior and anterior locus (parietal operculum/supramarginal gyrus) within the parietal lobe, and are thus closer to the auditory language zone as delineated by studies of passive listening.

SPEECH PERCEPTION, REHEARSAL, AND WERNICKE’S AREA

The emergence of event-related fMRI at the turn of the millennium allowed for a greater degree of flexibility in the tasks that might be used to isolate mnemonic processes in the brain. For instance, the temporal resolution of

Figure 3. The phonological store and the parietal lobe. Talairach coordinates for the location of the phonological store in five PET studies of verbal working memory conducted in the mid and late 1990s. Coordinates have been mapped to a cortical surface (in Talairach space) using AFNI program 3dVol2Surf.



fMRI allowed one to separately interrogate different “epochs” in a multiphase trial (e.g., stimulus encoding → maintenance → probe) without resorting to a series of complex cognitive subtractions. Using visual–verbal stimuli in a classic delayed-match-to-sample task, Postle, Berger, and D’Esposito (1999) showed that activity in single subjects during the rehearsal (or delay) period was often observed in the posterior superior temporal cortex. Buchsbaum, Hickok, and Humphries (2001), using auditory–verbal presentation of multisyllabic pseudowords, searched for regions that were active *both* during auditory stimulus perception and during a temporally extended delay period. They found, for each of the six subjects, two regions in the superior temporal cortex, one in the posterior-most part of the planum temporale (henceforth, Spt: Sylvian–parietal–temporal)² and the other in the posterior superior temporal sulcus (STS), that exhibited joint activity during perception and memory maintenance (i.e., silent rehearsal).³

Hickok, Buchsbaum, Humphries, and Muftuler (2003) further showed these two posterior temporal sites evinced the same pattern of activity (e.g., stimulus encoding + delay period maintenance) for a task requiring the perception and delay period maintenance of jabberwocky sentences and short piano melodies (also see Stevens, 2004). Buchsbaum, Olsen, Koch, and Berman (2005) dissociated the pattern of delay period activation between the more posterior and dorsally situated Spt and the relatively more lateral and anterior STS/STG, by showing that the latter region was modality-sensitive (i.e., greater delay-period activity for auditorily delivered items) and the former was not (i.e., equally active for visual–verbal and auditory–verbal input). In addition, activity in the STS/STG was not sustained across a 12-sec rehearsal phase, but tapered off 4 to 6 sec after stimulus encoding, consistent with the notion of a decaying acoustic-sensory trace. This same STS/STG region also showed increased activation to a positive item-recognition probe in an auditory–verbal Sternberg memory scanning paradigm (Buchsbaum, Olsen, Koch, & Berman, 2005), but only when the words were encoded in the auditory modality—a finding consistent with this region playing a role at the acoustic-sensory or phonological input level of representation. This conclusion is also supported by a neurological case study (Takayama, Kinomoto, & Nakamura, 2004) in which a patient with a lesion to the same region (see Figure 4, bottom panel, middle image) of the mid-lateral STG/STS showed a severe impairment (which included a reverse recency effect—poorer recall for last two items) in verbal STM with auditory presentation. Fiebach, Rissman, and D’Esposito (2006) have also shown that maintenance of visually presented words reveals sustained delay-period activity in the ventral temporal cortex, a region known to be involved in orthographic stimulus perception. In addition, Rama and Courtney (2005) have shown bilateral mid-STG/STS delay period activity during the mainte-

nance of voice identity. Thus, it appears that delay-period activity in tasks of immediate verbal memory is often found in regions that are involved in initial stimulus processing, whether orthographic, acoustic, or phonological.

How do these studies bear on the question of the localization of the phonological store? First, the studies by Hickok et al. (2003) and Buchsbaum et al. (2001) show that the parietal lobe does not meet the minimal logical requirements for the “neural correlate” of the phonological store because it does not activate during both auditory perception and covert rehearsal. Second, these studies show that the two regions that are active both during auditory–verbal perception and silent rehearsal—area Spt and the STG/STS, are positioned squarely within the classic posterior peri-sylvian language center, or Wernicke’s area. Third, the studies by Stevens (2004) and Hickok et al. (2003) show that posterior superior temporal memory areas are not speech-specific, and are therefore not necessarily “phonological” in nature (but see Baddeley & Logie, 1992), inasmuch as the term implies a language-specific level of representation. Lastly, Buchsbaum, Olsen, Koch, and Berman (2005) have shown that only area Spt shows auditory sensitivity during encoding coupled with delay-period activity that is independent of the modality of input—a pattern consistent with the phonological store as operating on modality-neutral code.

At this point, one might be tempted to make a slight amendment to the brain mapping of the phonological loop. One could simply nudge the phonological store (like a chess piece) from its position in the posterior

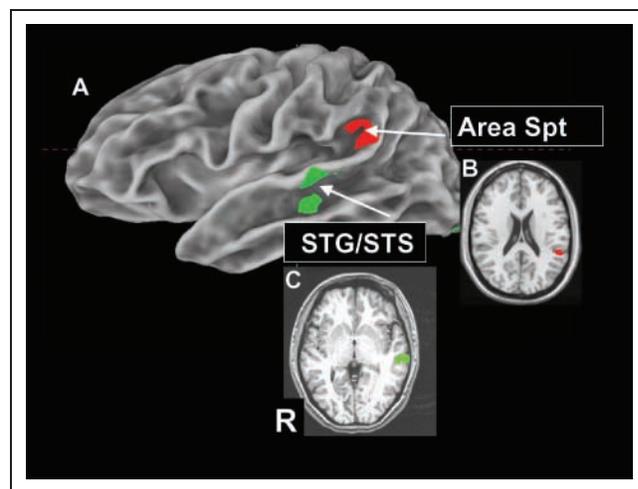


Figure 4. Auditory–verbal short-term memory in the temporal lobe. Figure adapted from Buchsbaum, Olsen, Koch, and Berman (2005). (A) Two regions showing sustained delay period activity in Buchsbaum, Olsen, Koch, and Berman: Area Spt and the STG/STS displayed on cortical surface. A third arrow indicates approximate location on surface of the inferior parietal lobe/supramarginal gyrus for reference. (B) Surface coordinates of Spt projected on to axial slice in Talairach space ($z = 20$). (C) Surface coordinates of STG/STS projected on to axial slice in Talairach space ($z = 1$).

