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Cortical memory mechanisms and language origins

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Abstract

We have previously proposed that cortical auditory-vocal networks of the monkey brain can be partly homologized with language networks that participate in the phonological loop. In this paper, we suggest that other linguistic phenomena like semantic and syntactic processing also rely on the activation of transient memory networks, which can be compared to active memory networks in the primate. Consequently, short-term cortical memory ensembles that participate in language processing can be phylogenetically tracked to more simple networks present in the primate brain, which became increasingly complex in hominid evolution. This perspective is discussed in the context of two current interpretations of language origins, the "mirror-system hypothesis" and generativist grammar.

Keywords: Broca's area; Mirror neurons; Syntax; Wernicke's area; Working memory

1. Introduction

In the last decade, there has been a growing interest in short-term memory phenomena that maintain the neuronal activation related to perceptual or long-term mnemonic items, in order to execute a near-future response (Fuster, 1995a; Fuster & Alexander, 1971; Levy & Goldman-Rakic, 2000). In humans, this kind of memory has been termed working memory (Baddeley, 1992; Baddeley & Hitch, 1974), and has been proposed to participate in several cognitive mechanisms, including language acquisition and processing (Baddeley, 1992, 2000, 2003; Baddeley, Papagno, & Vallar, 1988; Caplan, Alpert, & Waters, 1998; Caplan, Alpert, Waters, & Olivieri, 2000; Fiebach, Schelewsky, & Friederici, 2002; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Gathercole & Baddeley, 1990; Gibson, 1998; Just & Carpenter, 1992; King & Kutas, 1995; Müller & Basho, 2004). Furthermore, cognitive and neurobiological evidence suggests that the distinct aspects of language processing, including phonological, lexical, semantic, and syntactic domains, all rely importantly on short-term memory mechanisms (Bookheimer, 2002; Caplan & Waters, 1999; Hickock & Poeppel, 2000; Lieberman, 2002).

Working memory has been classically subdivided into a general, all-purpose executive system that manipulates the mnemonic items, and "slave" systems involved in sensorimotor rehearsal. The latter have been further subdivided into a visuospatial sketchpad, which maintains online visuospatial information, and a phonological loop, that allows internal rehearsal of phonological utterances (Baddeley & Hitch, 1974). Specifically, in humans, the phonological loop has been anatomically identified (see below) and shown to be important for language learning. For example, patients with phonological working memory deficits show impairments in long-term phonological learning, and a link has been observed between performance in the phonological loop and vocabulary level in children (Baddeley et al., 1988; Gathercole & Baddeley, 1990). Furthermore, specific language impairment, a developmental condition characterized by deficits in language learning, appears to have as a central characteristic a phonological working memory dysfunction (Webster & Shevell, 2004). According to Baddeley (2000), this evidence suggests that the loop might have evolved to enhance language acquisition.

