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Research report

Generalization from episodic memories across time: A route for semantic knowledge acquisition

Carly C.G. Sweegers* and Lucia M. Talamini

Department of Psychology, University of Amsterdam, The Netherlands

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ABSTRACT

The storage of input regularities, at all levels of processing complexity, is a fundamental property of the nervous system. At high levels of complexity, this may involve the extraction of associative regularities between higher order entities such as objects, concepts and environments across events that are separated in space and time. We propose that such a mechanism provides an important route towards the formation of higher order semantic knowledge. The present study assessed whether subjects were able to extract complex regularities from multiple associative memories and whether they could generalize this regularity knowledge to new items. We used a memory task in which subjects were required to learn face-location associations, but in which certain facial features were predictive of locations. We assessed generalization, as well as memory for arbitrary stimulus components, over a 4-h post-encoding consolidation period containing wakefulness or sleep. We also assessed the stability of regularity knowledge across a period of several weeks thereafter. We found that subjects were able to detect the regularity structure and use it in a generalization task. Interestingly, the performance on this task increased across the 4hr post-learning period. However, no differential effects of cerebral sleep and wake states during this interval were observed. Furthermore, it was found that regularity extraction hampered the storage of arbitrary facial features, resulting in an impoverished memory trace. Finally, across a period of several weeks, memory for the regularity structure appeared very robust whereas memory for arbitrary associations showed steep forgetting. The current findings improve our understanding of how regularities across memories impact memory (trans)formation.

1. Introduction

Episodic memory refers to memory for events and situations, organized in an autobiographical stream, and rich in contextual information (Tulving, 1983). The hippocampus is thought to be crucial for the encoding and retrieval of such vivid memories (Burgess, Maguire, & O'Keefe, 2002; McClelland, McNaughton, & O'Reilly, 1995; Nadel, Samsonovich, Ryan, & Moscovitch, 2000; Squire, 1992;

* *Corresponding author*. Department of Psychology, University of Amsterdam, Weesperplein 4, 1018 XA, The Netherlands.
E-mail addresses: sweegers@gmail.com, c.c.g.sweegers@uva.nl (C.C.G. Sweegers).
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Tulving & Markowitsch, 1998). Semantic memory, on the other hand, refers to general knowledge about the world (McClelland & Rogers, 2003; Moscovitch et al., 2005; Patterson, Nestor, & Rogers, 2007) and is stored in networks comprising widespread cortical regions (Binder, Desai, Graves, & Conant, 2009; Martin & Chao, 2001). Though there may be various routes towards creating semantic memories, the acquisition of complex semantic knowledge frames appears to involve episodic memory (Rosenbaum, Winocur, & Moscovitch, 2001; Moscovitch et al., 2005) and an intact hippocampus (Bayley & Squire, 2005; Hayman, Macdonald, & Tulving, 1993; Manns, Hopkins, & Squire, 2003; but see Gardiner, Brandt, Baddeley, Vargha-Khadem, & Mishkin, 2008 for a critical viewpoint). It has, in fact, been proposed that semantic memory is extracted from episodic memories through a hippocampo-cortical dialogue (Battaglia & Pennartz, 2011; McClelland et al., 1995; Meeter & Murre, 2005). According to the pertaining accounts, event memory would initially require a highly plastic memory system, the hippocampus, to quickly store the conjunction of different event components represented in widespread cortical circuits. Reinstatement of overlapping event memories, facilitated by the hippocampus, would allow less plastic extrahippocampal systems, to gradually discover the structure across ensembles of experiences. Thus, memories for statistical regularities, which are important for predicting behaviour in the long run, would acquire a neural representation that is relatively resistant to decay. On the other hand, arbitrary associations would tend to be forgotten at relatively high rate, consequent to fast overwriting of neural patterns in the hippocampus.

