Published in final edited form as:
J Exp Psychol Gen. 2010 February ; 139(1): 117–137. doi:10.1037/a0018200.

EVALUATING MODELS OF WORKING MEMORY THROUGH THE EFFECTS OF CONCURRENT IRRELEVANT INFORMATION

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Abstract

Working memory is believed to play a central role in almost all domains of higher cognition, yet the specific mechanisms involved in working memory are still fiercely debated. We describe a neuroimaging experiment using fMRI, and a companion behavioral experiment, both seeking to adjudicate between alternative theoretical models of working memory based on the effects of interference from articulatory suppression, irrelevant speech, and irrelevant nonspeech. Experiment 1 examined fMRI signal changes induced by each type of irrelevant information while subjects performed a probed recall task. Within a principally frontal and left-lateralized network of brain regions, articulatory suppression caused an increase in activity during item presentation, while both irrelevant speech and nonspeech caused relative activity reductions during the subsequent delay interval. In Experiment 2, the specific timing of interference was manipulated in a delayed serial recall task. Articulatory suppression was found to be most consequential when it coincided with item presentation, while both irrelevant speech and irrelevant nonspeech effects were strongest when limited to the subsequent delay period. Taken together, these experiments provide convergent evidence for a dissociation of articulatory suppression from the two irrelevant sound conditions. Implications of these findings are considered for four prominent theories of working memory.

Keywords

Working memory; Controlled attention; fMRI; Irrelevant sound effect; Articulatory suprression

Working memory, or the ability to actively maintain and manipulate information in the service of cognition, is a core cognitive construct implicated in a diverse range of higher cognitive abilities. Decades of research have taught us a great deal about the broad range of cognitive functions to which it contributes, the factors that limit its precision, and most recently, its neural correlates – yet the specific nature of the mechanisms and representations that underlie working memory remain hotly contested. Alternative models prove capable of explaining a similar body of evidence, even though these models take fundamentally different stances on the relationship between working memory, long-term memory, attention, and language processing (Baddeley, 1986; Gathercole, 1996; Miyake & Shah, 1999; Richardson, Engle, Hasher, Logie, & et al., 1996). Thus far, these models have primarily focused on accounting for patterns of behavioral

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results, such as the disruptive effects of irrelevant information on working memory performance (Baddeley & Larsen, 2003; Baddeley, 2000; Hanley & Bakopoulou, 2003; Jones & Tremblay, 2000; Larsen & Baddeley, 2003; Larsen, Baddeley, & Andrade, 2000; Macken & Jones, 2003; Neath, 2000; Neath, Farley, & Surprenant, 2003; Neath & Surprenant, 2001; Page & Norris, 2003). The goal of the current work was to show how functional neuroimaging data can serve to further constrain, and help to adjudicate between, competing models of working memory.

As a foundation for the present work, we turn to three types of irrelevant information that are known to disrupt working memory performance: 1) irrelevant articulations produced by the subject, referred to as *articulatory suppression, 2)* background *irrelevant speech* produced by an external source, and 3) background *irrelevant nonspeech,* also from an external source. The explanations for the disruptive effects of each type of irrelevant information differ considerably from theory to theory, as we outline below for four influential theoretical models of working memory: Baddeley's multiple component model (Baddeley, 1986; Larsen & Baddeley, 2003), the Object-Oriented Episodic Record (Jones, Beaman, & Macken, 1996), the Feature Model (Nairne, 1990; Neath, 2000), and the Embedded-Processes Model (Cowan, 1995, 1999). Importantly, these four perspectives make conflicting claims about the functional equivalence of the three irrelevant information effects. That is, they disagree on whether a given type of information affects memory in the same way, or in a different way, than does another type of information (see Figure 1a).

We exploit differences in the theoretical accounts of irrelevant information effects in the experimental work reported in this paper. We reason that a shared functional source for a behavioral effect implies a shared neural substrate; for example, if two different behavioral effects are linked to the same processing account (e.g., interference with an attentional control process), then there should be a brain region in which the activity is similarly modulated by both behavioral manipulations. While a putative location for the effect might also be hypothesized (e.g., within dorsolateral prefrontal cortex), this additional constraint is not necessary. Rather, the core idea centers around how the neural modulations induced by three different types of irrelevant information pattern together. As we outline below, four different theories of working memory each predict a unique patterning; thus, we should be able to identify a patterning of neuronal modulations that corresponds to only one of those predicted by the four different theories. Such a result would help to advance our understanding of working memory, and the many areas of cognitive research that incorporate working memory as a theoretical construct. It would also provide a powerful demonstration that functional neuroimaging can be an important tool for the advancement of psychological theory.

Theories of working memory posit different accounts for the effects of articulatory suppression, irrelevant speech, and irrelevant nonspeech. In order to substantiate the source attributions that are summarized in Figure 1, we provide below a relatively detailed explanation for how each model addresses each effect. Because the models differ in their assumptions about the shared versus distinct sources of each effect, each model leads to a unique pattern of sources that can be used to predict patterns of neuronal modulation.

The Multiple-Component model

The multiple-component model (Figure 1b) comes from the work of Baddeley and colleagues. They posit a dedicated short-term memory system in which temporal decay is the primary mechanism of forgetting. The verbal maintenance subsystem of the model, the *phonological loop,* is most relevant to the explanation of the three irrelevant information effects. The model divides this phonological loop into two subcomponents, a passive *phonological store* that retains verbal information as a set of phonological representations (each subject to decay), and an active *articulatory rehearsal process* that refreshes these representations in a manner akin to subvocalization, or inner speech. Articulatory rehearsal is a strategic way to retain information over durations that exceed the temporal decay limits of the store. Such rehearsal is also thought to allow recoding of visually presented verbal information into a form suitable for storage, whereas auditory-verbal information has direct access to the phonological store.

Within Baddeley's framework, articulatory suppression has two disruptive consequences for working memory, both a byproduct of preventing the subvocal rehearsal process. First, articulatory suppression is thought to engage the rehearsal mechanism during encoding, and to thus obstruct the conversion process allowing the registration of visually presented information into the phonological store. Second, by taxing the speech apparatus that supports subvocal rehearsal, articulatory suppression prevents decaying memoranda from being refreshed.

By contrast, the phonological loop account consigns irrelevant speech effects to the phonological store. Based on the work of Salamé & Baddeley (1982; 1986; 1990), it was initially proposed that irrelevant speech, by virtue of its phonological content, would gain obligatory access to the store. As a consequence, interactions between the irrelevant items and the memorial representations residing in storage would produce interference. Entry to the store was assumed to be filtered such that only phonological (speech-like) information could pass, thus explaining the null effects of noise (non-phonological sounds) on memory (Salamé & Baddeley, 1989). A revised view still attributes irrelevant speech effects to processes taking place within the phonological store (Larsen & Baddeley, 2003; Norris, Page, & Baddeley, 2004). However, it no longer maintains that there is corruption of the item representations themselves, and instead, irrelevant speech is proposed to add "noise" to the representation of order information in phonological memory. The revised account is somewhat ambiguous with respect to irrelevant nonspeech effects. However, the continued assumption that irrelevant speech effects take place in a storage medium devoted specifically to "phonological" representations seems to force the conclusion that nonspeech effects have an alternative origin. One explanation of the irrelevant nonspeech effect in the context of the multiple-component model is that it simply derives from dual-task interference occurring in the model's supervisory component, the *central executive* (Neath, 2000; Baddeley, 2000).

The O-OER model

A very different view of working memory is proposed by Jones and his colleagues (e.g., Jones et al., 1996; Jones, Macken, & Murray, 1993) in the Object-Oriented Episodic Record (O-OER) model (Figure 1c). The O-OER model assumes that temporary storage takes place on a unitary medium wherein all events (percepts and cognitions) are represented as amodal objects. For auditory stimuli, mental processes that detect boundaries in auditory perception (see e.g., Bregman, 1990) automatically create objects in short-term memory. Unique objects are established whenever there is a sufficient change in the energy of incoming information as to signal the arrival of a distinct event (and thus give rise to a discrete perception) – this is the *changing-state hypothesis* (e.g., Jones et al., 1993). Temporally successive events are thought to be chained together into streams of ordered objects, linked together by pointers.

In the O-OER model, the ability to recall a set of items is dependent on the maintained integrity of the pointers, which are thought to be susceptible to temporal decay. Both the rehearsal and retrieval of objects in short-term memory are achieved by following the pointers and sequentially visiting each object in the to-be-remembered stream, thereby "revivifying" the links between them (Jones & Macken, 1995a). In this model, the presence of other object streams in memory induces competition for a shared seriation mechanism, and thus hinders the ability to correctly navigate the connected stream of to-be-remembered. Such disruption of the streaming process provides an account for all three irrelevant information effects.

Accordingly, the irrelevant utterances associated with articulatory suppression are thought to give rise to their own object representations in memory, and to be chained together into a separate stream that can compete with the to-be-remembered item stream. Precisely the same account is provided to explain the effects of irrelevant speech and nonspeech. Changing-state irrelevant sounds of any type are assumed to be automatically registered into memory by the segmental processes of auditory perception. The links that represent order in these irrelevant streams again compete with those established between the to-be-remembered items, and disruption of memory ensues.

The Feature model

Nairne, Neath, and their colleagues (Nairne, 1990; Nairne, 2001; Neath, 2000; Neath & Nairne, 1995) embody their views of working memory in the Feature model and its extensions (see Figure 1d). The Feature model takes its name from the use of vectors of elements as a way to characterize information in memory, wherein each element of the vector represents some "feature" of stored information (see also Hintzman, 1991). According to the model, whenever a memory trace is formed, it is encoded simultaneously into two separate memory systems, *primary memory* and *secondary memory*, each having different properties. While secondary memory traces remain veridical, the traces encoded into primary memory are subject to interference from the encoding of subsequent items, and from the by-products (other traces) of ongoing cognitive processes operating independently from those responsible for item representation. However, only primary memory traces are available to conscious awareness. The primary memory system can therefore be thought of as "a repository of cues" (Nairne, 2002, p. 286), responsible for maintaining feature traces that are not themselves recallable, but permit access to the intact traces preserved in secondary memory. The success of this retrieval process is dependent on how well the available cues in primary memory match unique traces in secondary memory.

The Feature model offers a unique framework in which to interpret the three irrelevant information effects. Articulatory suppression is thought to disrupt memory by overwriting the features comprising to-be-remembered item traces in primary memory (Nairne, 1990). In the formalization of the Feature model, this overwriting is implemented as a process of "feature-adoption," in which modality-independent features of the memorial items are substituted with features of the irrelevant utterance (i.e., the memorial traces "adopt" features of the utterance).

Although the earliest version of the model was not designed to explain irrelevant speech effects, an extended model (Neath, 2000) assumes that irrelevant speech effects emerge from the same feature-adoption process used to explain the consequences of articulatory suppression. Accordingly, just as novel traces produced by articulatory suppression are thought to corrupt modality-independent features in the memory trace, so are the novel traces produced by irrelevant speech.

While the Feature model treats articulatory suppression and irrelevant speech similarly, irrelevant nonspeech effects are explained by other means. According to Neath (2000), the process of feature-adoption is not readily extended to irrelevant nonspeech since the modality-independent features produced for nonspeech traces would be unlikely to interact with those produced to represent speech tokens. Consequently, irrelevant nonspeech effects are argued to be better conceived as the simple result of the dual-task context they create – one task requiring subjects to maintain the to-be-remembered items, and the other requiring them to ignore irrelevant sounds (Neath, 2000; Neath & Surprenant, 2001).

The Embedded-Processes model

Proponents of the previously discussed theories participate most actively in the debate about irrelevant information effects, but a fourth viable position is conferred by a controlled attention view of working memory. The present work focuses on Cowan's Embedded-Processes model (Cowan, 1999), though similar accounts could be constructed in the context of other models that emphasize the role of a controlled attentional mechanism in working memory maintenance (e.g., Engle, 2002; McElree, 2001; Oberauer & Kliegl, 2006; Schneider & Chein, 2003). Following the tradition of Broadbent (1958) and Norman (1969), the main intent of the Embedded-Processes model is to account for a wide range of empirical findings in the fields of attention and working memory within one common framework.

Figure 1e shows the basic elements of the Embedded-Processes model. In the model, there is a single memory repository[1] that can be roughly equated with the long-term memory system. However, information in this system can be made more readily accessible, or brought into working memory. Entry into working memory occurs as an "embedded" subset of information in the long-term store takes on a temporarily heightened state of activation. This activation is time limited and subject to decay. A further embedded subset of the activated information can be made particularly salient when it falls under the *focus of attention*. The focus of attention, however, can cover only a small amount of information at any one time (the capacity is estimated to be four representational units, Cowan, 2001; cf. Oberauer & Kliegl, 2006; McElree, 2001). The Embedded-Processes model assumes a central controller that provides domain-general processing capacity. Among other functions, this controller supervises covert processes that serve to maintain information over time by reactivating decaying activity. Subvocal rehearsal may serve as one such reactivating mechanism. However, the model additionally suggests that searching through a set of memory items by iteratively subjecting them to the focus of attention can also serve to refresh their representations (Cowan, 1992, 1999). This alternative attentional reactivation strategy is hereafter referred to as *attentional refreshing* (Lewandowsky & Oberauer, 2008).

The effect of articulatory suppression could be explained in several ways within the Embedded-Processes model. However, Cowan's descriptions most strongly suggest a view analogous to that offered by the multiple-component model. Namely, that the articulatory suppression effect is derived from disruption of the speech-processing system used to subvocally rehearse items (Cowan, 1995, 2001).

The Embedded-Processes model, and other attentional control models of working memory, afford a different perspective on the origins of the irrelevant sound phenomena. Specifically, these models suggest that the deleterious influence of irrelevant sound on working memory arises from the diversion of the focus of attention away from to-be-remembered item representations during attentional refreshing. This diversion may be likened to the orienting response (Sokolov, 1963), wherein a novel, unexpected, or salient stimulus elicits an automatic attentional reaction. Similarly, novel components of the irrelevant sound stream may interfere with attentional refreshing by momentarily capturing attention.

Summary of theories

The contrasting positions afforded by the four alternative theoretical frameworks we considered are summarized in Figure 1a. The multiple-component model indicates that articulatory suppression, irrelevant speech, and irrelevant nonspeech effects each arise from a separate source (Baddeley, 1986, 2000); the O-OER model suggests that each effect has the

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[1] The embedded processes model includes a very brief sensory store in addition to the long-term memory store. This aspect of the model is not addressed in the present paper.

same origin (Macken & Jones, 1995); the Feature model likens the effects of articulatory suppression and irrelevant speech, while the irrelevant nonspeech effect is presumed to have a separate cause (Neath, 2000; Neath & Surprenant, 2001); the Embedded-Processes model assumes that the articulatory suppression effect has a unique origin, while irrelevant speech and irrelevant nonspeech effects arise from a common source (Cowan, 1995, 2001).

Prior attempts to empirically adjudicate between these fundamentally differing points of view have often focused on the interactions between various irrelevant information types (e.g., the interaction between articulatory suppression and irrelevant speech manipulations). Unfortunately, findings regarding these interactions have been inconsistent, and “there exists much uncertainty about the reliability, replicability, and interpretation of the … interactions” (Neath et al., 2003, p. 1269). For example, with auditory presentation of the to-be-remembered items, some studies report that articulatory suppression abolishes the affect of irrelevant speech (Hanley & Broadbent, 1987 Experiment 1; Jones, Macken, & Nichols, 2004), while others have found a persistence of the irrelevant speech effect under articulatory suppression (Hanley & Broadbent, 1987, Experiment 3; Hanley & Bakapoulou, 2003). Given these difficulties in evaluating competing theories on the basis of behaviorally observed interactions, it appeared that a different approach might be helpful.