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However, cortical short-term memory mechanisms are more diverse and involve other modalities or sensorimotor domains than the phonological loop and the visuospatial sketchpad (Fuster, 1995a). Furthermore, certain higher-level cognitive phenomena such as attention also imply short-term memory mechanisms that do not exactly fit the concept of "slave" sensorimotor systems (de Fockert, Rees, Frith, & Lavie, 2001). Although the concept of a central executive that distributes resources in different processing domains might adequately grasp some of these phenomena, the anatomical localization of this system in the dorsolateral prefrontal cortex has been questioned by some authors (Goldman-Rakic, 1996, 2000). Partly for this reason, we consider that the more general, neurophysiological concept of active memory (Fuster, 1995a; Fuster & Alexander, 1971) may be more appropriate in this context. This term implies "a broad network of associative memory" which is maintained "as a perceptual memory fragment in order to execute a motor act in the near future" (Fuster, 1995b, p. 64). In other words, active memory is a property of neuronal ensembles that consists of the capacity to maintain an activated state during the execution of a cognitive task, thus holding information online for a brief time interval (Fuster, 1995a, 1995b). Nevertheless, more than being specific memory circuits, the above networks are elements that link sensory and motor domains in the context of near-future behavior. Furthermore, the fact that active memory ensembles are associative as Fuster proposes implies that they are changeable, plastic, and that these overlap and interact with other active networks during the preparation and execution of complex behaviors, thus generating larger ensembles manipulating more than one memory item (for a more formal analysis, see Glassman, 2003). The mechanisms by which these networks maintain their activated state are not yet clear, but an intriguing possibility is that they do so through the establishment of reciprocally connected ensembles which oscillate synchronously (Engel, Fries, & Singer, 2001; Singer, 1999; Durstewitz, Seamans, & Sejnowski, 2000; Yuste, MacLean, Smith, & Lansner, 2005). There is accumulating evidence indicating that neural synchrony with a precision in the millisecond range participates in several cognitive phenomena including working memory, in a manner consistent with Hebb's postulate of maintained reciprocal activation. These studies show that short-term storage mechanisms involve an increase in neural synchrony between prefrontal cortex and posterior cortex, together with enhancing the activation of long-term memory representations (Engel & Singer, 2001; Fingelkurts et al., 2003; Palva, Palva, & Kaila, 2005; Ruchkin, Grafman, Cameron, & Berndt, 2003; Tallon-Baudry, Bertrand, & Fischer, 2001; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004).

In this article, we propose (1) that the neural circuits that participate in the phonological loop can be anatomically described in incipient form in the non-human primate brain, and that therefore these are homologous to the human circuits (Aboitiz, 1995; Aboitiz & García, 1997); and (2) that in part, language has evolved by virtue of an expanding short-term memory capacity, which has allowed the processing and manipulation of increasingly complex sequences of sounds, conveying elaborate meanings and eventually participating in syntactic processes. Thus, the language-specific areas of the human brain may have initially evolved as a circuit for phonological rehearsal involved in learning relatively long phonological utterances, which became conventionalized and acquired simple meanings by associative interactions with other sensorimotor domains. As the memory systems involved in this process expanded, it became possible to activate more complex memories representing several items that could be combinatorially manipulated (Glassman, 2003). This allowed utterances and their meanings to become also increasingly complex and specific. Eventually, primitive syntactic rules appeared within the context of a highly intricate short-term memory network that allowed to maintain previously perceived lexical items on line while others were still being processed. Although intuitively appealing, this proposal faces other recent hypotheses. One of them is the "mirror-system" hypothesis, which emphasizes the role of hand-grasping mirror neurons in language origins (Arbib & Bota, 2003; Rizzolatti & Arbib, 1998). Shortly, the hypothesis suggests that the manual mirror-neuron system provided the necessary plasticity for symbolic communication to arise in a gestural domain, which was eventually overcome by vocal communication. Although we feel that the concept of mirror neurons is in general complementary to our views, there are some points of disagreement which we will discuss. Another proposal relates to Chomsky's generativist approach which claims that syntax, and specifically the operation termed syntactic recursion (i.e., the ability to recursively embed sentences within larger sentences; see below), is the only faculty that is exclusive of human language and unlikely to result from evolution by natural selection (see Hauser, Chomsky, & Fitch, 2002). We claim that linguistic recursion demands significant working memory resources, and that at least partly, neural networks that participate in recursion were gradually elaborated from simpler networks involved in active memory in the primate brain.

In the rest of the article, we will discuss evidence in favor of our hypothesis. We will briefly update evidence on the location and connectivity of the human language areas and of the phonological loop, and their presumed homologues in the monkey. Then, we will face this evidence with the mirror-system hypothesis. Finally, we will analyze the role of short-term memory in syntactical processing, especially in the case of recursive structures, and will propose a neurobiological substrate for it and its evolution.

2. Neuroanatomy of phonological working memory and homologies between monkey and human

More than a century of analyses of focalized brain lesions in humans has evidenced that cortical language