parietal lobe 2 cm inferiorly so that it encircles Spt, lying in the posterior-most portion of planum temporale. Indeed, one might even use this example to demonstrate the triviality of linking brain regions to cognitive components: At any time, the arrow pointing from component *X* to brain region *Y* can be erased and made to point somewhere else, ad infinitum. The response to the above is that this type of maneuvering is extremely problematic once it is allowed that all positions on the “chess board” are not equally probable. For instance, can the arrow be moved to point to the cerebellum, or the portion of the primary motor cortex known to control the right hand? Probably not. Thus, a priori knowledge of the functional neuroanatomy of the brain severely constrains the space of “legal moves,” and therefore, arbitrary reconfigurations are difficult to justify. Indeed, the process of first linking a model’s components with its brain correlates leads by degrees to what might be called neural commitment, the fixing of the relations between the objects of cognition and the corresponding neural machinery. Nevertheless, in the following section, we will entertain what such a move—from parietal to temporal lobe—entails.

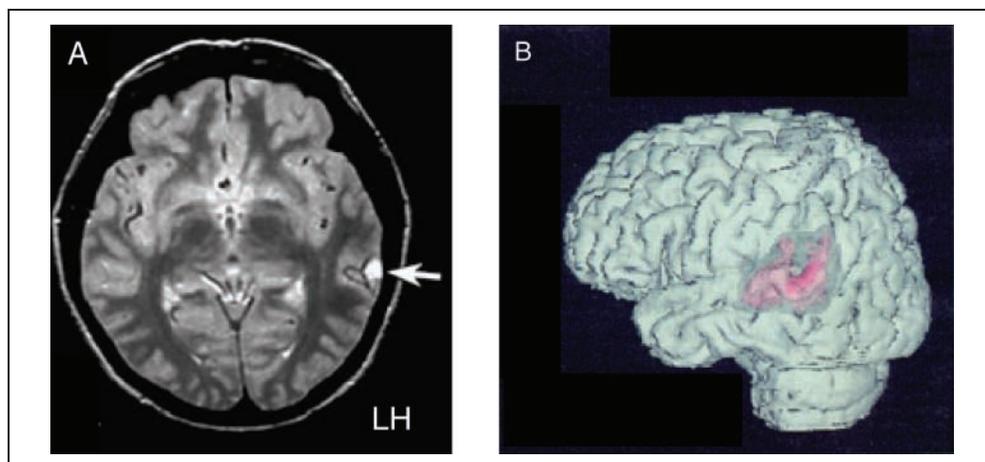
THE SUPERIOR TEMPORAL CORTEX: A BETTER HOME FOR THE PHONOLOGICAL STORE?

In many ways, the region of the posterior superior temporal lobe might seem to be a far more logical location for the phonological store than the parietal lobe. After all, it is well known from 150 years of clinical neurology, from Broca and Wernicke to Geschwind (1965), that language processes are highly localizable to the left peri-sylvian area. An obvious question to ask is whether, in the few cases in which immediate verbal STM dissociates from auditory–verbal processing, the site of neurological damage is also outside the classic peri-sylvian

language zone. As it turns out, in reports of patients with selective disturbances to verbal short-term memory, Shallice and Vallar (1990) show that, in seven of nine such cases, the site of damage includes the left temporal lobe. More recent cases in the literature that have published high-resolution MRI images of the lesion site associated with STM impairment have implicated the posterior superior temporal area (Takayama et al., 2004; Markowitsch et al., 1999; see Figure 5). Several other large studies of auditory–verbal repetition have also implicated the infra-sylvian cortex of the superior the temporal lobe as being the most critical region (Axer, von Keyserlingk, Berks, & von Keyserlingk, 2001; Selnes, Knopman, Niccum, & Rubens, 1985). Thus, evidence from neurological case reports indicates that lesions to the superior temporal area most often lead to severe language disturbances (i.e., classic aphasia) but, in rare cases, may also lead to more pure verbal STM impairment.

Given all the evidence in favor of the importance of the superior temporal lobe in verbal STM, it might seem strange that, in the context of neuroimaging work, the more superior portion of the parietal lobe was entertained so seriously as a plausible candidate for the phonological store. In point of fact, however, that the parietal lobe site of activation was relatively distant from classic peri-sylvian language cortex actually added to its plausibility as a candidate for the neural correlate of the phonological store. It has always been clear, in the specification of the phonological loop model, that the phonological store does not play a role in basic auditory–verbal language processing, such as speech perception and speech production (see Figure 1B). According to the model, these basic analytic processes occur earlier in the processing stream—as part of a perceptual analysis and identification system—outside the purview of the phonological loop. This is the classic division of labor often found in cognitive psychology between stimulus processing and short-term storage. Such a

Figure 5. Neuroanatomical lesion sites in two case studies of patients with severe auditory–verbal short-term memory impairments. (A) Superior temporal lesion shown on high-resolution MRI adapted from report of Takayama et al. (2004). (B) Temporo-parietal lesion shown on 3-D reconstruction of the cortex adapted from Markowitsch et al. (1999). Compare lesion sites with two regions showing of auditory–verbal maintenance-related activity reported in Buchsbaum, Olsen, Koch, and Berman (2005) and reproduced in Figure 4.



separation between perceptual processing and memory is not arbitrary, but rather serves to explain the characteristic profile of the “short-term memory patient,” who appears to have little difficulty with on-line language processing, but nevertheless has a digit span of two or three items. In contrast, patients with Wernicke’s or conduction aphasia show profound deficits in on-line language perception and production in addition to difficulty with short-term memory (Goodglass, 1993; Kohn, 1984; Green & Howes, 1977; Benson et al., 1973). The lesions associated with these posterior aphasias are well known to cluster around the posterior superior temporal gyrus (Axer et al., 2001; Damasio & Damasio, 1980; Benson et al., 1973). Thus, when many of the early PET studies found activity associated with the phonological store in the parietal lobe *outside the peri-sylvian language region*, this appeared to be in keeping with the specification of the phonological loop as operating outside the core language zone. The answer to the question posed in the title of this section, then, is that the superior temporal gyrus, because of its well-established role in the perception and production of speech, is indeed also a very poor candidate for the neural locus of Baddeley’s phonological store.

