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Memory mechanisms of hand gesture in communication and learning

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MEMORY MECHANISMS OF HAND GESTURE
IN COMMUNICATION AND LEARNING

by

Caitlin Hilliard

A thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Psychology
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The University of Iowa

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Thesis Supervisor: Professor Susan Wagner Cook

Graduate College
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CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

Caitlin Hilliard

has been approved by the Examining Committee for the thesis requirement for Doctor of Philosophy degree in Psychology at the August 2016 graduation.

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Dedicated to my mother, Lisa, who has inspired creativity, shouldered my insecurities, and motivated me to excel since the day I was born.

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ABSTRACT

Spontaneous co-speech hand gestures robustly affect learning and memory. Viewing or producing hand gestures during conversation facilitates the encoding, consolidation, and retention of the information in speech. Despite these effects, the cognitive and neural mechanisms supporting this relationship remains unknown. In Experiment 1, I explored the memory mechanisms supporting hand gesture by working with patients with damage to their hippocampus and thus their declarative memory system. Participants engaged in discourse tasks that disproportionately engaged the hippocampus. I found that patients gestured less overall than healthy comparisons across all tasks, suggesting that the hippocampus indeed plays a role in gesture production.

In order to test whether non-declarative memory supports gesture production as well, Experiment 2 directly manipulated features of memory representations (both visual and motor) to determine what would guide the form of gesture when participants later explained their experiences. On three visits, amnesic patients, healthy comparison and brain-damaged comparison groups completed a Tower of Hanoi task, involving moving disks between pegs following a set of rules. On each visit, participants completed the task with different visual and motor information. Comparisons' gestures tended to reflect both visual and motor experience, while patients' gestures tended to rely more heavily on their motor experiences. This suggests that gesture may be supported by non-declarative memory as well, particularly in the absence of a declarative memory for what is being discussed.

To directly test which properties of gesture facilitate learning, Experiment 3 examined how gesture affected the learning of novel labels for common, everyday objects. I again worked with patients with hippocampal amnesia, who are severely impaired in the learning of new

words, along with healthy and brain-damaged comparisons. Participants were exposed to novel word-object pairing that either was learned with a gesture or not. For the gestured-with trials, the gesture was either viewed and then produced by the participant or passively viewed, allowing me to determine if production of a gesture was necessary for learning. After adequately learning all the word-object pairings, there was a 30-minute delay followed by a free recall and object identification task. Both comparison groups showed good learning of the words regardless of whether they were learned with gesture. The amnesic patients performed poorly on the recall task. On the object identification task, they were significantly more likely to identify the label-object pairing if the pairing had been learned with gesture. This benefit was only seen for those learned by producing gesture. For the pairings learned without gesture and the pairings learned with only viewing gesture, the patients were at chance. These findings demonstrate that gesture can help rescue hippocampal amnesics' ability to bind labels with objects, and furthermore suggest that the self-production of gesture is critical for learning.

These findings are the first to demonstrate a link between gesture and memory systems. Experiments 1 and 2 demonstrate that gesture can reflect information from both declarative and non-declarative memory. Experiment 3 demonstrates that the link between gesture and non-declarative memory can be exploited to facilitate learning in patients with memory impairment. By understanding how memory and language interact we will be able to exploit this interaction to benefit memory and language more generally.

PUBLIC ABSTRACT

The spontaneous hand gestures that we produce when we talk affect the way we learn and remember. When we produce gestures ourselves or view the gestures of others, we better remember the content of their speech than if they did not gesture. Despite this, we know very little about how and why gesture facilitates memory. In the work described here, we test the relationship between gesture and memory to uncover what supports this relationship.

In order to examine this relationship, we tested patients with severe hippocampal amnesia who cannot form new declarative memories. If the hippocampal declarative memory system supports gesture's role in learning and memory then we expect that this group will not benefit from gesture in the same way as healthy people do.

In Experiment 1, we tested if the hippocampal declarative memory system supports gesture production by having amnesic patients and healthy comparisons engage in conversations about different events. We found that the patients gestured at a lower rate than healthy comparisons, suggesting that the hippocampus and the processes that it supports play a role in gesture production. In Experiment 2, we examined in more detail how the representations that people have for an event affect how they gesture. We found that for healthy people, their declarative memories for past events guide the form that their gestures take, while patients with amnesia rely more strongly on their past motor experiences when determining gesture form.

Experiment 3 tested whether gesture perception and production can be leveraged to help patients with amnesia learn new words. We found that producing – but not viewing – gesture when learning helped patients with amnesia identify objects by their novel labels later. These finding suggest that gesture is supported by multiple kinds of memory and that gesture production may be a crucial component in gesture aiding in learning and memory.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

General background and introduction

The spontaneous hand gestures that we produce along with our spoken language iconically reflect our thoughts. Take, for example, when we are giving instructions to a listener about how to make a sandwich. Our gestures may illustrate the spreading of butter across bread, the grasping of a knife, or the squeezing of a bottle of mustard. These gestures serve to illustrate the concepts that are being described in a visual and non-arbitrary way; we show on our hands what we have in our minds. In doing so, we provide an iconic form of what we are communicating that can facilitate the communicative interaction as well as well as our own memory and our listener's memory for the content of our spoken language. But where do our gestures come from? How does a representation in our mind get translated to our hands when we communicate? And how does the content of our gestures facilitate communication and learning?

In the work presented here I am to uncover and describe how the contents of minds end up on our hands and in turn, how the content communicated on our hands can help us learn and remember. To do this, I take the novel approach of considering gesture production and perception from a multiple memory systems framework. The reason for this is twofold. First, and somewhat obviously, the contents of our gesture necessarily rely on our memory. When we are communicating, our language is guided by our understanding in memory for what it is that we are discussing. Returning to the sandwich making example, we are able to gesture about this process because we remember what a knife, bread, and butter look like. We can reconstruct our past experiences of making sandwiches ourselves and watching others do so too, and use these memory representations to guide our spoken language and gesture production. By making inferences about the contents of memory representations and then examining how gestures reflect this information, I hope to uncover how different types of memory support the quantity and quality of our gesture production.

Second, there is already a well-established link between gesture and memory in the field of gesture studies. When we gesture when we talk, we are more likely to remember the content of our spoken language (Kelly, McDevitt, & Esch, 2009). The same goes for viewing the gestures of others: perceiving gesture with spoken language improves our memory for the content (Singer & Goldin-Meadow, 2005). These effects are found at multiple stages of memory: the encoding of new memories (Cook, Yip, & Goldin-Meadow, 2010), memory consolidation (Cook, Duffy, & Fenn, 2013), and memory retrieval (Nooijer, Gog, Paas, & Zwaan, 2013). Despite the repeated demonstrations of the effect of gesture on learning and memory, we still know very little about how this facilitation occurs. After uncovering how the contents of our memory representations affect our gesture, I then address how the contents of our gesture can be manipulated to facilitate learning. Although prior work has linked gesture to processes in memory, the details of the underlying links have not been examined. The work reported here is a first step towards determining how the contents of our memory representations affect how we gesture and how this link between memory content and gesture can be exploited for learning.

Although memory is a complex and multifaceted construct that likely involves a multitude of structures and processes, throughout this dissertation I construe memory within the classic multiple memory systems framework because decades of neurological research suggests that it can be simplified into two functionally and anatomically separate systems: declarative and non-declarative memory. Declarative memory supports the ability to rapidly acquire relational knowledge about the world such as vocabulary and facts (semantic memory) and information for time- and place-specific experiences that are autobiographical in nature (episodic memory). Non-declarative memory is an umbrella term used to refer to procedural memory (including skill and habit learning), classical conditioning and priming. I use this framework as an initial attempt at understanding how the contents of our memory affect our gesture because I use tasks and methods that differentially engage systems of memory. For example, when someone recalls a specific event from their past, I can infer that they are relying on declarative memory to retrieve and reconstruct this event. Their gestures, in turn, may reflect declarative memory as well. Conversely, when someone experiences a new motor behavior that they later discuss, I can test whether they are relying on their non-declarative memory for the experience by examining the form of their gestures.

Indeed, the three articles here attempt to empirically link the contents of the different memory systems with gestural behavior. I used knowledge of these memory systems and the content and information that they support to design experiments that engaged either or both memory system. All three articles contain data from both healthy, unimpaired participants and participant with severe memory impairment to determine when and how the contents of memory systems are reflected in gesture across diverse tasks. In Experiment 1, participants engage in discourse tasks that focus on prior events, a task that we consider to be supported in large part by hippocampal declarative memory. Within these tasks we expect that different prompts have different memory demands: past events that require situating oneself with an autobiographical, high episodic context should rely more heavily on hippocampal declarative memory than prompts that can be addressed with more generalized knowledge. In Experiment 2, participants engage in a spatial-motor task and then describe how to complete the task after a delay. Here, the memory demands are slightly different: rather than relying on a hippocampally generated representation of a past event, participants can rely on their knowledge of the task that was just presented. This may also differentially affect how systems of memory are engaged in gesture production. Lastly, in Experiment 3 we try to determine if visual and motor properties of gesture – that also implicate different systems of memory – can be leveraged to facilitate learning.

A critical component of the work presented here is the use of patient populations. For all studies reported here, I analyzed the behavior of healthy adult participants. Additionally, two groups of patients participated in our studies. Patients with damage bilateral damage to the hippocampus – who have severe declarative memory impairment – and patients with ventromedial prefrontal cortex (vmPFC) lesions – who have no obvious memory, language, or motor impairment. The participation of patients with hippocampal amnesia allowed me to draw causal inferences about the brain structures that support gesture: when they are successful at tasks, we can conclude that performance involves non-declarative memory processed. In contrast, when they are unsuccessful, we can infer that task performance might likely require declarative memory processed. The participation of patients with vmPFC damage allowed us to infer that any differences we found in the behavior of the patients with amnesia was indeed due to their specific memory impairment rather than due to brain damage more generally. Analyzing the behavior of all three groups provided a clearer picture of how distinct system of memory support how gestures are produced and can facilitate learning.

In Experiment 1, I sought to determine if and how hippocampal memory reconstructions affect gesture production. The hippocampus is responsible for the generation of rich, multifaceted representations, particularly those that are episodic or autobiographical in nature (Eichenbaum & Cohen, 2001). Because these representations contain imagistic components, it is possible that gesture reflects these imagistic components of the representation during communication. If this representation is impoverished in some way, as it is known to be in patients with amnesia, then gesture may be impoverished in some way as well. To examine this possibility, patients with amnesia and healthy comparison participants engaged in 4 discourse tasks that varied in how episodic of a representation was necessary: a description of how to make their favorite sandwich, their account of JFK's assassination, a description of their most frightening experience, and a description of how to go shopping in a supermarket. I calculated a gesture rate – the number of gestures per word – for each of the discourse tasks. If the hippocampus and the declarative representations that it generates indeed contribute to gesture production, then we should see a difference in the gesture rate of patients with amnesia relative to the healthy comparisons. This is indeed what we found: patients gestured less overall than healthy comparisons, suggesting that the hippocampus indeed plays a role in gesture production. Moreover, the proportion of episodic features that participants included in each discourse task positively predicted gesture rate for the comparison participants but not for the patients with amnesia. Taken together, these data suggest that the complexity of the hippocampal representation indeed affects how features of this representation are translated into hand gesture.

The findings of Experiment 1 are the first to our knowledge to relate the content of hippocampally-generated memory representations with hand gesture. Still, given the open-ended nature of the discourse task and our inability to examine memory representations directly, it remains unclear if non-declarative memory also affected how gesture was produced. Recent work has linked non-declarative memory processes to gesture production (Klooster, Cook, Uc, & Duff, 2015), and thus it is likely that non-declarative memory is also evident in how people gesture. To test this, in Experiment 2 we directly manipulated features of memory representations (both visual and motor) to determine what would guide the form of gesture when participants later explained their experiences. I reasoned that the visual features would likely engage the declarative memory system – participants could see and remember the moves that they made – while motor features might engage the non-declarative memory system. Thus the patients with amnesia would not readily encode the visual properties of the task over a delay but could potentially encode the motor properties via their intact non-declarative memory system.

On three visits, healthy comparison, patients with amnesia, and brain-damaged comparison groups completed a Tower of Hanoi task, involving moving a set of disks between three pegs with the goal of moving them all from the first to the third peg. The visual and motor properties necessary to complete the task varied on each visit: on the first visit, participants moved the disks by pressing buttons and there was no visual trajectory of the disks moving (they disappeared and reappeared). On the second visit, participants again moved the disks with button presses but this time they viewed a curved visual trajectory for disk movement. On the third visit, participants moved the disks by making curved movements with a mouse again without any visual trajectory. After a half hour delay, participants explained how to solve the Tower of Hanoi to an experimenter. The patients with amnesia had no declarative representation of the task at this point.

Our analysis of gesture assessed the presence of curvature in the gestures: if visual properties of what is being discussed guide gesture production, then we should expect the most curvature in gesture after session 2 when curvature was viewed but not produced. If motor properties for what is being discussed guide gesture production, then we should expect the most curvature in gesture after session 3, then curvature was produced but not viewed. We found that for the healthy participants, gesture contained the most curvature after session 2: after having viewed curved movements but not produced them. For the patients with amnesia, their gestures contained the most curvature after session 3: when they had produced curved mouse movements.

These findings suggest that both visual – declarative – and motor – non-declarative – experiences can affect the form that gesture takes. Interestingly, patients with amnesia, who did not have a declarative representation available to them when describing how to complete the task, nonetheless produced gestures that reflected their motor experiences. This suggests gestures can reflect the contents of memory even without explicit awareness for what is being communicated. Healthy participants did not produce as much curved gesture after producing curved motor movements without accompanying visual curved trajectories. It is possible that the healthy participants' explicit memory for the visual experience competed with the motor representation to decrease amount of curvature in gestures.

Taken together, the results of Experiments 1 and 2 demonstrate that the contents of our memory representations affect how we gesture. Experiment 1 showed that the integrity of hippocampal declarative memory representations can affect gesture production, with increasing episodic details leading to higher rates of gesture in healthy people but not in patients with amnesia. Experiment 2 showed that both visual, likely declarative features in memory and motor, likely non-declarative features in memory can affect the form that gestures take and when a hippocampal representation is not readily available, as is the case in patients with amnesia, motor properties from memory can still be evident in gesture. In Experiment 3 we tested if this relationship between gesture and the contents of our non-declarative memory could be leveraged to facilitate learning in the patients.

Because the patients with amnesia produced gestures that reflected their prior motor experiences, Experiment 3 investigated whether motor behavior experienced through gesture at encoding could enhance later recall of presented material. We examined how gesture affected the learning of novel labels for familiar objects. Patients with amnesia are known to be impaired at word learning. Participants were exposed to novel word-object pairing that either was learned with a gesture or not. For the gestured-with trials, the gesture was either viewed and then produced by the participant or viewed in order to test if gesture production was necessary to facilitate learning. After adequately learning all the word-object pairings, there was a 30-minute delay followed by a free recall and object identification task. Both comparison groups performed well above chance on both the free recall and object identification tasks regardless of gesture. The amnesic patients could not freely recall any labels with the exception of a single label by one patient (of a gestured-with word). On the object identification task, patients with amnesia were significantly more likely to identify the label-object pairing if the pairing had been learned with gesture. This benefit was only seen for those words learned when both observing and producing the gesture. For the pairings learned without gesture and the pairings learned with only viewing gesture, the patients were at chance at identifying objects by their novel label. These findings demonstrate that gesture can help rescue hippocampal amnesics' ability to bind labels with objects, and furthermore suggest that the self-production of gesture is critical for supporting this learning.

This series of studies have linked systems of memory to gesture production in multiple contexts. We have shown that both hippocampal declarative and non-declarative memory can affect how gesture manifests and that gesture production can facilitate learning and memory via non-declarative learning mechanisms. Together these studies establish clear and multifaceted links between gesture and memory that are described herein. A more thorough discussion of the implications of this work will immediately follow the articles.

Experiment 1: Hippocampal declarative memory supports gesture production: Evidence from amnesia

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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 (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 detriment was more extreme 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 specifically sensitive to the representation available in declarative memory, suggesting a potential mechanism supporting gesture production.

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 (Wesp et al., 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. 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, 2015). 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, multi-faceted 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). 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 and our ability to imagine events and scenarios of our distant futures. If gesture emerges from rich, relational memories, then gestures should 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 declarative memory representation extend to gesture? That is the question we address here.

The information carried by gesture can be information also expressed in the accompanying speech or this information can be 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 expressed 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 via the verbal descriptions in patients with hippcampal will extend to their gestures. Gesture may emerge directly from aspects of the memory representation supporting speech, or may emerge from memory representation outside the declarative memory system. 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 co-speech 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 non-declarative 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 experience, and how they heard about JFK’s assassination. While hippocampal declarative memory has long been defined in terms of its capacity for supporting rich, relational, and multimodal mental representations, the current study is the first to examine gesture production in the communication of patients with severe hippocampal amnesia. If hippocampal declarative memory supports gesture production, then we would expect the co-speech gestures of patients with hippocampal amnesia to differ in some way (e.g., fewer gestures) from those of demographically matched comparison participants. But if gesture just comes along with speech regardless of the underlying representation, or via non-declarative representations, we might expect that gesture is unaffected by hippocampal damage and thus independent of the hippocampal declarative memory system.

