



Neural mechanisms of information storage in visual short-term memory



John T. Serences*

Department of Psychology, Neurosciences Graduate Program, and the Kavli Institute for Mind and Brain, University of California, San Diego, United States

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ABSTRACT

The capacity to briefly memorize fleeting sensory information supports visual search and behavioral interactions with relevant stimuli in the environment. Traditionally, studies investigating the neural basis of visual short term memory (STM) have focused on the role of prefrontal cortex (PFC) in exerting executive control over what information is stored and how it is adaptively used to guide behavior. However, the neural substrates that support the actual storage of content-specific information in STM are more controversial, with some attributing this function to PFC and others to the specialized areas of early visual cortex that initially encode incoming sensory stimuli. In contrast to these traditional views, I will review evidence suggesting that content-specific information can be flexibly maintained in areas across the cortical hierarchy ranging from early visual cortex to PFC. While the factors that determine exactly where content-specific information is represented are not yet entirely clear, recognizing the importance of task-demands and better understanding the operation of non-spiking neural codes may help to constrain new theories about how memories are maintained at different resolutions, across different timescales, and in the presence of distracting information.

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1. Introduction

Perception and memory are limited by internal factors such as the finite processing capacity of neural systems, as well as by external factors such as the movement and occlusion of objects in the visual field. Covertly shifting attention and overtly shifting gaze can help to overcome some of these limits; however, occluded objects often remain inaccessible for short periods of time and are thus unavailable for attentive scrutiny, and exploratory eye-movements severely disrupt the continuity of inputs to the retina. As a result, short term memory – or the ability to maintain a coherent representation of sensory information that is no longer present in the visual field – is required to stitch together a useful perceptual representation that persists across discontinuities in the input stream (Goldman-Rakic, 1987; Irwin, 1991; James, 1890; Miller, Galanter, & Pribram, 1960; Rolf, 2015).

Experimental efforts to understand the cognitive and neural architecture of short term memory (STM) have long been guided by a high degree of cross-talk between experimental psychology and neuroscience (Baddeley, 1986; Baddeley & Hitch, 1974; Fuster & Alexander, 1971; see also: Atkinson & Shiffrin, 1968; Miller et al., 1960). In one of the most influential early models,

Baddeley and Hitch (1974) posited two memory buffers that independently store spatial and verbal information, coupled with a ‘central executive’ that is responsible for gating and manipulating information within these two content-specific buffers. The central-executive component of this model, or the source of control over STM, is thought to be supported largely via circuitry in the PFC. This account is consistent with well documented cognitive control deficits in patients with damage to the PFC (Badre & D’Esposito, 2009; Chao & Knight, 1998; Fuster, Bauer, & Jervey, 1985; Miller et al., 1960), as well as single-unit recording and functional neuroimaging evidence suggesting that areas of the PFC are involved in maintaining behavioral goals, task-switching, and adaptively manipulating information held in STM (D’Esposito, Postle, & Rypma, 2000; Miller & Cohen, 2001). Thus, even though some would include other non-PFC structures such as the basal ganglia as crucial nodes in an executive control network, few would dispute the key role played by PFC (e.g. McNab & Klingberg, 2008; Miller, 2013).

However, understanding the neural substrates that support the maintenance of content-specific information in STM has proven to be more controversial. Early evidence suggested a key role for maintenance in PFC, based on observations of sustained and stimulus-specific spiking activity during memory delays and on evidence from positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies showing that different sub-regions of the PFC can support different types of remembered

* Address: University of California, San Diego, Department of Psychology, 9500 Gilman Drive, La Jolla, CA 92093-0109, United States.

E-mail address: jserences@ucsd.edu

information (Courtney, Petit, Haxby, & Ungerleider, 1998; Funahashi, Bruce, & Goldman-Rakic, 1989; Funahashi, Bruce, & Goldman-Rakic, 1993; Goldman-Rakic, 1995; Mendoza-Halliday, Torres, & Martinez-Trujillo, 2014; Qi et al., 2010; Schumacher et al., 1996; Smith & Jonides, 1999; Smith et al., 1995; Wang, 2001).

However, evidence from other studies using a variety of techniques suggest instead that the storage of information in STM is primarily mediated by more specialized sub-regions of cortex that represent low-level visual features or the identity of whole objects (Awh & Jonides, 2001; Chelazzi, Miller, Duncan, & Desimone, 1993; Curtis & D'Esposito, 2003; D'Esposito, 2007; D'Esposito and Postle, 2015; Harrison & Tong, 2009; Lara & Wallis, 2015; Magnussen, 2000; Miller, Li, & Desimone, 1993; Pasternak & Greenlee, 2005; Serences, Ester, Vogel, & Awh, 2009; Sreenivasan, Curtis, & D'Esposito, 2014). This view is known as the *sensory-recruitment hypothesis*, and is based on the observation that neurons in early visual cortex are ideal candidates for storage because they exhibit highly selective tuning for different stimulus features such as orientation, spatial frequency and object identity. In effect, neural responses in visual cortex act as a bank of filters that are specialized to extract precise information about low-level properties of images. Thus, the tuning of neurons in early visual areas might be ideally suited to support both perception as well as mnemonic representations of these same features. This model has two intuitively appealing components. First, recruiting specialized regions of visual cortex to support STM might be a highly efficient way to avoid recoding remembered information using other distal anatomical structures or different types of neural codes (e.g. Stokes et al., 2013, see section below on *dynamic and activity (spike) silent codes*). Second, the high degree of feature-selectivity found in many areas of early visual cortex is not typically observed in PFC, and a high degree of selectivity may be critical when trying to remember very subtle distinctions between items stored in STM. On the other hand, others have argued that storing information within early visual cortex would leave memory representations susceptible to overwriting as new sensory stimuli are processed, and that circuits in these regions are not intrinsically wired to instantiate the type of recurrent activity that is often thought to support STM (Bettencourt & Xu, 2016; Riley & Constantinidis, 2015; Stokes, 2015; Wang, 2001). Thus, two general camps have emerged: those who believe that the PFC mediates both control and storage, and those who believe that the PFC largely regulates executive function and that content-specific information is stored primarily in highly-selective regions of early visual cortex.