WHITHER THE PHONOLOGICAL STORE?

To summarize, the early choice for the neural correlate of the phonological store, the posterior parietal lobe, was rejected because it lies *outside* the auditory–verbal processing zone (due to the requirement that auditory material have obligatory access to the store; see earlier discussion of the architecture of the phonological loop). On the other hand, the most plausible alternative candidate, the superior temporal lobe, must be rejected for precisely the opposite reason—that is, because it lies *inside* the auditory–verbal language zone. This leads unavoidably to the conclusion that either there is no proper “neural correlate” of the phonological store because there is something theoretically amiss in the construct itself, or that the error resides not in the logical formulation of the phonological loop but rather in the manner in which functional neuroimaging data are being applied to assess the validity of a cognitive component. This latter position might be formulated as a number of more or less specific objections to the functional neuroanatomical arguments that have been put forth here. Insofar as our thesis has been in favor of a role for functional neuroimaging in the context of models that may have been derived from cognitive psychology, it is important that we attempt to anticipate some of these potential objections. In the following discussion, we do not contend with the general argument that functional neuroimaging is inherently irrelevant to theories invented in the psychological domain because such theories make no predictions about functional neuroanatomy. This topic has been ably covered by sev-

eral recent reviews, including those of de Zubicaray (2006), Henson (2006), and Poldrack (2006) and, for the reverse point of view, Coltheart (2006) and Page (2006).

The first and most obvious criticism of our attempt to use functional neuroanatomy to “triangulate” the phonological store has to do with the presumption of an isomorphic mapping of the phonological store to a single brain area. That is to say, the failure to identify a single brain area that exhibits all the functional properties of the phonological store might reflect the fact that the store comprises a large area of brain tissue widely distributed across the brain. Just as one would never seek a single, isolated, and discrete neural correlate of “meaning,” because it is assumed that a great deal of the brain is in one way or another involved in conceptual representations, likewise one should not look for the phonological store in a single brain site. One problem with this objection is that even if the phonological store was spread out all over the cerebral cortex, the hypothetical network should still be identifiable as having the functional properties assumed in the phonological loop model. An additional problem with this objection is that the short-term memory syndrome has been associated with relatively focal lesions in temporoparietal cortex, a finding that is obviously incompatible with a distributed implementation of the phonological store. Thus, the existence of the short-term memory patient puts an upper bound on the neuroanatomical extent of the store.

An objection that might be considered the converse of the above “distributed” memory argument is the idea that although the phonological store is structurally discrete and localizable, it manifests itself as a particular functional state that emerges within the same region of the cortex that may carry out other related functions. Thus, according to this view, one may reconcile the assumption that the phonological store plays no role in language perception and production with its neuroanatomical location within the classic peri-sylvian language zone. That is to say, there may be a particular state of activity that is diagnostic of phonological storage, functionally distinct from other processes related to the perception and production of speech, and located in the very same region of the cortex. Once again, however, the idea of the store as one of several functional states coexisting within the same piece of brain tissue is hard to reconcile with the short-term memory patient, as it assumes that a lesion affecting one functional state (e.g., phonological storage) should also affect all other functional capacities that had been supported by the damaged area (e.g., speech perception).

Another objection to our thesis draws on the notion that functional neuroimaging cannot, in itself, distinguish between activity that is necessary for a function and activity that is merely incidental to it. For instance, area Spt in the posterior portion of the planum temporale was observed to have many of the properties one

would expect from the neural correlate of the phonological store: It activates to auditory material during passive listening, it shows sustained activation during the silent rehearsal of verbal material, and it is equally active during the maintenance of auditory- and visual-verbal information during a delay period. The only reason to disqualify area Spt as a candidate for the phonological store, we have argued, is its location within the posterior superior temporal language zone, damage to which is well known to cause deficits in language perception and/or production, such as are seen in conduction and Wernicke's aphasia. One may quibble with this line of reasoning, however. It is true that lesions to the posterior temporal area often lead to aphasia, but we do not know for certain what sort of deficit would be produced by a selective lesion to area Spt, as it has been defined in functional neuroimaging. It is conceivable that a lesion perfectly circumscribing area Spt would produce an STM impairment without any concomitant deficits in the perception or production of speech, an outcome that would be in full support of the phonological loop model. Thus, it may be that just because it is known that damage to tissue *in the vicinity* of Spt often causes perception and production deficits, a surgically precise removal of the area (defined in a single subject using with fMRI) would not necessarily lead to an aphasic impairment. Of course, although we will never know what the effect of removing the functionally defined area Spt would be, transcranial magnetic stimulation might be used to establish that a minimal disruption to the region does or does not lead to speech perception or production deficits (see e.g., Mottaghy et al., 1999).

The final objection to our analysis merely adverts to the existence of the short-term memory patient. We have stated that no region of the brain accords perfectly with the functional properties of the phonological store; namely, that (1) because auditory material has obligatory access to the store, the brain correlate must activate during passive listening to speech, and (2) because the phonological store does not play a role in the perception and production of speech (at least insofar as basic language processing does not draw on working memory; see Vallar & Baddeley, 1987), the brain correlate must exist outside the region of the cortex known to lead to impairments in language processing. Fifteen years of neuroimaging research, as well as over 150 years of neurological study of aphasia, strongly suggest that no brain region satisfies both of the above-listed properties. How, then, do we explain the existence of the short-term memory patient, whose impairment seems to demand recourse to some notion of a language-independent phonological store?