Materials and methods

2.1. Participants. Eighteen people participated in the study: nine individuals with bilateral hippocampal damage and severe declarative memory impairment (four females; seven right handed) and nine healthy adult participants (four females; seven right handed). At the time of data collection, the patients with amnesia were medically stable and in the chronic epoch of amnesia, with time-post-onset ranging from 1 to 25 years (M = 9.33; SD = 7.1). The patients were on average 50 years old (range 42–58) and had 14 years of education (range 9–16). Etiologies included anoxia/hypoxia (001, 1606, 1846, 2144, 2363, 2563, 2571), resulting in bilateral hippocampal damage and herpes simplex encephalitis (HSE) (1951, 2308), resulting in more extensive bilateral medial temporal lobe damage affecting the hippocampus, amygdala, and surrounding cortices (Figure 1). High-resolution volumetric MRI data were available for six patients (excluding 001, 2563, 2308) and revealed significant reduction to the hippocampus bilaterally with volumes reduced by at least 1.01 studentized residuals compared to age matched healthy comparison participants. The average reduction for the anoxic participants was 3.16 studentized residuals, compared to healthy participants. MRI images for 001 are published and reveal bilateral hippocampal volume reductions (Hannula, Tranel, & Cohen, 2006). Visual inspection of a CT scan from patient 2563, who wears a pacemaker, confirmed damage limited to hippocampus. Extensive bilateral medial temporal lobe damage in patient 2308 can be visualized in Figure 1.

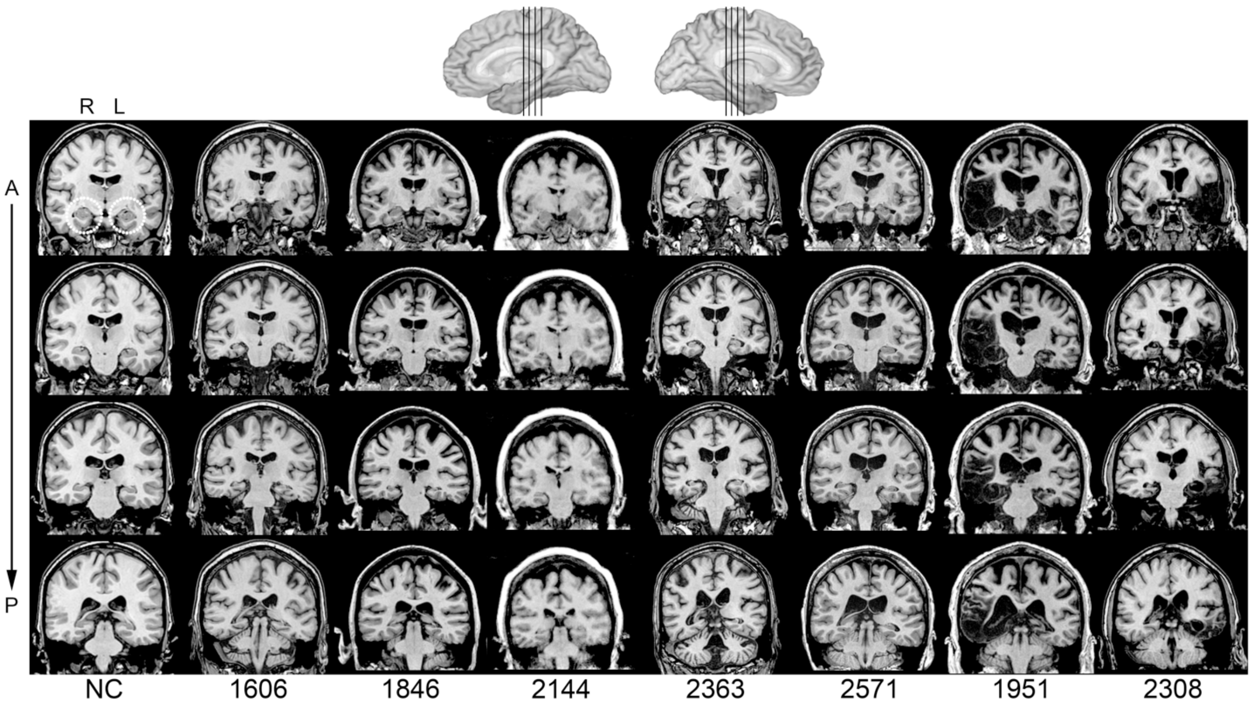

Figure 1. Magnetic resonance scans of hippocampal patients. Images are coronal slices through four points along the hippocampus from T1-weighted scans. R = right; L = left; A = anterior; P = posterior; NC = a healthy comparison brain.

Performance on tests of neuropsychological functioning revealed a severe and selective impairment in declarative memory functioning while performance across other cognitive domains was within normal limits (see Table 1). The Wechsler Memory Scale–III General Memory Index scores for each participant were at least 25 points lower than their scores on the Wechsler Adult Intelligence Scale–III, and the mean difference between Full Scale IQ and General Memory Index was 34.8 points. The average Delayed Memory Index was 63.3, almost 3 standard deviations below population means. This deficit in declarative memory was observed in the context of otherwise intact cognitive abilities. Participants performed within normal limits on standardized neuropsychological tests of intelligence, language, and executive function and experimental measures of non-declarative or procedural memory (Cavaco, Anderson, Allen, Castro-Caldas, & Damasio, 2004). The patients with hippocampal amnesia do not have aphasia as determined by standardized neuropsychological assessments of language and determination of a speech-language pathologist. These patients are well known to our group as we have studied their memory and language abilities for the over a decade (e.g., Duff & Brown-Schmidt, 2012). We have repeatedly documented deficits in declarative memory representations across a range of tasks (e.g., Duff, Hengst, Tranel, & Cohen, 2007; Klooster & Duff, 2015; Konkel, 2008; Kurczek et al., 2015).

Subject	**Sex**	**Age**	**Hand**	**Ed**	**Etiology**	**HC Damage**	**HC Volume**	**WMS III GMI**	**WAIS III FSIQ**	**BNT**	**TT**
001	F	54	R	9	Anoxia	Bilateral HC	N/A	54	90	56	44
1606	M	55	R	12	Anoxia	Bilateral HC	-3.99	66	91	32	44
1846	F	46	R	14	Anoxia	Bilateral HC	-4.23	57	84	43	41
2144	F	53	R	12	Anoxia	Bilateral HC	-3.92	56	99	56	44
2363	M	46	R	18	Anoxia	Bilateral HC	-2.64	73	98	58	44
2563	M	47	L	16	Anoxia	Bilateral HC	N/A	75	102	52	44
2571	F	39	R	16	Anoxia	Bilateral HC	-1.01	87	112	58	44
1951	M	50	R	16	HSE	Bilateral	-8.10	57	121	49	44

						HC +MTL					
2308	M	46	L	16	HSE	Bilateral HC +MTL	N/A	45	87	52	44
HC Mean	4F 5M	48.4 (±5.1)	7R 2L	14.3 (±2.8)				63.3 (±13.0)	98.2 (±12.1)	50.7 (±8.5)	43.6 (±1.0)

Table 1. Demographic, neuroanatomical, and neuropsychological characteristics of participants with hippocampal amnesia; Note: Hand.=Handedness. Ed.=years of completed education. HSE=Herpes Simplex Encephalitis. HC=hippocampus. +MTL=damage extending into the greater medial temporal lobes. N/A=no available data. Volumetric data are z-scores as measured through high resolution volumetric MRI and compared to a matched healthy comparison group (see Allen, Tranel, Bruss, & Damasio, 2006, for additional details). WMS-III GMI=Wechsler Memory Scale–III General Memory Index. WAIS-III FSIQ=Wechsler Adult Intelligence Scale–III Full Scale Intelligence Quotient. BNT=Boston Naming Test. TT=Token Test.

The healthy participants served as demographically matched comparison participants to the patients with amnesia and matched the patients on age, sex, education, and handedness. At the time of the study, these healthy participants were, on average, 50.6 years old (SD = 6.1) and had 14.4 (SD = 2.4) years of education, on average. All healthy comparison participants were free of neurological and psychological disease.

2.2. Procedures: Data analysis was conducted on data previously collected using the Mediated Discourse Elicitation Protocol (MDEP) (Hengst & Duff, 2007). The MDEP was designed to collect ecologically valid, interactional samples of multiple types of discourse following conventions in the literature (Cherney, Coelho, & Shadden, 1998). For the current study, four narrative discourse tasks were analyzed: two procedural discourse narratives (how to make a favorite sandwich and how to grocery shop in an American supermarket) and two episodic/autobiographical narratives (their most frightening experience and their account the JFK's assassination). We chose narrative samples (over conversational samples) as narratives are among the best studied discourse forms in the memory literature. Participants had all conversations with an experimenter (author M.D.) who was blind to hypotheses concerning gesture production. Prior to the discourse sampling sessions, participants were instructed that they would be talking about different topics, much like they do in their everyday conversations; there would be no right or wrong answers and they should try to communicate as naturally as possible.

The experimenter provided prompts for each discourse topic. For the first two topics, the prompts were "I want you to tell me about your most frightening experience," and "I want you to tell me where you were and how you learned about JFK's assassination." For the last two topics, the prompts were "Tell me how to make your favorite sandwich" and "I want you to pretend I'm from Timbuktu. Tell me everything I need to know about shopping in an American grocery store." While the participant spoke, the experimenter provided appropriate conversational feedback (e.g., verbal and non-verbal backchannels). For the procedural discourse narratives, the examiner took notes. The participant could speak as much or as little as deemed necessary. The instructions did not mention gesture, and the experimenter was not investigating gesture at the time of data collection and so did not explicitly attend to participant's gesture. However, the video recording of the sessions provided appropriate capture of gesture to support the current coding and analysis.

Consistent with work in our lab, and that of others, reporting impaired or impoverished declarative memory representations in the narratives of participants with amnesia, previous analyses of these narratives revealed significantly fewer details in the verbal productions of the participants with amnesia relative to the comparison participants (Duff et al., 2008; Kurczek & Duff, 2013).

2.3. Coding. Speech was transcribed from the videos. For each discourse topic, a total word count was determined to assess the amount of speech and allow for a calculation of gesture rate (total gestures divided by total words produced). All hand movements that accompanied speech were coded as gestures using ELAN (Lausberg & Sloetjes, 2009). Each gesture was categorized as one of three gesture types: iconic, deictic, and beat. Iconic gestures resembled the word or concept that was being communicated. For example, saying the word "up" while moving the hand upwards or saying the word house while making a triangle out of the hands to represent a roof. Beat gestures were simple movements produced in rhythm with speech and which carried no semantic content. Deictic gestures were typically pointing gestures that referred to something in space. Because the conversations were about past events or things that were not visually present, deictic gestures were relatively infrequent in this dataset. Still, participants would occasionally use a pointing gesture to refer to themselves or the experimenter.

2.4 *Analysis*. For our analyses, we used mixed effect regression models that predicted the dimension of interest as a function of participant status (amnesic patient versus healthy comparison). This allowed us to examine if there were indeed differences in the gesture produced for amnesic versus comparison participants. We determined the random effect structure for each model by using log-likelihood ratio testing; this allowed us to find the maximal random effect structure justified by the data for each model. Since there is no general consensus regarding how to determine degrees of freedom in mixed effects regression modeling (Barr, Levy, Scheepers, & Tily, 2013; Bates, Kliegl, Vasishth, & Baayen, 2015), we report the regression coefficient and test statistic for each model. Test statistics equal to or greater than an absolute value of 2 are considered to correspond to a p-value of less than .05. We used dummy coding in all of our models with patients with amnesia as the reference group for participant status.

Results

3.1. *Word Count.* All participants were highly variable in the amount of spoken language produced in the discourse topics. At the group level, amnesic participants and healthy comparison participants produced similar amounts of words across all tasks, with amnesic participants producing on average 268.1 words and comparison participants producing 281.3 words (SD = 179.95) per topic. Table 2 shows these broken down by discourse narrative topic.

		Shopping		Sandwich		FrightExp		JFK		All
		M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*
Amn.	Words	199.6	(56.7)	337.0	(341.2)	380.1	(269.3)	155.8	(75.5)	268.1
	Gestures	2.90	(1.12)	3.29	(2.90)	4.55	(1.80)	1.47	(0.55)	3.1
Com.	Words	275.8	(110.7)	166.0	(65.5)	443.8	(197.2)	239.4	(196.3)	281.3
	Gestures	3.02	(1.97)	5.70	(2.77)	7.81	(3.04)	5.20	(3.50)	5.4

Table 2. Number of words produced and the number of gestures produced per one hundred words for each of the discourse narrative types by group.

To assess whether there were differences in the total amount of speech produced as a function of participant status, we used a mixed effect model predicting word count, log-transformed for normality, with a fixed effect of participant status and random intercepts for participant and discourse topic. As expected, participant status did not predict word count (B = 0.16, t = 0.62). Thus, amnesic participants and comparisons participants produced similar amounts of words (Figure 2).

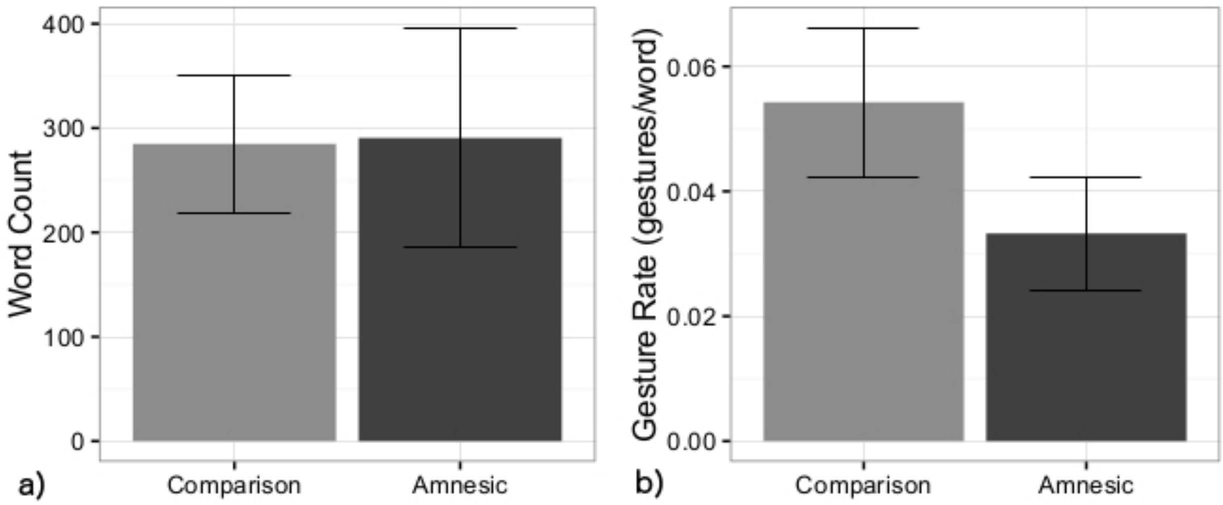

Figure 2. (a) Word count by participant group across all discourse narratives. The amount of speech produced was highly variable both within and across the different narratives. (b) Gesture rate by participant status across all discourse narratives. Participants with hippocampal amnesia gestured at a lower rate than comparison participants.

To additionally determine if there were any differences in the amount of spoken language produced in the individual discourse narratives, we reparameterized our model so that narrative type was a fixed effect. We also included a fixed effect for participant status and their interaction and a random intercept for speaker. Marginally more words were used when describing a frightening experience than when describing how to go shopping (β = 0.51, t = 1.98, p = .06) and marginally fewer words were used when describing JFK's assassination than when describing how to go shopping (β = -0.71, t = -1.98, p = .06). There was no reliable difference in the number of words produced when describing making a sandwich compared to describing going shopping (β = -.13, t = 0.48, p = 0.63). These main effects were accompanied by a significant interaction of participant status and discourse topic. Patients with amnesia produced marginally more words than healthy comparison participants when describing how to make a sandwich, (β = -0.71, t = -1.98, p = .06). The remaining two interactions were not significant (PSxFE: β = -0.08, t = -0.25, p = 0.80; PSxJFK: β = 0.17, t = 0.47, p = 0.64) and neither was the fixed effect of participant status (β = 0.35, t = 1.00, p = .32). Thus, the overall amount of spoken language was generally comparable across groups, but there was evidence that topic differentially affected the amount of spoken language across groups.

3.2. Gesture rate. All participants gestured during all narratives. Gesture rate was determined by dividing the number of gestures produced in a narrative by the total number of words produced. Across all narratives, amnesic patients gestured at a rate of 0.031 (3 gestures per 100 words; SD = 0.02) and healthy comparison gestured at rate of 0.054 (5 gestures per 100 words; SD = 0.03). See Table 2 for the gesture rate for each discourse narrative.

Our preliminary model of gesture rate had the same structure as the model of word count. Participant status significantly predicted gesture rate (β = 0.56, t = 2.41); amnesic patients had a significantly lower gesture rate than comparison participants did (Figure 2, panel b).

We next analyzed whether gesture rate varied as a function of discourse topic for participants with amnesia and comparison participants. Although the gesture rate of participants with amnesia was impaired when analyzed across all tasks, their gesture rate appeared relatively unimpaired for the shopping task. To investigate if this was indeed the case we used a mixed effect model predicting gesture rate as a function of participant status, task type, and their interaction. The explanation of grocery shopping topic was used as the reference group. The random effect structure included a random intercept for participant. There were two marginally significant interactions. Participant status interacted with the sandwich discourse topic (β = 0.96, t = 1.77, p = .08; Figure 3) and participant status interacted with the JFK discourse topic (β = 1.07, t = 1.88, p = .07) to predict gesture rate. Participant status and the frightening experience discourse topic did not predict gesture rate (β = 0.58, t = 1.12, p = 0.27). Additionally, no main effects had significant or trend level effects on gesture rate (participant status: β = -0.05, t = -

0.13, p = 0.89; making sandwich: β = -0.26, t = -0.62, p = 0.54; frightening experience: β = 0.28, t = -1.34, p = 0.18; JFK: β = -0.62, t = -1.34, p = .19). Thus, participants with amnesia gestured reliably less than comparison participants when describing how to make a sandwich and when describing learning about JFK's assassination.

