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Abnormal semantic knowledge in a case of developmental amnesia

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ABSTRACT

An important theory holds that semantic knowledge can develop independently of episodic memory. One strong source of evidence supporting this independence comes from the observation that individuals with early hippocampal damage leading to developmental amnesia generally perform normally on standard tests of semantic memory, despite their profound impairment in episodic memory. However, one aspect of semantic memory that has not been explored is conceptual structure. We built on the theoretically important distinction between intrinsic features of object concepts (e.g., shape, colour, parts) and extrinsic features (e.g., how something is used, where it is typically located). The accrual of extrinsic feature knowledge that is important for concepts such as *chair* or *spoon* may depend on binding mechanisms in the hippocampus. We tested HC, an individual with developmental amnesia due to a well-characterized lesion of the hippocampus, on her ability to generate semantic features for object concepts. HC generated fewer extrinsic features than controls, but a similar number of intrinsic features than controls. We also tested her on typicality ratings. Her typicality ratings were abnormal for nonliving things (which more strongly depend on extrinsic features), but normal for living things (which more strongly depend on intrinsic features). In contrast, NB, who has MTL but not hippocampal damage due to surgery, showed no impairments in either task. These results suggest that episodic and semantic memory are not entirely independent, and that the hippocampus is important for learning some aspects of conceptual knowledge.

1. Introduction

Developmental amnesia can result from early extended hippocampal system pathology, often due to perinatal hypoxia, and is characterized by a pronounced deficit in episodic recollection starting early in life. In addition to a lack of episodic recollection, individuals with developmental amnesia present with severe difficulties navigating in familiar environments, remembering where items are placed, and orienting themselves by date and time (Vargha-Khadem et al., 1997). In clinical neuropsychological tests of long-term memory, individuals with developmental amnesia score far below the general population. However, despite having severe episodic memory impairment, these individuals typically have normal IQs and progress successfully through mainstream schooling (Vargha-Khadem et al., 1997). Indeed, individuals with developmental amnesia typically show average academic performance, as well as normal performance on reading and spelling tests, standardized vocabulary tests, and general information questions, such as "What is the capital of France?" These observations have been taken as evidence that semantic knowledge is preserved in developmental amnesia (Vargha-Khadem et al., 1997; Gadian et al., 2000; Bindschaedler et al., 2011; Brizzolara et al., 2003). This view has received further support from experimental studies showing that new semantic knowledge can be acquired in developmental amnesia (Guillery-Girard et al., 2004; Bindschaedler et al., 2011; Martins et al., 2006; Martin, 2007; but see Gardiner et al., 2008).

Episodic and semantic memory are often considered to be separate, dissociable memory systems (Schacter and Tulving, 1994), and core retrieval processes from each system are thought to be independent. Despite being dissociable, there is a dependence between the two systems with respect to encoding of information; however, there are two *distinct* models of the direction of this dependence. According to the serial-parallel-independent (SPI) model (Tulving and Markowitsch, 1998; Tulving, 2002a, 2002b), episodic memory is a phylogenetically and ontogenetically later-developing system that grew out of semantic

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memory. As such, encoding episodic information critically depends on semantic memory, whereas semantic memory encoding is independent of episodic memory. By contrast, models of memory transformation or consolidation (Winocur et al., 2010; McClelland et al., 1995) suggest that semantic information is encoded initially as hippocampal-dependent episodic memory and then, either through repetition or gist extraction, becomes semantic. Evidence of intact semantic memory in developmental amnesia is considered one of the strongest sources of support for the SPI claim that semantic memory can be acquired independently of episodic memory (Vargha-Khadem, 1997; Tulving, 2002a, 2002b).

The extent to which semantic and episodic memory are dissociable at the neural level has been widely debated, with some researchers arguing that both semantic and episodic memory are dependent on the integrity of the medial temporal lobes, including the hippocampus (Squire, 1987; Shimamura and Squire, 1987; Gabrieli et al., 1988; Zola-Morgan, Cohen, and Squire, 1983; Squire and Zola, 1998). In contrast, others have argued that the medial temporal lobes are crucial for episodic but not semantic memory (Kinsbourne and Wood, 1975; Parkin, 1982). This latter view was supported largely by the finding that individuals with amnesia due to hippocampal damage seemed to show primarily deficits in episodic memory, with semantic memory being relatively preserved. The finding that individuals with developmental amnesia due to focal hippocampal damage had intact semantic memory added strong support to the notion that episodic but not semantic memory is dependent on the hippocampus.

Since the publication of Vargha-Khadem (1997), the prevailing view has been that semantic memory is normal in developmental amnesia. However, some interesting variations have been noted. For example, a few studies report that patients can acquire new semantic information, but that they require a greater number of repetitions than do control participants (Gardiner et al., 2008; Guillery-Girard et al., 2004). Furthermore, one patient did not acquire facts about the world at the same rate as normal control participants (Bindschaedler et al., 2011). Another individual with developmental amnesia showed below average performance on the “information” I.Q. subtest (although normal performance on a questionnaire about world facts), as well as poor naming and comprehension abilities (Vicari et al., 2007). These findings hint at possible subtle abnormalities in the development of semantic memory against a background of severe episodic memory impairment. However, it is critical to understand the nature of these abnormalities for a clearer view of the relative contribution of episodic memory and hippocampal function to the early formation of semantics.