REVISITING THE SHORT-TERM MEMORY PATIENT

We have previously alluded to the short-term memory patient as an instance of a perfect dissociation be-

tween language (perception and production) and short-term memory. In truth, however, certain of the patients that have been designated as exemplars of the syndrome, such as J.B. (Shallice & Butterworth, 1977), have turned out to have measurable, if not severe, impairments in language perception and production. For instance, Allport (1984) showed that although J.B. was virtually unimpaired in the context of self-directed spontaneous speech, he showed profound deficits in experimentally controlled speech production, such as object naming, nonword reading, and repetition. J.B.'s performance on auditory lexical decision and phonemic discrimination was also impaired, indicating a deficit in the perception of speech sounds. Of course, one may attribute these deficits to an impaired phonological store (Shallice & Vallar, 1990), but this argument could be used to undermine virtually any claim of language deficit accompanying an STM impairment; and, moreover, begs the question: How do we distinguish between tasks that rely on short-term memory and those that do not without first committing to the very idea in question, that is, that speech perception and short-term storage are governed by independent systems? At any rate, it is enough to note that some evidence of an accompanying deficit in language perception or production has been observed in most, if not all, of the documented STM patients (see Table 1.1 of Shallice & Vallar, 1990).

Finally, the sheer rarity of the STM patient, for there are no more than 10 to 15 cases reported in the literature, might indicate that there is something out of the ordinary in the underlying neurobiology of these particular individuals. For instance, it may be the case that an unusual capacity for the right hemisphere to effectively take over aspects of language perception and production has the effect of masking what might have otherwise been a more routine case of conduction aphasia. Consider also that although the vast majority of lesions affecting the temporo-parietal cortex do lead to an aphasic condition, the very fact that in the STM patients a similar lesion leads to a far milder syndrome⁴ indicates that, at some level, the STM patient represents a kind of statistical "outlier." Although the neuropsychological method emphasizes the value of "existence proofs" (i.e., the observation of a single white crow falsifies the assertion that all crows are black), it may be that the STM patient may be an example of an "exception that proves the rule."

RETHINKING THE PHONOLOGICAL STORE

Heretofore, we have focused on the question of whether functional neuroimaging evidence is consistent with the logical specification of the phonological store component of the phonological loop. We have concluded that the imaging evidence is indeed inconsistent with the

model as it is currently formulated. The major discrepancy stems from the assumption of a functional separation between basic auditory perceptual and speech processes, on the one hand, and phonological storage on the other. Although the existence of the short-term memory patient argues for a separation between “storage” and perceptual and motor processes, functional neuroanatomy tells us that there is no autonomous and isolable region of the cerebral cortex whose *only function* is to temporarily “hold phonemes.” One resolution to this apparent contradiction is that there exists a processing component located in the left temporo-parietal area that when damaged can, in rare circumstances, lead to a severe impairment in phonological short-term memory while leaving speech perception and speech production relatively less affected. If this hypothetical component is not a “store” (i.e., a passive receptacle of processed information), then what is its function? One possibility is that this processing component located in the temporo-parietal region acts as an *auditory–motor interface* that serves to bind acoustic representations of speech with articulatory counterparts stored in the frontal cortex (Jacquemot, 2006; Buchsbaum, Chang, et al., 2005; Buchsbaum, Olsen, Koch, & Berman, 2005; Buchsbaum, Olsen, Koch, Kohn, et al., 2005; Hickok & Poeppel, 2000, 2004; Nadeau, 2001; Wilson, 2001; Baddeley & Logie, 1992). The concept of an auditory–motor interface in the speech domain has been motivated (Hickok & Poeppel, 2000, 2007; Pa & Hickok 2007; Wise et al., 2001), in part, by the discovery of a neural system for sensory–motor integration in the visual system. For instance, regions in the posterior parietal cortex in both human and nonhuman primates have been identified as key components of visuomotor integration circuits (Andersen, Snyder, Bradley, & Xing, 1997; Milner & Goodale, 1995) that compute coordinate transformations in the mapping between sensory representations and motor commands. In addition, psycholinguistic models of speech production typically include an auditory–motor connection, such as the “internal loop” of Levelt, Roelofs, and Meyer (1999) and Nadeau’s (2001) “acoustic-to-articulatory” hidden units that act as a pattern associator in a connectionist framework.

The proposed anatomical location for this interface component is area Spt (Buchsbaum, Olsen, Koch, & Berman, 2005; Hickok et al., 2003), which lies at the junction of the temporal and parietal lobes, in the posterior part of the planum temporale of the auditory association cortex. Area Spt is a core component of the language system that happens to be particularly critical for performance in tasks requiring serial repetition of phonological information (Hickok & Poeppel, 2007). It is not a buffer for the temporary storage of phonological overflow, but is rather a processing component in its own right, and is essential for mediating between acoustic and articulatory representations of speech. Thus, a lesion primarily affecting area Spt would be predicted to severely affect auditory–verbal repetition due

to the need in such tasks for the formation of transient binding between acoustic and articulatory codes in the speech system. In addition, however, this interface component is also required for nonlexically mediated phonological encoding, which would be predicted to be especially important for learning new words, reading and repeating pseudowords, and for ordered recall of lists of letters or digits—all activities in which patient J.B. was shown to be impaired (Allport, 1984). In addition, Baddeley, Papagno, and Vallar (1988) showed that the STM patient P.V., although capable of learning paired-associate lists of meaningful words, was unable to learn a single word pair when the lists were composed of words drawn from an unfamiliar language. Again, such a deficit is consistent with a failure to instantiate bindings between phonological input and output codes. In circumstances where the temporary binding or the learning of new relationships between input and output speech codes may be circumvented, however, such as in the case of spontaneous speech (where low-frequency words may be avoided), one would expect relatively preserved function even in a patient with a damaged interface system. This is exactly what one finds in the case of the STM patient, whose spontaneous speech is virtually unimpaired. Thus, the reconceptualization of the phonological store as an auditory–motor interface, and thus, as a core member of the speech processing system, provides a parsimonious solution to the seeming contradiction between the functional neuroanatomy of verbal STM and the existence of the STM patient.

