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Research report

Hippocampal declarative memory supports gesture production: Evidence from amnesia



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ABSTRACT

Spontaneous co-speech hand gestures provide a visuospatial representation of what is being communicated in spoken language. Although it is clear that gestures emerge from representations in memory for what is being communicated (De Ruiter, 1998; Wesp, Hesse, Keutmann, & Wheaton, 2001), the mechanism supporting the relationship between gesture and memory is unknown. Current theories of gesture production posit that action - supported by motor areas of the brain – is key in determining whether gestures are produced. We propose that when and how gestures are produced is determined in part by hippocampally-mediated declarative memory. We examined the speech and gesture of healthy older adults and of memory-impaired patients with hippocampal amnesia during four discourse tasks that required accessing episodes and information from the remote past. Consistent with previous reports of impoverished spoken language in patients with hippocampal amnesia, we predicted that these patients, who have difficulty generating multifaceted declarative memory representations, may in turn have impoverished gesture production. We found that patients gestured less overall relative to healthy comparison participants, and that this was particularly evident in tasks that may rely more heavily on declarative memory. Thus, gestures do not just emerge from the motor representation activated for speaking, but are also sensitive to the representation available in hippocampal declarative memory, suggesting a direct link between memory and gesture production.

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1. Introduction

When we talk, we gesture with our hands. Our hand gestures are both temporally and semantically related to the speech that they accompany (McNeill, 1992). Hand gestures facilitate

communication for the speaker and for the listener (e.g., Hostetter, 2011) and enhance memory and learning (Cook, Yip, & Goldin-Meadow, 2010; Feyereisen, 2006). But, where do gestures come from? Although it seems intuitive that gestures emerge from representations in memory (De Ruiter,

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1998; Wesp, Hesse, Keutmann, & Wheaton, 2001), the mechanism supporting functional links between gesture and memory is unknown. The current study is part of a broader line of work bringing together the empirical study of gesture and of multiple memory systems (Klooster, Cook, Uc, & Duff, 2015). Here, we test the hypothesis that gesture is supported by hippocampal declarative memory representations, providing a starting point for the investigation of the neural and cognitive mechanisms linking gesture and memory.

Gestures reflect our thoughts iconically (Hilliard & Cook, 2015a, 2015b). Mental representations in the mind are translated into gestures, with the hands conveying a global and imagistic form of the message being communicated (McNeill, 1992). For example, when asked to describe how to make a sandwich, the speaker is likely to bring to mind a rich, multifaceted representation including, but not limited to, the ingredients needed to make the sandwich, the actions required and the temporal sequence of these actions, general semantic information about sandwich making, and autobiographical memories of previous contexts and occasions for making specific sandwiches. Relevant information will then be expressed in speech and in gesture.

As an initial attempt at understanding the nature of memory representations supporting gesture we investigated the hippocampal declarative memory system. The hippocampus and other medial temporal lobe structures have long been linked to the formation and subsequent retrieval of enduring (long-term) memory (Eichenbaum & Cohen, 2001; Gabrieli, 1998; Squire, 1992). The hippocampus plays a central role in support of relational (or associative) memory binding (Davachi, 2006; Eichenbaum & Cohen, 2001; Ryan, Althoff, Whitlow, & Cohen, 2000) which permits long-term encoding of the co-occurrences of people, places, and things along with the spatial, temporal, and interactional relations among them (see Konkel & Cohen, 2009) that constitute events, as well as representations of relationships among events across time, providing the basis for the larger record of one's experience. Another hallmark of the hippocampal declarative (relational) memory system is its representational flexibility, which permits the reconstruction and recombination of information and allows such information to be used in novel situations and contexts (Eichenbaum & Cohen, 2001). Hippocampal relational representations have also been implicated in supporting flexible cognition more broadly with hippocampal declarative memory deficits negatively impacting aspects of language and communication, decision making, and social cognition (for review see Rubin, Watson, Duff, & Cohen, 2014). Taken together, the role of the hippocampus in relational binding and representational flexibility supports our ability to reconstruct and recreate richly detailed, multimodal, memories of our remote past, our ability to imagine events and scenarios of our distant futures, and to flexibly act in and on the world. If gesture emerges from rich, relational memories, then gestures may depend on hippocampal representations.

When asked to construct and narrate a memory from their real past or to imagine what might happen in the future, patients with bilateral hippocampal damage and severe declarative memory impairment produce significantly fewer episodic details (e.g., Hassabis, Kumaran, Vann, & Maguire, 2007;

Kurczek et al., 2015; Race, Keane, & Verfaellie, 2011). That is, the verbal descriptions of past and future events of patients with hippocampal amnesia are impoverished, containing fewer details about the people, places, and things, as well as the spatial and temporal aspects of their experiences. But what about the information that is conveyed in gesture? Do disruptions in hippocampal declarative memory representation extend to gesture? That is the question we address here.

Although prior work has not directly tested the relationship between hippocampal memory representations and gesture, there is evidence for a link between working memory and the production of gesture. Producing gesture during communication can reduce the burden on working memory (Cook, Yip, & Goldin-Meadow, 2012; Goldin-Meadow, Nusbaum, Kelly, & Wagner, 2001). Moreover, lower scores on working memory tasks in healthy individuals are predictive of higher gesture rates (Gillespie, James, Federmeier, & Watson, 2014). These findings, coupled with work suggesting that gesture may aid in retrieval of words during discourse (Krauss, Chen, & Gottesman, 2000) and on vocabulary tests (Nooijer, van Gog, Paas, & Zwaan, 2013), indicate that people gesture more when memory demands are higher. It is unclear, however, if such patterns would be observed in patients with hippocampal amnesia, who can perform normally on standardized tasks of working memory but who also can exhibit deficits on relational memory tasks over very short delays (i.e., on the time scale of traditional working memory tasks) (e.g., Hannula, Tranel, & Cohen, 2006).

The information in gesture is sometimes also expressed in the accompanying speech and is sometimes unique to gesture (Alibali, Kita, & Young, 2000; Cassell, McNeill, & McCullough, 1998; Goldin-Meadow, 1999). For example, when describing making a sandwich, a speaker might say, "And, then you put the mustard on the bread," and accompany this description with either a spreading motion or a squeezing motion, depending on the type of mustard that the speaker has in mind. In this case, gesture expresses unique information, although if the speaker had instead chosen to say "squeeze" or "spread" the information in speech and gesture would have been the same. Because gesture and speech sometimes convey the same information and sometimes convey different, but complementary, information, it is not clear that the impoverished episodic representations observed in verbal descriptions in patients with hippocampal amnesia will extend to their gestures. Gesture may emerge directly from aspects of declarative (episodic) memory representations, or may emerge from memory representations that are not hippocampally mediated. Studies of healthy participants cannot reliably implicate specific memory systems as both systems are intact and possibly engaged, even in implicit tasks or processing. An alternative approach to test ideas about the relationship between memory and gesture is to examine cospeech gesture in neurological patients who have specific types of memory impairment.

We examined gesture production in a group of patients with severe declarative memory impairment (and intact procedural memory) due to bilateral hippocampal damage. Patients and comparison participants completed four discourse tasks: how to go shopping in an American supermarket, how to make their favorite sandwich, their most frightening

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