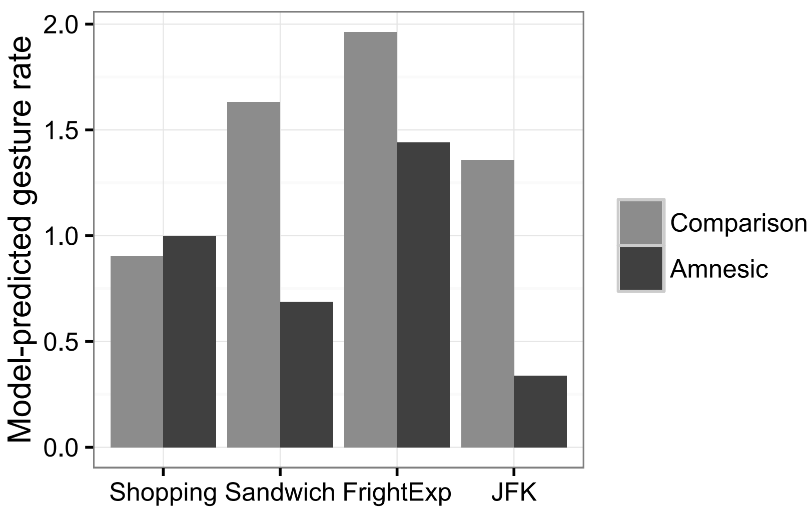

Figure 3. Model-predicted log-transformed gesture rate (gestures per 100 words). Patients with amnesia were significantly more impaired in gesture rate in the sandwich and JFK tasks than in the shopping task.

3.3. Gesture type. Finally, we examined the proportion of representational gestures produced by each participant for each narrative. Representational gestures were frequently produced in all narratives, and we reasoned that if hippocampal declarative memory is required for the rich reconstruction of an event then perhaps patients with hippocampal amnesia may produce fewer representational gestures overall. We divided the total number of representational gestures in each narrative by the total number of gestures in each task for all participants. Comparison participants produced representational gestures 68.9% of the time compared to the amnesic participants 70.1%. Using a mixed effect model predicting the logit of the proportion of representational gestures in each task, with a fixed effect of participant status and random effects of task and participant, we found no difference in the proportion of representational gestures (β = -0.30, t = -0.46). Thus, despite the fact that patients gestured less overall, they still produced the same relative amount of representational gestures as comparison participants.

We then reparameterized our model to assess if there were differences in the proportion of representational to non-representational gestures in each of the tasks. In addition to a fixed effect of participant status, we added a fixed effect of discourse task and its interaction with participant status into the model, along with a random effect for speaker. None of the interactions significantly predicted proportion of representational gestures (PSxMS: β = -0.37, *t* = -0.34, PSxFE: β = 0.35, t = 0.33; PSxJFK: β = -0.39, t = -0.34). Participant status again did not predict representational gesture use (β = -0.31, *t* = -0.32) nor did task (MS: β = -0.37, t = -0.34, FE: β = -0.21, t = -0.27; JFK: β = 1.18, *t* = 1.25). Therefore, participants did not alter their representational gesture production based on their memory impairment or discourse type.

Discussion

While it seems intuitive that gestures emerge from representations in memory for what is being communicated (Wesp et al., 2001), the mechanism supporting a link between gesture and memory is unknown. The current study investigated the hypothesis that gesture is, in part, supported by hippocampal declarative memory representations. The motivation for hypothesizing a relationship between the hippocampal declarative memory system and gesture stems from work pointing to the role of the hippocampus in relational binding and in representational flexibility for the reconstruction and recreation of richly detailed, multimodal, mental representations of experience (e.g., Eichenbaum & Cohen, 2001), and the disruptions in such representations following hippocampal amnesia (e.g., Hassabis et al., 2007; Kurczek et al., 2015; Race et al., 2011). We found that patients with hippocampal amnesia – who have impaired declarative memory – produced significantly fewer gestures than healthy comparison participants.

The role of hippocampus in the formation and subsequent retrieval of enduring (long-term) memory is incontrovertible (Eichenbaum & Cohen, 2001; Gabrieli, 1998; Squire, 1992). The hallmark processing features of hippocampus – relational binding and representational flexibility – support our ability to reconstruct and recreate richly detailed, multimodal memories of our remote past and our ability to imagine events and scenarios of our distant futures. Following hippocampal damage, these multifaceted relational representations are disrupted and the verbal descriptions of events by patients with hippocampal amnesia are impoverished, containing fewer details about the people, places, and things, and the spatial and temporal aspects of their experiences (e.g., Kurczek et al., 2015; Race et al., 2011). The critical question addressed here was: do these disruptions extend to the production of gesture? The answer is yes. Patients with hippocampal amnesia produced significantly fewer gestures than healthy comparison participants, suggesting that the rich, multifaceted representations supported by the hippocampus are important for gesture production.

Although these data are the first to demonstrate a link between gesture and hippocampal declarative memory, they fit with a growing body of work pointing to the breadth of cognitive and behavioral performances that receive hippocampal contributions. Hippocampal declarative memory has been shown to contribute to a range of abilities including, but not limited to decision making (e.g., Zeithamova, Schlichting, & Preston, 2012), creativity (e.g., Duff, Kurczek, Rubin, Cohen, & Tranel, 2013), social cognition (Spreng & Mar, 2012), and language processing (e.g., Duff & Brown-Schmidt, 2012) (see Rubin, Watson, Duff, & Cohen, 2014, for a review). The findings here extend the breadth and reach of the hippocampus and declarative memory to also include gesture production. An open question that warrants further investigation is if the nature of the relationship between gesture and memory is stable across tasks and behaviors, or if there are conditions or contexts in which gesture might engage non-declarative memory. Indeed, the findings of differential impairment in gesture across tasks suggest that there may be variability in the extent to which gestures are supported by hippocampally-mediated representations.

More specifically, the results argue against a pure action-based account of gesture production. For example, the Gesture as Simulated Action (GSA) framework argues that speakers simulate actions and perceptual states, that then activate motor and premotor cortices, leading to gesture production (Hostetter & Alibali, 2008). According to the GSA framework, the more a representation in the mind is grounded in action, the more likely it is that a gesture is produced. Although our findings are not in direct conflict with GSA, the reduced gesturing by patients with hippocampal amnesia suggests that action representations alone may not be sufficient to trigger a gesture or explain why and under which circumstances people gesture. There is a long history and large literature revealing that non-declarative memory (including procedural memory) is intact in patients with hippocampal amnesia (e.g., Cohen & Squire, 1980; Milner, 1962) including intact learning of and preserved memory for motor and action abilities (e.g., Cavaco et al., 2004). If action representations are intact in patients with hippocampal amnesia, and gesture emerges from action representation, then gesture should have been relatively unimpaired in patients.

Our findings do suggest one source of gesture is information supported by the hippocampal declarative memory system (i.e., details about the people, places, and things, as well as the spatial and temporal aspects of experience). The naming conventions of discourse tasks from the literature (e.g., procedural discourse for describing how to do things; episodic discourse for autobiographical events) make it tempting to assign direct mappings of discourse genre to specific memory systems (e.g., procedural discourse equates procedural memory). However, the data do not support such divisions. For example, if procedural discourse equated procedural memory we might have expected no group differences for the shopping and sandwich making tasks given the intact procedural memory status of the patients with amnesia (also see Duff, Hengst, Tranel, & Cohen, 2009). Instead, these data suggest a more complex picture of how and under what circumstances different types of memory representation are called upon in service of meeting the demands of different types of talk and communication. Future research should characterize co-speech gesture across a wider range of discourse tasks in patients with amnesia in order to better understand the interactions between communicative demands and distinct forms of memory representation.

Gestures are known to facilitate new learning and memory (Cook, Duffy, & Fenn, 2013; Cook, Mitchell, & Goldin-Meadow, 2008). Yet it is also not clear that the memory mechanisms that support gesture production during communication are the same mechanisms as those that implicate gesture in memory and learning. One way to address this question would be to examine if gesture can facilitate learning in patients with hippocampal amnesia, who necessarily rely on non-declarative learning mechanisms to acquire new information (see Cook & Tanenhaus, 2009; Klooster et al., 2015). If so, this would reveal the possibility of non-declarative mechanisms of learning via gesture.

Our gestures iconically represent our thoughts and thus reflect our representations in memory. By examining the gesture production of patients with hippocampal amnesia, we uncovered a potential mechanism for gesture production: hippocampal declarative memory representations. These representations are impoverished in patients with hippocampal amnesia, and these patients have a diminished gesture rate, without a concomitant reduction in speech rate. This finding is the first to empirically link gesture production with hippocampal declarative memory. By examining the cognitive and neural mechanisms that support gesture, memory, and their relationship, we can uncover how memory supports language and determine how gesture can be leveraged to facilitate learning and memory.

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Experiment 2: Visual and motor contributions to gesture: a multiple memory systems account of gesture production

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Abstract: The hand gestures that people produce when speaking provide an imagistic and motor representation of what is being described in spoken language. Despite the ubiquity of gesture, little is known about the cognitive and neural mechanisms that determine gesture form. To test this, we manipulated the visual and motor experience that participants received while completing the Tower of Hanoi task. Participants included four patients with severe hippocampal amnesia, four patients with lesions to the ventromedial prefrontal cortex (vmPFC), and healthy comparison participants. The Tower of Hanoi was completed three times across three sessions, with a different pairing of visual trajectories of disk movement and requisite motor movements: in session 1 participants pressed buttons and did not see a visible motion trajectory, in session 2 participants pressed buttons and viewed curved motion trajectories, and in session 3 participants made curved mouse movements and did not see a visible motion trajectory. In healthy and vmPFC participants, curvature was most evident in gesture when describing the task with visual curved trajectories. In contrast, for patients with hippocampal amnesia, curvature was most likely to be present in gesture when they had produced curved trajectories. These findings suggest that gesture reflects both visual and motor features of memory representations, and that the form that gesture takes during communication reflects information from multiple systems of memory.

Introduction

When we talk, we gesture with our hands. Hand gestures are related to spoken language semantically (McNeill, 1992), pragmatically (Holler & Beattie, 2003), and temporally (Habets, Kita, Shao, Ozyurek, & Hagoort, 2011). The form that the hands take when gesturing is typically iconic: gestures provide a visual, imagistic form of the message that is being communicated. Gestures reflect on the hands what is being represented in the mind. Little is known, though, about what underlies gesture production. What mechanisms support their production and what determines the form that gestures take?

One potential starting point in addressing these questions is to consider the role that memory plays in gesture production. Clearly the form of gestures stem from a representation in memory for what is being communicated; properties of what is being communicated are iconically reflected in gesture (McNeill, 1992). Conversely, gesture is known to affect memory; content learned with gesture at encoding is learned and remembered better than without gesture (Cook, Mitchell, & Goldin-Meadow, 2008; Kelly, McDevitt, & Esch, 2009). This suggests a bidirectional relationship between gesture and memory that may be useful in understanding mechanisms of gesture production.

Memory has classically been divided into two functionally and anatomically distinct systems. Declarative memory, supported mainly by the hippocampus, supports encoding and retrieval of information about episodic events and semantic facts that can be consciously recalled, and likely supports the generation of conscious visual images (Bird, Bisby, & Burgess, 2012; Eichenbaum & Cohen, 2001; Gabrieli, 1998). In contrast, non-declarative memory, formed and retrieved independently of the hippocampus, supports motor and cognitive skills below the level of consciousness (Knowlton, Mangels, & Squire, 1996; Knowlton & Moody, 2008).

Properties of these memory systems are related to properties of gesture: gesture is both imagistic and motor, and is both consciously and unconsciously produced. This overlap in features suggest that both memory systems can potentially support gesture production. We acknowledge there are likely a range of contributions to gesture production beyond just mechanisms of memory. Nevertheless, by situating gesture production a framework of multiple memory systems we are making critical first steps in forming and testing hypotheses about the nature of the relationship between gesture and memory. Under what circumstances do gestures reflect hippocampally-generated imagistic features from memory and under what contexts do they reflect non-declarative motor and action information? We discuss the potential contributions of each memory system to gesture production below. We then introduce the current study, which directly assesses the contribution of different forms of memory to gesture production in healthy individuals and in individuals with severe and selective memory impairment.

Hippocampal declarative memory and imagery in gesture production.

Gesture communicates information iconically (Hilliard & Cook, 2015a). Take for example, a speaker describing how to complete the Tower of Hanoi task. In this task, a series of disks must be moved from the first of three pegs to the third peg, only moving one disk at a time and not putting a larger disk on top of a smaller disk. When describing how to complete the Tower of Hanoi, speakers depict in gesture the specific trajectories that the disks move during task completion: completing the task on a computer (with straight mouse movements) yields flatter gesture trajectories than if the task had been completed with physical disks (with curved lifting movements) (Cook & Tanenhaus, 2009).

How is this representation generated? One likely possibility is the hippocampus and the declarative memory that it supports. The hippocampus and other medial temporal lobe structures have long been linked to the formation and subsequent retrieval of enduring (long-term) memory, particularly memory for episodes (Eichenbaum & Cohen, 2001; JGabrieli, 1998; Squire, 1992). Additionally, the hippocampus serves as a relational database to create, update, and juxtapose the mental representations that form the basis of declarative memory (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001). These representations are supported by binding elements that co-occur together, such as the people, places, and things involved and their spatial, temporal, and interactional components (Davachi, 2006; Eichenbaum & Cohen, 2001; Konkel, 2008). Returning to the Tower of Hanoi, when asked to describe how it is solved, the hippocampus will likely conjure a representation of the previous experience that may contain elements such as the disks and pegs used, the context in which it occurred, the steps taken, the temporal sequence, etc. This representation is a possible source of iconic representation in gesture production.

Support for this possibility comes from prior work with patients with hippocampal amnesia who have severely impaired declarative memory. Patients with hippocampal amnesia are known to be impaired in the generation of a multifaceted episodic memory representation for past, imagined, or future events (Kurczek et al., 2015)(Kurczek, Brown-Schmidt, & Duff, 2013) . 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 than comparison participants (e.g., Hassabis, Kumaran, Vann, & Maguire, 2007; Kurczek et al., 2015; Race, Keane, & Verfaellie, 2011). The impoverished hippocampal representation has also been shown to affect their gesture production. When communicating, these patients gesture at a lower rate (Hilliard, Cook, & Duff, *under review*) and use words that are higher frequency, more familiar, and shorter (Hilliard, Cook, & Duff, *in prep*). Thus, their hippocampal damage appears to affects both gesture and spoken language.

Aside from work with patients with amnesia, work with healthy people also demonstrates the potential importance of declarative memory, supported by the hippocampus, for gesture production. People gesture at higher rates when describing something from memory than when it is physically present (Wesp, Hesse, Keutmann, & Wheaton, 2001). Moreover, gesture rates are also higher when describing patterns from memory that are more difficult to conceptualize (Hostetter, Alibali, & Kita, 2007).

Although this previous work suggests that gesture may emerge from declarative memory representation, previous work did not take care to discriminate between different forms of memory. Most importantly, material likely was encoded across multiple memory systems, and so strong claims cannot be made regarding whether hippocampally-mediated representations were indeed the critical factor underlying differences in gesture production, even when tasks might appear to draw on hippocampal-dependent forms of representations. To directly test the role of memory systems in gesture production, we need to vary both the nature of the to-be-communicated material and the availability of memory systems.

Gesture production theories centered on imagery.

The role of imagery in language and gesture production has long been recognized in the field of gesture studies. According to McNeill's (1992; 1995)) *Growth Point* theory, the growth point – or core – of a to-be-communicated utterance contains both linear-segmented hierarchical linguistic structure and a global-synthetic image. By this account, the spoken language communicates the former while gesture communicates the latter. Spoken language and gesture are thought to be integrated to form a single message with gesture communicating the imagistic and analog parts of one's thinking. Similar to *Growth Point* theory is the *Information Packaging* hypothesis (Kita, 2000) that posits that gesturing helps speakers organize the visual, imagistic features of a message into units that are compatible with the linear, segmented format of spoken language. By this account, the movement of the hands guides the way that the speaker constructs their language. In both theoretical accounts there is the notion that the hands communicate the imagery inherent in a mental representation that is difficult to communicate through spoken language. For example, although an individual can readily communicate the details of a trip the museum in spoken language, it becomes difficult to describe precisely what a sculpture that they saw looks like without using hand gesture. The imagistic components of these representations are evident on the hands during gesture production, and these representations are likely hippocampally generated.

Another theory of gesture production that is reliant on imagery is the *Lexical Access* theory (Rauscher, Krauss, & Chen, 1996). According to this theory, gestures cross-modally prime lexical items and increase their activation, in turn making them easier to access. For example, if a speaker produced a grasping gesture while describing the Tower of Hanoi puzzle, they will more readily be able to produce the word "disk". Support for this theory comes from higher rates of gesture production when lexical access is more difficult (Morsella & Krauss, 2004). Although the mechanistic process underlying this phenomenon has not been fleshed out in detail, it is presumed that the iconic features of the gesture serve to activate the imagistic components of a lexical entry (Krauss, Chen, & Gottesman, 2000). Thus, although the details of theories of gesture production vary, it is clear that gesture's iconic nature plays a strong role throughout. However, it remains unclear precisely what imagery in gesture production is representing. Although that it is possible that gesture's iconic form reflects details of an underlying declarative memory representation, it is also possible that iconicity is depending on action and motor information.

Non-declarative memory and motor properties of gesture production.

In addition to its imagistic character, gesture is also motor behavior. When describing the Tower of Hanoi puzzle, the hands not only show imagistic properties of the task, but they also demonstrate the motor behaviors exhibited during task completion; the handshapes that gestures take are related to the handshapes made during task completion and the trajectories that demonstrate disk movement show how the hands moved during task completion (Cook & Tanenhaus, 2009). Thus, it is possible that these gestures directly reflect the motor movements made during task completion rather than the visual image of the disks moving through space. In prior work, the visual and motor trajectories of movement were confounded.

