

SPECIAL ISSUE

SEEKING THE NEURAL SUBSTRATES OF VISUAL WORKING MEMORY STORAGE

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ABSTRACT

It is widely assumed that the prefrontal cortex (PFC) is a critical site of working memory storage in monkeys and humans. Recent reviews of the human lesion literature and recent neuroimaging results, however, challenge this view. To test these alternatives, we used event-related fMRI to trace the retention of working memory representation of target faces across three delay periods that were interposed between the presentation of each of four stimuli. Across subjects, only posterior fusiform gyrus demonstrated reliable retention of target-specific activity across all delay periods. Our results suggest that no part of frontal cortex, including PFC, stores mnemonic representation of faces reliably across distracted delay periods. Rather, working memory storage of faces is mediated by a domain-specific network in posterior cortex.

Key words: working memory, prefrontal cortex, fusiform gyrus, short-term memory, fMRI

THE MULTIPLE MEANINGS OF “WORKING MEMORY”

The concept of working memory in primate cognition is broadly construed as the capacity to retain information no longer present in the environment, to manipulate and/or transform this information, and to use it to guide behavior. Within different traditions of the behavioral sciences, however, the term “working memory” can have different specific meanings. In neuroscience, the modern study of working memory was arguably launched by Jacobsen (1935; 1936), who described a deficit on a test of delayed response following large bilateral frontal lobe lesions. The profound and enduring influence of Jacobsen’s work is manifested in at least three ways. One has been the adoption of the delayed-response task and its variants – e.g., delayed alternation, delayed recognition, reversal learning – as the gold standard procedure for neuroscientific investigations of working memory. The basic procedure consists of first presenting a target stimulus, then imposing a delay during which the subject does not receive sensory information about the target, then prompting a response through which the subject reveals whether or not critical information about the target stimulus was retained across the delay period. “In a properly controlled experiment,” wrote Jacobsen (1936), information about the

target stimulus “must be supplied by the subject either through some sustained activity during the period of delay or by recall from past experience ...” (p. 12). A second influence of Jacobsen’s work has been the assumption that this task requires, and thus serves as an index of, what he, in the parlance of the day, termed “immediate memory” (Jacobsen, 1936). (In neuroscience, the use of this term to refer to the temporary retention of information was superseded by the 1960s with the term “short-term memory,” and in the 1990s by the term “working memory.”¹) A third influence of Jacobsen’s work is the idea that the frontal lobes, particularly the prefrontal cortex (PFC), are critical to working memory function (e.g., Stuss and Knight, 2002; Warren and Akert, 1964). (It is the details of this third idea that will be explored in this paper.) A quantum leap in the neuroscientific investigation of working memory occurred in the early 1970s when neurophysiologists recording from individual PFC neurons observed sustained activity throughout the delay period (Fuster and Alexander, 1971) that resembled the neural correlate of “immediate memory” that had been predicted by Jacobsen (1936) (as well as by Hebb (1949)).

Independent of these developments in neuroscience, Baddeley and Hitch, in 1974, proposed a multiple-component model of “working memory” that has been vastly influential within cognitive psychology (Baddeley and Hitch, 1974). This model comprised, in simplified outline, two independent buffers for the storage of verbal and of visuospatial information and a Central Executive to control attention and the management of information in the buffers (Baddeley, 1986). Human working memory is widely viewed as a fundamental cognitive capacity that contributes critically to such high level cognitive functions as learning, reasoning, and language comprehension (Baddeley, 1992; Jonides, 1995). Since the introduction of this multiple-component model of human working memory, many cognitive psychologists have proposed alternative models that employ a wide variety of mechanisms to produce working memory behavior (e.g., Miyake and Shah, 1999). Beginning in the 1980s, Goldman-Rakic has suggested that the sustained delay-period activity studied by neuroscientists and the multiple-component system proposed by Baddeley and colleagues were cross-species manifestations of the same fundamental mental phenomenon (Goldman-Rakic, 1987, 1990)². This assumption has been widely accepted up through the present day, although precise specification of the most useful points of comparison awaits further maturation in both fields. The advent of neuroimaging in the 1990s gave cognitive neuroscientists the opportunity to investigate the neural bases of working memory functions. Some of these neuroimaging studies have

¹ In the neuroscientific tradition, the term “working memory” was introduced in the early 1960s by Pribram (Miller et al., 1960; Pribram et al., 1964), who drew an analogy between the inferred mechanism that was disrupted by PFC lesions and the “working memory” built into contemporary computer simulations of human problem solving (Feigenbaum and Simon, 1961; Newell et al., 1958). However, this term didn’t enter the common lexicon of the neuroscience of primate cognition (see footnote #2) until the 1980s (e.g., Goldman-Rakic, 1987; Petrides, 1989; Petrides and Milner, 1982).

² “Working memory” is used in yet a different way in a third field within the behavioral sciences – rodent learning and memory – but this falls outside the scope of this brief review. For a helpful comparison of this third use of the term vs. its use in cognitive psychology, (see Becker and Morris, 1999).

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