This general framework accounts for a large spectrum of neurophysiological and behavioural observations regarding mammalian learning. In particular, the time-limited involvement of the hippocampus in (many forms of) memory (o.a. Kim & Fanselow, 1992) and the occurrence of temporally graded amnesia following brain damage (Brown, 2002; Ribot, 1881; Squire, Slater, & Chace, 1975), especially when such damage involves the hippocampus (Manns et al., 2003; Murre, Meeter, & Chessa, 2006; Scoville & Milner, 1957; Squire, Clark, & Knowlton, 2001). More recent support comes from studies on system-level consolidation, showing that hippocampus-dependent memories, over time, acquire a more cortically based representation (Frankland, Bontempi, Talton, Kaczmarek, & Silva, 2004; Paz, Bauer, & Paré, 2007; Takashima et al., 2006, 2009). Another study directly compared hippocampally and extrahippocampally stored aspects of events, and showed that memories preferentially lose hippocampus-dependent configurational components as they age (Talamini & Gorree, 2012). Hippocampal lesion studies in rodents suggest that such contextual impoverishment coincides with hippocampal disengagement from retrieval (Wiltgen et al., 2010; Winocur, Frankland, Sekeres, Fogel, & Moscovitch, 2009).

Several aspects of the model have thus been supported by experimental evidence, including hippocampo-neocortical memory recoding over time, and a parallel loss of memories' configural complexity, leading to memory semantization. On the other hand, the proposed hippocampus-mediated regularity extraction across episodic memories has long remained hypothetical.[1] A recent study from our lab generated initial support for this notion (Sweegers, Takashima, Fernández, & Talamini, 2013). In this study, subjects were required to learn associations between faces and screen locations. Half of the associations harboured complex regularities, in that facial features were predictive of screen locations; the other half did not. Importantly, regularities could only be extracted over hippocampus-encoded, associative aspects of the items. We will henceforward use the term 'associative regularity extraction' to denote this type of regularity extraction. The results indicated enhanced memory encoding and retention when associative regularities could be extracted. Moreover, the build-up of general knowledge regarding regular associations involved the coordinated activity of the hippocampus and mediofrontal regions, and the build-up of a functionally interconnected (neo)cortical network.

These findings suggest that cross episodic regularities gain preferential access to system-level consolidation processes, over arbitrary episodic memory components, leading to preferential maintenance of such regularities and, therewith, the build-up of general knowledge. Significant questions, however, remain. For one, our previous study (Sweegers et al., 2013) did not test whether acquired regularity knowledge could be generalized to new situations (c.q. new exemplars). Thus, definitive proof that flexibly applicable, general associative knowledge can be extracted across episodes is still lacking.

Ulterior questions regard the temporal dynamics of associative regularity extraction. In particular, does such extraction occur largely at the moment when a new episode occurs that holds overlap with a stored one, or might it proceed after encoding? There is some indication that the extraction of regularities across temporally spaced events may further develop during offline consolidation processes. In the pertaining studies sets of items were encoded, that – unbeknownst to the subjects – carried a hidden structure or grammar (Durrant, Cairney, & Lewis, 2012; Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Gómez, Bootzin, & Nadel, 2006; Tamminen, Davis, Merkx, & Rastle, 2012). While subjects immediately grasped some parts of such underlying structures, the extraction of additional relations evolved across time. In these studies, however, the encoding of the individual items may not have been crucially dependent upon hippocampal functioning.

If generalization of associative regularities does continue post-encoding, this might occur differentially during the wake and sleep state. Indeed, sleep has been shown to contribute importantly to both the consolidation (Gais, Lucas, & Born, 2006; Payne, Stickgold, Swanberg, & Kensinger, 2008; Plihal & Born, 1997; Talamini, Nieuwenhuis, Takashima, & Jensen, 2008) and the reorganization of memories (Djonlagic et al., 2009; Ellenbogen et al., 2007; Lau, Alger, & Fishbein, 2011; Orban et al., 2006; see Lewis & Durrant, 2011 for a model on

[1] Of note, many studies have investigated category formation and generalization, but in most of these the acquisition of exemplars is not crucially hippocampus-dependent and neither, therefore, is the extraction of regularities.