Aside from work with healthy populations, work with neurological populations also suggest that gesture may be supported by the non-declarative memory system. Patients with hippocampal amnesia are more likely to correctly identify an object when given a novel label if the label was learned with gesture at encoding than if it was learned without gesture (Hilliard, Duff, & Cook, *in prep*). Importantly, this effect of gesture is only found if the gesture was produced at encoding; just viewing a gesture does not facilitate object identification. Additionally, patients with hippocampal amnesia produce gestures that reflect their experiences with the Tower of Hanoi when they describe the task immediately after completing it, suggesting that the mechanisms that support gesture may be available to them (Klooster, Cook, & Duff, in prep). Finally, patients with Parkinson's disease are not affected by the movement properties of the gestures that they see (Klooster, Cook, Uc, & Duff, 2012). These patients are known to have damage to the basal ganglia, a structure involved in non-declarative learning. Thus, neurological and behavioral data both suggest that gesture is in part supported by non-declarative learning mechanisms, making non-declarative memory a plausible mechanism support gesture production.

In addition, the non-declarative memory system also supports the learning of motor skills and habits and is usually thought to contain information that cannot be explicitly accessed (Eichenbaum & Cohen, 2001). Gesture is also often produced and comprehended without conscious awareness. Speakers are typically unable to report whether or not they have gestured when asked after the fact, and even more rarely can describe what or how they gestured. Listeners also do not consciously process gesture; they are typically unaware that they are responding to information from gesture rather than speech (Alibali, Flevares, & Goldin-Meadow, 1997). Thus, gesture, like information in non-declarative memory, tends to be processed below the level of explicit awareness, suggesting that it may be supported by non-declarative memory.

Gesture production theories centered on motor action.

Like imagery, action is also a central feature in several gesture production theories. The Interface model proposed by Kita and Ozyurek (Kita & Özyürek, 2003) is an extension of the aforementioned theories, and argues that gestures stem from an action generator and verbal utterances stem from a message generator. Although there are bidirectional interactions between the two at the planning stage, gesture and spoken language are thought to stem from two distinct systems.

An alternative account of gesture production that offers a potential mechanistic explanation for gesture production is the Gesture as Simulated Action framework (Hostetter & Alibali, 2008). This account posits that speakers activate simulations of actions and perceptual states when they are communicating. These simulations in turn activate motor cortex and premotor cortex that control movement production. When activation of these cortices reaches a certain threshold then the speaker produces a gesture. For example, when explaining how to solve the Tower of Hanoi, the speaker will form a mental simulation of how it is completed. Because the simulation includes a great deal of action information, this will activate motor cortex and if this motor activation exceeds the predetermined gesture threshold, gestures are produced.

Although theories of gesture production have considered action as a source of information for gesture, the structure of memory has not been considered. One possibility is that the “action generator” posited by the Interface model is the non-declarative information associated with declarative information in the message that is being communicated. Gesture then may serve as a vehicle for this non-declarative information not communicated in spoken language. Similarly, the motor simulations used in the GSA may draw on non-declarative, motor representations. Thus, it is possible that the representation that supports gesture production is supported by non-declarative memory structures.

Testing declarative and non-declarative contributions to gesture production.

Clearly, properties of gesture map onto properties of multiple systems of memory. Gesture’s imagistic form – that resembles visual properties of the concept being described – implicates hippocampally-generated declarative representation as a potential mechanism for gesture production. Additionally, gesture’s motoric and unconscious nature implicate non-declarative mechanisms of memory supporting gesture production. Although we have separated these possibilities theoretically, they are not mutually exclusive. Instead, it is also possible that both memory systems contribute to gesture production.

In order to determine if and how memory systems contribute to gesture, we must first know precisely what is being represented in memory when a speaker is talking. This can be done by controlling the experiences that the speaker has prior to speaking, and creating experiences that are likely to implicate, or place differential on demands on, different memory systems. In the current study, we did this by varying characteristics of the Tower of Hanoi task. Participants completed the task in three different sessions, one month apart each time. During each session they completed the task differently with respect to the visual and motor information that they were receiving. After a delay, they explained how to solve the Tower of Hanoi. By manipulating the visual and motor information available during task completion, we were able to determine how visual and motor experience was subsequently expressed in gesture in order to assess the nature of the representations underlying gesture production.

During session 1, participants completed the Tower of Hanoi by pressing buttons on a computer to move the disks on the computer screen. When they performed a disk movement with a button press, the disk disappeared and then reappeared in the desired area. During session 2, participants again pressed buttons to move the disks. When they initiated a disk movement, this time, however, they viewed the disk moving up and over to the desired location in a curved trajectory. In the final session, participants completed the task with a mouse and were required to make curved movements to move the disks up and over the pegs. Once they initiated the movement, the disk disappeared and they did not see it again until it was dropped on the desired location. Thus, participants either saw or produced no curved movements, saw curved movements but did not produce them, or produced curved movements but did not see them.

Although we expected that the visual information was likely declarative and the motor information was likely non-declarative, to specifically discern the role of memory systems in driving gesture production, we also included patient populations. To more directly assess non-declarative contribution to gesture production, four participants with hippocampal amnesia – and severe declarative memory impairment – were included in the study. Assessing behavior of these patients is important because after a delay, these patients have very little to no declarative memory for having experienced the task before. Thus, any information in their gestures has to come from non-declarative memory.

Methods.

5.1. Participants. Participants included 4 (one female) hippocampal amnesic (HC) patients, 4 (three female), brain-damaged comparison (BDC) patients with damage outside of the medial temporal lobe and no declarative memory impairment, and 12 (4 female) healthy comparison (HC) participants that were matched both patient groups on age, handedness, sex, and years of education. The patients were recruited from the Patient Registry at the University of Iowa's Division of Behavioral Neurology and Cognitive Neuroscience. All patients in the HC and BDC groups have non-progressive lesions.

For the HC group, three patients experienced anoxic/hypoxic episodes (1846, 2363, 2563) resulting in bilateral hippocampal damage and the fourth had herpes simplex encephalitis (1951) leading to more extensive bilateral medial temporal lobe damage affecting the hippocampus, amygdala, and surrounding cortices (Figure 4). Structural MRI examiniations completed on 3 of the 4 patients confirmed bilateral hippocampal damage and volumetric analyses revealed significantly reduced hippocampal volumes. Participant 2563 wears a pacemaker and was unable to undergo MRI examination and thus their damage was confirmed by computerized tomography; damage was confined to the hippocampus. For the three anoxic patients there is no damage to the lateral temporal lobes or anterior temporal lobes. Patient 1846's medial temporal lobe structures were judged to be within the normal range through volumetric analyses.

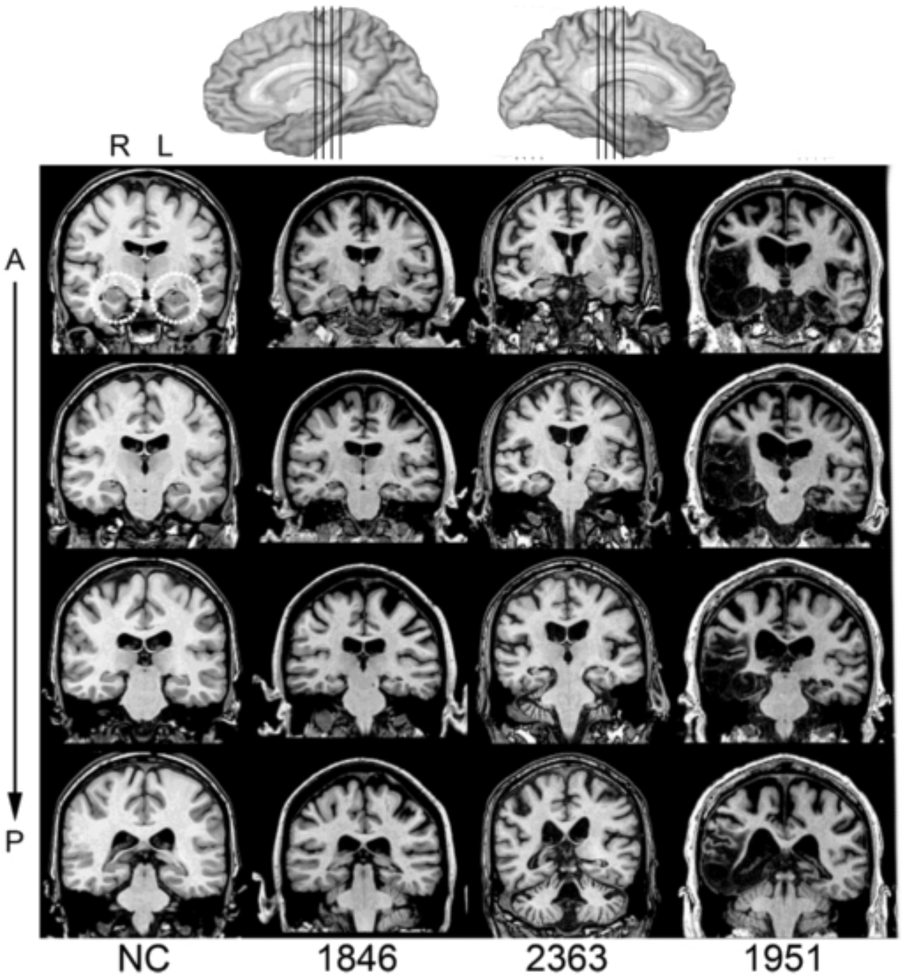

Figure 4. Magnetic resonance scans of hippocampal patients. Images are coronal slices through four points along the hippocampus from T1-weighed scans. Volume changes can be noted in the hippocampal region for patients 1846 and 2363 and significant bilateral MTL damage including the hippocampus can be noted in patient 1951. R = right, L = left, A = anterior, P = posterior, NC = healthy comparison brain.

Tests of neuropsychological functioning revealed a severe and selective impairment in declarative memory (M =57.6; Wechsler Memory Scale-III General Memory Index) while measures of verbal IQ, vocabulary, and semantic knowledge was within a normal range (Appendix A). Intact performance on naming and semantic knowledge suggests that lexical and semantic access is relatively normal as measured by standard neuropsychological testing. Patients were free of aphasia and had no motor impairments that interfered with the ability to gesture.

The BDC group was used to differentiate any deficits due to hippocampal damage from deficits due to brain damage more generally. BDC participants all had focal and bilateral damage to the ventromedial prefrontal cortex. Like the participants with hippocampal amnesia, the BDC performed in the normal range on neuropsychological tests of intelligence and language, were free of aphasia, had no motor impairments that prevented them from gesturing. In critical contrast to the participants with hippocampal amnesia, the BDC group had no lesions in the medial temporal lobe and performed within normal limits on standardized tests of declarative memory.

Patient	**Sex**	**Age**	**Hand**	**Ed**	**Chron**	**Etiology**	**WAIS-III FSIQ**	**WMS-III GMI**	**BN**	**TT**
318	M	73	R	14	38	Meningioma Resection	143	109	60	44
2025	F	64	R	14	15	SaH; ACoA	106	109	54	44
2391	F	67	R	12	14	Meningioma Resection	109	132	57	43
3534	F	74	R	12	4	Meningioma Resection	107	112	57	44
Mean (SD)	N/A		N/A			N/A				

Table 3. Demographic and neuropsychological characteristics of the vmPFC participants.

Non-brain damaged healthy comparison participants (NC) included 19 individuals without any neurological or psychiatric disease that were case matched to the AM and BDC participants on sex, age, handedness, and education.

5.2. Procedure. Participants visited the lab three times with four weeks in between each visit. They were told they would be completing and explaining a problem solving task called the Tower of Hanoi. In this task there is a tower of disks arranged from largest to smallest on the leftmost of three pegs. The goal is to move the disks one at a time from the first peg to the third peg, without putting a larger disk on top of a smaller disk. At the beginning of each visit, an experimenter described the rules to the participant with a picture of the ToH (Figure 5) present. Immediately after hearing the rules the picture was removed and the participant was prompted to explain to the experimenter how they think they would solve the ToH problem. They were given no feedback during their explanation. After their explanation, they had to solve the problem themselves.

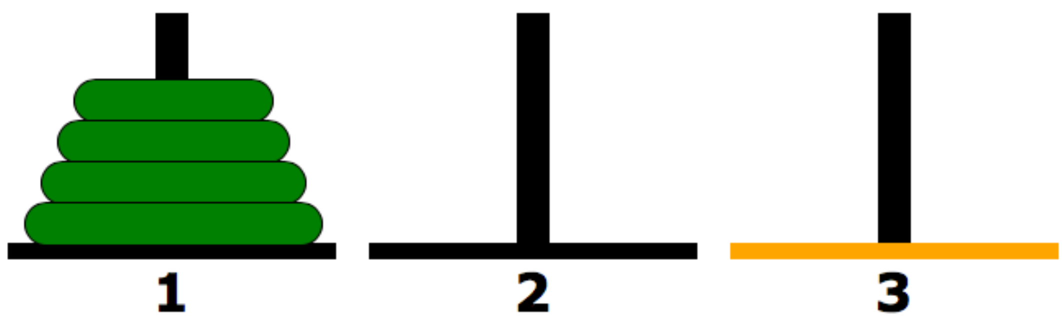

Figure 5. The Tower of Hanoi. The goal is to move all disks to the third peg only moving one disk at a time and not putting a bigger disk on top of a smaller disk.

On each visit, the visual and motor properties associated with the task varied (Figure 6). Visually, the disks either disappeared when moved and reappeared on the selected peg or visibly moved over the pegs in a curved trajectory. Motorically the task was either completed with button pressing to move the disks or by clicking and dragging the disks with the computer mouse. If declarative memory guides gesture production, then we should expect hand gestures to reflect what they have seen: if they have seen curved movements they should produce curved gestures. If non-declarative memory guides gesture production, then we should expect hand gestures to reflect what they have done: if they have used a mouse to move the disks in a curved way they should produce curved hand gestures.

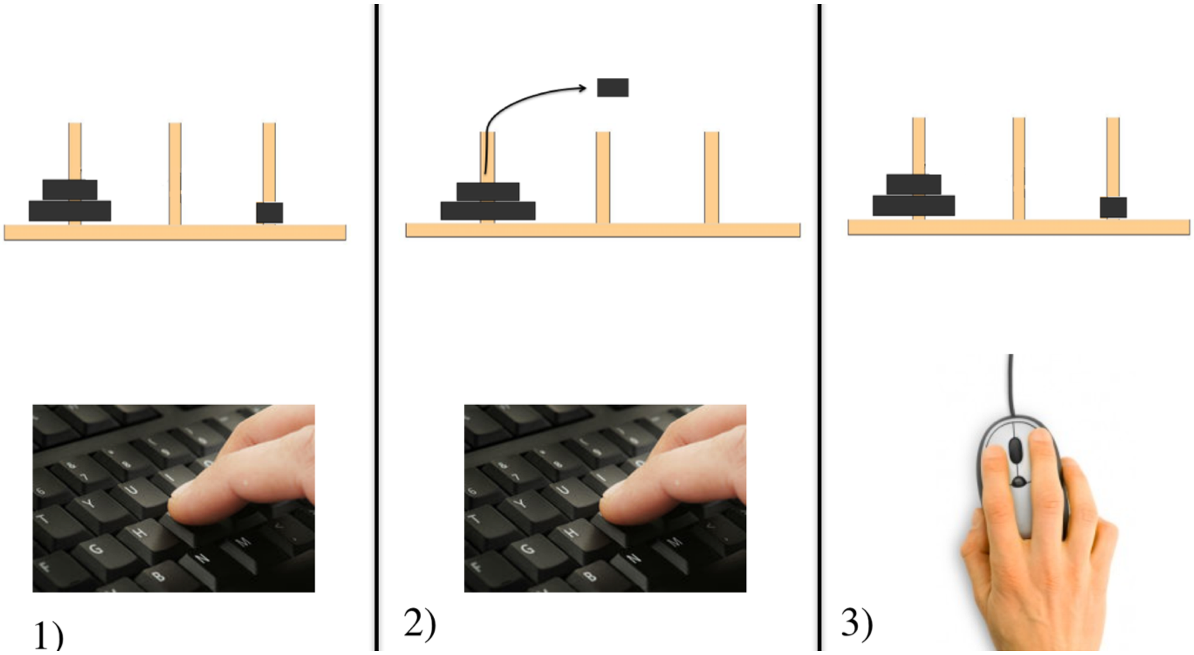

Figure 6. The visual and motor experiences received by participants on each session. In session 1, they pressed buttons and did not see visual disk trajectories. In session 2, they pressed buttons and viewed curved disk trajectories. In session 3, they made curved mouse movements and did not see visual disk trajectories.

On the first visit, participants pressed buttons and saw no visual trajectory. They used buttons 1, 2, and 3 on a standard keyboard. When they pressed a button, it highlighted the top disk on the corresponding peg. The next button that they pressed resulted in the disk moving to the indicated peg. In this first session trajectories of motion were not visible: the disk disappeared and then reappeared in the desired location. On the second visit, participants again pressed buttons. This time, they did see a visual trajectory: when they pressed a button to move the disk to the desired location, they viewed the disk moving up and over to the new peg in curved trajectory. On the final visit, participants used the mouse to move the disks. They had to click on the desired disk, hold down the button and move it to the desired location, and then let go of it. In order to force a curved trajectory, the disk would not make any lateral movement until it reached the top of the peg. When they initially clicked on a disk, the disk disappeared. As they moved it, the pegs that it was hovering over were highlighted so participants would know where the disk was. When they let go of the button, the disk was dropped onto the highlighted peg. After completing the ToH on each session, there was then a half-hour delay in which the participant engaged in a variety of other tasks. After the delay, an experimenter again presented the rules of the ToH along with a picture (Figure 5). The participant was asked if they had ever done the task before. The picture was then removed and the participant was prompted to explain how they would solve the task.