An important component of semantic memory that has yet to be explored in developmental amnesic cases is the structure of their conceptual knowledge. This can be explored through knowledge of concrete concepts such as “chair” and “dog”, and we focus on these types of concepts in this article. One of the dominant theoretical frameworks for understanding concrete concepts is feature-based models in which concepts are represented in terms of semantic features (Martin, 2007; Tyler et al., 2013). In these models, theoretically and empirically important distinctions have been made among the types of features of which concepts may be composed (Cree and McRae, 2003; Wu and Barsalou, 2009). Consider “hammer”. Learning the concept of hammer can be thought of in terms of learning its features, such as how it looks (elongated, has a handle), how it is used (grip the handle, swing back and forward), what it is used for (pounding nails into the wall), and where it is commonly found (the garage). Some aspects of people's knowledge of objects such as hammers are intrinsic to, or physically part of, the object itself, whereas other aspects can be considered to be part of the contexts in which an object is encountered (Barr and Caplan, 1987). Contextually based information may include how or where a hammer is used, and can be considered as extrinsic to the object. For concrete living (cow) and nonliving things (hammer), important aspects of extrinsic information involve relations between the physical object itself and other types of objects and locations, as well as the ways in which people interact with the object.

During development, individuals acquire both intrinsic and extrinsic feature knowledge as part of learning concrete concepts. In terms of neural mechanisms, the hippocampus may play an important role in binding extrinsic features to the intrinsic features that compose the object. A large body of evidence suggests that *relational binding*, or the forming of associations among an object and its context, is a core function of the hippocampus (Olsen et al., 2012; Eichenbaum & Cohen, 1993). Anatomically, the hippocampus is well suited to the task because it receives object information from the visual ventral stream, as well as contextual information (e.g., found in a garage) from a number of unimodal and multimodal cortical areas (Lavenex and Amaral, 2000). Although typically this type of learning is considered with reference to individual episodes, some evidence suggests that acquisition of new conceptual knowledge may also rely on hippocampally mediated binding, particularly across multiple episodes that share regularities in object-context relationships (Kumaran et al., 2009). To the extent that developmental amnesia is the result of damage to the hippocampus or the extended hippocampal system in most, if not all, cases, one might expect extrinsic aspects of conceptual knowledge to develop abnormally.

If extrinsic aspects of concept knowledge are impaired in developmental amnesia, how might this affect the structure of semantic memory? There exists a correspondence between Barr and Caplan's (1987) distinction between intrinsic and extrinsic features and the distinction that has been made between sensory and functional features (or sensory and non-sensory features). Sensory information corresponds to intrinsic knowledge because people's (somewhat abstract) knowledge of how something looks, smells, and sounds is intrinsic to the entity or object itself. In contrast, functional information reflects extrinsic information because how an object is used and what it is used for are based on relationships between the object and something else, such as actions performed on the object by some agent. In some cases, the term functional information has been used to refer to all knowledge about a concept that is not sensory (Warrington and Shallice, 1984). In this sense, in addition to information about how an object is used and what it is used for, functional (or actually “nonsensory”) information includes other extrinsic information, such as where an entity or object typically is located, when an object typically is used (e.g., during the winter), or what an object typically is used with. Note that researchers differ with regard to how various types of information are labelled or classified, and detailed classification schemes have been proposed and used (Cree and McRae, 2003; Wu and Barsalou, 2009). For our present purposes, what is centrally important is that sensory information is intrinsic to an object itself, whereas other types of knowledge about concrete concepts are extrinsic (Barr and Caplan, 1987).

Interestingly, a recent study showed that patient D.A., an individual with adult-onset amnesia associated with hippocampal damage, was impaired in learning new functional knowledge in an experimental setting. Specifically, although D.A. learned movements related to new, unfamiliar tools as quickly as control participants, he was subsequently unable to recall the functional significance of those object (what they were used for) as well as controls (Roy and Park, 2010). An intriguing possibility, therefore, is that for concrete concepts, the learning of extrinsic features outside the laboratory also depends on hippocampal integrity, and may be impaired in developmental amnesia.

Our goal was to test whether some aspects of semantic knowledge depend on the same relational binding mechanisms in the hippocampus that subserve episodic memory. Specifically, we explored whether extrinsic feature knowledge for concrete concepts is impaired in developmental amnesia. We investigated a previously described individual with developmental amnesia, HC, with well-documented impairments in episodic memory and a well-characterized lesion of the extended hippocampal system (Olsen et al., 2013). We tested HC on a semantic feature production task and a typicality rating task, both of which are sensitive to knowledge that underlies individual concepts. Although