The present study thus began with an attempt to assess alterative theoretical positions using neuroimaging methods. In our first experiment, which uses fMRI, we obtained a pattern of results that generally supports the Embedded-Processes framework. The neuroimaging results also point to intriguing differences in the timing of the three irrelevant information effects. In Experiment 2, we exploit these temporal distinctions through a convergent behavioral study. The findings from this second experiment also lend support to the Embedded-Processes model of working memory. Our experimental findings illustrate the value of using functional neuroimaging to probe theoretical models of cognition, and they bring to the forefront a theoretical model that posits a strong interconnection between working memory, attention, and long-term memory.

EXPERIMENT 1

Advancements in neuroimaging methods (e.g., fMRI, PET) have established these techniques as an important new source of evidence that can be employed to triangulate on a specific cognitive theory, and an impressive number of neuroimaging studies have sought to explore the neural basis of working memory. What is readily apparent from these myriad studies is the consistent network of neuroanatomical regions implicated in working memory function (Chein et al., 2002; D’Esposito et al., 1998; Fiez et al., 1996; Owens, 1997). The major constituents of the verbal working memory network, in which irrelevant information effects on verbal items are likely to take place, are shown in Figure 2a.

Baddeley’s multiple-component framework has been used to motivate and interpret the majority of prior neuroimaging studies. Based upon a large body of experimental results, a specific mapping between components of the model and particular regions of the brain has been forwarded (e.g., Henson, 2001; Smith & Jonides, 1999; Smith et al., 1998), as represented in Figure 2b. On the surface, investigations in the domain of verbal working memory thus seem to reflect a success in establishing close links between neuroimaging results and cognitive theory. However, alternative theoretical accounts that may actually prove more accommodating of the data have not been frequently considered (c.f., Chein, Ravizza, & Fiez, 2003).

While the three irrelevant information effects are not tested together in a prior neuroimaging study, a pair of fMRI studies conducted by Gruber and von Cramon (Gruber, 2001; Gruber & von Cramon, 2003; related data is also discussed in Gruber & von Cramon, 2001) examined the neural basis of articulatory suppression effects, and a pair of PET studies conducted by Gisselgard and colleagues (2003 (2004) sought to explore the neural basis of the irrelevant speech effect. The results obtained across these studies point toward an intriguing functional distinction between articulatory suppression and irrelevant speech effects, in that one seems to increase activity within the verbal working memory network, and the other seems to reduce it. However, the absence of within-subjects comparisons of articulatory suppression and irrelevant speech, the deployment of different methods and different working memory tasks across studies, and a difficulty in replicating the findings, all suggest the need for caution in drawing strong conclusions based on these previous studies. Furthermore, an assessment of irrelevant nonspeech effects on neural processing has yet to be made. These limitations are addressed in the present trial-based fMRI experiment.

A simple logic can be employed to form predictions. Effects having a common source should influence fMRI signal during working memory processing in the same way. That is, the pattern of brain activity observed under conventional (quiet) working memory conditions should be modified in the same way by separate irrelevant information effects that derive from the same source. By contrast, effects having different sources should accordingly have dissociable consequences for brain activity. Such influences on brain function may materialize as an alteration of the signal magnitude or temporal processing within the “classic” working memory network, or as a shift in the neuroanatomical substrates of performance (i.e. a change in the set of regions activated during working memory). Importantly, the predictions formed through this logic are neutral with respect to the type of neural modulation expected for each effect (e.g., a magnitude increase or decrease). Moreover, while interpretation of the results can be informed by proposed mappings of a given model onto the brain (e.g., Chein et al., 2003; Cowan, 1999; Smith & Jonides, 1997), the logic of the experiment is similarly neutral with regard to specific anatomical localization.

Participants

Fourteen right-handed, native English speaking, subjects (mean age ~ 22 years, range 19–29, 8 females) selected from the University of Pittsburgh community volunteered to take part in the fMRI experiment. All subjects were naïve to the specific hypotheses being tested, but had completed a brief prior behavioral session to demonstrate their individual sensitivity to the types of irrelevant information being tested, and to ensure roughly equivalent working memory spans across subjects (80–95% accuracy on quiet trials). Participants gave informed, written consent, and received monetary compensation. All subjects reported normal hearing and normal, or corrected-to-normal, vision.

Design

The experiment included four working memory conditions: quiet (WMQ), concurrent silent articulatory suppression (WMAS), concurrent irrelevant speech (WMIS), concurrent irrelevant nonspeech (WMIN), and three non-mnemonic conditions: silent articulation, irrelevant speech, irrelevant nonspeech. In a roughly two hour long scan session, subjects completed 13 experimental blocks,[2] each lasting 6.6 minutes and comprised of 11 task trials; two trials of each working memory condition, and one trial of each non-mnemonic condition. In total, subjects completed 26 trials for each working memory condition, and 13 trials for each non-mnemonic condition. The trials were sampled in a pseudo-random fashion such that no two successive trials were of the same condition.

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[2] The full experimental session could not be finished for two subjects. Consequently, one subject completed only ten blocks, and the other only seven.

Stimuli

A list of seven items was presented for each working memory trial. The lists were constructed by sampling seven items in random order (without replacement) from the consonants B, F, H, K, L, M, Q, R, S, and Z. The letters were displayed sequentially, just above a centrally located fixation cross, in upper-case, 26-point, white, Garamond font on a black background. For non-mnemonic trials, a series of dashes (--) was presented in place of the to-be-remembered letters.

Irrelevant background sounds were constructed using Goldwave (GoldWave Inc., Newfoundland, CA) sound editing software. Irrelevant background speech sequences consisted of the spoken digits one through four, presented in pseudo-random order (the same digit was never spoken twice in succession). These speech sequences were derived from digital recordings of a male speaker, obtained at 16-bit resolution and a sampling rate of 44 kHz. After recording, each spoken digit was isolated and edited to be 350 ms long. Eight irrelevant speech sequences, lasting 20 s each, were then assembled by sampling one of the four speech tokens once every 500 ms (i.e. a 150 ms gap separated each speech sound).

Irrelevant nonspeech sequences consisted of changing-state broadband noise bursts (Tremblay, Macken, & Jones, 2001). White noise (with equal energy over audible frequencies) was generated digitally, and then filtered at each of five center frequencies: 250, 500, 1000, 2000, and 4000 Hz. As in Tremblay et al. (2001), the filter was designed to produce broadband noise with a center frequency-to-bandwidth ratio of 1.66, and to thus yield sounds with a low degree of tonality. Sound tokens lasting for 350 ms were created from the five center frequencies. These five sound tokens were then assembled in pseudo-random fashion at a rate of one token every 500 ms (with 150 ms gaps) to form irrelevant nonspeech sequences. Eight nonspeech sequences, each lasting 20 s, were constructed.

All irrelevant background sounds (speech and nonspeech) were delivered through MRI compatible headphones (Avotec Inc., Stewart, Florida) at approximately 70dB, as measured by a digital sound level meter (Extech Instruments, Waltham, MA). The headphones attenuated approximately 15–20dB of the ambient sounds produced by the MRI scanner during data collection, and additional sound-insulating material was packed around the headphones to further reduce the amount of scanner noise heard by participants. For all participants, an initial sound test was conducted to insure that the irrelevant background sequences were audible well above the operating sounds of the scanner.

Procedure

Cognitive Task Procedure—Subjects were scanned while performing a probed recall task under various irrelevant information conditions. The task required that subjects view a series of items, maintain the series over a delay, and then recall a specific item when given the item that preceded it in the series as a probe. Figure 3 shows a schematic diagram of a task trial. It should be highlighted that while this working memory task requires that only one item be recalled per trial, accurate responding required that subjects maintain an ordered representation of the entire series (see also Sternberg, 1967). Experimental programming and presentation was implemented with the E-Prime experimental software suite (Psychology Software Tools, Pittsburgh).

Working Memory Trials: Trials associated with the working memory conditions differed only according to the type of irrelevant information present during the trial, as described below. Each working memory trial began with a 3 s instruction period that indicated the nature of irrelevant information, if any, that would be imposed. The subsequent presentation period consisted of seven to-be-remembered English letters presented sequentially at a rate of one item per second (on for 0.8 s, off for 0.2 s). Following the final list item, a *wait* prompt appeared, and remained visible on the screen for the duration of 10 seconds. Subjects were instructed to covertly maintain the list items throughout this delay period.

At the end of the delay, an item-probe appearing in the middle of the display prompted the subject to begin recall. The probe item was always a to-be-remembered letter from one of the first six serial positions of the effective trial.[3] Subjects were instructed to respond to the recall probe by writing the successive item from the series (i.e. the single letter that followed the probe letter during presentation) onto a paper notepad positioned on their torso or lap. Although participants could not see the notepad, the responses for each trial could be easily discriminated from one another (and a fresh sheet of the notepad was used for each run). Responding was allowed for 4 seconds, following which time the recall probe was removed from the display.

For the remainder of the trial, subjects passively viewed a centrally located fixation cross. The cross remained on the display for 12 seconds, allowing the hemodynamic response evoked by cognitive components of the task to decay back to baseline. Subjects were encouraged to treat this baseline period as an opportunity to relax.

Non-mnemonic Trials: The inclusion of non-mnemonic trial types allowed for the identification of brain regions engaged by the “irrelevant” processes in the absence of a working memory demand. Accordingly, trials associated with the three non-mnemonic conditions were closely matched to the working memory trials with respect to visual input, response, and irrelevant information, but differed from the working memory trials in that they placed no demands on the memory system. To-be-remembered letters were not shown in non-mnemonic trials, and instead, subjects saw a pair of dashes flash seven times at the same presentation rate (0.8s on, 0.2s off). At the “recall” probe for non-mnemonic trials (--), subjects responded by writing a pair of hyphens on the notepad.

Irrelevant Information Type: Irrelevant information type was manipulated from trial to trial, with four possible conditions: quiet (i.e., no irrelevant information), irrelevant speech, irrelevant nonspeech, and articulatory suppression. The irrelevant information was identical for working memory and non-mnemonic trials, but only the working memory trials were performed under quiet conditions.

The type of irrelevant information associated with a given trial was indicated by a colored frame first appearing around the stimulus display during the 3s trial instruction period. The frame was color-coded allowing subjects to determine which type of irrelevant information was being tested. The colored frame remained visible on the display throughout the presentation and delay periods (20 seconds), and was removed as the recall probe appeared. On irrelevant speech and nonspeech trials, one of the eight constructed sound sequences (selected at random) was initiated and terminated concurrent with the appearance and disappearance, respectively, of the colored frame. Subjects were instructed to ignore the background sounds, and to focus on the working memory task. On articulatory suppression trials, subjects were required to initiate covert repetition of the word “*the”* at an approximate rate of two repetitions per second, as soon as the appropriately colored frame appeared on the display. Subjects were instructed to continue silent articulatory suppression at this rate until the colored frame disappeared from the screen. To avoid movement artifact in the imaging data, subjects were asked to refrain from any overt movements of the articulatory musculature during silent articulation. The reader should note that the present use of *covert* articulation reflects a departure from standard articulatory suppression methodology, which typically involves overt articulation. In pilot

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[3] Interference effects are largest in the latter part of the serial position curve. To optimize the likelihood of obtaining significant effects, selection of the probe item was accordingly biased with serial positions 1 and 2 each used as the probe on 10% of trials, and serial positions 3 through 6 each used as the probe on 20% of trials.

studies, we found strong, and similarly patterned, within-subjects, effects for both overt and covert suppression, which gave us confidence in proceeding with the silent articulatory suppression procedure.

FMRI data acquisition—Scanning was conducted on a 3-Tesla head-only Siemens Allegra magnet equipped with a standard transmit/receive head coil. Subjects lay supine, and stimuli were projected onto a visual display positioned inside the magnet's bore (viewed through a mirror placed above the subjects' eyes).

Prior to functional scanning, a 34 slice oblique-axial structural series was collected parallel to the AC-PC plane with a T1-weighted inversion recovery pulse sequence (TE = 14 ms, TR = 1570 ms, FOV = 200 mm, slice thickness = 2.7 skip 0.3, flip angle = 180, inversion time = 800 ms). This slice prescription provided coverage from the top of the brain through the upper third of the cerebellum in all subjects. The structural series served as an "in-plane" anatomical reference for all functional series, which were acquired in the same slices using a T2*-weighted echo-planar imaging (EPI) sequence (TE=30 ms, TR=2 s, FOV=200 mm, slice-thickness=3.0 skip 0 mm, flip angle=70, in-plane resolution = 3.125 mm). Functional data were collected in thirteen separate runs, each associated with one block of the cognitive paradigm. To support more precise anatomical localization and spatial co-registration of the data, a separate high-resolution 3D structural volume (Siemens MPRAGE) was collected from each subject after the completion of functional scanning.

FMRI data analysis—Data analysis was conducted off-line using select utilities from a range of neuroimaging software packages (Brain Voyager, AIR, NIS, FSL, AFNI), with format conversion and integration provided by Fiswidgets (Fissell et al., 2003). A series of preprocessing steps were employed to correct for artifacts and individual subject differences. To compensate for variation in acquisition timing, a slice scan time correction using sinc interpolation was first applied. Images were then adjusted for subject motion through a six-parameter rigid-body automated registration algorithm (Woods, Cherry, & Mazziotta, 1993).

In order to obtain group composite results, structural images[4] from each subject were transformed into a common reference space using first a linear (12-parameters), and then a nonlinear (60-parameters), alignment step (Woods, Grafton, Watson, Sicotte, & Mazziotta, 1998). The same transformation matrix was then applied to the functional data. Global mean scaling (to account for differences in subject means) and 3D isotropic Gaussian smoothing (8mm FWHM) were also applied to adjust for between-subjects differences. For final reporting and anatomical localization, the reference anatomy and statistical maps were warped into standard stereotaxic space (Talairach & Tournoux, 1988).

Statistical analysis of the functional data employed least-squares estimation based on the general linear model (GLM) approach, allowing fMRI BOLD signal changes occurring during particular temporal stages of the task trial to be assessed (see Zarahn, Aguirre, & D'Esposito, 1999). The full model included four temporally shifted covariates (shown in Figure 3) for each task condition. These four covariates corresponded with square-wave functions representing the presentation (p), early delay (d1), late delay (d2), and recall (r) portions of each trial, each convolved with a canonical model of the hemodynamic response[5] (Boynton, Engel, Glover, & Heeger, 1996). While the two middle covariates (d1 & d2) are of greatest relevance in

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[4] For the 12 subjects who completed the entire session, the whole-brain high resolution volume scan was used for coregistration. For two subjects who could not complete the session, the 34 slice T1-weighted structural scan was used.

[5] The use of a canonical hemodynamic model may be problematic in that different subjects, and even different regions within a subject may produce a differential hemodynamic response. Accordingly, statistical contrasts were repeated using a more flexible inferential approach similar to that employed by Chein & Fiez, 2001. Highly consistent results were obtained, and only the GLM findings are reported.

assessing working memory function, the inclusion of the surrounding covariates allowed presentation and retrieval components of the task to be assessed, and caused variance explained by the d1 and d2 covariates to be specific to delay-period activity (Zarahn et al., 1999).

As detailed in the results section, several statistical contrasts based on this full model were conducted. To form group-composite statistical maps, voxel-wise parameter estimates (beta coefficients) provided by the GLM were first obtained for each subject independently. A t-test of the significance of the subjects' coefficients at each voxel relative to zero was then conducted, thus constituting a random-effects analysis. All statistical maps were thresholded using a false discovery rate (FDR) algorithm (Genovese, Lazar, & Nichols, 2002), with the probability of a false detection set at $q = 0.01$.