5.3. Coding. All sessions were video recorded for later analysis. Spoken language was transcribed and a total word count was generated for each explanation. Hand gestures were identified and annotated in ELAN (Lausberg & Sloetjes, 2009). Gestures were categorized as either transfer (representing disk movement) or non-transfer (not representing disk movement). Physical properties of the gestures were determined by using a technique that we developed to capture body movement (Hilliard & Cook, 2015a). The total number of gestures produced in each explanation was used to calculate a gesture rate (gestures per 100 words) for each explanation.

5.4. Analysis. Mixed effects regression models were used to predict each dimension of interest. Random effect structure was determined by using model comparison. Since there is no consensus regarding how to determine degrees of freedom for these models, we present coefficients and t-values, with t-values with an absolute value greater than 2 corresponding to a p-value of .05 or less.

Results

6.1. Declarative memory for task. At the start of the second explanation on each session, the experimenter asked the participant if they had completed the Tower of Hanoi before. All of the comparison participants reported memory for their previous experience on all sessions, indicating that they were able to encode and retrieve a declarative representation of their prior experience. For the patients with amnesia only one participant – patient 2363, who had prior experience with and semantic knowledge of the task – reported that he had done the task earlier that day, and this was only on session 2. Thus, three of the patients with amnesia clearly had a severely degraded declarative representation of the task or no declarative representation at all upon explaining how to complete it, and one patient with amnesia had some declarative knowledge of the task.

6.2. Spoken language. A total word count was generated for each individual explanation (Table 4). We assessed differences in the amount of spoken language produced with a mixed effect model predicting word count, log-transformed for normality, as a function of session number (one, two, or three), phase (pre- or post-task experience), group (amnesic, NC, BDC), and their two-way and three-way interactions. There were random intercepts for participant and comparison pair. There were no significant differences in word count for any of the predictors mentioned (Appendix B).

	1: Buttons, no motion		2: Buttons, curved motion		3: Mouse, no motion	
	pre: *M* (*sd*)	post: *M* (*sd*)	pre: *M* (*sd*)	post: *M* (*sd*)	pre: *M* (*sd*)	post: *M* (*sd*)
NC	212.2 (116.5)	249.5 (161.1)	226.3 (87.6)	290.2 (385.8)	170.3 (128.5)	187.5 (198.7)
AM	511.3 (635.8)	506.3 (411.1)	242.5 (225.2)	220.8 (214.9)	350.8 (244.5)	177.8 (88.7)
BDC	310.3 (107.6)	250.7 (15.9)	291.3 (413.0)	247.2 (78.7)	214.5 (39.9)	205.2 (19.8)

Table 4. The number of words produced by group in each explanation.

Since there appeared to be a decreasing trend in the number of words produced over the three sessions, we analyzed this possibility with a mixed effect model predicting word count, log-transformed for normality, as a function of explanation number (1-6), group, and their interaction with random intercepts for participant, session, and phase. Again, none of our fixed effects or interactions significantly predicted word count (Appendix B). Thus, the length of the explanations did not systematically vary between different explanations and did not appear to systematically change over time.

6.2. Gesture rate. Gesture rate was calculated by dividing the number of gestures produced in a single explanation by the number of words produced in that explanation. We analyzed gesture rate with a mixed effect model predicting gesture rate as a function of session, phase, group, and their two-way and three-way interactions. There were random intercepts for participant and comparison pair. None of our fixed effects or interactions reliably predicted gesture rate (Appendix A). Thus, gesture rate did not appear to be affected by an impairment in declarative memory (Table 5).

	Session 1		Session 2		Session 3	
	pre: *M* (*sd*)	post: *M* (*sd*)	pre: *M* (*sd*)	post: *M* (*sd*)	pre: *M* (*sd*)	post: *M* (*sd*)
AM	0.15 (0.09)	0.14 (0.05)	0.12 (0.11)	0.16 (0.05)	0.10 (0.08)	0.11 (0.15)
BDC	0.11 (0.05)	0.14 (0.12)	0.15 (0.09)	0.18 (0.14)	0.13 (0.04)	0.18 (0.16)
NC	0.14 (0.07)	0.19 (0.07)	0.16 (0.05)	0.17 (0.09)	0.13 (0.10)	0.15 (0.11)

Table 5. Gesture rate by group for each explanation.

6.3. Gesture curvature. A key feature of our design was the curvature that the participants experienced. In session 1, participants experienced no curvature: they pressed buttons to initiate disk movement and did not see any trajectories. In session 2, participants used button presses to initiate disk movement and viewed curved trajectories. If visual, declarative representations guide gesture production then we should observe gesture with the most curvature after this session. In session 3, participants used curved mouse movements to initiate disk movement but saw no visual trajectory. If motor, non-declarative representations guide gesture production then we should observe gesture with the most curvature after this session.

To assess curvature, we used the lmList function from the nlme package in R to fit a quadratic model to each gesture produced in each explanation. If the model for a gesture had significant negative curvature then that gesture was categorized as a curved gesture. The proportion of curved gestures to overall gestures can be seen in Figure 7. We then analyzed the likelihood of producing a curved gesture with a logistic regression model predicting the production of a curved gesture as a function of session, group, and their interaction, with a random intercept for participant. Session 3 served as the reference group, as our amnesic group yielded specific predictions about motor behavior and this session was the only session predicted to have curved motor movements. There was a main effect of session for session 1 ($B = -1.02$, $z = -3.54$, $p < .001$); the likelihood of a gesture being curved was significantly greater in session 3 than in session 1, indicating that gestures had the highest likelihood of being curved when curvature had been experienced motorically. This effect was not significant for session 2 ($B = -0.46$, $z = -3.54$, *ns)*. There were no significant differences in likelihood of a curved gesture between amnesic patients and healthy comparisons ($B = -0.57$, $z = -1.51$, *ns*) or amnesic patients and BDCs ($B = -0.61$, $z = -0.27$, *ns*). There was a significant interaction between session 1 and the NC group ($B = 1.39$, $z = 4.07$, $p < .001$); healthy participants were less likely to produce a curved gesture than amnesic participants in session 3 relative to session 1. This interaction was also significant in the same direction for the BDC group ($B = 1.16$, $z = 2.68$, $p <.01$). There was also a significant interaction between session 2 and the NC group ($B = 0.92$, $z = 2.40$, $p < .05$); healthy participants were significantly more likely to produce a curved gesture than amnesic patients in session 2 relative to session 3, indicating that viewing a curved trajectory affected the likelihiood of curvature showing up in their gesture more than it did for the patients with amnesia. This interaction was not significant for the BDC group interaction with session (B = -0.12, z = -0.27, *ns)*.

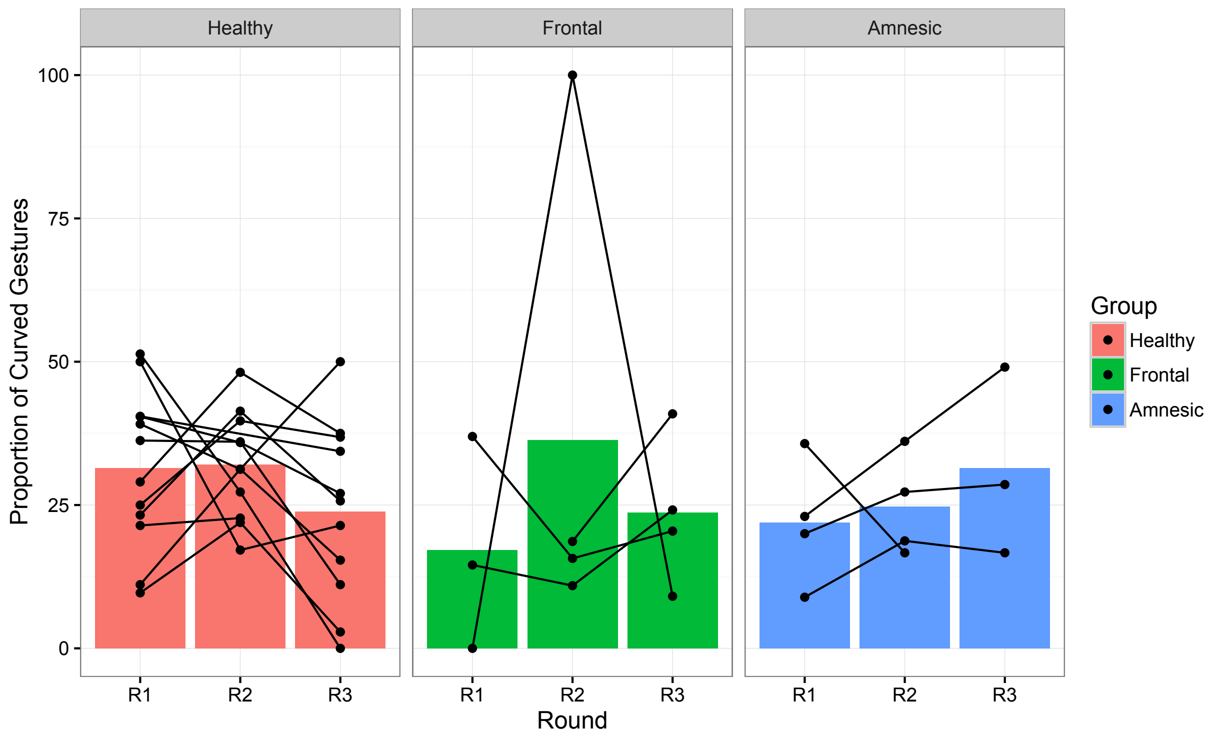

Figure 7. The proportion of curved gestures produced by participant by round. Healthy comparison participants were significantly more likely to produce a curved gesture in session 2, when they had viewed curved motion trajectories, than in session 3, when they had produced curved mouse movements. Patients with amnesia were significantly more likely to produce a curved gesture in session 3, when they had produced curved mouse movements, than in session 1.

We next subset the data by group to assess differences between rounds within each group. For the healthy comparisons, we used a model predicting the logit of the proportion of curved gestures in each explanation with fixed effect for round and a random intercept for participant. There was a significant difference between the likelihood of producing a curved gesture in session 2 and session 3 (B = 0.45, z = 2.47, $p < .05$); the likelihood of a curved gesture was greater in session 2 than in session 3; they were more likely to produce a curved gesture after viewing curvature than after producing curvature. There was also a significant difference between session 1 and session 3 ($B = 0.37$, $z = 2.01$, $p < .05$); the likelihood of a curved gesture was greater in session 1 than in session 3; even after experiencing no curvature they produced curved gestures more often than when they had produced curved mouse movements. Thus, for the healthy comparison group, they produced fewer curved gestures after producing curved movements compared with viewing curved trajectories.

For the amnesic group, the model predicted the likelihood of a curved gesture as a function of round with a random intercept for participant. There was a significant difference between session 1 and session 3 ($B = -1.02$, $z = -3.50$, $p < .001$); patients were significantly less likely to produce a curved gesture in session 1 than in session 3. There was no reliable difference between session 2 and session 3 ($B = -0.46$, $z = -1.37$, *ns*). Thus, amnesic patients were most likely to produce curved gestures in session 3 than in session 1, indicating more curvature after producing curved trajectories than after experiencing no curvature. Also, amnesic patients trended toward being more likely to produce curved gestures in session 3 than in session 2, indicating that their motor experience with curvature has a more robust effect on their gesture than their visual experience with curvature.

Finally, for the BDC group, there was a significant difference between session 2 and session 3 ($B = 0.58$, $z = 2.00$, $p <.05$); the likelihood of a curved gesture was greater in session 2 than in session 3, indicating that they, like the healthy comparisons, were more likely to produce curved gestures if they had viewed curved movements than if they had produced them. This difference did not reach significance for session 1 and session 3 ($B = 0.13$, $z = 0.40$, *ns*). Thus, their behavior followed that of the normal comparisons.

General Discussion.

We investigated if and how the visual and motor experience that people receive during the Tower of Hanoi task affects their gesture production when they later explain how to complete the task. Prior work investigating gesture production by using the Tower of Hanoi task has demonstrated that gestures reflect properties of the speaker's previous experience; gestures reflect the movement of the disks (Cook & Tanenhaus, 2009; Hilliard & Cook, 2015b). However, visual and motor experience are typically confounded. Here, we manipulated visual and motor properties of the task across three sessions to determine which information later appeared in gesture. We tested healthy and patient populations in order to assess the memory systems involved in gestures production. Our findings suggest that both memory systems can serve as mechanisms of gesture production.

7.2. Visual contributions to gesture production. We measured visual contributions to gesture production by examining whether the visual properties that participants experienced during task completion were evident later in gesture when they described how to complete the task. We predicted that after a delay, only the comparison groups would be readily able to conjure a declarative representation for their prior experience while the patients with amnesia would not. This prediction was borne out. The gestures produced by comparison participants after session 2 – when they had viewed curved trajectories and pressed buttons – contained a higher rate of curved gestures relative to session 3 – when they had produced curved gestures. This suggests that the visual properties of their task experience was affecting the form of their gestures. Despite the high rates of curvature, this did not comprise all of the gestures produced by comparison groups; a majority of the gestures that they produced were not curved. Although we cannot make any direct claims about what was being represented in the gestures that lacked curvature, it is certainly possible that these gestures were reflecting their motor behavior. Prior work with the ToH task in healthy adults has demonstrated that the handshapes produced in gesture reflect those experienced during task completion (Beilock & Goldin-Meadow, 2010; Cook & Tanenhaus, 2009). Our coding of gesture trajectory and analysis of curvature may not have captured this possibility.

The performance of the comparison groups relative to the amnesic patients on session 2 indicates that the visual information experienced during task completion is likely hippocampally reconstructed. The amnesic patients did not appear to encode and later retrieve the curvature information that was evident visually during task experience like the healthy and brain damaged comparison groups did. In session 3 – when participants did not view disk trajectories but did completed the task with curved mouse movements – healthy comparisons produced significantly fewer curved gestures than amnesic participants. This is further evidence that the healthy participants, who have the ability to access a declarative representation of their previous experience with the Tower of Hanoi, may be representing visual information in their gesture form. The amount of curved gestures that they produced in session 3 was lower than in session 2 as well, also supporting this interpretation. It is also possible that they are accessing something else.

7.3. Motor contributions to gesture production. Session 3 was the only session in which participants produced curved movements. Amnesic participants produced more curved gestures in session 3 than in session 1 and session 2. This suggests that their motor experiences can influence their gesture form, even in the absence of a declarative representation. This is striking because although hippocampal amnesic patients can improve on motor skills (Cavaco et al., 2011; Gabrieli & Stebbins, 1997), in this case, they are not actually performing the task again but instead just discussing it after a delay by being shown the tower and re-told the rules. One possibility for how this happens is that viewing and re-hearing the rules of the task later that day may activate motor representations that then influence gesture form. Further research with this population is necessary to determine how – in the absence of a fully-functioning hippocampal memory system – they are able to relate the motor information experienced during the task with their representation of the task itself.

7.4. Rate of gesture production: discourse versus action tasks. In the data present here, there were no significant differences in gesture rate by group: patients with amnesia gestured at similar rates to the comparison groups. This stands in contrast with our prior work demonstrating that patients with amnesia gesture at a lower rate than healthy comparison participants when engaged in discourse tasks (Hilliard, Cook, & Duff, submitted). In the previous work, participants were given a prompt about a past event – their account of JFK's assassination, their most frightening experience, how to make their favorite sandwich, and how to go grocery shopping – and had to describe them, and amnesic patients gestured at a lower rate than comparison participants. Why then are they unimpaired in gesture rate relative to comparisons in the task here? One possibility is that the tasks differentially rely on the hippocampus. Here, participants are describing an action task. Even though it does arguably require generating a representation of what is being discussed, it does not necessitate the access of a specific episode. Amnesic participants reported that they had not done the task before they produced their explanations. Thus, it did not appear that they were accessing a specific episode but rather using knowledge created on the fly based on the rules that were just presented, and they were able to effectively communicate this knowledge in speech. Nonetheless, their gestures communicated the actions that they would produce should they complete the task themselves. The discourse tasks, on the other hand, did require that the participants access and communicate about a specific episode. Because patients with amnesia are impaired at the reconstruction of past events (Kurczek et al., 2013) and have also likely not been able to update these memories in the same way as healthy comparison are able to do (Hupbach, Gomez, Hardt, & Nadel, 2007), we might expect that communication of this impoverished representation gesture rate would be impaired in tasks that require a rich recreation of a scene or event relative to the description of something motor.

7.5. Conclusion. Gesture is both visual and motor and thus is well-suited to communicate imagistic and motor information. The findings reported here suggest that both visual experience and motor experience are evident in gesture production. In healthy and vmPFC participants, curvature was most evident in their gesture when they had visual experience with curved visual trajectories. This suggests that while explaining their solution to the task, they mentally represented their early experiences with the task in a way that incorporated visual information. It is possible that this representation was hippocampally generated. In amnesic participants, curvature was most likely to be present in their gesture when they had motor experience with curved mouse trajectories. This suggests that gesture can also reflect motor experience. By understanding the mechanisms in memory that contribute to the rate and form of gesture production, we can better understand how and why gesture is produced across a variety of contexts.

Appendix A.

