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The effect of rehearsal rate and memory load on verbal working memory

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ABSTRACT

While many neuroimaging studies have investigated verbal working memory (WM) by manipulating memory load, the subvocal rehearsal rate at these various memory loads has generally been left uncontrolled. Therefore, the goal of this study was to investigate how mnemonic load and the rate of subvocal rehearsal modulate patterns of activity in the core neural circuits underlying verbal working memory. Using fMRI in healthy subjects, we orthogonally manipulated subvocal rehearsal rate and memory load in a verbal WM task with long 45-s delay periods. We found that middle frontal gyrus (MFG) and superior parietal lobule (SPL) exhibited memory load effects primarily early in the delay period and did not exhibit rehearsal rate effects. In contrast, we found that inferior frontal gyrus (IFG), premotor cortex (PM) and Sylvian-parietal-temporal region (area Spt) exhibited approximately linear memory load and rehearsal rate effects, with rehearsal rate effects lasting through the entire delay period. These results indicate that IFG, PM and area Spt comprise the core articulatory rehearsal areas involved in verbal WM, while MFG and SPL are recruited in a general supervisory role once a memory load threshold in the core rehearsal network has been exceeded.

Introduction

Working memory (WM) is what allows one to maintain and manipulate task-relevant information over short time periods and is critical for various cognitive tasks such as problem solving, reasoning and comprehension (Daneman and Merikle, 1996; Kyllonen and Christal, 1990; Logie et al., 1994). At the center of many theoretical models of WM is an attempt to explain how task-relevant information is maintained in an activated state over a delay period. For example, Baddeley and colleagues' classic WM model consists of domain-specific storage components for visuospatial and verbal information coupled with rehearsal processes that serve to update and refresh items currently held in memory (Baddeley, 1986). Current neuroscientific models of WM such as the "emergent property view" (Postle, 2006) propose that information is effectively "stored" in memory by the repeated reactivation of the same cortical regions that were involved in the initial perception of the task-relevant information (Buchsbaum and D'Esposito, 2008; D'Esposito, 2007; Postle, 2006). In these models rehearsal is one mechanism by which transient representations can be reactivated and is defined as the repeated selection of, or the repeated attention to, task-relevant mnemonic representations (Curtis and D'Esposito, 2003). However, despite the importance of strategic rehearsal processes to theoretical WM models, neuroscience investigations of WM typically allow subjects to freely choose the rate and manner in which they maintain information in working memory. A drawback of this naturalistic approach is that a subject's internal rehearsal strategy may change as a function of other experimentally manipulated variables, such as memory load (i.e. the number of items that must be retained in memory). Indeed, memory load manipulations are often used as a way of indexing working memory storage processes (Awh et al., 1996; Todd and Marois, 2005), and to the extent that these manipulations are used to make inferences about the informational capacity of a brain region or system, it is important to understand how rehearsal processes scale with memory load.

The primary question of the current study is whether the neural systems that vary as a function of rehearsal rate are modulated by changes in memory load, and vice versa. While it has been established in behavioral studies that verbal WM capacity is strongly correlated with a person's ability to rapidly produce speech (Cowan et al., 1998; Dasí et al., 2008; Hulme et al., 1984), the connection between rehearsal rate and memory load has never been examined to our knowledge in neuroscience studies of WM. Indeed, in the context of manipulations of memory load, a corresponding increase in the rate of subvocal rehearsal acts as a confounding variable. Moreover, the confounding of load and rate of rehearsal may partially account for the between-study variability in neural localization of load effects in previous neuroimaging studies (Postle et al., 1999; Rypma and D'Esposito, 1999; Rypma et al., 1999, 2002; Zarahn et al., 2005) contributing to what has already

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been described about the issue (Feredoes and Postle, 2007). Thus, because memory load manipulations are not particularly well-suited to dissociate domain-general executive processes (i.e. attentional, executive, internal monitoring) from rehearsal or reactivation processes (Buchsbaum and D'Esposito, 2008), previous verbal WM load studies have demonstrated activity across numerous cortical areas including middle frontal gyrus (MFG, BA 9/46), inferior frontal gyrus (IFG, BA 44/45), premotor cortex (PM, BA 6), Sylvian-parietal-temporal area (area Spt) and superior parietal lobule (SPL, BA 7). While MFG and SPL are generally thought of as domain-general executive regions and known to be activated by high memory loads (Cohen et al., 1997; Rypma and D'Esposito, 1999; Zarahn et al., 2005), the involvement of these regions in subvocal rehearsal is less clear. In particular, while it is known that MFG and SPL are not required for WM tasks with low memory loads (Barbey et al., 2013; D'Esposito and Postle, 1999; Hamidi et al., 2008; Postle et al., 1999) and thus not required for rehearsal of task-relevant items, it may be the case that these areas may be recruited at higher rates of rehearsal. On the other hand, in areas such as IFG, PM and area Spt, which are known to be involved in articulatory rehearsal and speech production more generally (Hickok et al., 2003; Shergill et al., 2002; Wildgruber et al., 1999, 2001), it is not clear if memory load influences rehearsal processing in these regions independently of subvocal rehearsal rate. In summary, it is currently unknown whether domain-general executive regions (MFG, SPL) exhibit selective activity related to the rehearsal of task-relevant items, and if domain-specific nodes of the verbal rehearsal network (IFG, PM, Spt) display memory load effects. Understanding how activity in the nodes of the WM circuit are modulated by rehearsal rate and memory load will lead to a deeper understanding of the computations that each of these cortical regions are performing and is vital to our understanding of WM.