Recent work in computational modeling of speech production and serial verbal STM also supports a tighter integration between phonological storage and speech production. For instance, Page, Madge, Cumming, and Norris (2007) have argued that the phonological store is a key component in the planning of speech, especially in the ordering of a sequence of lexical items for an upcoming utterance. The dissociation observed between serial verbal memory and ordinary speech production observed in the STM patient, they argue, is a result of the fundamental difference between exogenous and endogenous speech output. Tasks of verbal short-term memory are exogenous in the sense that the content of speech is entirely constrained by external factors, where the subject has scant control over the timing and content of the utterance. Ordinary speech production is an endogenous process where timing and content are controlled by the speaker, a factor that might allow an injury to the speech production system to go unnoticed in ordinary conversation. In support of this distinction, Page et al. (2007) showed that in a task requiring the rapid reading aloud of words and nonwords, the types of speech errors that were committed are the same kinds of errors that occurred as a result of a phonological similarity manipulation in an STM recall task. This evidence strongly supports a common locus for the two

effects and argues, again, for a primary role for the phonological store in speech production (see also Dell, Schwartz, Martin, Saffran, & Gagnon, 1997).

Although we have proposed that phonological memory may be conceived as strongly dependent on the operation of an auditory–motor interface system in the left posterior planum temporale, one might ask how this proposed component is related to the classic cognitive psychological concept of a memory store or “buffer.” In the famous “levels of processing” proposal, Craik and Lockhart (1972) suggested that there are no dedicated stores or buffers, only dedicated processes that encode information in a more or less durable form. Thus, in their view, short-term memory is part and parcel of the hierarchy of processes that successively encode and transform information. As Monsell (1984) has observed, however, although representations are undoubtedly the by-products of processing, “. . . they do not float in vacuo, and the capacity and organization of the storage substrate at each level of processing is surely an important question complementary to that of processes that generate and use representations” (Monsell, 1984, p. 331). Thus, even if one assumes that processing and storage cannot be neatly individuated, as appears to be true in regard to phonological STM, it remains the case that such an integrated processor must make use of some kind of buffering when informational processing extends across a temporal interval, as is required in the production and comprehension of multiword utterances and, of course, for short-term verbal memory. Buffering, however, is in itself not enough without some way of representing serial order, or the relation between an item and its context: Without such a mechanism, it is difficult to conceive how a person could repeat the digit sequence “1 4 5 6 7 8 5 2” or produce the sentence “the little bear followed the big bear,” where the same token (“5” and “bear”) is repeated in the short period of time. The problem of memory for serial order is present regardless of whether the temporary storage substrate is part of the same cortical processor that mediates between perception and long-term memory or whether it is a neuroanatomically separate structure in its own right. In either case, some mechanism for the representation of serial order and the ability to maintain and distinguish between multiple instances of the same token in temporary memory must exist. Precisely how this is achieved at the level of the neural information processor has long been recognized as an important problem (Burgess & Hitch, 2005; Lashley, 1951) and must be worked out in future research. With respect to the broader question of how temporary memories are stored in the brain, however, neurobiological evidence increasingly points to a shared anatomical substrate for the representation of the objects of perception, action, and temporary memory (D’Esposito, 2007; Postle, 2006; Ranganath, 2006; Postle, Druzgal, & D’Esposito, 2003; Ruchkin, Grafman, Cameron, & Berndt, 2003; Fuster, 1997).

CONCLUSIONS

We have examined how functional neuroimaging over the last 15 years has taken a classic cognitive psychological model of memory and attempted to relocate its components in the brain. The search for the phonological store first led to the parietal lobe, then moved to the superior temporal cortex, and ended with the realization that no single brain region has a functional profile matching perfectly with that of the phonological store. The solution to this mismatch between psychological theory and functional neuroanatomy is not to conclude that mixing the realms only leads to contradiction and confusion. Rather, we have shown that knowledge about the functional architecture of the brain may constrain and inform classic psychological models of cognition. In the case of the phonological store, the inability to find a perfect match in the brain argues that phonological storage emerges from the inherent capacities of the sensory–motor speech processing system. A particularly important processing component that enables phonological memory, we argue, is located in the left posterior planum temporale, which acts as an auditory–motor interface that has an important role in speech perception, speech production, as well as verbal short-term memory.

Finally, as the phonological loop has evolved as a model with a brain implementation, the need to continually translate between the two media (mind and brain) is increasingly gratuitous. Even the most tentative links that are drawn between structure and function lead by degrees to the development of models that regard cognitive components and brain regions (or networks) as single entities. Thus, we may begin to regard heuristic models, such as the phonological loop, as intrinsically neurobiological, where the specification of its logic and neural implementation are combined in a single theoretical picture.

Reprint requests should be sent to Bradley R. Buchsbaum and Mark D’Esposito, Department of Psychology, Helen Wills Neuroscience Institute, University of California, Berkeley, 132 Barker Hall, MC #3190, Berkeley, CA 94720-3190, or via e-mail: bbuchsbaum@berkeley.edu; or despo@berkeley.edu.

Notes

1. It is interesting to note that, in contrast to the phonological store, the articulatory rehearsal process *was* observed to be associated with activity distributed across a number of brain regions. Clearly, though, the intuitive expectation for a one-to-one correspondence between a “process” and its neural correlate is not the same as it is for a “store” and its neural correlate. The idea of a store, as a receptacle of information, *seems* to demand a physical implementation that is moderately “local.”
2. The region identified as Spt, although at the boundary of the parietal and temporal lobes, is to be distinguished from both the “supramarginal gyrus” and BA 40, which are typically defined as constituting the gray matter of the inferior parietal lobe. Spt, as identified in single subjects with high-resolution

MRI underlays, is located at the most posterior portion of the planum temporale, lying along the Sylvian fissure, inferior the supramarginal gyrus (see Figure 5 and Buchsbaum, Chang, et al., 2005; Buchsbaum, Olsen, Koch, & Berman, 2005; Buchsbaum, Olsen, Koch, Kohn, et al., 2005; Buchsbaum et al., 2001). Spt probably comprises the cytoarchitectonic region “Tpt,” the most dorsal and caudal subdivision of the auditory association cortex in man (see Galaburda & Sanides, 1980).