Word count model:

Predictors	**Estimate**	**t-value**
Intercept	5.10	14.63
Session 1	0.77	1.97
Session 2	0.39	-.01
Phase - pre	0.59	1.50
Group - Frontal	0.21	0.44
Group - Healthy	-0.07	-0.18
Session 1: Phase - pre	-0.80	-1.43
Session 2: Phase – pre	-0.56	-1.00
Session 1: Group – frontal	-0.62	-1.08
Session 2: Group – frontal	0.15	0.28
Session 1: Group – healthy	-0.45	-0.98
Session 2: Group – healthy	0.18	0.40
Phase - pre: Group – frontal	-0.56	-1.00
Phase - pre: Group – healthy	-0.68	-1.45
Session 1: Pre : Frontal	0.94	1.15
Session 2: Pre : Frontal	0.05	0.06
Session 1: Pre : Healthy	0.78	1.19
Session 2: Pre : Healthy	0.79	1.20

Gesture rate model:

-0.03	**-0.45**	**-0.03**
Intercept	0.12	2.97
Session 1	0.01	0.30
Session 2	0.04	0.77
Phase - pre	-0.02	-0.46
Group - Frontal	0.06	1.08
Group - Healthy	0.03	0.53
Session 1: Phase - pre	0.37	0.53
Session 2: Phase – pre	-0.02	-0.31
Session 1: Group – frontal	-0.50	-0.69
Session 2: Group – frontal	-0.39	-0.57
Session 1: Group – healthy	0.02	0.43
Session 2: Group – healthy	-0.02	-0.40
Phase - pre: Group – frontal	-0.003	-0.05
Phase - pre: Group – healthy	-0.03	-0.45
Session 1: Pre : Frontal	-0.02	-0.19
Session 2: Pre : Frontal	0.04	0.40
Session 1: Pre : Healthy	-0.06	-0.79
Session 2: Pre : Healthy	0.04	0.49

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Experiment 3: Hand gesture engages non-declarative memory mechanisms: evidence from word learning in amnesia

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Viewing and producing co-speech hand gesture facilitates learning and retention of the information being communicated. Despite the robust effects of gesture on memory, the cognitive and neural mechanisms by which gesture affects memory systems remains unclear. One possibility is that gesture's imagistic and iconic form leads to a more detailed declarative memory representation. This possibility implicates the hippocampus and surrounding medial temporal lobe as being instrumental in gesture's effects on memory. Alternatively, gesture's motor properties may engage the procedural memory system, implicating areas outside of the hippocampus and medial temporal lobe. To investigate these alternatives, we conducted a word learning task in which participant were presented with names for known objects both with and without gesture. Participants included 4 patients with bilateral hippocampal damage and severe declarative memory impairment and intact procedural memory, 4 patients with bilateral ventromedial prefrontal cortex (vmPFC) damage and no memory impairment, and 18 healthy comparison participants. Participants were presented with novel word forms while producing gesture, viewing gesture, or hearing without gesture. After a delay, free recall and object identification were assessed. Both the patients with vmPFC damage and the healthy comparisons performed well above chance at both the recall and object identification tests regardless of whether gesture was present at encoding. The patients with hippocampal damage were unable to recall the words. However, they were significantly more likely to correctly match an object to its novel label if it they had produced a gesture at encoding, but not if they had viewed a gesture or learned the word without gesture. These findings suggest that producing gesture can affect learning by engaging the non-declarative memory system and maybe be a promising avenue for improving learning outcomes in patients with severe declarative memory impairment.

Introduction.

When we talk, we gesture spontaneously with our hands. The gestures that we produce are related to spoken language both temporally and semantically (McNeill, 1992) and thus are integrated with the spoken message to construct and convey meaning (Goldin-Meadow & Singer, 2003; Hostetter & Alibali, 2008; Kendon, 2004). Gesture is known to facilitate learning and memory in a number of ways. When people gesture when they are learning something new, they are more likely to retain the new information, whether the gesture be spontaneous (Cook & Goldin-Meadow, 2006) or taught (Cook, Mitchell, & Goldin-Meadow, 2008). Moreover, passively viewing gesture leads to better memory for the content of spoken language than hearing the same content without gesture (Kelly, McDevitt, & Esch, 2009). Despite the robust effects of gesture on learning and memory, the cognitive and neural mechanisms supporting this relationship remain unknown.

One domain in which gesture's effects on learning have become most evident is recalling material presented verbally. Iconic gestures – or gestures that have a form that reflects the semantic content of speech (McNeill, 1992) – enhance memory for words and phrases relative to when the same information is presented only verbally (Zimmer, 2001). Although the passive viewing of iconic gestures has been shown to facilitate language learning (Kelly et al., 2009), the production of gestures – either spontaneous or instructed – also leads to better learning (Cook, Yip, & Goldin-Meadow, 2010). Producing gesture during learning appears to function similarly to producing action more generally: having people learn action phrases while producing the actions themselves – called the "enactment effect" – has been shown to lead to better learning outcomes (Engelkamp & Krumnacker, 1980). This facilitative effect of action while learning has also been found in both children (Thompson, Driscoll, & Markson, 1998) and elderly adults

(Feyereisen, 2009), and in patients with mild dementia (Hutton, Sheppard, Rusted, & Ratner, 1996). These benefits are evident in the quantity, retention, and ease of retrieval of the items learned with gesture.

Despite its action properties, it is not clear what form of memory is engaged or affected by gesture. Memory is classically divided into two functionally and anatomically distinct systems. Declarative memory, receiving critical support by the hippocampus and other MTL structures, supports the acquisition of new knowledge such as vocabulary and facts (semantic memory) and the details of time- and place- specific autobiographical experiences (episodic memory). Declarative memory supports relational representations by rapidly binding the arbitrary co-occurences of people, places, and things and their spatial, temporal, and interactional components (Davachi, 2006; Eichenbaum & Cohen, 2001; Konkel, 2008). Because these representations are relational, an entire memory and its individual elements can be created and retrieved separately or together. Thus, experiencing just one element of an experience can reactivate an entire memory. Moreover, this flexibility permits rapid integration with representations across modalities and accessibility to other processing systems.

Non-declarative memory, formed and retrieved independently of the hippocampus, supports motor and cognitive skills (Knowlton, Mangels, & Squire, 1996; Knowlton & Moody, 2008). In stark contrast to the flexibility of the declarative memory system, the representations created by the non-declarative memory system are incremental, inflexible, and inaccessible to conscious introspection or verbal report (Eichenbaum & Cohen, 2001; Reber, et al., 1996). Although non-declarative memories can be comprised of multiple elements, these elements are considered to be blended into an inseparable or unitized representation (Cohen & Eichenbaum, 1993; Henke, 2010) and cannot be individually reactivated. Learning via non-declarative memory mechanisms is typically slow and gradual and requires repeated exposure and practice. Thus, although both declarative and non-declarative mechanisms of memory are engaged during learning, they differ greatly in the representations that they support and the timecourse at which new information is acquired.

Properties of gesture seem to implicate different systems of memory. Gesture is distinct from speech in providing an imagistic, iconic representation. Thus, one possibility is that gesture facilitates the creation of an imagistic representation in the mind of the listener. Indeed, language comprehension has been shown to activate mental images (Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Glenberg & Kaschak, 2002), and the details of these mental images can be altered by changing the context in which a word is heard (e.g., processing a sentence with a flying eagle tends to lead to an image of an eagle with wings spread versus talking about an eagle in its nest (Zwaan, Stanfield, & Yaxley, 2002)). Mental images likely implicate hippocampal declarative memory as the neural circuitry involved in learning from gestures as the hippocampus would be a prime candidate for binding visuospatial information in gesture with the verbal information in speech together into one declarative memory representation.

Gesture is also motor behavior. An alternative possibility is that gesture could invoke a motoric and embodied form of the message that is processed via structures that support non-declarative memory. Gestures are motor actions and are often produced and comprehended without conscious awareness. Thus gestures may be processed in areas independent of the hippocampus, such as the motor cortex or striatum, potentially leading to deeper semantic encoding of the novel information. Behavioral support for this possibility comes from the aforementioned studies demonstrating the enactment effect; the production element seems to be critical for the enactment effect, as simply viewing a movement does not yield learning

(Macedonia, 2014). Moreover, an fMRI study demonstrating that novel words learned with the production iconic gestures yielded larger activation in a semantic network than those learned without gestures (Kroenke, Mueller, Friederici, & Obrig, 2013). However, the same study failed to find a behavioral benefit of iconic gesture production, making the implications of this findings less clear.

Previous research has been unable to address the effects of gesture on memory systems because both memory systems are typically active during encoding, consolidation, and retrieval. We addressed this issue by studying the behavior of a rare group of neurological patients with severe and selective impairment to just one system of memory: declarative memory. Patients with bilateral hippocampal damage have clear behavioral dissociations between what they can report in speech and what their motor movements reveal about past experience; these patients show distinct improvements over time in performance on motor tasks, such as rotary pursuit, without being able to report any evidence in speech that they remember ever previously experiencing the task (Gabrieli & Stebbins, 1997). Because these patients have only one fully-functioning memory system, this makes them an ideal group for examining questions regarding how gesture affects learning via their intact non-declarative memory system.

In order to examine how gesture affects learning in this population we focused on one specific type of verbal learning: word learning. Patients with hippocampal amnesia are known to be severely impaired at word learning (Gabrieli, Cohen, & Corkin, 1988; Postle & Corkin, 1998; Warren & Duff, 2014). This is due in part to the nature of word learning itself which requires the binding of an arbitrary relation between a word form and its meaning, a hippocampally-supported process. However, there have been demonstrations in this population of sparse, incremental semantic learning over hundred of trials (Hayman & Macdonald, 1992; Holdstock, Mayes, Isaac, Gong, & Roberts, 2002), particularly when the learned information can be anchored to old semantic memories (Skotko et al., 2004; Stark, Stark, & Gordon, 2005). Thus, structures exterior to the hippocampus and MTL may also play a role in the acquisition of new words (Sharon, Moscovitch, & Gilboa, 2011; Vargha-Khadem, Gadian, Watkins, Connelly, & Paesschen, 2009). Because patients with amnesia have severely impaired declarative memory, they are an ideal population for testing whether gesture can be leveraged to facilitate word learning by capitalizing on their intact non-declarative memory system.

In order to determine if gesture facilitates word learning via the non-declarative memory system, we exposed patients, both those with hippocampal damage and brain-damaged comparison participants, and demographically-matched healthy comparison participants to novel words that were assigned to common, everyday objects. Half of the words were learned with gesture and half the words were learned without gesture. There were two sessions: on the first, participants gestured during encoding and on the second, participants passively watched gestures, allowing us to determine the role of self-production in learning. After the encoding phase, there was a 30-minute delay followed by recall and object identification tasks. After 30 minutes, patients with amnesia would have lost all short term memory of the learning experience and so any difference in performance should reflect long-term memory processes. If gesture can support word learning via non-declarative learning mechanisms, then we expect to see a benefit from gesture in the patients with amnesia. If gesture can only support word learning via declarative mechanisms, we should see no benefit to learning through gesture in patients with amnesia.

Methods.

Participants. Participants included 4 (one female) hippocampal amnesic (HC) patients, 4 (three female), brain-damaged comparison (BDC) patients with damage outside of the medial temporal lobe and no declarative memory impairment, and 19 (8 female) healthy comparison (HC) participants that were matched to both patient groups on age, handedness, sex, and years of education. The patients were recruited from the Patient Registry at the University of Iowa's Division of Behavioral Neurology and Cognitive Neuroscience. All patients in the HC and BDC groups have non-progressive lesions.

For the HC group, three patients experienced anoxic/hypoxic episodes (1846, 2363, 2563) resulting in bilateral hippocampal damage and the fourth had herpes simplex encephalitis (1951) leading to more extensive bilateral medial temporal lobe damage affecting the hippocampus, amygdala, and surrounding cortices (Figure 8). Structural MRI examinations completed on 3 of the 4 patients confirmed bilateral hippocampal damage and volumetric analyses revealed significantly reduced hippocampal volumes. Participant 2563 wears a pacemaker and was unable to undergo MRI examination and thus their damage was confirmed by computerized tomography; damage was confined to the hippocampus. For the three anoxic patients there is no damage to the lateral temporal lobes or anterior temporal lobes.

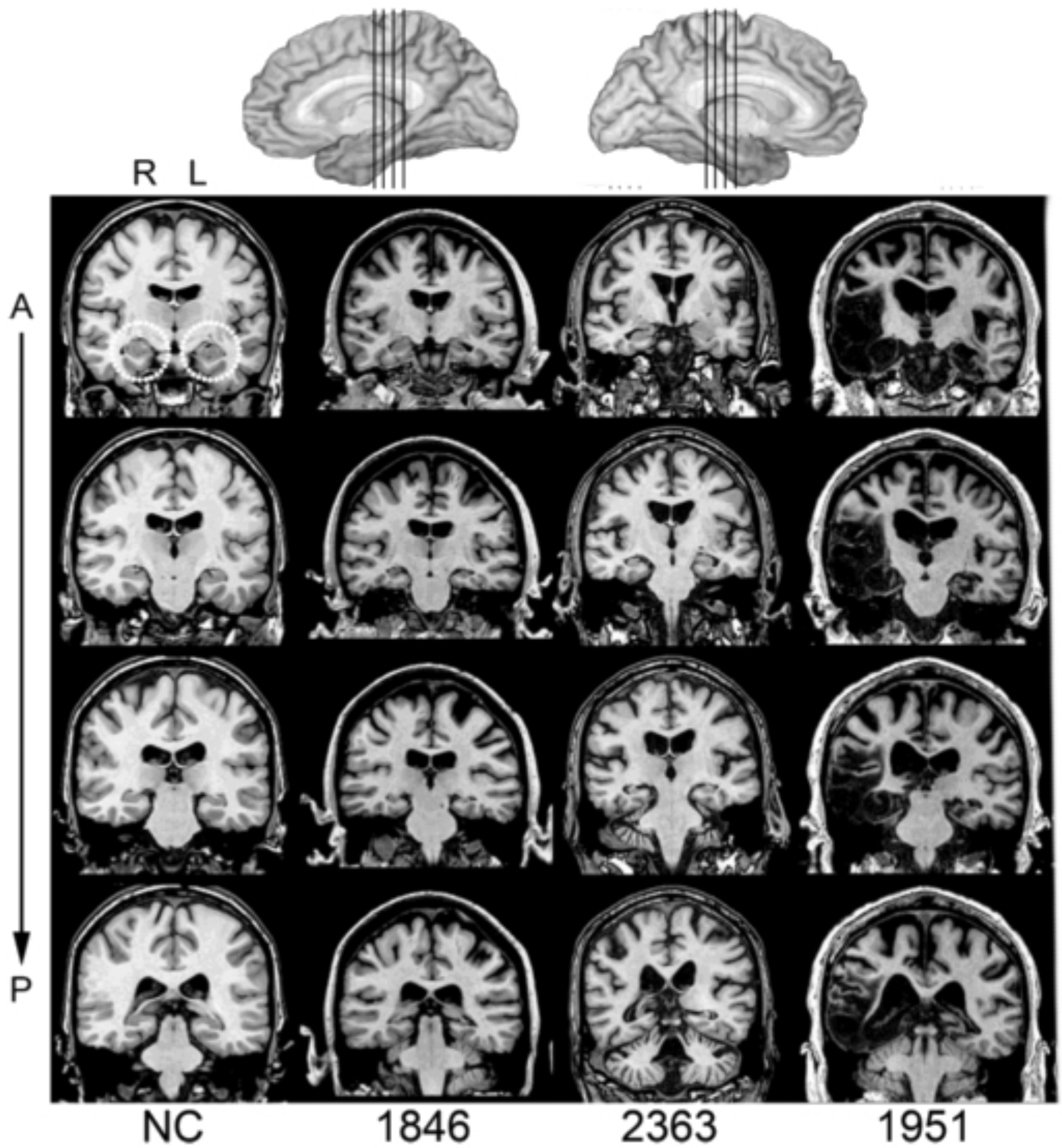


Figure 8. Magnetic resonance scans of hippocampal patients. Images are coronal slices through four points along the hippocampus from T1-weighed scans. Volume changes can be noted in the hippocampal region for patients 1846 and 2363 and significant bilateral MTL damage including the hippocampus can be noted in patient 1951. R = right, L = left, A = anterior, P = posterior, NC = healthy comparison brain.

Tests of neuropsychological functioning revealed a severe and selective impairment in declarative memory (M =57.9); Wechsler Memory Scale-III General Memory Index) while measures of verbal IQ, vocabulary, and semantic knowledge was within a normal range

(Appendix A). Intact performance on naming and semantic knowledge suggests that lexical and semantic access is relatively normal as measured by standard neuropsychological testing.

The BDC group was used to differentiate any deficits due to hippocampal damage from deficits due to brain damage more generally. BDC participants all had bilateral damage to the ventromedial prefrontal cortex. Like the participants with hippocampal amnesia, the BDC performed in the normal range on neuropsychological tests of intelligence and language, were free of aphasia, had no motor impairments that prevented them from gesturing. In critical contrast to the participants with hippocampal amnesia, the BDC group had no lesions in the medial temporal lobe and performed within normal limits on standardized tests of declarative memory (Table 6).

Patient	Sex	Age	Hand	Ed	Chron	Etiology	WAIS-III FSIQ	WMS-III GMI	BN	TT
318	M	73	R	14	38	Meningioma Resection	143	109	60	44
2025	F	64	R	14	15	SaH; ACoA	106	109	54	44
2391	F	67	R	12	14	Meningioma Resection	109	132	57	43
3534	F	74	R	12	4	Meningioma Resection	107	112	57	44
Mean (SD)	N/A		N/A			N/A				

Table 6. Demographic and neuropsychological characteristics of the vmPFC participants.

Non-brain damaged healthy comparison participants (NC) included 19 individuals without any neurological or psychiatric disease that were case matched to the AM and BDC participants on sex, age, handedness, and education.

Materials. Eight object-label pairings were generated, four for each session. Pilot data suggested that four was the maximum number of pairings that an amnesic could learn to criterion within an hour session. Objects were selected so that a gesture could be produced that resembled the action associated with the object, resulting in the following objects: *cup, hairbrush, phone, computer, violin, shovel, flute,* and *toothbrush (*for pictures, see Appendix A). All objects were paired at random with labels.