Results

Behavioral Results—Probed recall task performance was analyzed to identify the behavioral effects of silent articulatory suppression, irrelevant speech, and irrelevant nonspeech on working memory. Subject accuracy in each working memory condition was calculated by determining the proportion of trials on which subjects correctly recalled the item that succeeded the probe. The mean accuracy of performance in each condition is shown in Figure 4. The overall disruptive effects of irrelevant information were first assessed in a one-way repeated measures ANOVA with irrelevant information type (WMQ, WMAS, WMIS, WMIN) as a within-subjects factor, which produced a significant result [$F(3,13)=12.61$, $p < 0.001$)]. Planned comparisons were used to contrast performance under each of the concurrent processing conditions to that in the quiet condition (WMAS vs. WMQ, WMIS vs. WMQ, WMIN vs. WMQ). Each type of irrelevant information produced a performance decrement, with the proportion of accurate trials under silent articulatory suppression [mean = 0.49, SD = 0.19, $T(13) = 6.12$, $p < 0.001$, one-tailed], irrelevant speech [mean = 0.58, SD = 0.17, $T(13) = 4.56$, $p < 0.01$, one-tailed], and irrelevant nonspeech [mean = 0.68, SD = 0.15, $T(13) = 2.39$, $p < 0.05$, one-tailed] all significantly reduced relative to quiet (mean = 0.77, SD = 0.10). These behavioral effects were also very reliable within subjects (all subjects showed a performance decrement with suppression, 13 of 14 with irrelevant speech, and 11 of 14 with irrelevant nonspeech). Additional *post-hoc* contrasts (Newman-Keuls) yielded further significant differences between the articulatory suppression and both irrelevant sound conditions ($p < 0.01$), but a nonsignificant difference between irrelevant speech and irrelevant nonspeech ($p = 0.07$).

Imaging Results

Working Memory Effects: The first goal of analysis was to localize the network of regions supporting short-term maintenance during probed recall task performance. To identify these regions, the four covariates associated with quiet working memory trials (WMQ) were tested for significant contributions to the overall variance in each voxel's time-series. This analysis revealed regions contributing to the encoding, maintenance, and/or retrieval of information in working memory in the absence of irrelevant information.

Since the essential function of working memory is to maintain information in the absence of external stimulation (i.e. over a delay), analysis of the two delay-period covariates (d1 & d2) could be regarded as the purest measure of a region's involvement in working memory. Thus, brain regions exhibiting significant loading on these two delay covariates were of greatest interest. Areas exhibiting significant delay-based activation are shown in Figure 5 and detailed in Table 1.

Foci of activation associated with the presentation and retrieval stages of task performance were similarly assessed by identifying regions with significant contributions from the presentation (WMQ_p) and recall (WMQ_r) covariates in quiet working memory trials. Presentation and retrieval related activations were found in regions overlapping those implicated in delay-based processing, as well as in regions that were not significantly engaged during the delay period (see Table 1)

Irrelevant Information Effects: The primary objective of the experiment was to characterize the neural correlates of articulatory suppression, irrelevant speech, and irrelevant nonspeech effects in working memory. To examine the neuroanatomical loci of these effects, regions exhibiting significant delay-related activity during quiet working memory trials (i.e. those showing activation associated with covariates WMQ_{d1} and/or WMQ_{d2}) were treated as regions-of-interest (ROIs), and were further probed for effects of irrelevant information. To identify ROIs exhibiting significant irrelevant information effects, we contrasted regional activity during quiet working memory to that during each form of irrelevant processing. This ROI analysis was repeated for each stage of the trial (presentation, delay 1, delay 2, recall) by using the stage-based trial covariates shown in Figure 3. Accordingly, there were twelve linear contrasts tested, each comparing signal from an irrelevant information condition to that in the quiet condition during a particular trial sub-stage, as follows: articulatory suppression contrasts – $WMAS_p$ vs. WMQ_p, $WMAS_{d1}$ vs. WMQ_{d1}, $WMAS_{d2}$ vs. WMQ_{d2}, and $WMAS_r$ vs. WMQ_r; irrelevant speech contrasts – $WMIS_p$ vs. WMQ_p, $WMIS_{d1}$ vs. WMQ_{d1}, $WMIS_{d2}$ vs. WMQ_{d2}, and $WMIS_r$ vs. WMQ_r; irrelevant nonspeech contrasts – $WMIN_p$ vs. WMQ_p, $WMIN_{d1}$ vs. WMQ_{d1}, $WMIN_{d2}$ vs. WMQ_{d2}, and $WMIN_r$ vs. WMQ_r.

Table 2 shows the pattern of significant activity change under each form of irrelevant processing, for each stage of the trial. As the table shows, the overall pattern of regional modulation was very different for articulatory suppression as compared to the two irrelevant sound conditions, while the two irrelevant sound conditions had nearly identical affects on activity. Specifically, articulatory suppression was generally found to evoke activity *increases*, while both irrelevant sound conditions tended to produce activity *decreases*. Moreover, articulatory suppression produced its activity changes coincident with item *presentation*, while the effect of both irrelevant sound conditions on regional activity was not realized until the *delay* stage of the trial. This difference in the valence and relative timing of each effect is further illustrated in the time-series shown in Figure 5 (right). Relative to quiet control trials, articulatory suppression caused an increase in fMRI signal that was significant for acquisitions 4–8 (corresponding with presentation and early delay) in the region shown, while both irrelevant speech and nonspeech caused a decrease in fMRI signal that was significant for acquisitions 6–10 (corresponding with early and late delay) in the same region. For interested readers, we describe below the specific regions showing modulation from each irrelevant processing condition. However, we remind readers who are less familiar with neuroanatomy (and claims regarding putative regional functions) that the predictions from alternative working memory models can be evaluated by considering the overall pattern of modulation across the three irrelevant processing conditions, and without regard to the specific regions where modulation occurs.

Articulatory Suppression Effects: In general, articulatory suppression was found to **increase** activity in working memory regions. Significant activity enhancements were found in five of the sixteen delay-related ROIs (see Table 2). These included the medial frontal (BA 6/32), premotor (lateral BA 6), left dorsal and ventral inferior frontal (BA 44/9 and BA 45/44, respectively), and the left anterior insular (BA 45/13) regions. In all of these regions, the increase in activity was significant in a contrast of the presentation covariate for articulatory suppression trials to the presentation covariate for quiet trials ($WMAS_p$ vs. WMQ_p). In the medial frontal, ventral inferior frontal, and anterior insular areas, the activity increase associated with suppression was shown to persist into the early delay period, as shown via a linear contrast of the early delay covariates for each condition ($WMAS_{d1}$ vs. WMQ_{d1}). Similar patterns of increase that failed to reach statistical significance were also present in the anterior cingulate cortex (BA 24/32), bilateral cerebellum, and right lateralized homologues of the premotor and anterior insular regions. The only additional significant difference between suppression and quiet trials was a relative reduction of activity under suppression in the left basal ganglia (putamen), identified by a contrast of the late delay covariates (WMAS_{d2} vs. WMQ_{d2}). No differences were present in the recall period (WMAS_{r} vs. WMQ_{r}).

Irrelevant Speech Effects: In contrast to the effects obtained under articulatory suppression, irrelevant speech tended to **reduce** activity in working memory areas, and this reduction emerged later in the trial than did the increases observed with articulatory suppression. A contrast of the presentation period covariate for irrelevant speech and quiet trials (WMIS_{p} vs. WMQ_{p}) produced no significant results. However, significant decreases in the magnitude of regional activity were found within the anterior cingulate, left dorsal and ventral inferior frontal, bilateral anterior insula, and left basal ganglia ROIs in a contrast based on the early delay covariates (WMIS_{d1} vs. WMQ_{d1}). These decreases remained significant into the late delay period (WMIS_{d2} vs. WMQ_{d2}) in the left ventral inferior frontal, left anterior insula, and left basal ganglia regions. Once again, no differences were found during the recall period (WMIS_{r} vs. WMQ_{r}), and the only observed activity increase was during the latter half of the delay period in the left middle temporal cortex.

Irrelevant Nonspeech Effects: The results obtained from comparison of concurrent irrelevant nonspeech to quiet working memory trials were highly consistent with those obtained for the concurrent irrelevant speech contrasts. Significant irrelevant nonspeech effects were found in the anterior cingulate, the left dorsal and ventral inferior frontal gyrus, the left anterior insula, and the left basal ganglia. A nonsignificant, but similarly patterned difference was also present in the right anterior insula. As with irrelevant speech, these irrelevant nonspeech effects could be characterized as reductions in the magnitude of working memory activity occurring specifically during the delay portion of the trial. The contrast for the presentation period (WMIN_{p} vs. WMQ_{p}) again produced no significant differences. Meanwhile, activity reductions from irrelevant nonspeech were significant in all listed regions during the early delay period (WMIN_{d1} vs. WMQ_{d1}), and for the left ventral inferior frontal and left anterior insula in the late delay period (WMIN_{d2} vs. WMQ_{d2}). No differences were obtained in the recall period, nor did any region exhibit an increase in activity with concurrent irrelevant nonspeech.

Irrelevant information effects in correct-only trials: A concern often raised in the neuroimaging literature is that regional activity differences may derive solely from differences in the accuracy of performance, rather than from actual processing differences induced by the intended experimental manipulation (e.g., Barch et al., 1997). It seems unlikely that such an explanation could account for the present results, in that conditions having similarly detrimental effects on performance were found to have opposite effects on neural activity (increases with WMAS, decreases with WMIS and WMIN). However, it could be argued that the additional performance decrements in the WMAS condition were responsible for some of the observed differences. To address this potential confound, the data were sorted *post-hoc* to allow examination of the subset of trials for which subjects produced an accurate response. Analysis of correct-only trials produced a pattern of irrelevant information effects qualitatively consistent with those observed in the full dataset (though sub-sampling of correct-only trials limits the statistical power of these tests). In some regions (e.g., left anterior insula) the size of the irrelevant information effects actually appeared to be enhanced for correct-only trials.

Competition for Cognitive Resources: A common assumption among the considered models of working memory is that irrelevant information effects derive from competition between the primary working memory task and the secondary interference conditions (in some models the competition is for processing resources, and in others it is for representational resources). In neuroanatomical terms, one might expect that the locus of competition could be revealed as shared territory (overlap) between the working memory network and the set of areas engaged when interfering conditions are present in the absence of a working memory demand. To identify the possible anatomical loci of such resource competition, a set of activation maps was generated from the delay covariates associated with each of the non-mnemonic trial types (silent articulation, irrelevant speech, irrelevant nonspeech), and these maps were inspected for anatomical overlap with the ROIs identified in the working memory effects analysis.

For non-mnemonic silent articulation trials, only the left precentral gyrus was found to overlap with the identified set of working memory regions, though activation in this condition was notably weaker than in the memory conditions. For non-mnemonic irrelevant speech trials, an overlapping activation was found in the left middle temporal gyrus. No other delay-based activity from non-mnemonic trials occurred within the working memory ROIs.

Recruitment of Compensatory Resources under Interference from Irrelevant Information: The work of Gruber and von Cramon (Gruber & von Cramon, 2001, 2003) suggests that partially distinct cortical networks may be used to support working memory performance when it occurs with and without concurrent interference. That is, working memory performance under interfering conditions may be supported by an additional set of cognitive processes, and thus, by distinct brain regions from those engaged during quiet working memory. A similar argument is found in the cognitive theoretical literature, where it is suggested that irrelevant information can lead to the abandonment of processes normally used to support working memory (e.g., phonological storage and rehearsal), and to the recruitment of compensatory processes (see e.g., Larsen & Baddeley, 2003). Thus, a potential limitation of the ROI-based approach employed above, which considered the data from only quiet working memory (WMQ) trials to identify the ROIs, is that it may have excluded regions engaged to support working memory only under interfering conditions. To detect any such regions, the data from each concurrent irrelevant information trial (WMAS, WMIS, WMIN) were analyzed separately by an analogous approach to that used to identify maintenance regions for quiet working memory trials.

All three working memory irrelevant information conditions engaged the same broad network of regions as was identified in the quiet working memory trial analysis. For concurrent articulatory suppression trials, the regions engaged in delay-based processing almost completely subsumed the set of voxels comprising the quiet working memory network. Interestingly, despite observed reductions of signal with irrelevant speech (WMIS) and nonspeech (WMIN) conditions, activity associated with these conditions also remained above the statistical criteria in all working memory ROIs (though select voxels in certain ROIs did fall below the statistical threshold).

Beyond those areas implicated in the working memory network for quiet trials, concurrent articulatory suppression trials (WMAS) also produced significant delay-period activity in bilateral anterior middle frontal gyri (BA 46/10), bilateral inferior parietal lobes (BA 40/39), and a right cerebellar region (lateral to that found for the quiet presentation and early delay periods). While activation in these regions did not reach statistical significance for any of the other working memory trial types, inspection of the time-series in these regions indicated that similar, sub-threshold, temporal patterns were present for quiet and concurrent irrelevant sound trials. The increased activity observed in these regions during articulatory suppression trials is consistent with the overall pattern of increases seen in the working memory network discussed above.

As expected given the additional auditory input associated with concurrent irrelevant speech and nonspeech trials, these irrelevant sound conditions also produced large activations in the primary auditory and adjacent cortices. However, no additional areas were recruited to support performance in the presence of irrelevant sounds of either type.

Discussion

This trial-based fMRI experiment represents the first within-subjects test of irrelevant information effects (articulatory suppression, irrelevant speech, and irrelevant nonspeech) in neuroimaging. With respect to the primary goal of the experiment, the main finding was that the articulatory suppression effect was dissociated from the effects of irrelevant speech and nonspeech in the directional valence and timing of the influence it exerts on cortical function. Specifically, articulatory suppression caused a generalized *increase* in the BOLD fMRI response relative to control working memory conditions, and this increase tended to materialize *early* during task trials in the affected regions. In contrast, both irrelevant speech and irrelevant nonspeech caused a distributed *decrease* in the signal, which was found to emerge *later* in the trial (especially in inferior frontal and anterior insular regions).

Several consistencies with previously published work point to the reliability of the results afforded by the present experiment. Although the use of probed recall is novel to fMRI, the obtained pattern of working memory activity closely parallels that observed in an earlier trial-based fMRI study of verbal working memory using serial, rather than probed, recall (Chein & Fiez, 2001). In both studies, delay-based processing was found to be principally supported by a frontal network including pre-SMA, premotor, middle and inferior frontal, anterior insular, and basal ganglia regions. Engagement of these regions in verbal working memory is also highly consistent with the broader literature (Cabeza & Nyberg, 2000; Smith & Jonides, 1999; Fiez, 1996; Chein et al., 2002).

The present findings also generally converge with previous neuroimaging studies examining the consequences of irrelevant information in working memory. As in the prior work of Gruber and von Cramon (2003), we found that the behavioral effect of silent articulatory suppression corresponds with relative increases in activity in left inferior prefrontal and bilateral anterior insular regions. The present observation of similar increases in the pre-SMA and left precentral regions also appears to be consistent, though this is somewhat difficult to assess due to the "interaction" method used in the prior studies. Specifically, Gruber & von Cramon (2003) reported significant activation of analogous pre-SMA and left precentral regions during silent articulation performed in the absence of a mnemonic demand (see Gruber & von Cramon, 2003, Table 2), but subtracted out these activations in the process of comparing the articulatory suppression to control working memory conditions. While non-mnemonic articulatory engagement of the left premotor cortex was also found in the present study, the statistical approach ensured that data from this condition did not influence the detection of irrelevant information effects present during working memory trials. Importantly, this difference in statistical approach explains a further apparent disparity between the present findings and those of Gruber and von Cramon (2003), in that the present study produced no evidence that verbal working memory regions are abandoned during articulatory suppression (though it is possible that the observed activations reflect processing of the secondary task, and not storage or rehearsal in WM per se).