3. The studies of Buchsbaum et al. (2001) and Postle et al. (1999) examined brain activation in single-subject fMRI data rather than presenting a composite statistical map based on a group average of stereotaxically normalized brains. Buchsbaum, Chang, et al. (2005), Buchsbaum, Olsen, Koch, and Berman (2005), Buchsbaum, Olsen, Koch, Kohn, et al. (2005) showed that large regions, both anterior and posterior to the Sylvian fissure, deactivate during silent reading of pseudowords, and that detection of rehearsal-related activity in the posterior temporal cortex is strongly affected by anatomical variability in the configuration of the posterior part of the Sylvian fissure as well as the amount of smoothing applied to the single-subject contrast image. Too large a smoothing kernel (10 mm or greater) has the effect of blending together neighboring regions that exhibit opposite patterns of activation.

4. When compared to Wernicke’s or conduction aphasia which involve deficits in language processing in addition to a verbal STM impairment.

REFERENCES

- Allport, D. A. (1984). Auditory-verbal short-term memory and conduction aphasia. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance: X. Control of language processes* (Vol. 10, pp. 313–325). Hillsdale, NJ: Erlbaum.
- Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, 20, 303–330.
- Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in working memory: PET evidence. *Psychological Science*, 7, 25–31.
- Axer, H., von Keyserlingk, A. G., Berks, G., & von Keyserlingk, D. G. (2001). Supra- and infrasyllabic conduction aphasia. *Brain and Language*, 76, 317–331.
- Baddeley, A., Lewis, V., & Vallar, G. (1984). Exploring the articulatory loop. *Quarterly Journal of Experimental Psychology*, 36, 2233–2252.
- Baddeley, A. D. (1986). *Working memory*. Oxford: Oxford University Press.
- Baddeley, A. D. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, 4, 829–839.
- Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation* (Vol. 7, pp. 47–90). New York: Academic Press.
- Baddeley, A. D., & Logie, R. (1992). Auditory imagery and working memory. In D. Resiberg (Ed.), *Auditory imagery* (1st ed., p. 274). Hillsdale, NJ: Erlbaum.
- Baddeley, A. D., Papagno, C., & Vallar, G. (1988). When long-term learning depends on short-term storage. *Journal of Memory and Language*, 27, 586–595.
- Baddeley, A. D., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of Verbal Learning and Verbal Behavior*, 14, 575–589.
- Becker, J. T., MacAndrew, D. K., & Fiez, J. A. (1999). A comment on the functional localization of the phonological storage subsystem of working memory. *Brain and Cognition*, 41, 27–38.
- Benson, D. F., Sheremata, W. A., Bouchard, R., Segarra, J. M., Price, D., & Geschwind, N. (1973). Conduction aphasia. A clinicopathological study. *Archives of Neurology*, 28, 339–346.
- Besner, D. (1987). Phonology, lexical access in reading and articulatory suppression: A critical review. *Quarterly Journal of Experimental Psychology*, 39A, 467–478.
- Billingsley, R. L., McAndrews, M. P., Crawley, A. P., & Mikulis, D. J. (2001). Functional MRI of phonological and semantic processing in temporal lobe epilepsy. *Brain*, 124, 1218–1227.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Springer, J. A., Kaufman, J. N., et al. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, 10, 512–528.
- Broadbent, D. (1958). *Perception and communication*. London: Pergamon Press.
- Buchsbaum, B., Hickok, G., & Humphries, C. (2001). Role of left superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science*, 25, 663–678.
- Buchsbaum, B. R., Chang, W., Furman, D., Sarpal, D., Koch, P. F., Apud, J., et al. (2005). An fMRI study of serial position effects in a Sternberg item-recognition task. *Society for Neuroscience Abstracts*. Online.
- Buchsbaum, B. R., Olsen, R. K., Koch, P., & Berman, K. F. (2005). Human dorsal and ventral auditory streams subserve rehearsal-based and echoic processes during verbal working memory. *Neuron*, 48, 687–697.
- Buchsbaum, B. R., Olsen, R. K., Koch, P. F., Kohn, P., Kippenhan, J. S., & Berman, K. F. (2005). Reading, hearing, and the planum temporale. *Neuroimage*, 24, 444–454.
- Burani, C., Vallar, G., & Bottini, G. (1991). Articulatory coding and phonological judgments on written words and pictures: The role of the phonological output buffer. 3, 379–398.
- Burgess, N., & Hitch, G. (2005). Computational models of working memory: Putting long-term memory into context. *Trends in Cognitive Sciences*, 9, 535–541.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12, 1–47.
- Caplan, D., Rochon, E., & Waters, G. S. (1992). Articulatory and phonological determinants of word length effects in span tasks. *Quarterly Journal of Experimental Psychology A*, 45, 177–192.
- Caramazza, A., Basili, A. G., Koller, J. J., & Berndt, R. S. (1981). An investigation of repetition and language processing in a case of conduction aphasia. *Brain and Language*, 14, 235–271.
- Chein, J. M., & Fiez, J. A. (2001). Dissociation of verbal working memory system components using a delayed serial recall task. *Cerebral Cortex*, 11, 1003–1014.
- Chein, J. M., Ravizza, S. M., & Fiez, J. A. (2003). Using neuroimaging to evaluate models of working memory and their implications for language processing. *Journal of Neurolinguistics*, 16, 315–339.
- Coltheart, M. (2006). What has functional neuroimaging told us about the mind (so far)? *Cortex*, 42, 323–331.
- Conrad, R., & Hull, A. J. (1964). Information, acoustic confusion and memory span. *British Journal of Psychology*, 55, 429–432.
- Craik, F., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior*, 11, 671–684.
- D’Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 362, 761–772.