The labels generated were monosyllabic nonsense words selected from

All followed a CVC pattern and no two words learned in a session had the same onset or rhyme. Moreover, none of the words overlapped in onset or rhyme with the object with which it was paired. Two lists were created for each session such so a gesture was paired with a different object-label pairing in each list. Participants were randomly assigned a list for each session.

The gestures that were chosen for each label were iconic and depicted functional use of the objects. See Table 7 for information on each of the gestures paired with each object.

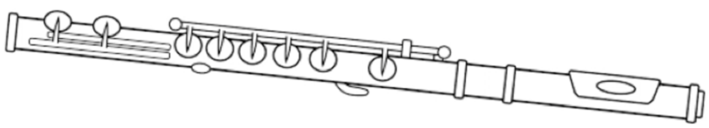
Object	Label (IPA)	Gesture (location)
cup	fat	*drinking motion (mouth)*
hairbrush	dok	*brushing motion (hair)*
computer	pʌm	*typing motion (chest)*
violin	sIg	*stroking motion (neck)*
shovel	gɛf	*digging motion (chest)*
flute	kIb	*playing motion (mouth)*
toothbrush	vær	*brushing motion (mouth)*
phone	mag	*phone motion (ear)*

Table 7. The object, its novel label, and the gesture that it was paired with. Gestures were paired with two of the objects from each session in two lists.

Procedure. Participants came to the lab for two sessions (as part of a 3 session study requiring a variety of cognitive and communicative tasks) and were told that they would be completing a word learning task in which they would be required to learn novel names for four common, known objects. The procedure was identical on each of the two days. There were three phases: 1) exposure, 2) free recall, and 3) object identification. After the learning phase there was a 30-minute delay during which participants engaged in conversation with the experimenter about an unrelated topic.

In the exposure phase, a familiar object (e.g., cup, phone) appeared on the screen for 4 seconds on each trial. A video then appeared of an experimenter providing the novel label (e.g., mog) in a sentence frame, "This is a [*label*]". The participant was instructed to repeat the sentence and the trial ended (Figure 9). Half of the trials were gesture trials: the experimenter in the video also produced a gesture with a novel label (Table 7). The participant's response after viewing the gesture with the sentence varied by session according to experimental instructions. In the first session, participants were instructed to produce the gesture while repeating the sentence – herein called the *production session.* In the section session, participants were instructed to only repeat the sentence, not the gesture – herein called the *perception session*. After the initial exposure to each of the object-label pairings, participants were instructed to attempt to produce the novel label prior to viewing the video again. If they did produce the label correctly the video was skipped. If they could not generate the label or generated it incorrectly, they again watched the video and repeated the sentence (and gesture, if applicable). This procedure continued until the participant produced all four novel words correctly in succession.

b)



a)

Figure 9. Picture showing the procedure of the experiment: a) the picture of the image is present for 2 seconds and then b) a video appears above it. The experimenter presents the label in the sentence “This is a *sib*”. If it is a gestured-with word, the gesture is produced in time with the object label.

After a 30-minute delay there was a recall phase. During this phase, an image of each of the objects was shown and the participant attempted to freely recall the novel label for each object. They were given no feedback during this phase.

Immediately after free recall, the object identification phase occurred. In this phase, all four objects were shown on a screen and the label for one of the objects was produced out loud by the experimenter (the same voice was used during exposure and object identification). The participant was instructed that they had to select the object that they thought matched the label, and if they were not sure to make a guess. Again, no feedback was provided during this portion of the experiment. Each object was the target in 4 trials for a total of 16 trials of object identification per session.

Analysis.

Our analyses consisted of mixed effects regression models. The random effect structure of each model was determined by using model comparison. We report coefficients and *t*-values for all of our models, with *t*-values with an absolute value of 2 of greater corresponding to a *p*-value of .05 or less. In the event that a model did not converge, we subset the data by session (session 1 and session 2).

Results.

Exposure phase. As expected, patients with amnesia took many more trials than participants from both comparison groups to learn the mappings between labels and objects (Table 8). To assess these differences, we used a mixed effect regression model that predicted the total number of trials taken to reach criterion (producing all 4 labels correctly in a row). There were fixed effects for session (production, perception) group (amnesic, BDC, NC), and their interaction and random intercepts for participant and list. The amnesic group served as the reference group. Group significantly predicted trials to reach criterion such that amnesic participants took more trials than both the BDCs ($B = -31.5$, $t = -2.57$) and NCs ($B = -28.24$, $t = -2.99$). Session also predicted trials to exposure ($B = 18.25$, $t = 3.57$); it took more trials to reach criterion in the perception session, when gestures were viewed but not produced, than the production session, when gestures were both viewed and produced. Session also significantly interacted with group for both BDCs ($B = -18.25$, $t = -2.52$) and NCs ($B = -16.83$, $t = -3.02$); patients with amnesia performed significantly worse in the perception session relative to the remaining two groups.

Group	Production session	Perception session
NC	15.68 (8.83)	17.10 (9.78)
BDC	11.00 (3.83)	11.00 (3.83)
AM	60.75 (11.44)	79.00 (17.34)

Table 8. Mean number of trials to reach criterion in each of the sessions. It took patients with amnesia significantly longer to reach criterion.

We then assessed the role that gesture played during learning. Because the comparison groups reached criterion so quickly, we restricted this analysis to patients with amnesia. We again analyzed the production and perception sessions separately. For the production sessions, we used a mixed effect logistic regression model that predicted the correct naming of an object as a function of trial number, trial type, and their interaction with random intercepts for participant and list. Trial type significantly predicted correctness such that words learned with gesture were *less* likely to be correctly produced ($B = -2.40$, $z = -3.10$, $p < .01$), indicating that words learned with gesture were learned more slowly. There was also a significant interaction between trial number and trial type; gestured-with words were more likely to be correctly produced as trial number increased relative to words that were not gestured with ($B = 0.04$, $z = 1.96$, $p = .05$). Trial number on its own did not predict correctness ($B = -0.0001$, $z = -0.01$, *ns).*

For the perception session, we used model of the same structure as for the production condition with the amnesic group. This time, gesture did not significantly predict correctness ($B = 0.30$, $z = 0.53$, *ns*), nor did it interact with trial number ($B = -0.01$, $z = -0.83$, *ns*). Trial number on its own did not significantly predict correctness ($B = 0.01$, $z = 1.38$, *ns*). Thus, patients with amnesia were influenced by gesture at encoding only in session 1, when gesture was produced.

Recall. Not surprisingly, amnesic patients performed poorly on recall (Figure 10). Only patient 2563 correctly produced a single new label when given an object (a word that had been gestured with during exposure). We analyzed performance on recall with a mixed effect model predicting total number of words correctly recalled as a function of group, session, and their interaction. There was a random intercept for participant. Group marginally predicted recall performance for the NCs (B = 2.24, t = 1.91); NCs recalled reliably more words after a delay. This difference did not reach significance for the BDCs (B = 2.00, t = 1.32). Session did not significantly predict recall performance (B = -0.25, t = -039), nor did session interaction with group for NCs (B = -0.25, t = -0.27) or BDCs (B = 0.24, t = 0.34).

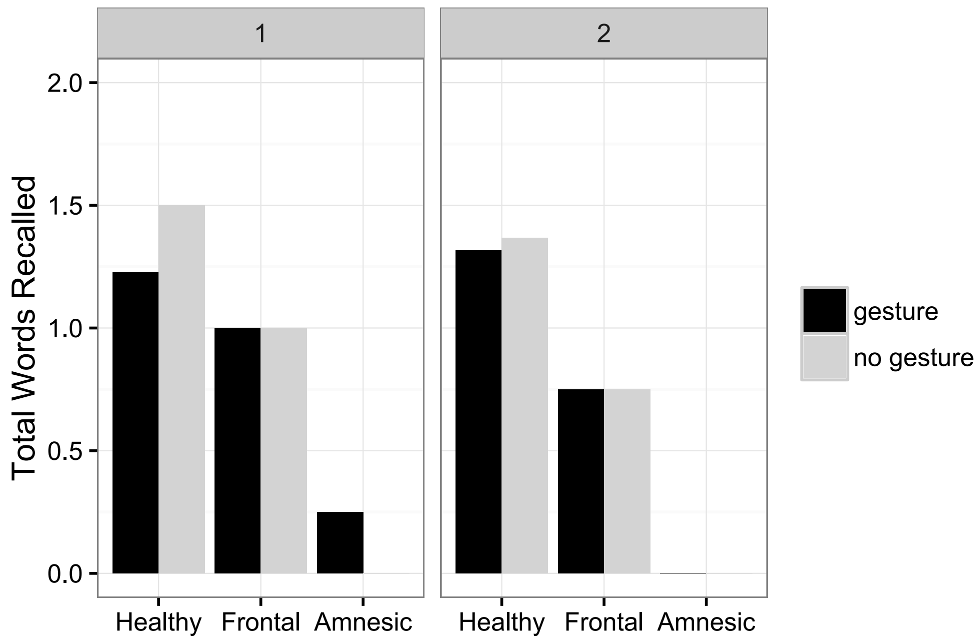


Figure 10. The average number of words correctly recalled by trial type (gestured-with and not gestured-with). There were a total of 4 words per session, 2 of each type. Session 1 is the production session, while session 2 is the perception session.

Object Identification. In the production session, NCs on average correctly identified 14.18 (SD = 3.42) objects, BDCs correctly identified 15.25 (SD = 0.96), and amnesic patients correctly identified 7 (SD = 2.58) (Figure 11). In the perception session, NCs correctly identified 15.24 (SD = 2.47), BDCs correctly identified 12.25 (SD = 4.92), and amnesic patients correctly identified 5.5 (SD = 2.38). Our first model assessed performance of all groups with a mixed effect logistic model predicting the correct identification of an object as a function of trial type, group, and their interaction with random intercepts for participant and list. We again subset the data into the production session and perception session. For the production session, trial type significantly predicted correctness ($B = 1.12$, $z = 2.17$, $p < .05$); a label was significantly more likely to be correctly mapped to an object if the label was learned with a gesture at encoding. Group also significantly predicted correctness; both the NC group ($B = 5.46$, $z = 3.97$, $p < .001$) and BDC group ($B = 4.60$, $z = 2.55$, $p < .05$) were significantly more likely to correctly identify an object compared to the amnesic group. Trial type also interacted with the NC group ($B = -2.71$, $z = -3.59$, $p < .001$); amnesic patients benefitted more from gesture than the NC group. This interaction was not significant with the BDC group ($B = -0.42$, $z = -0.30$, *ns*).

For the perception session, a model with the same structure was used. This time trial type did not significantly predict performance. Group again predicted performance; the NC group was more likely to correctly identify an object by its label than the amnesic group ($B = 6.35$, $z = 4.30$, $p < .001$). This effect did not reach significance for the BDC group ($B = 2.43$, $z = 1.52$, *ns)*, perhaps due to poor performance by BDC patient 2025. The interactions of trial type with both group did not predict performance for the NC group ($B = -1.33$, $z = -1.52$, *ns*) nor the BDC group ($B = 0.52$, $z = 0.55$, *ns*). Thus, it appears that learning with gesture helps with later object identification only if the gesture was produced at encoding. Moreover, amnesic patients were particularly more likely to benefit from gesture relative to the NC group.

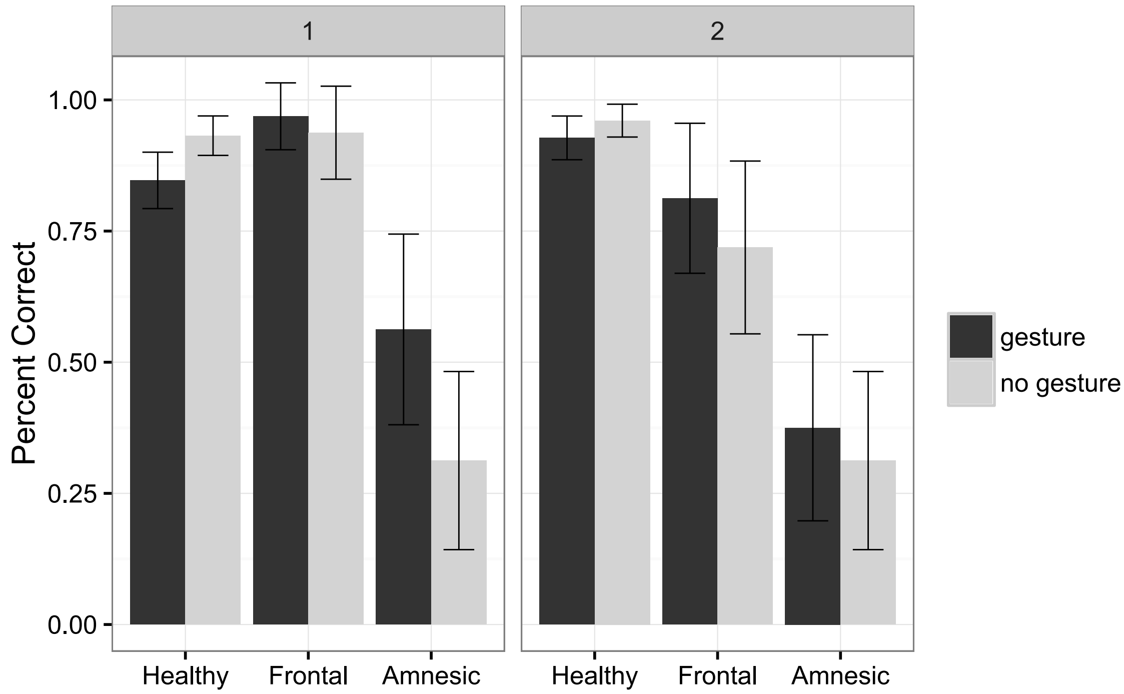


Figure 11. The average percent correct in the object identification task by group in each session. In session 1, patients with amnesia were more likely to identify an object correctly if they had produced a gesture with it at encoding than if they did not. This finding did not hold in session 2 – the perception session – when gestures were only viewed and not produced.

To ensure that gesture's facilitative effect on the amnesic patients' identification performance held without the NCs in the model – who appeared to perform worse for gestured-with trials – we ran another model restricting analysis to just the amnesic group in the production session. This model predicted correctness as a function of trial type with random intercepts for participant and list. Trial type significantly predicted performance ($B = -1.06$, $z = 02.00$, $p < .05$; Figure 12); patients with amnesia were significantly more likely to correctly map a label to its object when they had learned the label with the production of a gesture. When the same model was applied to session 2, trial type did not predict performance ($B = -0.28$, $z = -0.53$, *ns*).

Lastly, we tested whether or not the amnesic patients' performance in the object identification task differed from chance for both the gestured-with and not gestured-with objects in the production session. We used two two-sample t-tests to examine whether the mean of the observed values differed from a mean of 2, which is the number of objects that would be correctly identified at chance levels for each type of trial. For the gestured-with objects, amnesic patients selected the correct object-label mapping at above chance levels ($t(3) = 5, p < .05$). For the not gestured-with objects, amnesic patients selected the correct object-label mapping at chance levels ($t(3) = 0.52, p = .64$).

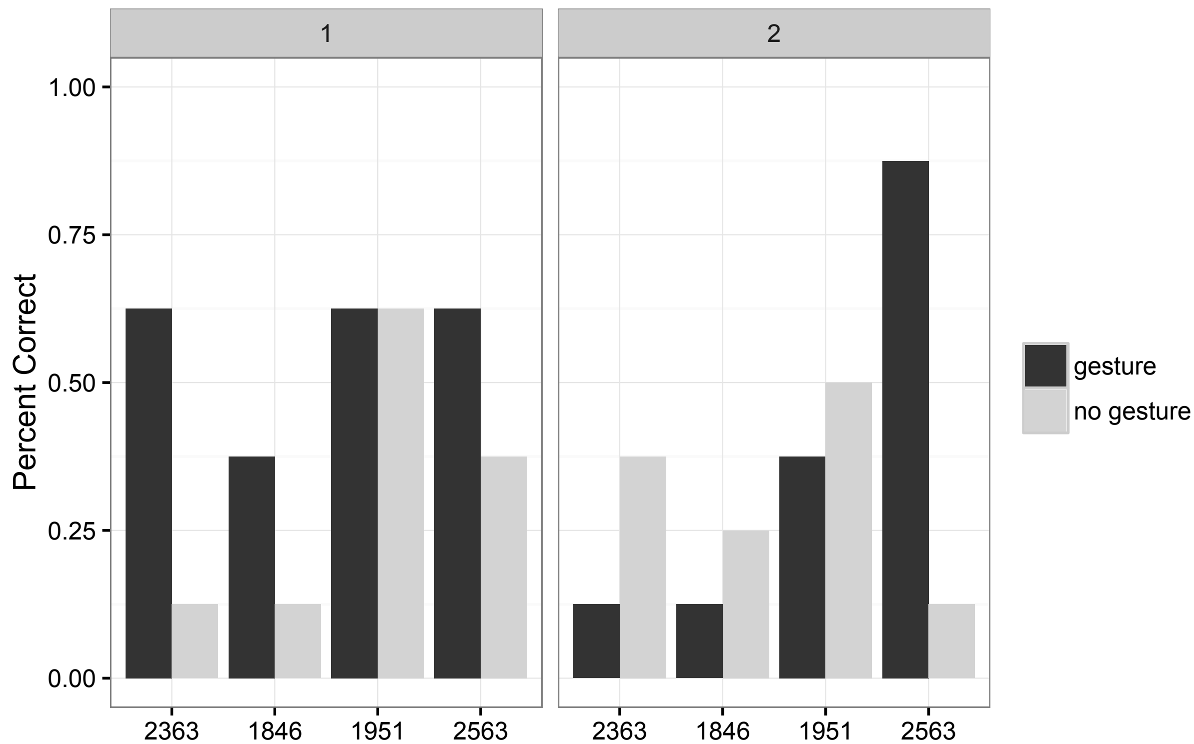


Figure 12. Percentage correct on the object identification task by the four patients with amnesia in both sessions. In the production session, gestured-with objects were significantly more likely to be identified by their label than objects not gestured-with. This was not found in perception condition.