Gruber (2001) and Gruber & von Cramon (2003) assert that the demands of articulatory suppression cause subjects to recruit additional maintenance resources, as evidenced by their observation of an additional "bilateral prefrontal-parietal network" specifically during concurrent articulatory suppression trials. They contend that this recruited network is unlikely to reflect domain-general (e.g., central executive) contributions, since the same regions are not engaged to support visuospatial working memory under correspondingly damaging interference. The results of the present study replicate the emergence of these additional regions under articulatory suppression, but shed further light on interpretation by providing a characterization of their relative engagement across task conditions. While articulatory suppression drives activation above the statistical threshold, we find that the same regions are similarly engaged at sub-threshold levels in each of the other working memory conditions. The data thus suggest that rather than being recruited only when articulatory mechanisms are burdened, the processes supported by these regions are just more heavily emphasized under articulatory suppression.

The results from the present experiment are also broadly consistent with the irrelevant speech effects reported by Gisselgard et al., (2003). In both, the presence of irrelevant speech during working memory task performance is shown to be reflected as a distributed reduction of activity in working memory related regions. Gisselgard et al. (2003), however, obtained significant reductions in only the left superior temporal gyrus, with a nearly significant reduction in the right prefrontal cortex. In the present study, significant irrelevant speech effects were found to be somewhat more widespread, and occurred within regions commonly implicated in verbal working memory processing (anterior cingulate, left dorsal and ventral inferior frontal, and bilateral anterior insular sites). This difference in the sensitivity of the present experiment to irrelevant speech effects likely derives from an advantage of trial-based fMRI, which allowed us to detect effects limited to just the delay stage of each trial.

The results from this experiment indicate that the affect of articulatory suppression on working memory processing is distinct from the affects of irrelevant sound, while no further distinction between irrelevant speech and irrelevant nonspeech was apparent. This new piece of information allows us to evaluate the four theories reviewed in the introduction to this paper: the Multiple-Component model, the O-OER model, the Feature model, and the Embedded-Processes model. As summarized in Figure 1, each of the models makes a specific prediction about how the various effects of irrelevant information should pattern together. Only the alternative forwarded by the Embedded-Processes model accurately predicted the outcome of the study. The findings thus appear to have satisfied the objective of the experiment, by uniquely endorsing one theoretical view (the Embedded-Processes model) while seeming to disconfirm the explanations afforded by competing theories.

EXPERIMENT II

In the first experiment it was shown that articulatory suppression effects are differentiated from irrelevant sound effects (speech and nonspeech) according to the influence they have on neural processing during a working memory task. An intriguing aspect of the time course data was that these differences appeared at distinct stages of the trial, with articulatory suppression effects emerging most strongly very early in the trial (during presentation), and irrelevant sound effects emerging more strongly later in the trial (as delay-based processing sets in). While neuroimaging experiments are often derived from earlier behavioral findings, rarely have neuroimaging results been used to motivate novel behavioral experiments. The temporal differences observed in our fMRI experiment suggested to us, however, a potential behavioral method for dissociating the effects of articulatory suppression and irrelevant sound; by manipulating the specific timing of irrelevant information relative to trial stages. Accordingly, the goal of the second experiment was to corroborate the neuroimaging findings through a behavioral experiment exploring whether articulatory suppression and irrelevant sounds have different consequences to behavior when limited temporally to a particular stage of the working memory task trial.

Behavioral differences in the relevant timing of articulatory suppression and irrelevant sound effects are suggested in the literature. A number of studies have investigated the impact of “stage-limited” irrelevant speech on working memory (Hanley & Bakopoulou, 2003; Macken, Mosdell, & Jones, 1999; Miles et al., 1991; Norris, Baddeley, & Page, 2004; Tolan & Tehan, 2002). While these studies sought to investigate distinct theoretical issues, and therefore included additional manipulations, each of the experiments contained two relevant conditions: one in which irrelevant background speech occurred only during presentation (input), and another in which irrelevant background speech occurred only during a delay period (rehearsal). Unfortunately, direct statistical contrasts between these two conditions were not reported in several of the experiments, thereby leaving it ambiguous whether a statistically significant difference was obtained. However, as shown in Table 3, there is a clear tendency for the irrelevant speech effect to be smaller when speech occurs during presentation, and larger when speech occurs during the delay.

In addition to examining effects of irrelevant speech, Miles et al. (1991) tested the effects of articulatory suppression at separate stages. In these experiments, articulatory suppression was found to be more damaging than irrelevant speech, as is usually the case (e.g., Salamé & Baddeley, 1982). However, the pattern obtained for articulatory suppression was opposite to that obtained for irrelevant speech, with articulatory suppression effects being larger during presentation, and smaller during the delay (Table 3). The authors reported that this apparent interaction between irrelevant information type (irrelevant speech, articulatory suppression) and stage (presentation, delay) was not significant. However, the tested interaction included a third disruptive condition (irrelevant speech and articulatory suppression in combination) which may have diluted the interaction test. Moreover, stage of interference was a between-subjects factor, raising some concern over the statistical power of the comparisons. A more recent study conducted by Toppino and Pisegna (2005) replicates the finding that articulatory suppression is most damaging when it is concurrent with presentation, and less damaging when performed during a subsequent delay. In this study, both steady-state (same digit repeated) and changing-state (counting) articulatory suppression led to more recall errors when restricted to the presentation period.

The present experiment employs a delayed serial recall task in a procedure modeled on the work of Miles and colleagues (1991), with three relevant distinctions. First, the experiment includes conditions in which irrelevant nonspeech is deployed to disrupt memory. The inclusion of the nonspeech conditions allows for direct comparison of the temporal effects of irrelevant nonspeech to those of irrelevant speech and articulatory suppression. Second, for completeness, the experiment includes conditions in which the presence of each type of irrelevant information is limited to the retrieval period. Third, while stage of interference was a between-subjects factor in Miles et al., in the present study all manipulations were performed using a more statistically powerful within-subjects design.

If, as both the imaging results and trends in the literature suggest, articulatory suppression and irrelevant sound effects have their peak influence during separate temporal stages of the trial, it should be possible to demonstrate these differences as interactions in the within-subjects design. Whereas articulatory suppression effects are predicted to be greatest when suppression is required during the presentation period, irrelevant speech effects are predicted to be greatest when the background speech is isolated to the delay interval. Moreover, on the basis of the imaging findings, it is predicted that irrelevant nonspeech will pattern with irrelevant speech, and thus also be most effectual during the delay.

Participants

Twenty introductory level psychology students from the University of Pittsburgh participated in the experiment in partial fulfillment of a course requirement. All subjects were tested individually, and reported normal hearing and normal, or corrected-to-normal, vision.

Design

The experiment employed a 3 × 3 factorial design with two within-subjects factors: irrelevant information type (articulatory suppression, irrelevant speech, irrelevant nonspeech) and stage of interference (presentation, delay, retrieval). In an additional control condition (quiet), performance was tested in the absence of irrelevant information. Subjects completed six trials from each cell of the design, with trials sampled by random selection without replacement.

Stimuli

Both the to-be-remembered items and the stimuli used for irrelevant information were identical to those employed in Experiment 1, with the exception that the duration of the irrelevant sound sequences was shortened to 10s. Sounds were presented to participants through headphones at approximately 65dB (A), as measured by a digital sound level meter (Extech Instruments, Waltham, MA).

Procedure

Each subject participated in a one hour long experimental session in which they performed repeated trials of a delayed serial recall task. At the beginning of the session, subjects were given instructions about the possible nature and timing of irrelevant information in a given trial. Subjects also completed a set of practice trials to ensure a clear understanding of the task demands.

After the practice period, subjects completed six blocks of trials. Each block consisted of one trial from each of the experimental conditions. Subjects initiated trials with a keypress. The basic trial consisted of three stages: presentation, delay, and recall. Presentation included a 3.0s instruction event, followed by the presentation of a seven item list of to-be-remembered English consonants. List items were presented in the center of a computer monitor just above a fixation cross. Items appeared in random order on each trial, and were shown at a rate of one item per second (each item was shown for 0.8 s, and separated by an interstimulus interval of 0.2 s).

Following the presentation of the last list item, the word *wait* appeared on the screen, denoting the start of the delay interval. The delay interval lasted for 10 seconds. Subjects were instructed to covertly maintain the memoranda during this period.

Retrieval was prompted with a graphic depicting a pen against a paper tablet. Subjects were instructed to respond to this recall prompt by immediately writing down as many of the to-be-remembered items as they could recall onto a provided response sheet. Subjects were required to recall the items in strictly forward order, leaving blank any boxes associated with items that could not be recalled, and attempting to place each remembered item in the box associated with its appropriate serial position. Responding was allowed for 10 seconds, following which time the recall prompt was removed from the display and an auditory cue signaling the end of the trial was heard through the headphones.

As in Experiment 1, a color-coded frame appeared around the stimulus display to signal the onset and offset of the irrelevant information in each trial. Irrelevant information processing coincided with specific trial stages (presentation, delay, or retrieval), and always lasted for a duration of 10s. For irrelevant sound trials, subjects were instructed to ignore any background sounds, and to focus on the working memory task. Sounds were heard through headphones worn by subjects throughout the duration of the experimental session. For articulatory suppression trials, subjects were required to initiate overt repetition of the word "*the*" at an approximate rate of two repetitions per second and as soon as the appropriately colored frame appeared around the display. Subjects were told to continue suppression at this rate until the frame disappeared from the screen (for a total duration of 10 seconds). All subjects were informed that their overt suppression was being recorded to ensure that the temporal boundaries of the suppression were tightly matched to the appropriate task stage, and to verify general compliance with the suppression instructions.

Results

Subjects' responses were scored according to a strict serial recall criterion, wherein an item was considered correct only if it was written in the appropriate serial position. Data were pooled across serial positions, and a two-way (3×3) analysis of variance (ANOVA) was performed, with type of irrelevant information and stage of interference as within-subjects factors. The mean probability of correct recall for each of the experimental conditions is shown in Figure 6. The main effect of irrelevant information type was significant, $F(2,38)=22.41$, $p < 0.001$, with the effect driven by reduced overall performance under articulatory suppression (mean = 0.53) relative to the irrelevant speech and nonspeech conditions (means = 0.67 and 0.68, respectively). Stage also produced a significant main effect, $F(2, 38)=17.46$, $p < 0.001$, due to an increase in overall mean performance during recall (mean = 0.68) relative to presentation (mean = 0.63) and delay (mean = 0.57) conditions. Most importantly, the predicted interaction between irrelevant information type and stage was also observed [$F(4, 76)=14.22$, $p < 0.001$].

To further delineate the nature of this interaction, planned simple main effects analyses and pair-wise contrasts were conducted. These tests indicated that the overall effect of stage was significant for each type of irrelevant information independently: articulatory suppression [$F(2, 59) = 12.49$, $p < 0.001$], irrelevant speech [$F(2,59)=3.37$, $p < 0.05$], and irrelevant nonspeech [$F(2,59) = 3.28$, $p < 0.05$]. Newman-Keuls *a posteriori* tests (alpha = 0.05) further specified these simple main effects, and explained the irrelevant information type by stage interaction. For articulatory suppression, the Newman-Keuls test showed that the degree of impairment differed significantly at each stage, with suppression during presentation producing a larger impairment than during either delay or recall, and suppression during the delay also producing significantly more impairment than that during recall. In contrast, for both irrelevant speech and irrelevant nonspeech, only the pair-wise comparison between presentation and delay was significant, with delay producing the *greater* degree of impairment. Thus, the significant interaction between irrelevant information type and stage is understood by recognizing that articulatory suppression is most damaging during presentation and less so during delay, whereas the effects of irrelevant speech and nonspeech were weak during presentation and comparatively strong during the delay.

Comparison of each experimental condition to performance under the quiet (control) condition further clarifies the effects of stage-limited irrelevant information. When collapsed across stages, the data reveal typical and significant effects of articulatory suppression ($T(19)=9.14$, $p < 0.001$, one-tailed), irrelevant speech ($T(19)=3.45$, $p < 0.001$, one-tailed), and irrelevant nonspeech ($T(19)=3.57$, $p < 0.001$, one-tailed), relative to quiet trials. However, independent inspection of the irrelevant information effects at each stage shows that significant differences relative to quiet are not always obtained. Specifically, while articulatory suppression significantly impairs performance relative to quiet at all stages [presentation $T(19)=13.77$, $p < 0.001$; delay $T(19)=7.38$, $p < 0.001$; recall $T(19)=2.56$, $p < 0.05$], irrelevant speech and nonspeech differed significantly from quiet only in the delay condition [speech: presentation $T(19)=0.50$, $p = 0.63$; delay $T(19)=5.05$, $p < 0.001$; recall $T(19)=1.79$, $p = 0.09$; nonspeech: presentation $T(19)=0.24$, $p = 0.81$; delay $T(19)=6.50$, $p < 0.001$; recall $T(19)=1.47$, $p = 0.16$].

Discussion

The main objective of this experiment was to differentiate the articulatory suppression effect from irrelevant speech and nonspeech effects on the basis of their temporal specificity. Recall performance under stage-limited irrelevant information of each type showed precisely the expected pattern of dissociation, with articulatory suppression having its most damaging influence when it occurred during the presentation stage, and both irrelevant speech and nonspeech being most effectual when they occurred during the post-presentation delay. These findings dovetail nicely with patterns observed in the fMRI data provided by Experiment 1 of this study, and demonstrate that trends apparent in the extant behavioral literature (e.g., Miles et al., 1991) are statistically reliable when tested in a within-subjects paradigm. In addition, they extend the behavioral literature by characterizing the pattern of disruption produced by stage-limited irrelevant nonspeech. The current behavioral experiment bolsters the results of the earlier imaging experiment (Experiment 1) in revealing a pattern of dissociation predicted only by the Embedded-Processes model, and not by the alternative models.

Of greatest importance to the aim of the present experiment was the detection of a statistically significant interaction between type of irrelevant information and stage of interference (Figure 6). This interaction resulted from strong effects of articulatory suppression during presentation that were reduced in later stages (delay, recall), as compared to small effects of irrelevant sound during presentation that became larger during the delay (and were intermediate in size during recall).

Although the direction of the interaction was precisely as predicted, the results do deserve some scrutiny. The present findings seem to indicate a critical period of vulnerability to irrelevant sounds during the delay period, and the absence of interference from irrelevant sounds that are restricted to the presentation period. However, the exposure period in the presentation-only trials included 3s of instruction that preceded the arrival of the first to-be-remembered item. Consequently, the overall "dose" of irrelevant sound exposure was slightly smaller for presentation-only as compared to delay-only irrelevant sound trials. Moreover, several prior studies report significant irrelevant speech effects with *immediate* serial recall (e.g. Beaman & Jones, 1998), and three prior studies have found small, but significant, presentation-only irrelevant speech effects in delayed serial recall (Miles et al., 1991; Tolan & Tehan, 2002; Norris et al., 2004). We believe that the apparent inconsistency with these earlier findings can be explained by assuming that performance is susceptible to interference from irrelevant sounds whenever the sounds coincide with the engagement of active maintenance processes (e.g., subvocal rehearsal, attentional refreshing). Methodological factors that extend the duration of the presentation period (e.g., longer list lengths, Tolan & Tehan, 2002; slower presentation rates, Miles et al., 1991) may encourage active maintenance processes to be engaged even while items are still arriving, thus causing performance to be vulnerable to disruption by irrelevant sounds occurring during item presentation (Jones, Hughes, & Macken, 2006; Macken et al., 1999; Miles et al., 1991). Since the present study used relatively short list lengths and comparatively faster item presentation, active maintenance during item presentation may have been limited, causing vulnerability to disruption from irrelevant sounds to be restricted principally to the delay-period.