- Damasio, H., & Damasio, A. R. (1980). The anatomical basis of conduction aphasia. *Brain*, *103*, 337–350.
- de Zubizaray, G. I. (2006). Cognitive neuroimaging: Cognitive science out of the armchair. *Brain and Cognition*, *60*, 272–281.
- Dell, G. S., Schwartz, M. F., Martin, N., Saffran, E. M., & Gagnon, D. A. (1997). Lexical access in aphasic and nonaphasic speakers. *Psychological Review*, *104*, 801–838.
- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*, 475–483.
- Fiebach, C. J., Rissman, J., & D'Esposito, M. (2006). Modulation of inferotemporal cortex activation during verbal working memory maintenance. *Neuron*, *51*, 251–261.
- Fiez, J. A., Raife, E. A., Balota, D. A., Schwarz, J. P., Raichle, M. E., & Petersen, S. E. (1996). A positron emission tomography study of the short-term maintenance of verbal information. *Journal of Neuroscience*, *16*, 808–822.
- Fuster, J. M. (1997). Network memory. *Trends in Neurosciences*, *20*, 451–459.
- Galaburda, A., & Sanides, F. (1980). Cytoarchitectonic organization of the human auditory cortex. *Journal of Comparative Neurology*, *190*, 597–610.
- Geschwind, N. (1965). Disconnexion syndromes in animals and man: I. *Brain*, *88*, 237–294.
- Glanzer, M., & Cunitz, A. R. (1966). Two storage mechanisms in free recall. *Journal of Verbal Learning and Verbal Behaviour*, *5*, 357–360.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In F. Plum (Ed.), *Handbook of physiology—The nervous system* (Vol. 5, pp. 373–417). Bethesda, MD: American Physiological Society.
- Goodglass, H. (1993). *Understanding aphasia*. San Diego: Academic Press.
- Green, E., & Howes, D. H. (1977). The nature of conduction aphasia: A study of anatomic and clinical features and of underlying mechanisms. In H. Whitaker & H. A. Whitaker (Eds.), *Studies in neurolinguistics* (pp. 123–156). New York: Academic Press.
- Henson, R. (2006). What has (neuro)psychology told us about the mind (so far)? A reply to Coltheart (2006). *Cortex*, *42*, 387–392.
- Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory–motor interaction revealed by fMRI: Speech, music, and working memory in area Spt. *Journal of Cognitive Neuroscience*, *15*, 673–682.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, *92*, 67–99.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*, 393–402.
- Hickok, G., & Poeppel, I. D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences*, *4*, 131–138.
- Jacquemot, C., & Scott, S. K. (2006). What is the relationship between phonological short-term memory and speech processing? *Trends in Cognitive Sciences*, *10*, 480–486.
- Jones, D., & Morris, N. (1992). Irrelevant speech and serial recall: Implications for theories of attention and working memory. *Scandinavian Journal of Psychology*, *33*, 212–229.
- Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., et al. (1998). The role of parietal cortex in verbal working memory. *Journal of Neuroscience*, *18*, 5026–5034.
- Kleiman, G. M. (1975). Speech recoding in reading. *Journal of Verbal Learning and Verbal Behavior*, *14*, 323–329.
- Kohn, S. E. (1984). The nature of the phonological disorder in conduction aphasia. *Brain and Language*, *23*, 97–115.
- Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior* (pp. 112–136). New York: Wiley.
- Levelt, W. J. M., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences*, *22*, 1–38.
- Levy, B. A. (1971). Role of articulation in auditory and visual short-term memory. *Journal of Verbal Learning and Verbal Behavior*, *10*, 123–132.
- Majerus, S., Bastin, C., Poncelet, M., Van der Linden, M., Salmon, E., Collette, F., et al. (2007). Short-term memory and the left intraparietal sulcus: Focus of attention? Further evidence from a face short-term memory paradigm. *Neuroimage*, *35*, 353–367.
- Markowitsch, H. J., Kalbe, E., Kessler, J., von Stockhausen, H. M., Ghaemi, M., & Heiss, W. D. (1999). Short-term memory deficit after focal parietal damage. *Journal of Clinical and Experimental Neuropsychology*, *21*, 784–797.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Monsell, S. (1984). Components of working memory underlying verbal skills: A “distributed” capacities view—A tutorial review. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance: X. Control of language processes* (Vol. 10). Hillsdale, NJ: Erlbaum.
- Mottaghy, F. M., Hungs, M., Brugmann, M., Sparing, R., Boroojerdi, B., Foltys, H., et al. (1999). Facilitation of picture naming after repetitive transcranial magnetic stimulation. *Neurology*, *53*, 1806–1812.
- Mueller, S. T., Seymour, T. L., Kieras, D. E., & Meyer, D. E. (2003). Theoretical implications of articulatory duration, phonological similarity, and phonological complexity in verbal working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 1353–1380.
- Nadeau, S. E. (2001). Phonology: A review and proposals from a connectionist perspective. *Brain and Language*, *79*, 511–579.
- Nystrom, L. E., Braver, T. S., Sabb, F. W., Delgado, M. R., Noll, D. C., & Cohen, J. D. (2000). Working memory for letters, shapes, and locations: fMRI evidence against stimulus-based regional organization in human prefrontal cortex. *Neuroimage*, *11*, 424–446.
- Pa, J., & Hickok, G. (2007). A parietal-temporal sensory-motor integration area for the human vocal tract: Evidence from an fMRI study of skilled musicians. *Neuropsychologia*.
- Page, M. P. (2006). What can't functional neuroimaging tell the cognitive psychologist? *Cortex*, *42*, 428–423.
- Page, M. P. A., Madge, A., Cumming, N., & Norris, D. (2007). Speech errors and the phonological similarity effect in short-term memory: Evidence suggesting a common locus. *Journal of Memory and Language*, *56*, 49–64.
- Paulesu, E., Frith, C. D., & Frackowiak, R. S. (1993). The neural correlates of the verbal component of working memory. *Nature*, *362*, 342–345.
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*, 59–63.
- Posner, M. I., Petersen, S. E., Fox, P. T., & Raichle, M. E. (1988). Localization of cognitive operations in the human brain. *Science*, *240*, 1627–1631.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- Postle, B. R., Berger, J. S., & D'Esposito, M. (1999). Functional neuroanatomical double dissociation of mnemonic and