Finally, we analyzed the structure of errors in the object identification task. We did not predict that our comparison groups would benefit in the same way from gesture as the amnesic patients, as our criterion for ending exposures meant that would receive many fewer trials than the amnesic patients (as they indeed did). However, we also did not expect to see a detriment in object identification for labels learned with gesture, as we saw in the production session. We reasoned that the NC group may not have had enough exposures to sufficiently bind the label, object, and gesture. If this is the case, then we might expect their errors to reflect that they have formed a category of words learned with gesture but have not yet correctly bound the label to the specific gestured-with objects. To test this, we examined whether errors were systematically more likely to be made within a category (substituting a gestured item with another gestured item) than across a category (substituting a gestured item with a non-gestured item or vice versa). Given an error on a single trial, there is a 33.33% chance that an error made will be within the category and a 66.67% chance that an error will be made across the category. If the rate of errors is more likely to be within then across, this would indicate that a category has been formed. Indeed, normal comparisons appear to make within-category errors at a disproportionately high rate for the gestured-with items in session 1 (Table 9).

		Gesture				No Gesture				Total Errors All Trials
		Within	Across	**Total**	Percent within chance=33%	Within	Across	**Total**	Percent within chance=33%	
Prod	AM	2	9	**11**	22%	13	12	**25**	52%	36
	BDC	0	1	**1**	0%	1	1	**2**	50%	3
	NC	15	10	**25**	60%	2	12	**14**	14%	39
Perc	AM	6	16	**22**	27%	6	14	**20**	30%	42
	BDC	0	8	**8**	0%	1	6	**7**	17%	15
	NC	5	6	**11**	45%	0	6	**6**	0%	17

Table 9. Errors made in the object identification task. Normal comparisons were reliably more likely to make a within-category error on the gestured-with items in session 1

We used a mixed effect logistic model predicting the likelihood of a within-category swap error (swapping a gestured object with another gesture object or non-gestured object with another non-gestured with object) as a function of the trial type, group, and their interaction with a random effect for participant. For the production session, trial type significantly predicted the likelihood of a within-category error ($B = -2.71$, $z = -2.63$, $p < .01$); for the items that were gestured with at encoding, there was less of a chance of a within-category error. This effect appears to be driven by the amnesic and BDC participants. There was also a marginal interaction of trial type and the NC group ($B = 2.82$, $z = 1.78$, $p = .075$); NC participants were more likely to make a within-category error than patients with amnesia. As can be seen in Table 9, a majority of the errors made by NC participants on the gestured trials were within-category errors. To assess if these errors occurred at a level greater than chance, we used a t-test that compared the percentage of within category errors to a value of 33.3 percent. Healthy comparison participants did indeed make within category errors a rate that was significantly greater than chance $t(41) = 4.80$, $p < .001$).

We used a model of the same structure for the perception session. This type, none of the fixed effects reliably predicted the likelihood of making a within-category error. Trial type ($B = 0.30$, $z = 0.42$), BDC group ($B = -1.12$, $z = -0.89$), NC group ($B = -18.56$, $z = -0.003$), trial type x BDC group ($B = -16.75$, $z = -0.004$), and trial type x NC group ($B = 19.00$, $z = 0.003$) did not reliably predict performance. Thus, there were no systematic differences in error structure in the object identification task in the second session.

Discussion.

We investigated if the production and perception of hand gesture facilitated word learning in patients with severe hippocampal amnesia, patients with vmPFC damage, and healthy comparison participants. A substantial body of research on gesture has demonstrated that presenting new verbal information with gesture leads to better learning of the material than presenting it without gesture (Cook et al., 2010; Kelly et al., 2009; Macedonia, 2014). We sought to uncover the mechanisms in memory that support this facilitative effect. Our findings demonstrate that gesture can indeed affect the ability to bind novel labels with objects. Producing gesture during encoding affected participants' ability to identify objects by name after a delay. Most notably, the patients with amnesia were significantly more likely to correctly identify an object by name when they had learned that name in tandem with the production of a gesture. This suggests that gesture engages non-declarative learning mechanisms in order to facilitate memory. The patients with amnesia are severely impaired at the acquisition of new declarative information, and our findings suggest that learning new verbal information in tandem with a gesture may have the potential to rescue this ability.

Critically, this benefit in object identification was only observed when the patients with amnesia had gestured at encoding. Passively viewing a gesture did not lead to enhanced object identification performance; the amnesic patients identified objects at chance levels when they had learned the novel names with a viewed gesture, perhaps because the producing gesture may have engaged non-declarative learning mechanisms.

Indeed, many features of the learning context here implicate non-declarative memory. The first concerns the information that was learned: novel word forms were mapped on to familiar objects, and the gesture was related to the object in a non-arbitrary way. Prior work with hippocampal amnesic patients has demonstrated that the acquisition of new information is more likely if the new information can be anchored to an already existing memory (Skotko et al., 2004). Gesture, particularly with an iconic, non-arbitrary form, may have enhanced the likelihood of anchoring the new label to already existing information. Second, like previous studies demonstrating the acquisition of semantic knowledge in patients with amnesia, learning was slow relative to the comparison groups (O'Kane, Kensinger, & Corkin, 2004; Stark et al., 2005); it took more than triple the exposures for the patients to reach criterion. Non-declarative learning typically occurs on a much slower timecourse than declarative learning. Still, the patients with amnesia were still able to successfully bind all the objects to the labels in around a twenty minute exposure phase. Lastly, although they were able to identify objects by their labels after a delay if they had learned the labels with the production of a gesture, they were not able to freely recall the object names. There is no evidence for declarative learning, but rather, they have been able to associate the label, object and gesture to succeed on the object identification task.

An alternative interpretation of these findings is that gesture may have facilitated unitization, a process through with multiple disparate pieces of information can be combined into a single functional unit to be maintained in memory (Tulving & Patterson, 1968). More recent work on this processing mechanism has demonstrated that action, particularly self-generated action, may promote unitization to the extent that is rescues declarative-like learning in hippocampal amnesics (Ryan, Moses, Barense, & Rosenbaum, 2013). The same mechanism may be at work here; the non-arbitrary gesture produced in temporal coordination with the label may have led the label, gesture, and the object (represented by the gesture form) to be bound together into one representation. This would potentially explain how the patients with amnesia were able to identify objects at levels above chance after a delay, a skill at which they are known to be significantly impaired.

Although patients with amnesia clearly benefitted from producing gesture, this same benefit was not evident for the comparison groups. The reasons for this are twofold. First, the performance of the comparison groups was near ceiling; the BDC group was nearly perfect at identifying objects regardless of whether a gesture was seen or produced or not. Surprisingly, the healthy comparison group was not at ceiling; it appeared that they had some detriment in object identification when they had learned the labels with a production of a gesture (production session) relative to without gesture (perception session). However, analysis of the structure of the errors made by healthy comparisons during the object identification phase showed that for words learned with gesture, they were more likely to select another gestured item than they were an item that was not gestured with in session 1. This indicates that that may have suffered some detriment in object identification because the label, object, and gesture may not have all been sufficient bound together. The normal comparisons may not have had enough exposure to the mappings to have created a lasting link between all three components. This may explain why rather than being at ceiling at object identification, they instead performed less well on the gestured-with label-object mappings, for which they frequently transposed the labels.

Both the error structure data and the object identification performance in patients with amnesia suggest that non-declarative learning mechanisms are engaged when learning via gesture. Gesture is motor behavior and non-declarative memory supports the learning of motor skills and habits. The relationship between non-declarative memory and gesture is evident in gesture production as well; the gestures that people produce can reflect their prior motor experiences, even at the level of the handshapes made (Cook & Tanenhaus, 2009). Still, our results do not suggest that motor behavior is the only property of gesture that affects learning. The temporal coordination of gesture with spoken language (Habets, Kita, Shao, Ozyurek, & Hagoort, 2011; Wagner, Malisz, & Kopp, 2014) and gesture's iconic, non-arbitrary form (McNeill, 1992) likely also contributed to learning. Motor behavior was the feature that was critical to learning for the patients with amnesia and this feature appeared to affect healthy comparison participants as well. Future work is necessary to examine how features of gesture engage different memory systems, both independently and in conjunction with each other.

These findings also provide exciting new opportunities for rehabilitative strategies for patients with amnesia, who are typically severely impaired at word learning (Ullman et al., 1997; Warren & Duff, 2014). Here, we found that their ability to identify objects was partially rescued if they learned the object labels while producing iconic gesture. They were still severely impaired relative to comparison groups, particularly at recall of object names. This is likely because recall is thought to be a declarative memory task. Object identification likely relies on structures that support recognition memory external to the hippocampus. However, the patients with amnesia exhibited more than just pure recognition memory. Rather, they recognized a label and bound it to an object. This presents gesture as a potential rehabilitative or compensatory strategy for this population. More work is needed to determine if gesture is enhancing a system already in place or if gesture engages an entirely new type of learning in these patients.

From this work, we have uncovered that gesture can engage non-declarative memory mechanisms in service of word learning. After producing gesture at encoding, patients with severe hippocampal amnesia were subsequently able to identify an object by a novel label at above chance levels.

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Summary

Together, these works comprise an initial attempt at directly relating the contents of memory representations with gesture production. We have demonstrated that hand gesture is supported by and reflects information from both declarative and non-declarative systems of memory. Additionally, we have found that producing gestures during learning can facilitate memory for new label-object mappings in patients with amnesia, who are typically severely impaired at this task. The results of each experiment will first be discussed and synthesized and future lines of work will be addressed.

The first study demonstrated that hippocampally-generated memory representations can affect whether or not a gesture is produced when describing past declarative content; patients with amnesia gestured at a lower rate than healthy comparison participants. Moreover, healthy comparisons gestured at a higher rate when they communicated information that contained a higher proportion of episodic content. This is the first demonstration that has linked the complexity of hippocampally-generated representations to gesture rate and will serve as the groundwork for future work linking memory and gesture.

First, the mechanistic account of what causes more gestures with higher rates of episodic memory content remains to be understood. Although we have inferred that the representations that contain more episodic details are in turn more complex – or more hippocampally dependent – the precise content of these representations is yet to be discovered. One possibility is that the ability to generate complex spatial and relational representations directly underlies this finding; indeed, existing theories of gesture production focus on space and action as a potential mechanism of gesture production (Hostetter & Alibali, 2010; Kita & Davies, 2009). If this is the case then it is possible that the patients with amnesia – who are known to be impaired at relational memory – simply choose to discuss fewer spatial and relational details in their narrative, leading to fewer gestures overall. The use of discourse tasks in the future that are more constrained in content - in tandem with a complex coding scheme capturing content – will help elucidate precisely what leads to less gesture in patients with amnesia in conversation.

Another factor that may affect gesture rate that we did not address in Experiment 1 the effect of the presence of a listener. My prior work has indicated that speakers alter their gesture rate and form as a function of their listener's knowledge (Hilliard & Cook, 2015; Hilliard, O'Neal, Plumert, & Cook, 2015). It may be that patients with amnesia – who have impaired declarative memory – are not able to readily represent their listener's knowledge states in the same way that healthy people can. This may be in part responsible for why we do not find the same increase in gesture rate with increasing episodic information as we do for the patients with amnesia; they may have not been able to encode what their listener does and does not know, and thus default to gesturing at a low rate. This possible finding would be at odds with work examining the effect of increasing listener knowledge on patients' speech; with increasing listener knowledge, speakers persist in their use of the indefinite article *"a"* for repeated referents while comparisons switch to the definite article *"the"*. Still, the findings of Experiment 1 cannot directly tease apart these two possibilities, and I thus plan to do so in future work.

While Experiment 1 addressed only how gesture rate was affected by memory representations, Experiment 2 manipulated variables that we hypothesized may lead to differences in gesture form as well. Healthy participants produced fewer curved gestures when they did not view curved visual motion trajectories than whey they did, despite producing curved mouse movements (visit 3). This suggests that the healthy participants were representing the task mainly by relying on what they had seen visually rather than what they had produced motorically. Because they were able to readily generate a multifaceted hippocampal representation for their earlier experience, they were in turn able to incorporate a multitude of elements into their Tower of Hanoi explanation.

Although they had this representation available to them, it is quite likely that comparisons did not rely solely on their visual memory for the event to guide their motor behavior. Indeed, their representation likely included motor information as well. This may be why 1) the curvature that they produced in the first visit – when no curvature was viewed – was similar to that of the second visit – when they viewed curvature visually and 2) they produced a mixture of curved and other gestures, some of which may have been reflecting motor movements. Our findings in this population have only demonstrated that taking away visually-presented curvature information lead to less curved gesture. My future work will focus more greatly on other aspects of form beyond curvature, like handshape, to help further uncover precisely how what is being represented in each utterance affects the form that gesture takes.

The patients with amnesia - who had no hippocampally-generated representation available to them at all – produced the most curvature in their gesture when they had produced curved mouse movements than when they had viewed curved trajectories. Although this finding may initially seem obvious, it was yet unknown if *any* of their prior experience would be evident in their gesture. This is because in order for their gesture to illustrate their prior experience, they would have had to someone encode that the Tower of Hanoi task was bound with the movements that they made when they were later presented with the task. It is unclear exactly how they succeeded at this. It may be that presenting them with the picture of the Tower of Hanoi activated their prior movement representations even though they were not physically repeating the task; amnesic patients improve at new motor skills despite not explicitly recalling encountering them. Alternatively, one less likely possibility is that completion of the task primed a particular set of motor movements, which were still primed after the half an hour delay. This alternative is unlikely, given that there were a multitude of intervening tasks. Still, our future work will address this.

Taken together, Experiments 1 and 2 suggest that addressing gesture from a multiple memory systems perspective is a useful framework for considering how our hands reflect what we have in our minds. Clearly, both hippocampal declarative representations and non-declarative representations affect the way that we gesture. What remains to be uncovered is how these representations differentially affect rate and form. Patients with amnesia gestured at a lower rate when describing past events. However, this same deficit in gesture rate was not seen in the Tower of Hanoi task. It is possible that the task demands – and the memory systems that support these demands – may have led to the different findings. In the first study, the task required the generation of a hippocampally-mediated representation, something that patients with amnesia are known to be impaired at doing. In the second study, the task required describing how to solve a motor task. In may be that the motor properties of the task, along with the visual presentation immediately before the explanation, allowed the patients with amnesia to access a representation of the task that was not hippocampally mediated. It would be possible to address this possibility by directly varying the task demands in a variety of discourse tasks to determine if and when patients with amnesia demonstrate impaired rates of gesture relative to comparisons, and, in fact, I am currently conducting this work.

More generally, these data will serve as a starting point in the creation of a gesture production framework that is biologically plausible and can directly explain what underlies the content of our gestures. Current gesture production theories tend to focus on gesture rate as the central component of the theory: what causes a gesture to be produced? Our data suggest that aside from spatial or action properties, it is possible that the imageability of the underlying representation determines the rate of gesture production: if an idea or concept can be clearly and readily brought to mind, then there are more features available to gesture about. This describes why patients with amnesia gestured less than comparison participants in the discourse tasks: they cannot conjure an imageable representation in the same way that people with an unimpaired hippocampus can. Additionally, both systems of memory contribute to the form that gesture takes during production: we found that gesture can reflect both prior motor experience and a visual representation that people have for a task. By continuing to examine how people alter their gesture as a function of the task demands and of the quality and complexity of their own representations in memory, I hope to flesh out a theory of gesture production that can speak to both how and when gestures are produced.

The findings of Experiment 3 address the link between gesture and memory from a different angle, by investigating how gesture production may seek to enhance learning and memory for the learner. We designed our study in such a way that it focused on the patients with amnesia; since the findings of Experiment 2 suggested a link between non-declarative motor representations and gesture production, it seemed possible that gesture could potentially enhance learning in this population as well. It is generally accepted that the ability of patients with hippocampal amnesia to acquire new declarative information is severely impaired. Our findings have demonstrated that by requiring gesturing at encoding, patients with amnesia can acquire new label-object mappings in a period of just 20 minutes, and these mappings can be maintained over a 30-minute delay.

The implications of this finding are twofold: first, it offers a potential avenue for rehabilitation for patients with amnesia and potentially those with less severe memory impairments. Here, we stopped in training as soon as they reached criterion. Several of the training studies that currently exist demonstrating new learning in this population have included hundreds of training trials over a multitude of days (O'Kane, Kensinger, & Corkin, 2004; Verfaellie, Kose, & Alexander, 2000). Since this type of slow, laborious learning likely engages non-declarative learning mechanisms, it is possible that with more repetitions of the gesture-label-object mappings that their outcomes would continue to improve.

Second, this suggests that systems of memory may not be as distinct as commonly thought. Although the information that was acquired was something that was thought to be a declarative skill: the binding of an object and label, the features of this learning context suggest that this learning emerged from the non-declarative memory system. Clearly, this binding is not as robust as the binding supported by the hippocampal system; patients could only identify objects and could not recall them. Still, that they could recognize any bound pairs at all suggests that there may be some engagement of their declarative system, although impaired, in order to show learning. Future work will seek to uncover precisely how this learning occurs mechanistically.

Ultimately, the work presented in this dissertation is novel in its attempt to bridge literatures on hand gesture and memory. This work has provided a framework for thinking about gesture production that can explain a wide range of gesture data and hints at the cognitive and neural mechanisms that support this behavior. Moreover, it has set the stage for a fruitful research career in which I plan to continue to elucidate the relationship between memory and language. By continuing to work with patient populations, employing new methods, and approaching and situating my research questions within both the language and memory literatures, I plan to address the open questions that this dissertation poses throughout my career. Memory and language are crucial for everyday functioning, and uncovering as much as possible about how they function and interact can benefit rehabilitative strategies, educational principles, and daily life.