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From storage to manipulation: How the neural correlates of verbal working memory reflect varying demands on inner speech

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ABSTRACT

The ability to store and manipulate online information may be enhanced by an inner speech mechanism that draws upon motor brain regions. Neural correlates of this mechanism were examined using event-related functional magnetic resonance imaging (fMRI). Sixteen participants completed two conditions of a verbal working memory task. In both conditions, participants viewed one or two target letters. In the "storage" condition, these targets were held in mind across a delay. Then a probe letter was presented, and participants indicated by button press whether the probe matched the targets. In the "manipulation" condition, participants identified new targets by thinking two alphabetical letters forward of each original target (e.g., f → h). Participants subsequently indicated whether the probe matched the newly derived targets. Brain activity during the storage and manipulation conditions was examined specifically during the delay phase in order to directly compare manipulation versus storage processes. Activations that were common to both conditions, yet disproportionately greater with manipulation, were observed in the left inferior frontal cortex, premotor cortex, and anterior insula, bilaterally in the parietal lobes and superior cerebellum, and in the right inferior cerebellum. This network shares substrates with overt speech and may represent an inner speech pathway that increases activity with greater working memory demands. Additionally, an inverse correlation was observed between manipulation-related brain activity (on correct trials) and test accuracy in the left premotor cortex, anterior insula, and bilateral superior cerebellum. This inverse relationship may represent intensification of inner speech as one struggles to maintain performance levels.

1. Introduction

An influential model of working memory includes a sub-component known as the phonological loop, (Baddeley, 1992). The phonological loop is comprised of 1–2 s of passive storage of phonological content (i.e., sounds, words, and phrases), which is followed by a secondary active rehearsal process that retains this information beyond 1–2 s. The passive and active phases of the phonological loop enable everyday tasks, such as following navigational commands while driving or adhering to a written recipe while cooking. The phonological loop may have evolved from speech systems as a way to enhance language acquisition (Aboitiz, Garcia, Bosman, & Brunetti, 2006; Baddeley, Gathercole, & Papagno, 1998). For example, a simple mechanism for the rehearsal of phonological utterances could have developed into a more complex system to incorporate several items at once, leading to an ability to create specific and meaningful sound combinations. According to Baddeley et al. (1998), the modern day function of the phonological loop is to create a reliable representation of a novel speech event (e.g., a new word). This concept has direct implications for language skills because the ability to hold unfamiliar phonemes in mind is a critical aspect of learning and expanding one's vocabulary. The ability to immediately recall non-words, for example, has been correlated to vocabulary skills in young children (Gathercole & Baddeley, 1989). This same ability was found to be specifically impaired in language disordered children, even after perceptual processing and articulation rates were considered (Gathercole & Baddeley, 1990). Thus, from an evolutionary and developmental perspective, the phonological loop may be intrinsically involved in the acquisition and refinement of language skills.

The act of vocalization – even merely mouthing or whispering – while learning verbal content (e.g., letters) improves the immediate recall of that information, relative to silent reading without any mouth movements (Murray, 1965). Moreover, producing speech responses that conflict with the acoustic nature of the verbal content (e.g., repeating "the, the, the" while reading) impairs immediate recall performance, relative to reading the verbal content aloud (Levy, 1971; Murray, 1967). It seems, therefore, that engaging speech mechanisms can enhance verbal learning, as long as the motor

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and auditory patterns are consistent with the phonological form of the content. Internalization of this vocalization process (inner speech) may provide similar benefits. For example, one study found that the covert repetition of pseudowords subsequently improved the pronunciation accuracy for pseudowords that had been presented multiple times relative to those that had been presented only once (Rauschecker, Pringle, & Watkins, 2008). The authors speculated that subjects had learned to articulate pseudowords using inner speech mechanisms in conjunction with the phonological loop. A separate experiment showed that studying a picture of an object speeded subsequent word reading if the object-word pair began with the same phoneme (Roelofs, Ozdemir, & Levelt, 2007). Thus, inner speech may interact with working memory in order to enhance the encoding of new material.

The term inner speech has been defined variably in the literature (for an informal, yet lengthy review, see Conrad, 1971). One common feature is that inner speech is inaudible. In this report, inner speech is broadly defined as internalized, inaudible verbal thought that may or may not reach conscious awareness and may or may not be accompanied by subliminal vocal activity. To a certain extent, our views concur with those of Vygotsky (1986) who posited that inner speech would not resemble spoken language as we know it, but would be compressed. Thus, inner speech may represent a variant of external speech, but is not necessarily a direct emulation of it (i.e., speech without sound). Conceivably, though, inner speech engages a verbal code, drawing upon motor planning and preparatory brain regions that precede overt speech (Ackermann, Mathiak, & Riecker, 2007). An internal code for motor sequences related to the vocalization (even if not executed) may serve as a memory trace that enhances verbal working memory (Marvel & Desmond, 2010b; Ravizza, Delgado, Chein, Becker, & Fiez, 2004). A motor memory trace would provide redundancy with visual and auditory traces also involved in the encoding process of verbal content. Presumably, without this redundancy, working memory would still be possible, but more effortful. The first step in creating a motor trace would begin during encoding with the creation of an articulatory trajectory for the phonological information that is then entered into a phonological loop (Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997). From there, information can be rehearsed, refreshed, and held in mind. Based on this model, the creation of an articulatory trajectory would be directly involved in verbal encoding but would be less important for phonological rehearsal. Accordingly, dissociative neural systems for phonological encoding versus rehearsal have been demonstrated in several event-related fMRI studies (Chang, Crottaz-Herbette, & Menon, 2007; Chein & Fiez, 2001; Chen & Desmond, 2005a, 2005b; Marvel & Desmond, 2010a).