In summary, the results of this experiment demonstrate a clear dissociation in the temporal specificity of articulatory suppression and irrelevant sound effects, while also showing equivalent temporal specificity for irrelevant speech and irrelevant nonspeech. Accordingly, the results corroborate the neuroimaging evidence from Experiment 1, and lend further backing to only the Embedded-Processes model of working memory. This model not only predicts the observed dissociations between irrelevant information effects, but can also explain the observed temporal patterns. The strong influence of articulatory suppression during presentation-only trials can be addressed by assuming that subvocal rehearsal becomes progressively automated, and thus gradually more robust to disruption from articulatory suppression (Cowan, 2001; Naveh Benjamin & Jonides, 1984; Baddeley, 1986). Accordingly, the "critical period" of articulatory suppression may be limited to the earlier presentation portion of the trial, when the intended rehearsal sequence is first being established.

Through the lens of an attentional control model of working memory it is also possible to account for the limited impact of irrelevant sounds occurring only during item presentation. First, the physical presence of memorial stimuli during presentation may be sufficient to hold the focus of attention in place, and thus limit orienting toward irrelevant stimuli. Second, strong initial activation at presentation may allow item representations to endure through brief periods of attentional distraction. In contrast, once the delay period commences, memorial stimuli are no longer physically present, and their representations are likely to drop below initial levels of activation (despite covert maintenance processes). So, delay-only irrelevant sounds may be most disruptive because attention is more susceptible to distraction during this period, and such attentional distraction will have a more damaging effect on item retention by allowing representations to slip below recoverable levels of activation.

GENERAL DISCUSSION

Considered together, the two experiments in this series provide convergent evidence regarding the functional equivalence, and non-equivalence, of the three irrelevant information effects. Both the neuroimaging evidence from Experiment 1, and the complementary behavioral findings from Experiment 2, point toward a dissociation of the articulatory suppression effect from the functionally equivalent effects of irrelevant speech and irrelevant nonspeech. Leverage in understanding the basis for this global pattern of dissociation is afforded by a further point of consistency across the two experiments, the relative timing of interference produced by each irrelevant information type. In particular, both experiments indicate the same temporal dissociation of the effects, with articulatory suppression having its greatest influence on working memory at the beginning of each trial (presentation) and the irrelevant sounds having their greatest impact during the post-presentation delay interval. Four competing theories of working memory, each widely applied to address the effects of irrelevant information, were detailed in the introduction. It was argued that the differential predictions afforded by each theory could be exploited as a way to adjudicate between their alternative accounts. Indeed, the coherent pattern of results produced in the two above experiments appear to endorse specifically the account provided by an attentional control theory of working memory; the Embedded-Processes model.

While it is encouraging that the pattern of findings from both experiments lends backing to this attentional model of working memory, we must acknowledge that there remain important challenges to this view. For example, although the attentional account predicts that irrelevant sound effects should habituate over repeated or extended exposures (e.g. Morris & Jones, 1990), the results from prior studies are mixed, with some indicating that effect size is not attenuated over repeated trials (Jones & Macken, 1995a; Tremblay & Jones, 1998), but others showing that the irrelevant speech effect is dampened after several minutes of pre-exposure to the irrelevant sequence (Banbury & Berry, 1997; Morris & Jones, 1990). More recent behavioral work using auditory oddball events to directly test an attentional capture hypothesis has also yielded mixed, but potentially challenging, results. While the presentation of an auditory oddball during serial recall task performance does appear to capture attention and thus disrupt recall for earlier presented items (Lange, 2005), the temporal locus of this auditory deviant effect may be different from that found for the traditional irrelevant speech manipulation (Hughes, Vachon, & Jones, 2005) and the two forms of auditory distraction (auditory deviant, irrelevant speech) appear to have different impacts across various tasks (e.g. serial recall, missing item). Results to date thus generally point to a role for attention in some task contexts but not others, and suggest that we may need to invoke distinct mechanisms to account for the separate effects of irrelevant speech and auditory oddballs (Hughes, Vachon, & Jones, 2007). Further investigations are clearly needed to address these contemporary challenges to an attentional control account.

A Revised Neuroanatomical Mapping of Working Memory Processes

Prior neuroimaging research has shown that it is possible to adopt the perspective of Baddeley's multiple-component model and to corroborate many of its predictions. The prevailing view of how working memory processes map onto specific brain structures is derived from this earlier work. The results of the present study, however, seem to resist interpretation under the Multiple-Component model, and thus add to a growing body of evidence that challenges the established neuroanatomical mapping (see also Chein & Fiez, 2001; Chein, Ravizza, & Fiez, 2002; Ravizza et al., 2004; Postle, 2006). The present data suggest instead that a mapping of theory to brain based on a controlled attention theory of working memory may prove more accurate. To support future testing of novel predictions based on this alternative theory, a revised *neuroanatomical* theory of working memory processing is also needed. While the available data does not fully constrain a revised model, the rudiments of an alternative mapping can be constructed from Cowan's (1995, 1999) speculations on the probable neural substrates of working memory, and from the available neuroimaging evidence.

The resulting neuroanatomical theory, shown in Figure 7, assigns regions activated by a working memory task to one of three sources – executive processing, covert maintenance, or active memory. Executive processes are assumed to be housed in frontal areas, especially the dorsolateral prefrontal cortex (Cowan, 1995; the same is normally assumed about the executive system of Baddeley's model). To support covert maintenance in verbal working memory, both attentional refreshing and subvocal rehearsal areas may be recruited. Cowan (1995) assumes that the inferior parietal cortex is the neural substrate for the focus of attention. Accordingly, attentional refreshing may be mediated by parietal shifting of the attentional focus. Attribution of this attentional function to the inferior parietal cortex is highly consistent with the broader literature (e.g., Corbetta & Shulman, 2002), but represents an important departure from a proposed mapping based on Baddeley's model, which holds this region to be the site of phonological storage (Henson, 2001;Paulesu et al., 1993;Smith & Jonides, 1999). Data from the present paper can also be construed as support for this reinterpretation. Specifically, increased inferior parietal activity during articulatory suppression can be interpreted as reflecting an increased demand on attentional refreshing when subvocal rehearsal is disrupted. Likewise, modest (nonsignificant) reductions of activity in this region during irrelevant sound trials may reflect strategic inhibition of the attentional refreshing process to limit the effect of the distracting irrelevant sounds when subvocal rehearsal is possible.

Controlled attention accounts of working memory provide few constraints on the appropriate localization of the rehearsal process. However, an assumption used earlier to explain the temporal specificity of articulatory suppression effects in the context of the Embedded-Processes model can be similarly employed to inform a speculative mapping of the rehearsal process. The relevant assumption is that rehearsal should be conceptualized as a dynamic multistaged process, wherein the rehearsal sequence becomes more stable (automatic) in later stages (see e.g., Naveh-Benjamin & Jonides, 1984, Chein & Fiez, 2001). Accordingly, regions exhibiting only transient contributions at the onset of each working memory trial may be thought to make essential contributions to rehearsal by supporting the "set-up" stage, while regions showing sustained delay-related activity may be thought to mediate automatic aspects of rehearsal. By this account, cerebellar and dorsal inferior frontal regions, both of which were found to exhibit transient activity in the present study (and in Chein & Fiez, 2001), may support the early stage of rehearsal by retrieving and assembling the motoric plans that will comprise the final rehearsal sequence. Similarly, as suggested by Cowan (2001), the focus of attention may also be engaged to initiate rehearsal, thus explaining transient parietal contributions. Meanwhile, the final rehearsal sequence may become stabilized, and hence sustained, within premotor and pre-supplementary motor areas, both found to exhibit significant activity throughout the trial.

While previous research treats Broca's area as the most likely site of subvocal rehearsal (e.g., Awh et al., 1996; Henson, 2001; Paulesu et al., 1993; Smith & Jonides, 1999), the ventral portions of this region may be more appropriately interpreted as a site of representation for novel phonological sequences (Chein et al., 2003). The latter interpretation is consistent with Cowan's (1995) more general assumptions regarding the nature of active memory. Specifically, representations of existing knowledge are assumed to be distributed throughout the neocortex. When external stimuli or internal processes activate a given memory representation, the particular activated (encoded) features determine where in the cortex this active representation is processed and preserved. For sensory features, activated areas are assumed to be the same as, or adjacent to, the brain areas involved in perceiving a stimulus (i.e. primary sensory cortex). In contrast, non-sensory features (e.g., semantic, phonological) are likely to be represented in association cortices. In verbal maintenance tasks, activated memory representations are likely generated or contained within ventral inferior frontal areas (e.g., Broca's area and the adjacent insular cortex). Thus, Broca's area may serve not as the site of rehearsal, but as a general source of phonological representation and processing that becomes active when a phonological sequence of to-be-remembered items is presented.

Conclusions

As we seek to explain the relationships between working memory, long-term memory, attention, and language, and to elucidate the role of working memory in cognition more generally, we must be sure to adopt an appropriate theoretical framework. As proponents of the historically dominant theoretical view of working memory now construe neuroimaging findings as confirmatory of their position (see e.g., Baddeley, 2000; Larsen & Baddeley, 2003), there is a real danger that the ability and motivation to advance alternative theories will diminish. In demonstrating that other models can be reasonably tested through neuroimaging, the present work thus has important implications for both the future of neuroimaging research and the development of cognitive theory. Importantly, the obtained results do not lend support to the historically prevailing view, and instead appear to advocate an alternative controlled attention theory of working memory embodied by the Embedded-Processes model. The present work thus suggests a need to reassess existing theoretical claims, and demonstrates how a cognitive neuroscientific approach can serve to inform theoretical development while elucidating the links between theoretical processes and putative biological mechanisms.

BIBLIOGRAPHY

Awh E, Jonides J, Smith EE, Schumacher EH, Koeppe RA, Katz S. Dissociation of storage and rehearsal in verbal working memory: Evidence from positron emission tomography. Psychological Science 1996;7(1):25–31.

Baddeley A, Larsen JD. The disruption of STM: A response to our commentators. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 2003;56A(8):1301–1306.

Baddeley, AD. Working memory. New York, NY, US: Clarendon Press/Oxford University Press; 1986.

Baddeley, AD. The development of the concept of working memory: Implications and contributions of neuropsychology. In: Vallar, GS.; Tim, editors. Neuropsychological impairments of short term memory. New York, NY: Cambridge University Press; 1990. p. 54-73.

Baddeley AD. Is working memory working? The fifteenth Bartlett Lecture. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1992;44a(1):1–31.

Baddeley AD. The phonological loop and irrelevant speech effect: Some comments on Neath (2000). Psychonomic Bulletin and Review 2000;7(3):544–549. [PubMed: 11082863]

Baddeley, AD.; Hitch, G. Working Memory. In: Bower, GH., editor. The Psychology of Learning and Motivation. Vol. 8. New York: Academic Press; 1974. p. 47-89.

Baddeley AD, Lewis V, Vallar G. Exploring the articulatory loop. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1984;36a(2):233–252.

Baddeley, AD.; Logie, RH. Working memory: The multiple-component model. In: Miyake, AS.; Priti, editors. Models of working memory: Mechanisms of active maintenance and executive control. New York, NY: Cambridge University Press; 1999. p. 28-61.

Baddeley AD, Thomson N, Buchanan M. Word length and the structure of short-term memory. Journal of Verbal Learning and Verbal Behavior 1975;14(6):575–589.

Banbury S, Berry DC. Habituation and dishabituation to speech and office noise. Journal of Experimental Psychology: Applied 1997;3(3):181–195.

Barch DM, Braver TS, Nystrom LE, Forman SD, Noll DC, Cohen JD. Dissociating working memory from task difficulty in human prefrontal cortex. Neuropsychologia 1997;35(10):1373–1380. [PubMed: 9347483]

Beaman CP, Jones DM. Role of serial order in the irrelevant speech effect: Tests of the changing-state hypothesis. Journal of Experimental Psychology: Learning, Memory, and Cognition 1997;23(2): 459–471.

Beaman CP, Jones DM. Irrelevant sound disrupts order information in free recall as in serial recall. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1998;51A(3):615–636.

Boynton GM, Engel SA, Glover GH, Heeger DJ. Linear systems analysis of functional magnetic resonance imaging in human V1. J Neurosci 1996;16(13):4207–4221. [PubMed: 8753882]

Bregman, AS. Auditory scene analysis: The perceptual organization of sound. Cambridge, MA, US: The MIT Press; 1990.

Bridges AM, Jones DM. Word dose in the disruption of serial recall by irrelevant speech: Phonological confusions or changing state? Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1996;49a(4):919–939.

Broadbent, DE. Perception and communication. New York: Pergamon Press; 1958.

Cabeza R, Nyberg L. Imaging cognition II: An empirical review of 275 PET and fMRI studies. J Cogn Neurosci 2000;12(1):1–47. [PubMed: 10769304]

Campbell T, Beaman CP, Berry DC. Auditory memory and the irrelevant sound effect: Further evidence for changing-state disruption. Memory 2002;10(3):199–214. [PubMed: 11958724]

Chein JM, Fiez JA. Dissociation of verbal working memory system components using a delayed serial recall task. Cereb Cortex 2001;11(11):1003–1014. [PubMed: 11590110]

Chein JM, Fissell K, Jacobs S, Fiez JA. Functional heterogeneity within Broca's area during verbal working memory. Physiology and Behavior 2002;77(4–5):635–639. [PubMed: 12527011]

Chein JM, Ravizza S, Fiez JA. Using neuroimaging to evaluate models of working memory and their implicaions for language processing. Journal of Neurolinguistics 2003;16(4–5):315–339.

Chein, JM.; Schneider, W. Designing Effective FMRI Experiments. In: Grafman, J.; Robertson, I., editors. The Handbook of Neuropsychology. Amsterdam: Elsevier; 2003.

Clifton C, Tash J. Effect of syllabic word length on memory-search rate. Journal of Experimental Psychology 1973;99(2):231–235.

Colle HA. Auditory encoding in visual short-term recall: Effects of noise intensity and spatial location. Journal of Verbal Learning and Verbal Behavior 1980;19(6):722–735.

Colle HA, Welsh A. Acoustic masking in primary memory. Journal of Verbal Learning and Verbal Behavior 1976;15(1):17–31.

Collette F, Salmon E, Van der Linden M, Chicherio C, Belleville S, Degueldre C, Delfiore G, Franck G. Regional brain activity during tasks devoted to the central executive of working memory. Cognitive Brain Research 1999;7(3):411–417. [PubMed: 9838207]

Conrad R, Hull AJ. Information, acoustic confusion and memory span. British Journal of Psychology 1964;55(4):429–432. [PubMed: 14237884]

Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci 2002;3(3):201–215. [PubMed: 11994752]

Cowan N. Verbal memory span and the timing of spoken recall. Journal of Memory and Language 1992;31(5):668–684.

Cowan N. Activation, attention, and short-term memory. Memory and Cognition 1993;21(2):162–167.

Cowan, N. Attention and memory: An integrated framework. New York, NY, US: Oxford University Press; 1995.

Cowan, N. An Embedded-Processes Model of working memory. In: Miyake, A.; Shah, P., editors. Models of working memory: Mechanisms of active maintenance and executive control. New York, NY, US: Cambridge University Press; 1999. p. 62-101.

