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High frequency gamma activity in the left hippocampus predicts visual object naming performance

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ABSTRACT

Access to an object's name requires the retrieval of an arbitrary association between it's identity and a word-label. The hippocampus is essential in retrieving arbitrary associations, and thus could be involved in retrieving the link between an object and its name. To test this hypothesis we recorded the iEEG signal from epileptic patients, directly implanted in the hippocampus, while they performed a picture naming task. High-frequency broadband gamma (50–150 Hz) responses were computed as an index of population-level spiking activity. Our results show, for the first time, single-trial hippocampal dynamics between visual confrontation and naming. Remarkably, the latency of the hippocampal response predicts naming latency, while inefficient hippocampal activation is associated with "tip-of-the-tongue" states (a failure to retrieve the name of a recognized object) suggesting that the hippocampus is an active component of the naming network and that its dynamics are closely related to efficient word production.

1. Introduction

A core aspect of our ability to speak lies in the process of word retrieval, during which our brain establishes a link between an idea or a concept ("a particular fragrant flower from a prickly bush") and the corresponding linguistic form ("rose"). Usually, there is no natural motivation why a particular word form has been attached to a particular concept, and hence this link has been described as arbitrary (de Saussure, 1916; see also Shakespeare, 1599; some limits to the arbitrariness of the sign are discussed by Marchand, 2010). For a speaker that knows a given word, the arbitrary link is presumably stored in memory and retrieved when the word is to be produced (for example, during visual object naming: Glaser, 1992).

In models of memory and language production, the retrieval of arbitrary links is construed rather differently. In memory models, some have proposed that formation and retrieval of arbitrary associations, also known as relational memory, is a critical function of the hippocampus (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, 2004; Konkel & Cohen, 2009; Mayes, Montaldi, & Migo, 2007; Moses & Ryan, 2006), and one of the basic mechanisms that could account for its involvement in a variety of mnesic processes (Ludowig et al., 2008; Manning, Sperling, Sharan, Rosenberg, & Kahana, 2012; Rutishauser, Schuman, & Mamelak, 2008; Sederberg et al., 2007; Zeineh, Engel, Thompson, & Bookheimer, 2003). For instance, hippocampal activity subserves the successful association between an item and its paired-associate or between an item and its context (Brasted, Bussey, Murray, & Wise, 2003; Henke, Weber, Kneifel, Wieser, & Buck, 1999; Petrides, 1985; Preston, Shrager, Dudkovic, & Gabrieli, 2004; Ranganath, Cohen, Dam, & D'Esposito, 2004; Wirth et al., 2003). In models of word production, the arbitrary link between meanings and word forms is captured by the distinction between the semantic and the lexical levels of representation (Caramazza, 1997; Dell, Schwartz, Martin, Saffran, & Gagnon, 1997; Levelt, Roelofs, & Meyer, 1999). In the neurocognitive versions of these models, such levels of processing have been tied to a distributed large scale 'language network' comprising frontal and temporal cortices. In particular, semantic processes engage the temporal pole, the medial temporal gyrus, the angular gyrus, and the superior and

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inferior frontal gyri, while word retrieval primarily engages the inferior frontal gyrus, middle temporal gyrus, and posterior/lateral and ventral inferior temporal gyrus (e.g. DeLeon et al., 2007; Vidal et al., 2012, for reviews see: Binder, Desai, Graves, & Conant, 2009; Indefrey, 2011; Price, 2012). In contrast to memory models, the description of word retrieval processes do not usually consider the hippocampal formation as an important node of the network, at least not beyond semantics. For instance, the speech production section of the most recent neuroimaging meta-analysis states: "When word retrieval became more semantically demanding (...) activation (...) was also reported in (...) the left hippocampus. However, these anatomically distributed brain areas are likely to reflect silent conceptual processing (see Speech comprehension section) rather than word retrieval per se" (Price, 2012, p. 829). Indeed, only a handful of neuroimaging studies have reported significant hippocampal activity during language production tasks (Bonelli et al., 2011; Hocking, McMahon, & Zubicaray, 2008; Pihlajamaki et al., 2000; Whitney et al., 2009).

The absence of the hippocampus in the language production models described above might stem from two sources. On one hand, imaging studies, which are able to accurately measure spatial patterns of activation, lack the temporal resolution to describe its fast dynamics. This means that a possible link between temporal aspects of the hippocampal activity (e.g. latency) and behavior (e.g. successful object naming), would be missed by conventional imaging techniques. On the other hand, the clinical evidence regarding a potential link between hippocampal damage and word finding difficulties is somewhat mixed. First, patient HM, whose prototypical medial temporal lobe (MTL) resection comprised both hippocampi, had massive memory problems and a normal score in most language comprehension and production tests (note however that slight naming difficulties were also reported; Corkin, 1984).[1] Second, more recent neuropsychological studies suggest that naming capabilities can be compromised in hippocampal sclerosis (Bonelli et al., 2011; Davies et al., 1998; Hamberger et al., 2007; Sawrie et al., 2000) and after anteromedial resective surgery, but not in all cases. The variable impact of MTL resection on naming performance has been linked to the presence of pre-surgical sclerosis (Hamberger, Seidel, Goodman, & McKhann, 2010; Seidenberg, Geary, & Hermann, 2005), to different degrees of plasticity from spared structures (Sabsevitz et al., 2003; Swanson, Sabsevitz, Hammeke, & Binder, 2007), and to differences in neuropsychological assessment (Trébuchon-Da Fonseca et al., 2009). Overall, the strongest predictor of naming decline after MTL resection appears to be the absence of structural hippocampal pathology before surgery; post-operative naming difficulties are likely if the resected hippocampus was structurally healthy before surgery (see Ives-Deliperi & Butler, 2012, for a review). Together, this evidence suggests a possible role for structurally healthy hippocampus in naming, but it does not specify at which level of word production it may participate (perceptual, semantic or lexical).