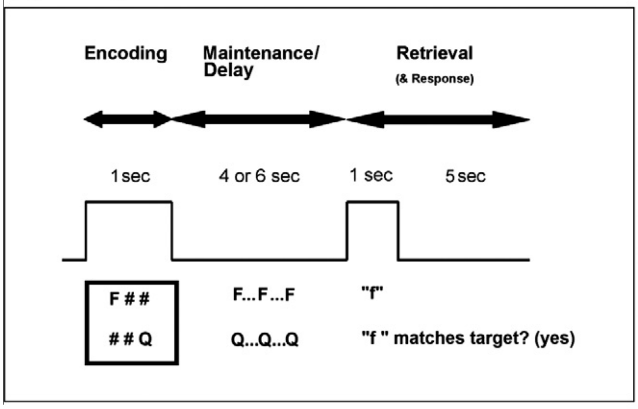
There is considerable overlap between the neurobiology of speech (overt and covert) and verbal working memory. Neuroimaging studies of overt speech implicate primary motor areas, such as the motor cortex (M1) and the medial anterior cerebellum (Lobule IV–V, rostral to the primary fissure) (Bohland & Guenther, 2006; Ghosh, Tourville, & Guenther, 2008; Turkeltaub, Eden, Jones, & Zeffiro, 2002). However, these studies have also identified secondary motor areas as part of the process. Such regions include the left inferior frontal cortex (IFC–Broca's area), ventral premotor cortex, supplementary motor area (SMA), pre-SMA, striatum, and lateral superior cerebellum (Lobule VI and Crus I, between the primary and horizontal fissures). These secondary motor areas have been shown to support motor functions (such as a button press) by activating prior to motor execution (Hulsmann, Erb, & Grodd, 2003), suggesting that their role is supportive but not directly responsible for overt motor execution. In studies of verbal working memory, activations in many of these secondary motor areas have also been observed when sensorimotor variables were controlled (Chang et al., 2007; Chein & Fiez, 2001; Chen & Desmond, 2005a, 2005b; Desmond et al., 1997; Durisko & Fiez, 2010; Marvel & Desmond, 2010a; Ravizza et al., 2004). Therefore, it appears that a secondary motor system may contribute to both overt speech and verbal working memory via motor planning and preparatory mechanisms, which would be consistent with the notion of an inner speech process that creates a motor trace of internally verbalized content to support working memory.

Verbal working memory is often tested in the laboratory using a delayed item recognition paradigm known as the Sternberg task (Sternberg, 1966). Although many variations have been used, the Sternberg task generally consists of a list of items, such as letters, that are briefly presented for study, or encoding (Fig. 1a) (encoding phase). This is followed by a delay period in which the items are rehearsed and maintained (maintenance phase). Finally, a probe is presented and a comparison is made between the probe and target items presented at the beginning of the trial (retrieval phase).

Coupling functional magnetic resonance imaging (fMRI) with the Sternberg task allows researchers to examine the neural correlates of the cognitive mechanisms associated with each phase of

Sternberg Verbal Working Memory Task

(a) Storage Condition



(b) Manipulation Condition

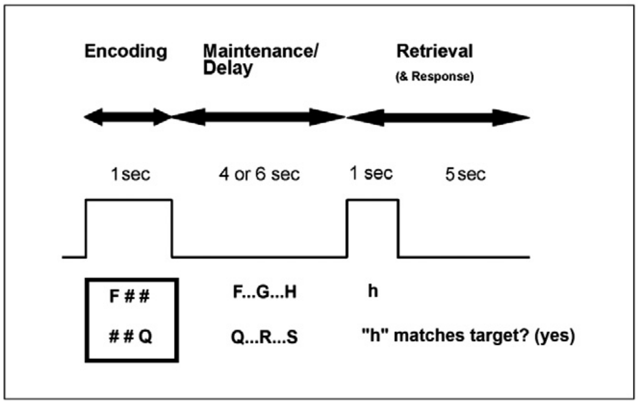


Fig. 1. A variation of the Sternberg working memory task was given under two conditions. (a) In the storage condition, subjects encoded 1 or 2 targets (encoding phase). Note that in the example, two targets are shown, but on half the trials, only one target was shown. Then, subjects silently rehearsed these targets across a delay (traditionally called the maintenance phase, but here we use the term "delay" phase). Finally, at the presentation of a letter probe, subjects indicated whether the probe matched either of the targets (retrieval phase). (b) In the manipulation condition, the encoding phase was identical to that in the storage condition. However, in the delay phase, instead of simply rehearsing the targets, subjects counted two alphabetical letters forward of each. Then they rehearsed these newly identified targets. In the retrieval phase, subjects indicated whether the probe matched either of the newly identified targets (rather than the original targets). In both figures, the box wave indicates when stimuli were visible on the screen.