A second question regarding WM is how the representation of task-relevant information changes as it is being rehearsed at a constant rate over time. Behavioral studies have shown that WM tasks with long retention intervals involve an effortful first stage followed by an automatized and less effortful second stage (Aldridge et al., 1987; Greene, 1987; Naveh-Benjamin and Jonides, 1984; Phaf and Wolters, 1993). Several fMRI studies of WM maintenance have found decreasing activity as the delay period progressed in the cortical regions involved in maintaining task-relevant information (Chein and Fiez, 2001; Jha and McCarthy, 2000). The finding of decreasing activity over time may reflect a “sharpening” of task-relevant neural representations. With time and increasing number of rehearsals, neural activation associated with the coding of irrelevant features may begin to wane, a phenomenon that has been referred to as “repetition suppression” (Desimone, 1996; Wiggs and Martin, 1998). However, because these previous studies of WM maintenance did not directly control rehearsal it is not known if these cortical regions demonstrated decreasing activity over the delay period because participants slowed or stopped rehearsing before the delay period was over, or whether activity decreases might be genuinely attributed to a neural phenomenon such as repetition suppression. These alternatives can be better distinguished by explicitly controlling rehearsal rate and examining activity changes over the delay period.

A third question that we will examine is how activity in regions supporting subvocal rehearsal is modulated by rehearsal rate. While several fMRI studies investigating speech found a linear relationship between rehearsal rate and cortical activity (Riecker et al., 2005, 2006; Shergill et al., 2002; Wildgruber et al., 2001), it is unclear if this same pattern of activation holds for WM rehearsal as these speech studies did not contain a memory component and simply had subjects repeatedly rehearse single syllables like “ta.” The attentional demands associated with a WM task may affect the neural systems involved in subvocal rehearsal. For example, top-down attention may lead to synaptic potentiation, a form of synaptic plasticity that may result in less activity as the rate of activation is increased. If there is synaptic efficiency at higher rehearsal rates then this would result in a nonlinear relationship between cortical activity and rehearsal rate with proportionately less cortical activity required.

In order to investigate how neural activity during the maintenance of task-relevant information changes with memory load, time, and rehearsal rate, we employed a novel WM paradigm that explicitly and directly controlled subvocal rehearsal rate as well as memory load over 45-s delay periods. We then addressed the above questions by investigating: 1) which cortical regions are involved in computations related to memory load, rehearsal rate, or both and if these cortical areas can be dissociated on the basis of these factors (behaviorally, the relationship of memory load and rehearsal rate will be tested in a related behavioral task), 2) how neural activity changes through time while keeping rehearsal rate constant, and 3) how neural activity changes with different subvocal rehearsal rates, especially in the critical rehearsal regions PM and area Spt.

Methods

Subjects

Twenty-eight subjects gave informed written consent according to procedures approved by the University of California and participated in the study. All were right-handed, native English speakers, had normal or corrected-to-normal vision, and normal hearing. All subjects were healthy with no neurological or psychiatric disease. One subject was eliminated due to falling asleep in the scanner and three subjects were eliminated for failing to follow the instructions properly (subvocally rehearsing when not explicitly prompted by the task). Thus, a total of 24 subjects (13 females; age: 18–32, mean: 21.3) were included in the final analyses.

Experimental stimuli

Letters were chosen pseudorandomly from a pool of 19 consonants (b, c, d, f, g, h, j, k, l, m, n, p, q, r, s, t, v, x, z) with the only constraint being that a letter could not be repeated within the same trial. Vowels (a, e, i, o, u) and the letter “y” were excluded to minimize chunking of letter sequences into words; and the letter “w” was excluded because it has three syllables. Letters were spoken by a female voice that was generated with text-to-speech software (Nuance Speechify, Burlington, MA).

Behavioral task performed prior to fMRI scanning

Before being informed of any of the details of the fMRI experiment, subjects performed a verbal WM task to determine the effect of memory load on rehearsal rate. Subjects were presented with 2, 4, 6, or 8 letters at a rate of one letter per second. Each letter was presented simultaneously in the visual and auditory modalities. Following the presentation of the final letter in the sequence there was a 1-s pause before a 500 ms beep sounded informing subjects to begin overtly rehearsing the letter sequence over a 15-s delay period. Subjects were instructed to rehearse the letters one letter at a time, in the original order, at a normal speaking voice at whatever rate was comfortable for them. After the delay period subjects were prompted with a recall probe (green triangle that appeared in the center if screen) and given 4 s to recall in order as many of the letters as possible. Overt rehearsal and recall responses were recorded by a digital recorder and then manually transcribed and scored.

Each subject was given a total of five blocks of trials with 2-min breaks between blocks. The first block was a practice block that was not scored and the remaining four blocks were test blocks with the first trial of each block also counted as practice. Each block contained eight scored trials, two at each memory load, which were pseudorandomly ordered for each subject. Therefore, each subject had a total of eight trials at each memory load.