Here we report evidence that the left hippocampus is involved in overt visual object naming, a task that is highly relevant for both clinicians and researchers who want to test word production. We took as a working model the current consensual view in which word production can be divided in several sub-components (Caramazza, 1997; Dell et al., 1997; Levelt et al., 1999): conceptual processing, lexical retrieval, and response encoding processes (the latter variably ranging from phonological and phonetic encoding to articulatory programming and triggering). On the basis of memory models, where hippocampal function is to establish and retrieve arbitrary associations, (Diana et al., 2007; Eichenbaum, 2004; Konkel & Cohen, 2009; Mayes et al., 2007; Moses & Ryan, 2006), we expected that hippocampal activity should be involved in retrieving the link between semantic and lexico-phonological knowledge (i.e. between a concept and its name).

Picture naming, which we used as the main experimental protocol, is arguably the most commonly used task to elicit word production processes in healthy and neurological populations (cf. DeLeon et al., 2007; Glaser, 1992; Salmelin, Hari, & Lounasmaa, 1994). Here we analyzed behavioral measures of performance in conjunction with neurophysiological activity recorded directly from hippocampus. The behavioral measures of performance included naming latencies, which are indicative of the whole production process (Alario et al., 2004), as well as certain errors that are known to signal failures at specific stages of the naming process. In particular, we focused on those errors in which participants correctly identify the presented object, but fail to retrieve its name, a common situation known as 'tip-of-the-tongue' (TOT) state (Brown, 1991). This subjective state occurs frequently among healthy (Brown, 2012) and neurological populations (Trébuchon-Da Fonseca et al., 2009). It reflects a difficulty in accessing linguistic information (Brown, 2012 p. 169), whereby successful perceptual and semantic processing (recognizing an object) does not lead to successful lexico-phonological access (retrieving its name). This is a capital distinction in theories of word production at least since Badecker, Miozzo, and Zanuttini (1995).

Neurophysiological activity was obtained with intracranial EEG (iEEG) recordings, performed as pre-surgical investigation of drug-resistant partial epilepsy. These recordings lack the full spatial coverage of fMRI, but they benefit from high temporal and spatial resolution. Therefore, they allow measuring electrophysiological activity from a targeted neural structure in a time-scale meaningful for single word production. Moreover, high-frequency components of the iEEG signal (50–150 Hz) can be regarded as an index of multi-unit spiking activity (Le Van Quyen et al., 2010; Manning, Jacobs, Fried, & Kahana, 2009; Ray & Maunsell, 2011), providing a robust tool for functional mapping (Crone, Sinai, & Korzeniewska, 2006; Jerbi et al., 2009; Lachaux, Axmacher, Mormann, Halgren, & Crone, 2012), in real time (Hamamé et al., 2012), and with no risks of contamination from articulatory artifacts. Intracranial EEG research has already advanced our understanding of language-production networks by clarifying the functional role of specific brain areas depending on their temporal course of activity (Sahin, Pinker, Cash, Schomer, & Halgren, 2009; Edwards et al., 2010; Flinker et al., 2010; Wu et al., 2012; Perrone-Bertolotti et al., 2012; for review see: Llorens, Trébuchon-Da Fonseca, Lliégeois-Chauvel, & Alario, 2011). Nevertheless, none of the cited iEEG studies included patients with recording sites (depth-electrodes) directly implanted in the hippocampus.

2. Materials and methods

2.1. Participants

A total of 28 pharmaco-resistant epilepsy patients, implanted with multi-lead depth-electrodes and candidates for resective neurosurgical treatment (La Timone Hospital, Marseille, France), were asked to participate in the protocol. They had been

[1] Language function in patient HM is a long-lived debate. Neuropsychological testing showed mostly normal scores in both comprehension and production, with the notable exception of verbal fluency, an impairment attributed to extra-surgical factors (e.g. education level; Corkin, 1984). Interestingly, clinical examination and more demanding language production tests (DeRenzi & Ferrari, 1978) showed slight (yet significant) naming difficulties. Additionally, more detailed examination of H.M.'s language production revealed a higher frequency of different types of errors, particularly omission errors (Mackay, James, Hadley, & Fogler, 2011). Other aspects of language such as the retrieval and production of verbal material (Mackay, Burke, & Stewart, 1998) together with grammatical and figurative features of speech were also found to be impaired (Mackay, Stewart, & Burke, 1998; MacKay, James, & Hadley, 2007; MacKay, James, Taylor, & Marian, 2007). However, since H.M. resection comprised an important part of the medial and anterior temporal lobe (i.e. not only the hippocampus), the link that can be established between hippocampal function and language on the basis of this patient's performance remains unclear.