Cowan N. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. Behavioral and Brain Sciences 2001;24(1):87–185. [PubMed: 11515286]

Cowan N, Wood NL, Wood PK, Keller TA, Nugent LD, Keller CV. Two separate verbal processing rates contributing to short-term memory span. Journal of Experimental Psychology: General 1998;127(2): 141–160. [PubMed: 9622911]

D'Esposito M, Aguirre GK, Zarahn E, Ballard D, Shin RK, Lease J. Functional MRI studies of spatial and nonspatial working memory. Brain Res Cogn Brain Res 1998;7(1):1–13. [PubMed: 9714705]

D'Esposito M, Detre JA, Alsop DC, Shin RK, Atlas S, Grossman M. The neural basis of the central executive system of working memory. Nature 1995;378(6554):279–281. [PubMed: 7477346]

Donovos, DK.; Chein, JM.; Fiez, JA. Links between verbal working memory, concurrent articulation effects, and the cerebellum: Converging fMRI and behavioral studies. Abstracts of the 10th Annual Meeting of the Cognitive Neuroscience Society; 2002.

Engle RW. Working memory capacity as executive attention. Current Directions in Psychological Science 2002;11(1):19–23.

Eysenck, MW.; Keane, MT. Cognitive Psychology. Hove, UK: Laurence Earlbaum Associates Ltd; 1995.

Fiez JA, Raife EA, Balota DA, Schwarz JP, Raichle ME, Petersen SE. A positron emission tomography study of the short-term maintenance of verbal information. J Neurosci 1996;16(2):808–822. [PubMed: 8551361]

Fissell K, Tseytlin E, Cunningham D, Carter C, Schneider W, Cohen JD. Fiswidgets: A graphical computing environment for neuroimaging analysis. Neuroinformatics 2003;1(1):111–125. [PubMed: 15055396]

Gathercole, S. Models of short-term memory. Hove, UK: Psychology Press; 1996.

Gathercole SE. The modality effect and articulation. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1986;38(3-A):461–474.

Gathercole, SE.; Baddeley, AD. Working memory and language. Hove, England UK: Lawrence Erlbaum Associates, Inc; 1993.

Genovese CR, Lazar NA, Nichols T. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. Neuroimage 2002;15:870–878. [PubMed: 11906227]

Gisselgard J, Petersson KM, Baddeley AD, Ingvar M. The Irrelevant Speech Effect: A PET study. Neuropsychologia 2003;41(14):1899–1911. [PubMed: 14572523]

Gruber O. Effects of domain-specific interference on brain activation associated with verbal working memory task performance. Cereb Cortex 2001;11(11):1047–1055. [PubMed: 11590114]

Gruber O, von Cramon DY. Domain-specific distribution of working memory processes along human prefrontal and parietal cortices: a functional magnetic resonance imaging study. Neurosci Lett 2001;297(1):29–32. [PubMed: 11114477]

Gruber O, von Cramon DY. The functional neuroanatomy of human working memory revisited: Evidence from 3-T fMRI studies using classical domain-specific interference tasks. Neuroimage 2003;19:797–809. [PubMed: 12880808]

Gupta P, MacWhinney B. Is the articulatory loop articulatory or auditory? Reexamining the effects of concurrent articulation on immediate serial recall. Journal of Memory and Language 1995;34(1):63–88.

Hanley JR. Does articulatory suppression remove the irrelevant speech effect? Memory 1997;5(3):423–431. [PubMed: 9231151]

Hanley JR, Bakopoulou E. Irrelevant speech, articulatory suppression, and phonological similarity: A test of the phonological loop model and the feature model. Psychonomic Bulletin and Review 2003;10 (2):435–444. [PubMed: 12921421]

Hanley JR, Broadbent C. The effect of unattended speech on serial recall following auditory presentation. British Journal of Psychology 1987;78(3):287–297.

Hartley AA, Speer NK. Locating and fractionating working memory using functional neuroimaging: storage, maintenance, and executive functions. Microsc Res Tech 2000;51(1):45–53. [PubMed: 11002352]

Henson, R. Neural working memory. In: Andrade, J., editor. Working memory in perspective. Philadelphia, PA: Psychology Press; 2001. p. 151-173.

Henson RN, Burgess N, Frith CD. Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. Neuropsychologia 2000;38(4):426–440. [PubMed: 10683393]

Hickok G, Poeppel D. Functional anatomy of speech perception and speech production: psycholinguistic implications. J Psycholinguist Res 2001;30(3):225–235. [PubMed: 11523272]

Hintzman DL. Classification and aural coding in short-term memory. Psychonomic Science 1965;3(4): 161–162.

Hintzman, DL. Why are formal models useful in psychology?. In: Hockley, WEL.; Stephan, editors. Relating theory and data: Essays on human memory in honor of Bennet B. Murdock. Hillsdale, NJ: Lawrence Erlbaum Press; 1991. p. 39-56.

Hughes RW, Vachon F, Jones DM. Auditory attentional capture during serial recall: Violations at encoding of an algorithm-based neural model? Journal of Experimental Psychology: Learning Memory and Cognition 2005;31(4):736–749.

Hughes RW, Vachon F, Jones DM. Disruption of Short-Term Memory by Changing and Deviant Sounds: Support for a Duplex-Mechanism Account of Auditory Distraction. Journal of Experimental Psychology: Learning Memory and Cognition 2007;33(6):1050–1061.

Jones D, Alford D, Bridges A, Tremblay S, Macken B. Organizational factors in selective attention: The interplay of acoustic distinctiveness and auditory streaming in the irrelevant sound effect. Journal of Experimental Psychology: Learning, Memory, and Cognition 1999;25(2):464–473.

Jones, D.; Beaman, CP.; Macken, WJ. The object-oriented episodic record model. In: Gathercole, S., editor. Models of short-term memory. London: Erlbaum; 1996. p. 209-238.

Jones D, Morris N. Irrelevant speech and serial recall: Implications for theories of attention and working memory. Scandinavian Journal of Psychology 1992;33(3):212–229. [PubMed: 1488646]

Jones DM. Disruption of memory for lip-read lists by irrelevant speech: Further support for the changing state hypothesis. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1994;47a(1):143–160.

Jones DM, Alford D, Macken WJ, Banbury SP, Tremblay S. Interference from degraded auditory stimuli: Linear effects of changing-state in the irrelevant sequence. Journal of the Acoustical Society of America 2000;108(3 Pt1):1082–1088. [PubMed: 11008810]

Jones DM, Macken WJ. Irrelevant tones produce an irrelevant speech effect: Implications for phonological coding in working memory. Journal of Experimental Psychology: Learning, Memory, and Cognition 1993;19(2):369–381.

Jones DM, Macken WJ. Organizational factors in the effect of irrelevant speech: The role of spatial location and timing. Memory and Cognition 1995a;23(2):192–200.

Jones DM, Macken WJ. Phonological similarity in the irrelevant speech effect: Within- or between-stream similarity? Journal of Experimental Psychology: Learning, Memory, and Cognition 1995b;21(1): 103–133.

Jones DM, Macken WJ, Murray AC. Disruption of visual short-term memory by changing-state auditory stimuli: The role of segmentation. Memory and Cognition 1993;21(3):318–328.

Jones DM, Macken WJ, Nichols A. The phonological store of working memory: is it phonological and is it a store? Journal of Experimental Psychology: Learning, Memory, and Cognition 2004;30(3): 656–674.

Jones DM, Madden C, Miles C. Privileged access by irrelevant speech to short-term memory: The role of changing state. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1992;44a(4):645–669.

Jones DM, Hughes RW, Macken WJ. Perceptual organization masquerading as phonological storage: Further support for a perceptual-gestual view of short-term memory. Journal of Memory and Language 2006;54:265–281.

Jones DM, Tremblay S. Interference in memory by process or content? A reply to Neath (2000). Psychon Bull Rev 2000;7(3):550–558. [PubMed: 11082864]

Jonides, J. Working memory and thinking. In: Smith, EEO.; Daniel, N., editors. Thinking: An invitation to cognitive science. An invitation to cognitive science. Vol. 2. Cambridge, MA, US: The MIT Press; 1995. p. 215-265.

Just MA, Carpenter PA. A capacity theory of comprehension: Individual differences in working memory. Psychological Review 1992;99(1):122–149. [PubMed: 1546114]

Klatte M, Kilcher H, Hellbrueck J. Wirkungen der zeitlichen Struktur von Hintergrundschall auf das Arbeitsgedaechtnis und ihre theoretischen und praktischen Implikationen. The effects of the temporal structure of background noise on working memory: Theoretical and practical implications. Zeitschrift fuer Experimentelle Psychologie 1995;42(4):517–544.

la Pointe LB, Engle RW. Simple and complex word spans as measures of working memory capacity. Journal of Experimental Psychology: Learning, Memory, and Cognition 1990;16(6):1118–1133.

Lange EB. Disruption of attention by irrelevant stimuli in serial recall. Journal of Memory and Language 2005;53(4):513–531.

Larsen JD, Baddeley A. Disruption of verbal STM by irrelevant speech, articulatory suppression, and manual tapping: Do they have a common source? Quarterly Journal of Experimental Psychology: Human Experimental Psychology 2003;56A(8):1249–1268.

Larsen JD, Baddeley AD, Andrade J. Phonological similarity and the irrelevant speech effect: Implications for models of short-term verbal memory. Memory 2000;8(3):145–158. [PubMed: 10889899]

LeCompte DC. Extending the irrelevant speech effect beyond serial recall. Journal of Experimental Psychology: Learning, Memory, and Cognition 1994;20(6):1396–1408.

LeCompte DC. An irrelevant speech effect with repeated and continuous background speech. Psychonomic Bulletin and Review 1995;2(3):391–397.

LeCompte DC. Irrelevant speech, serial rehearsal, and temporal distinctiveness: A new approach to the irrelevant speech effect. Journal of Experimental Psychology: Learning, Memory, and Cognition 1996;22(5):1154–1165.

LeCompte DC, Neely CB, Wilson JR. Irrelevant speech and irrelevant tones: The relative importance of speech to the irrelevant speech effect. Journal of Experimental Psychology: Learning, Memory, and Cognition 1997;23(2):472–483.

LeCompte DC, Shaibe DM. On the irrelevance of phonological similarity to the irrelevant speech effect. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1997;50A(1):100–118.

Lewandowsky S, Oberauer K. The word length effect provides no evidence for decay in short-term memory. Psychonomic Bulletin & Review. in press.

Logie R, Baddeley AD, Mane AM, Donchin E, et al. Working memory in the acquisition of complex cognitive skills. Acta Psychologica 1989;71(1–3):53–87.

Logie, RH.; Gilhooly, KJ., editors. Working memory and thinking. Hove, England: Psychology Press/ Erlbaum (UK) Taylor and Francis; 1998.

Longoni AM, Richardson JT, Aiello A. Articulatory rehearsal and phonological storage in working memory. Memory and Cognition 1993;21(1):11–22.

Macken WJ, Jones DM. Functional characteristics of the inner voice and the inner ear: Single or double agency? Journal of Experimental Psychology: Learning, Memory, and Cognition 1995;21(2):436–448.

Macken WJ, Jones DM. Reification of phonological storage. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 2003;56A(8):1279–1288.

Macken WJ, Mosdell N, Jones DM. Explaining the irrelevant-sound effect: Temporal distinctiveness or changing state? Journal of Experimental Psychology: Learning, Memory, and Cognition 1999;25(3): 810–814.

Marshuetz C, Smith EE, Jonides J, DeGutis J, Chenevert TL. Order information in working memory: fMRI evidence for parietal and prefrontal mechanisms. Journal of Cognitive Neuroscience 2000;12 (Suppl2):130–144. [PubMed: 11506653]

McElree B. Working Memory and Focal Attention. Journal of Experimental Psychology: Learning, Memory, and Cognition 2001;27(3):817–835.

Miles C, Jones DM, Madden CA. Locus of the irrelevant speech effect in short-term memory. Journal of Experimental Psychology: Learning, Memory, and Cognition 1991;17(3):578–584.

Miyake, A.; Shah, P., editors. Models of working memory: Mechanisms of active maintenance and executive control. New York: Cambridge University Press; 1999.

Morris N, Jones DM. Habituation to irrelevant speech: Effects on a visual short-term memory task. Perception and Psychophysics 1990;47(3):291–297. [PubMed: 2326151]

Murray DJ. The effect of white noise upon the recall of vocalized lists. Canadian Journal of Psychology 1965;19(4):333–345. [PubMed: 5847751]

Murray DJ. Articulation and acoustic confusability in short-term memory. Journal of Experimental Psychology 1968;78(4 Pt 1):679–684.

Murray DJ, Rowan AJ, Smith KH. The effect of articulatory suppression on short-term recognition. Canadian Journal of Psychology 1988;42(4):424–436.

Nairne JS. A feature model of immediate memory. Mem Cognit 1990;18(3):251–269.

Nairne, JS. A functional analysis of primary memory. In: Roediger, HL., III; Nairne, JS., editors. The nature of remembering: Essays in honor of Robert G. Crowder. Science conference series. Washington, DC, US: American Psychological Association; 2001. p. 283-296.

Nairne JS. Remembering over the short-term: The case against the standard model. Annual Review of Psychology 2002;53(1):53–81.

Naveh Benjamin M, Jonides J. Maintenance rehearsal: A two-component analysis. Journal of Experimental Psychology: Learning, Memory, and Cognition 1984;10(3):369–385.

Neath I. Modeling the effects of irrelevant speech on memory. Psychon Bull Rev 2000;7(3):403–423. [PubMed: 11082850]

Neath I, Farley LA, Surprenant AM. Directly assessing the relationship between irrelevant speech and articulatory suppression. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 2003;56A(8):1269–1278.

Neath I, Nairne JS. Word-length effects in immediate memory: Overwriting trace decay theory. Psychonomic Bulletin and Review 1995;2(4):429–441.

Neath, I.; Surprenant, AM. The irrelevant sound effect is not always the same as the irrelevant speech effect. In: Roediger, HL., III; Nairne, JS., editors. The nature of remembering: Essays in honor of Robert G. Crowder. Science conference series. Washington, DC, US: American Psychological Association; 2001. p. 247-265.

Neath I, Surprenant AM, LeCompte DC. Irrelevant speech eliminates the word length effect. Memory and Cognition 1998;26(2):343–354.

Norman, DA. Memory and attention: An introduction to human information processing. 1969.

Norris D, Page MP, Baddeley AD. Retroactive effects of irrelevant speech on serial recall from short-term memory. J Exp Psychol Learn Mem Cogn. 2004

Oberauer K, Kliegl R. A formal model of capacity limits in working memory. Journal of Memory and Language 2006;55 (4):601–626.

Owen AM. The functional organization of working memory processes within human lateral frontal cortex: the contribution of functional neuroimaging. Eur J Neurosci 1997;9(7):1329–1339. [PubMed: 9240390]

Page MPA, Norris DG. The irrelevant sound effect: What needs modelling, and a tentative model. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 2003;56A(8): 1289–1300.

Paulesu E, Frith CD, Frackowiak RS. The neural correlates of the verbal component of working memory. Nature 1993;362(6418):342–345. [PubMed: 8455719]

Peterson LR, Johnson ST. Some effects of minimizing articulation on short-term retention. Journal of Verbal Learning and Verbal Behavior 1971;10(4):346–354.