Here, I will review evidence about the respective roles of PFC and visual cortex in supporting executive control and the storage of content-specific information. For the purpose of focusing on the control/storage distinction, I will not review other important and related topics about the total storage capacity of STM or about the discrete or continuous nature of information in STM (see reviews by Luck & Vogel, 2013; Ma, Husain, & Bays, 2014; van den Berg, Awh, & Ma, 2014; Xu & Chun, 2009 that cover these topics in great detail). Instead, I will focus on the idea that the storage of information in STM can vary along a continuum that depends on task demands, and that considering other types of neural codes beyond the classically described sustained spiking in PFC may reveal previously overlooked mechanisms for adaptively storing remembered information.

2. Sustained activity and executive control functions in the PFC

Given its intuitive appeal, sustained neural activity during memory delay periods has been traditionally viewed as the most widely accepted signature of information storage in STM. For

example, in a delayed-match-to-sample (DMTS) task, a to-be-remembered stimulus (*sample stimulus*) is encoded, and during the retention interval, the sub-set of neurons involved in maintaining a representation of the sample spike in a continuous and highly stereotyped manner until the memory probe (*test stimulus*) is presented for comparison. In one early paper, Fuster and colleagues used a DMTS task in which a monkey had to covertly encode the spatial position of an occluded object (Fuster & Alexander, 1971). The majority of PFC neurons that were identified – as well as neurons in the dorsomedial nucleus of the thalamus that provides input to the PFC – exhibited elevated and sustained spiking activity across memory delay periods that lasted up to 30 s. However, these sustained delay-period responses were not selective for the spatial position that the animal was remembering, which led the authors to conclude that sustained spiking in PFC was related to the maintenance of general task rules or behavioral goals as opposed to a spatial memory engram per se.

However, following these initial observations of non-selective sustained responses in PFC, other groups developed variants of the DMTS task in which an animal had to encode a peripheral spatial location that was the target of a saccadic eye movement after a brief 1–6 s delay period. In contrast to the non-selective responses reported by Fuster, many neurons around the principal sulcus, a sub-region of PFC, exhibited a spatially-selective response that carried information about the remembered location (Funahashi et al., 1989). However, the role of these neurons in supporting spatial STM as opposed to motor planning is not entirely clear, as the remembered position was yoked to the endpoint of the planned saccade. Thus, even in the domain of relatively simple tasks, early unit recording data did not fully distinguish between content-specific memory signals and more general executive control functions related to task-set and motor planning.

Complementing the single-unit data, early work using fMRI in human subjects also showed sustained activation profiles in PFC during memory delays. However, many of the same issues arose regarding whether these sustained activations reflect mnemonic storage or executive functions such as motor planning. In one early study, Courtney and coworkers used fMRI and a DMTS task in which subjects had to remember either the identity or the location of a series of faces (Fig. 1; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Courtney, Ungerleider, Keil, & Haxby, 1997). Persistent activity across the memory delay period was observed in different sub-regions of PFC depending on what type of information the subjects were remembering, suggesting a ventral/dorsal split between the storage of object and spatial information, respectively (Courtney, Petit, Haxby et al., 1998; Courtney, Petit, Maisog et al., 1998; Courtney et al., 1997; Petit, Courtney, Ungerleider, & Haxby, 1998). In contrast, other investigators argued that the site of delay-period activation in the PFC was more influenced by factors such as covertly planning eye-movements to spatial locations during STM. In support of this view, Curtis and colleagues designed two versions of a DMTS task: in one version subjects were able to plan a saccadic response during the delay period, and in another version subjects were not able to pre-plan the motor response and just had to remember the sensory attributes of the sample stimulus. Many regions of PFC (and parietal cortex) tracked the motor intention of subjects during the memory delay, particularly the dorsal areas that were previously tied to spatial STM (Curtis & D'Esposito, 2003; Curtis, Rao, & D'Esposito, 2004). Thus, the authors proposed that the dorsal/ventral functional division of PFC was not as tightly associated with representing remembered spatial positions and objects, but instead was likely influenced by other factors including planning spatially covert motor plans (Curtis & D'Esposito, 2003, 2004; Curtis, Rao, & D'Esposito, 2004; Postle, Berger, Taich, & D'Esposito, 2000; Postle & D'Esposito, 1999).

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