- executive control processes contributing to working memory performance. *Proceedings of the National Academy of Sciences, U.S.A.*, 96, 12959–12964.
- Postle, B. R., Druzgal, T. J., & D'Esposito, M. (2003). Seeking the neural substrates of visual working memory storage. *Cortex*, 39, 927–946.
- Postman, L., & Phillips, L.-W. (1965). Short-term temporal changes in free recall. *Quarterly Journal of Experimental Psychology*, 17, 132–138.
- Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., et al. (1996). Cerebral organization of component processes in reading. *Brain*, 119, 1221–1238.
- Rama, P., & Courtney, S. M. (2005). Functional topography of working memory for face or voice identity. *Neuroimage*, 24, 224–234.
- Ranganath, C. (2006). Working memory for visual objects: Complementary roles of inferior temporal, medial temporal, and prefrontal cortex. *Neuroscience*, 139, 277–289.
- Ravizza, S. M., Delgado, M. R., Chein, J. M., Becker, J. T., & Fiez, J. A. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *Neuroimage*, 22, 562–573.
- Repovs, G., & Baddeley, A. (2006). The multi-component model of working memory: Explorations in experimental cognitive psychology. *Neuroscience*, 139, 5–21.
- Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: A state of activated long-term memory. *Behavioural Brain Sciences*, 26, 709–728; discussion 728–777.
- Saffran, E. M., & Marin, O. S. (1975). Immediate memory for word lists and sentences in a patient with deficient auditory short-term memory. *Brain and Language*, 2, 420–433.
- Salame, P., & Baddeley, A. D. (1982). Disruption of short-term memory by unattended speech: Implications for the structure of working memory. *Journal of Verbal Learning and Verbal Behavior*, 21, 150–164.
- Salmon, E., Van der Linden, M., Collette, F., Delfiore, G., Maquet, P., Degueldre, C., et al. (1996). Regional brain activity during working memory tasks. *Brain*, 119, 1617–1625.
- Schumacher, E. H., Lauber, E., Awh, E., Jonides, J., Smith, E. E., & Koeppel, R. A. (1996). PET evidence for an amodal verbal working memory system. *Neuroimage*, 3, 79–88.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery and Psychiatry*, 20, 11–21.
- Seghier, M. L., Lazeyras, F., Zimine, S., Maier, S. E., Hanquinet, S., Delavelle, J., et al. (2004). Combination of event-related fMRI and diffusion tensor imaging in an infant with perinatal stroke. *Neuroimage*, 21, 463–472.
- Selnes, O. A., Knopman, D. S., Niccum, N., & Rubens, A. B. (1985). The critical role of Wernicke's area in sentence repetition. *Annals of Neurology*, 17, 549–557.
- Shallice, T., & Butterworth, B. (1977). Short-term memory impairment and spontaneous speech. *Neuropsychologia*, 15, 729–735.
- Shallice, T., & Vallar, G. (1990). The impairment of auditory-verbal short-term storage. In G. Vallar & T. Shallice (Eds.), *Neuropsychological impairments of short-term memory* (pp. 11–53). Cambridge: Cambridge University Press.
- Shallice, T., & Warrington, E. K. (1970). Independent functioning of verbal memory stores: A neuropsychological study. *Quarterly Journal of Experimental Psychology*, 22, 261–273.
- Smith, E. E., Jonides, J., & Koeppel, R. A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, 6, 11–20.
- Smith, E. E., Jonides, J., Koeppel, R. A., Awh, E., Schumacher, E., & Minoshima, S. (1995). Spatial vs. object working memory: PET investigations. *Journal of Cognitive Neuroscience*, 7, 337–358.
- Smith, E. E., Jonides, J., Marshuetz, C., & Koeppel, R. A. (1998). Components of verbal working memory: Evidence from neuroimaging. *Proceedings of the National Academy of Sciences, U.S.A.*, 95, 876–882.
- Sperling, G. (1967). Successive approximations to a model for short term memory. *Acta Psychologica (Amsterdam)*, 27, 285–292.
- Sternberg, S. (1969). Memory-scanning: Mental processes revealed by reaction-time experiments. *American Scientist*, 57, 421–457.
- Stevens, A. A. (2004). Dissociating the cortical basis of memory for voices, words and tones. *Brain Research, Cognitive Brain Research*, 18, 162–171.
- Takayama, Y., Kinomoto, K., & Nakamura, K. (2004). Selective impairment of the auditory-verbal short-term memory due to a lesion of the superior temporal gyrus. *European Neurology*, 51, 115–117.
- Vallar, G. (2006). Mind, brain, and functional neuroimaging. *Cortex*, 42, 402–405; discussion 422–427.
- Vallar, G., & Baddeley, A. D. (1984). Phonological short-term store, phonological processing and sentence comprehension: A neuropsychological case study. *Cognitive Neuropsychology*, 1, 121–141.
- Vallar, G., & Baddeley, A. D. (1987). Phonological short-term store and sentence processing. *Cognitive Neuropsychology*, 4, 417–438.
- Vallar, G., & Cappa, S. F. (1987). Articulation and verbal short-term memory. *Cognitive Neuropsychology*, 4, 55–78.
- Warrington, E., & Shallice, T. (1969). Selective impairment of auditory verbal short-term memory. *Brain*, 92, 885–896.
- Waugh, N. C., & Norman, D. A. (1965). Primary memory. *Psychological Review*, 72, 89–104.
- Wilson, M. (2001). Perceiving imitable stimuli: Consequences of isomorphism between input and output. *Psychological Bulletin*, 127, 543–553.
- Wise, R. J., Scott, S. K., Blank, S. C., Mummery, C. J., Murphy, K., & Warburton, E. A. (2001). Separate neural subsystems within “Wernicke's area”. *Brain*, 124, 83–95.
- Zurowski, B., Gostomzyk, J., Gron, G., Weller, R., Schirmer, H., Neumeier, B., et al. (2002). Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing. *Neuroimage*, 15, 45–57.