Petrides M, Alivisatos B, Meyer E, Evans AC. Functional activation of the human frontal cortex during the performance of verbal working memory tasks. Proc Natl Acad Sci U S A 1993;90(3):878–882. [PubMed: 8430101]

Postle BR, Berger JS, D'Esposito M. Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. Proc Natl Acad Sci U S A 1999;96(22):12959–12964. [PubMed: 10536030]

Postle BR. Working memory as an emergent property of the mind and brain. Neuroscience 2006;139(1): 23–38. [PubMed: 16324795]

Ravizza SM, Delgado MR, Chein JM, Becker JT, Fiez JA. Functional dissociations within the inferior parietal cortex in verbal working memory. Neuroimage 2004;22(2):562–573. [PubMed: 15193584]

Repovs G, Baddeley AD. The multi-component model of working memory: Explorations in experimental cognitive psychology. Neuroscience 2006;139(1):5–21. [PubMed: 16517088]

Richardson, JTE.; Engle, RW.; Hasher, L.; Logie, RH., et al. Working memory and human cognition. New York, NY, US: Oxford University Press; 1996.

Salamé P, Baddeley A. Noise, unattended speech and short-term memory. Ergonomics 1987;30(8):1185–1194. [PubMed: 3691472]

Salamé P, Baddeley A. The effects of irrelevant speech on immediate free recall. Bulletin of the Psychonomic Society 1990;28(6):540–542.

Salamé P, Baddeley AD. Disruption of short-term memory by unattended speech: Implications for the structure of working memory. Journal of Verbal Learning and Verbal Behavior 1982;21(2):150–164.

Salamé P, Baddeley AD. Phonological factors in STM: Similarity and the unattended speech effect. Bulletin of the Psychonomic Society 1986;24(4):263–265.

Salamé P, Baddeley AD. Effects of background music on phonological short-term memory. Quarterly Journal of Experimental Psychology: Human Experimental Psychology 1989;41(1-A):107–122.

Salamé P, Baddeley AD. The effects of irrelevant speech on immediate free recall. Bulletin of the Psychonomic Society 1990;28(6):540–542.

Salthouse TA. Working-memory mediation of adult age differences in integrative reasoning. Mem Cognit 1992;20(4):413–423.

Schneider W, Chein JM. Controlled & automatic processing: behavior, theory, and biological mechanisms. Cognitive Science 2003;27(3):525–559.

Schneider, W.; Detweiler, M. A connectionist/control architecture for working memory. In: Bower, GH., editor. The psychology of learning and motivation: Advances in research and theory. Vol. 21. San Diego, CA: Academic Press; 1987.

Smith EE, Jonides J. Working memory: A view from neuroimaging. Cognitive Psychology 1997;33(1): 5–42. [PubMed: 9212720]

Smith EE, Jonides J. Storage and executive processes in the frontal lobes. Science 1999;283(5408):1657–1661. [PubMed: 10073923]

Smith EE, Jonides J, Koeppe RA. Dissociating verbal and spatial working memory using PET. Cerebral Cortex 1996;6(1):11–20. [PubMed: 8670634]

Smith EE, Jonides J, Marshuetz C, Koeppe RA. Components of verbal working memory: evidence from neuroimaging. Proc Natl Acad Sci U S A 1998;95(3):876–882. [PubMed: 9448254]

Sokolov EN. Orientirovochnyi refleks kak kiberneticheskaia sistema. Orienting reflex as a cybernetic system. Zhurnal Vysshei Nervnoi Deyatel'nosti 1963;13(5):816–830.

Sternberg S. Retrieval of Contextual Information from Memory. Psychonomic Science 1967;8(2):55–56.

Stevenson, AK. On individual differences in noise susceptibility: Methodology and implications for models of the irrelevant speech effect. Stevenson,-Adam-Krystopher; Purdue U., US: 2002.

Surprenant AM, Neath I, LeCompte DC. Irrelevant speech, phonological similarity, and presentation modality. Memory 1999;7(4):405–420.

Talairach, J.; Tournoux, P. Co-planar Stereotaxic Atlas of the Human Brain. New York: Thieme; 1988.

Tolan GA, Tehan G. Testing feature interaction: Between-stream irrelevant speech effects in immediate recall. Journal of Memory and Language 2002;46(3):562–585.

Toppino TC, Pisegna A. Articulatory suppression and the irrelevant-speech effect in short-term memory: does the locus of suppression matter? Psychonomic Bulletin & Review 2005;12(2):374–9. [PubMed: 16082821]

Tremblay S, Jones DM. Role of habituation in the irrelevant sound effect: Evidence from the effects of token set size and rate of transition. Journal of Experimental Psychology: Learning, Memory, and Cognition 1998;24(3):659–671.

Tremblay S, Macken WJ, Jones DM. Elimination of the word length effect by irrelevant sound revisited. Mem Cognit 2000;28(5):841–846.

Tremblay S, Macken WJ, Jones DM. The impact of broadband noise on serial memory: changes in band-pass frequency increase disruption. Memory 2001;9(4–6):323–331.

Waugh NC, Norman DA. Primary memory. Psychological Review 1965;72(2):89–104. [PubMed: 14282677]

Woods, Cherry; Mazziotta. MRI-PET registration with automated algorithm. Journal of Computer Assisted Tomography 1993;17:536–546. [PubMed: 8331222]

Woods RP, Grafton ST, Watson JD, Sicotte NL, Mazziotta JC. Automated image registration: II. Intersubject validation of linear and nonlinear models. J Comput Assist Tomogr 1998;22(1):153–165. [PubMed: 9448780]

Zarahn E, Aguirre GK, D'Esposito M. Temporal isolation of the neural correlates of spatial mnemonic processing with fMRI. Brain Res Cogn Brain Res 1999;7(3):255–268. [PubMed: 9838152]

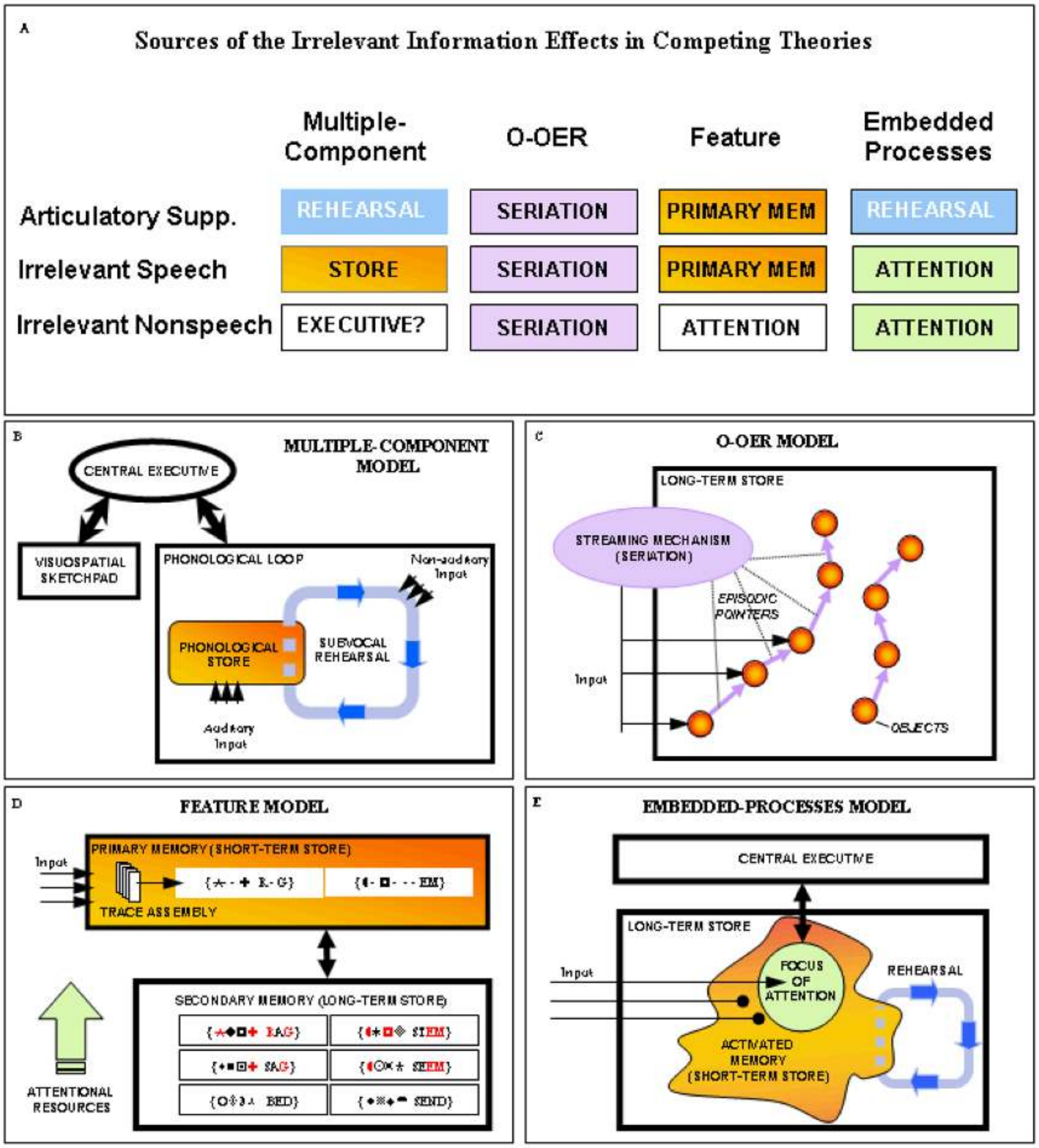

Figure 1.

Alternative explanations for the irrelevant information effects. (A) Putative origins of the irrelevant information effects in four competing theories of working memory. The main structural and processing components of the (B) multiple-component model (adapted from Baddeley, 1986), (C) O-OER model (adapted from Jones, 1996), (D) Feature model (adapted from Nairne, 2002), and (E) Embedded-Processes model (adapted from Cowan, 1999).

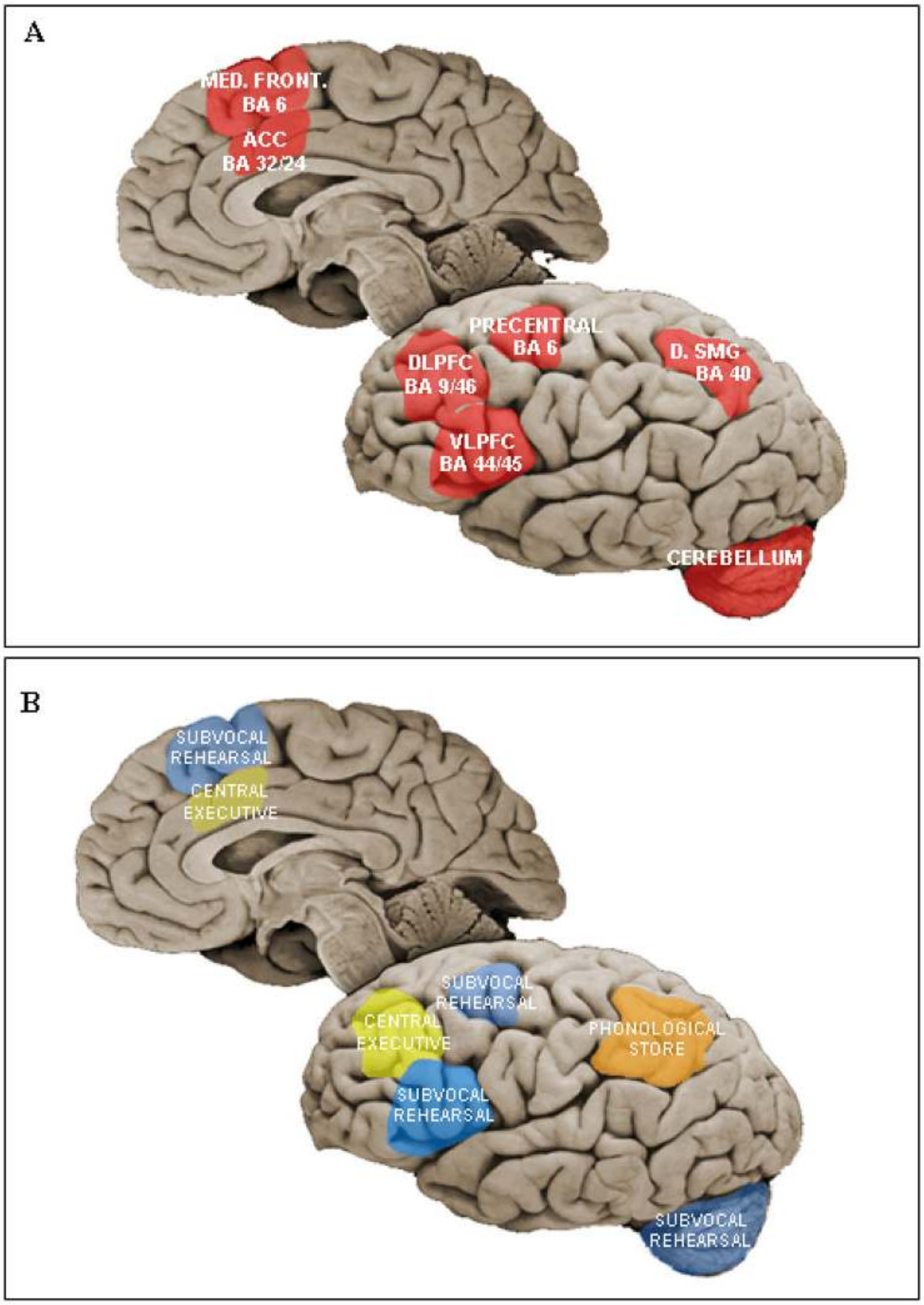

Figure 2.

The neuroanatomy of working memory and a mapping of function according to the Multiple-Component model. (A) The network of regions consistently implicated in neuroimaging studies of verbal working memory. This network is comprised of the dorsolateral prefrontal cortex (DLPFC), the ventrolateral prefrontal cortex (VLPFC), the premotor cortex, the pre-supplementary motor area (pre-SMA), the anterior cingulate cortex (ACC), and the cerebellum. (B) The prevailing interpretation of regional function based on Baddeley's Multiple-Component model.

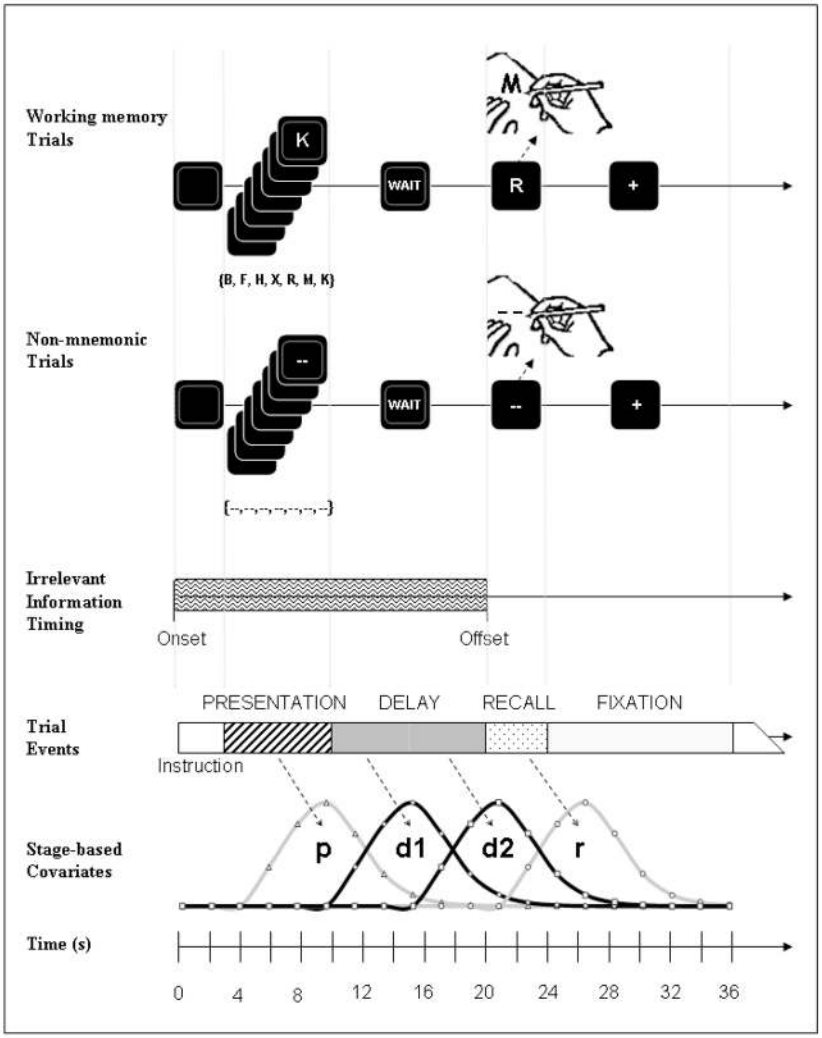

Figure 3.

Schematic of the experimental protocol used in Experiment 1. (Top) Display sequence for working memory and non-mnemonic trials. (Middle) Timing of irrelevant information relative to the stages comprising each trial (presentation, delay, recall, rest). (Bottom) The four covariates used in the GLM analysis of BOLD fMRI activity associated with the presentation (p), early delay (d1), late delay (d2), and recall (r) stages of task performance. Stage-covariates reflect a convolution of trial stages with the hemodynamic response function, and thus accommodate the time-lag of the brain's hemodynamic response to trial events.

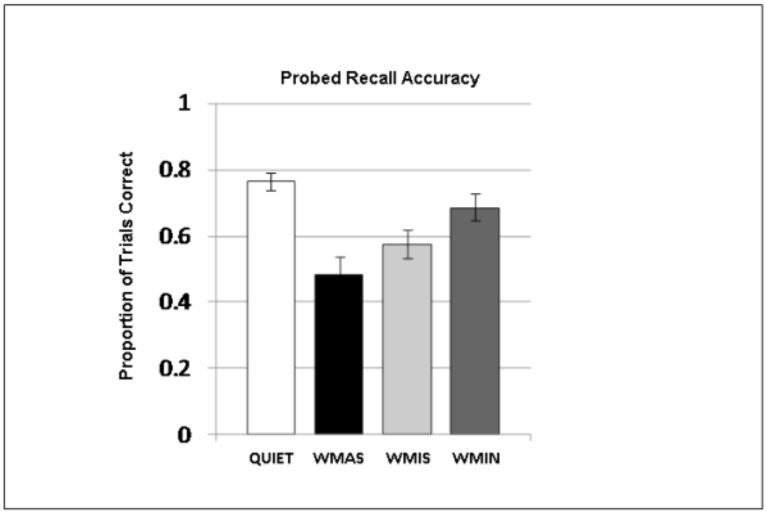

Figure 4.

The effects of irrelevant information on probed recall accuracy in Experiment Statistically significant decrements in accuracy were present for articulatory suppression (WMAS), irrelevant speech (WMIS), and irrelevant nonspeech (WMIN) conditions, relative to quiet control trials (WMQ).

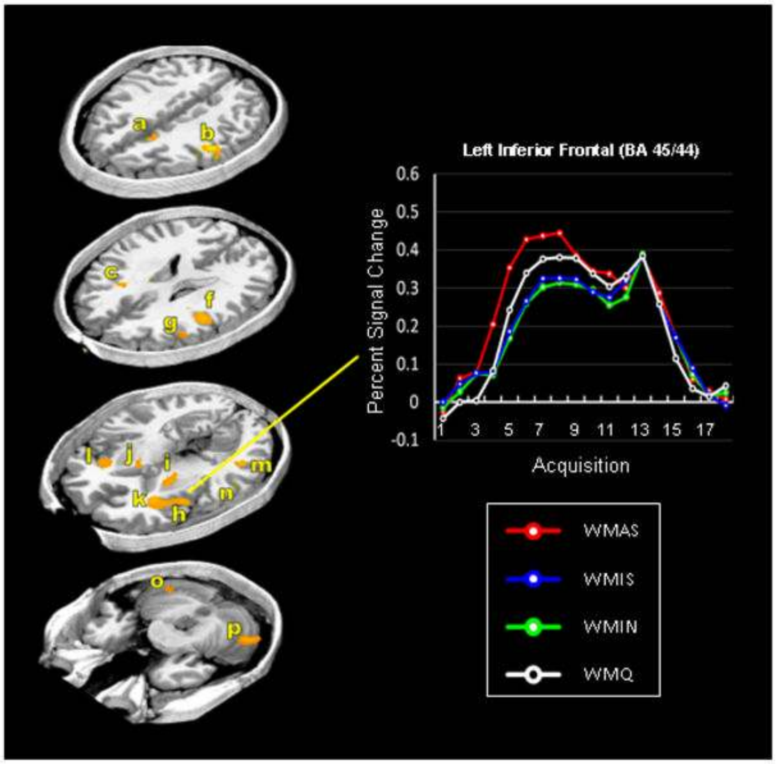

Figure 5.

“Quiet” working memory regions identified in Experiment 1. (Left) Regions in which activity surpassed a false discovery rate threshold of 0.01 in the group composite data for the early delay covariate (d1), late delay covariate (d2), or both. The statistical images are shown overlaid onto horizontal sections of the reference structural image at +40mm, +25mm, +5mm, and −25mm from the anterior commissure to posterior commisure plane. Regions are labeled according to their designation in Table 1 (not all regions listed are shown). (Right) An illustrative example of the trial-averaged fMRI time-series for each condition, showing an early onset increase in activity for articulatory suppression trials (WMAS) relative to quiet trials (WMQ), and a later onset decrease in activity for the both the irrelevant speech (WMIS) and irrelevant nonspeech (WMIN) trials relative to quiet trials.

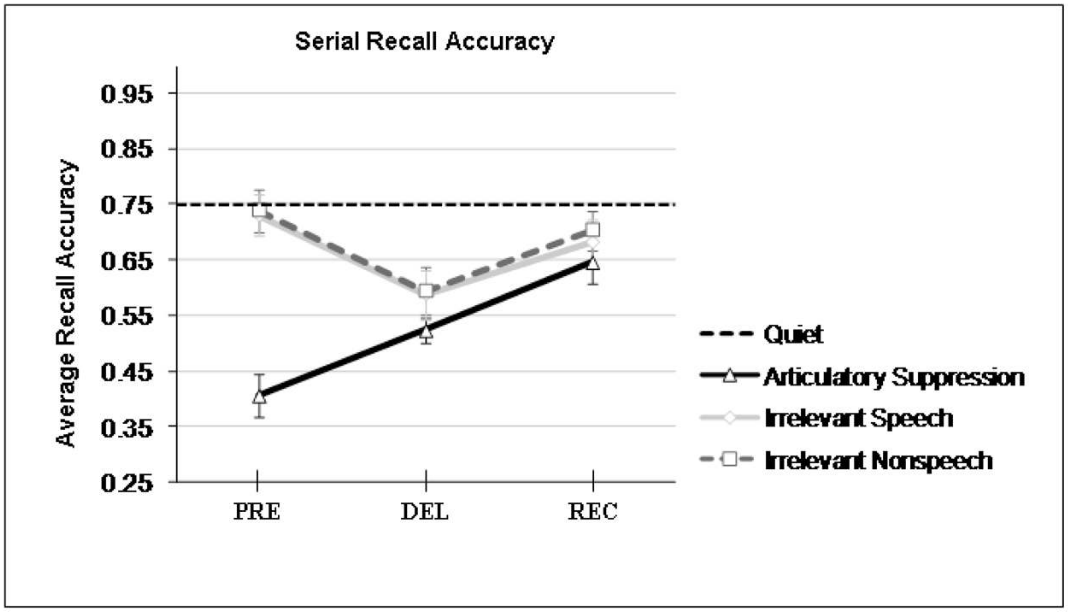

Figure 6.
Delayed serial recall task performance under stage-limited irrelevant information in Experiment 2. Average accuracy (pooled across subjects and serial positions) is shown for quiet, articulatory suppression, irrelevant speech, and irrelevant nonspeech conditions when limited temporally to the presentation (PRE), delay (DEL), or recall (REC) stages. A significant interaction between irrelevant information type and stage of interference was obtained.

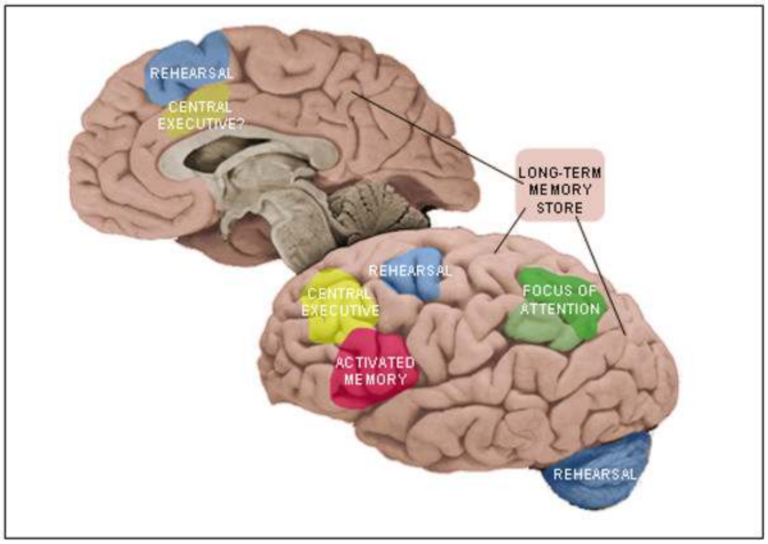

Figure 7.
A revised neuroanatomical model of working memory based on a controlled attention theory of working memory, such as the Embedded-Processes model.

Table 1

Local maxima of regions showing significant activity during presentation, delay, and recall periods in quiet working memory trials

	Presentation (p)				Early Delay (d1)				Late Delay (d2)				Recall (r)			
Delay-Period Activations†	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**
a. Medial Frontal (BA 6/32)	ns				**	−8	9	41	**	−8	15	42	***	−8	5	41
b. L Precentral (BA 6)	***	−49	−8	38	***	−46	−9	38	**	−49	−10	39	***	−54	−5	31
c. R Precentral (BA 6)	*	39	1	23	**	50	−11	34	ns				*	47	1	25
d. Anterior Cingulate (BA 24/32)	ns				**	11	12	27	*	12	19	25	*	7	11	34
e. L Precentral/Inferior Fr (BA 6/9)	ns				ns				***	−32	9	33	ns			
f. L Inferior Frontal (BA 44/9)	**	−43	4	24	**	−45	1	24	ns				***	51	6	18
g. L Middle Frontal (BA 46)	ns				ns				*	−50	25	25	*	−40	38	19
h. L Inferior Fr (BA 45/44)	*				**	−40	11	8	**	−43	19	12	***	−37	11	9
i. L Basal Ganglia (Putamen)	ns				***	−22	2	17	ns				***	−19	5	5
j. R Basal Ganglia (Putamen)	ns				**	15	0	8	ns				***	12	5	4
k. L Ant Ins (BA 13/45)	ns				***	−29	27	7	**	−31	27	7	**	−32	23	6
l. R Ant Ins (BA 13/45)	ns				**	29	21	7	**	29	18	2	*	36	17	1
m. L Post Middle Temporal (BA 21)	ns				*	−42	−51	5	ns				ns			
n. L Middle Temporal (BA 21)	ns				ns				**	−58	−34	1	ns			
o. R Cb	**	39	−53	−24	*	36	−62	−23	ns				ns			
p. L Cb	*	−46	−65	−27	**	−44	−59	−27	ns				*	−43	−56	−27
Presentation & Recall Activations																
R Sup Par/Intraparietal (BA 7/40)	*	24	−64	44	ns				ns				*	35	−49	49
L Pre/Postcentral (BA 4/3/2)	ns				ns				ns				***	−33	−25	48
R Precentral (BA 4/6)	ns				ns				ns				***	26	−6	47
L Inferior Parietal (BA 39/40)	*	−26	−74	26	ns				ns				***	−31	−51	42
R Inf Parietal (BA 39/40)	*	24	−69	29	ns				ns				ns			
L Ant Middle Frontal (BA 10)	ns				ns				ns				*	−39	54	5
R Ant Middle Frontal (BA 10)	ns				ns				ns				*	38	54	4
L Thal	ns				ns				ns				***	−11	−19	2
R Thal	ns				ns				ns				***	3	−17	1
L Fusiform (BA 37)	**	−40	−63	−11	ns				ns				*	−43	−63	−14
L Inferior Occipital (BA 18)	**	−26	−87	−15	ns				ns				ns			

	Presentation (p)				Early Delay (d1)				Late Delay (d2)				Recall (r)			
Delay-Period Activations[†]	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**	**P**	**x**	**y**	**z**
R Inferior Occipital (BA 18)	*	18	−90	−15	ns				ns				ns			
R Fusiform (BA 37)	**	39	−52	−21	ns				ns				ns			
M Cb	ns				ns				ns				*	4	−77	−33

ns = not significant,

[*] P <.001,

[**] P<.0001,

[***] P <.00001

[†] Regions in Figure 5 are labelled according to their designation in the table (a.-p.)

Table 2

Regions showing significant irrelevant information effects in Experiment 1

	Articulatory Suppression				**Irrelevant Speech**				**Irrelevant Nonspeech**			
	p	**d1**	**d2**	**r**	**p**	**d1**	**d2**	**r**	**p**	**d1**	**d2**	**r**
Medial Frontal (BA 6/32)	+	+										
L Precentral (BA 6)	+											
Anterior Cingulate (BA 24/32)						−				−		
L Inferior Fr (BA 45/44)	+	+				−	−			−	−	
L Ant Ins (BA 13/45)	+	+				−	−			−	−	
R Ant Ins (BA 13/45)						−						
L Middle Temporal (BA 21)						+						
L Inferior Frontal (BA 44/9)	+					−				−		
L Basal Ganglia (Putamen)			−			−	−			−		

p = presentation, d1 = early delay, d2 = late delay, r = recall

+ Indicates a relative increase compared to quiet working memory trials

− Indicates a relative decrease compared to quiet working memory trials

Table 3

Prior studies examining the temporal-specificity of irrelevant information effects

			Effect Size (%E)		% Difference
			Presentation	**Delay**	
A. **Irrelevant Speech**					
Miles et al., 1991	Experiment 1		12.1	15.9	31.4
Miles et al., 1991	Experiment 2		2.8	1.2	−58.4
Miles et al., 1991	Experiment 3		5.6	11.7	108.9
Macken et al., 1999*			8.0	9.0	12.5
Tolan & Tehan, 2002	Experiment 1		8.0	23.8	195.4
Hanley & Bakopoulou, 2003	Experiment 1		3.5	7.3	107.1
Norris et al., 2004	Experiment 1		5.0	4.4	−13.0
		MEAN	***6.4***	***10.4***	**54.9**
B. **Articulatory Supression**					
Miles et al., 1991	Experiment 2		11.8	8.2	−30.6
Miles et al., 1991	Experiment 3		24.1	14.8	−38.5
Toppino & Pisegna, 2005	Steady-state AS		37.7	26.0	−31.0
Toppino & Pisegna, 2005	Changing-state AS		41.9	32.4	−22.6
		MEAN	***28.9***	***20.3***	***−30.7***

Effect Size (%E) was computed as %E=100((Q−I)/Q), where Q is the mean percent accuracy in the quiet condition, and I is the mean percent accuracy under the interference condition (see Logie, Della Sala et al, 1996, see also Neath et al., 2003 for an application of the measure). % Difference is $(\%E_{presentation} - \%E_{delay})/\%E_{presentation} *100$

[*] Results averaged across two sub-stage conditions