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Time- but not sleep-dependent consolidation promotes the emergence of cross-modal conceptual representations

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ABSTRACT

Conceptual knowledge about objects comprises a diverse set of multi-modal and generalisable information, which allows us to bring meaning to the stimuli in our environment. The formation of conceptual representations requires two key computational challenges: integrating information from different sensory modalities and abstracting statistical regularities across exemplars. Although these processes are thought to be facilitated by offline memory consolidation, investigations into how cross-modal concepts evolve offline, over time, rather than with continuous category exposure are still missing. Here, we aimed to mimic the formation of new conceptual representations by reducing this process to its two key computational challenges and exploring its evolution over an offline retention period. Participants learned to distinguish between members of two abstract categories based on a simple one-dimensional visual rule. Underlying the task was a more complex hidden indicator of category structure, which required the integration of information across two sensory modalities. In two experiments we investigated the impact of time- and sleep-dependent consolidation on category learning. Our results show that offline memory consolidation facilitated cross-modal category learning. Surprisingly, consolidation across wake, but not across sleep showed this beneficial effect. By demonstrating the importance of offline consolidation the current study provided further insights into the processes that underlie the formation of conceptual representations.

1. Introduction

Every day we automatically discriminate between hundreds of objects, and assign meaning to them. This process often requires the integration of information from different modalities. For instance, when discriminating a donkey from a mule, information about its shape, the colour of its fur, or its location overlaps between the two species and is therefore, individually, not sufficient for correct categorisation. However, when the information is integrated, the two exemplars can be pulled apart, which allows us to rapidly discriminate between them. To account for this ability and to allow for generalisation to novel objects or situations, the conceptual representation of an object enables the capture of regularities and variations across the different modalities (Medin & Rips 2005; Lambon Ralph, Sage, Jones, & Mayberry 2010; Lambon Ralph, 2014). The formation of many real-world concepts therefore seems to depend on two crucial mechanisms: the abstraction of the statistical variation across exemplars and the integration of information from different modalities (Rogers & McClelland, 2004; Lambon Ralph et al., 2010). How new conceptual representations form with on-going category training has been studied in great detail (Ashby & Maddox 2005; Smith & Minda, 2002; Kumaran, Summerfield, Hassabis, & Maguire 2009; Jiang et al., 2007; van der Linden, Murre, & van Turennout, 2008; van der Linden, van Turennout, & Indefrey, 2010; van der Linden, van Turennout, & Fernandez, 2011). To date, however, very little research has focused on how conceptual representations evolve over time (Djonlagic et al., 2009).

Memory consolidation describes a post-encoding process of reorganisation, through which new memories become stabilised and integrated into long-term memory (Frankland & Bontempi, 2005). In addition to its stabilising effect, memory consolidation, including that which occurs across sleep, has been associated with a qualitative change of memories towards more abstract and general representations (McClelland, McNaughton, & O'Reilly, 1995; Winocur, Moscovitch, & Bontempi, 2010; Walker & Stickgold, 2010). Specifically, memory consolidation has been shown to facilitate the integration of distinct elements into coherent constructs (Walker & Stickgold 2010;

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Kuriyama, Stickgold, & Walker, 2004; Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Lau, Alger, & Fishbein, 2011). This has been demonstrated, for example, using a relational memory task in which participants were taught objects pairs, embedded in a hidden hierarchy (Ellenbogen et al., 2007). Consolidation across sleep promoted the links between individual items and the hierarchical structure. A similar but weaker benefit was observed during sleep-independent consolidation. Other evidence suggests that sleep-dependent consolidation facilitates the incorporation of newly learned information into the network of pre-existing knowledge (Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010). Besides this integrative function, memory consolidation also seems to play a role in the abstraction of rules (Gomez, Bootzin, & Nadel, 2006; Wagner, Gais, Haider, Verleger, & Born, 2004; Sweegers, Takashima, Fernandez, & Talamini, 2013), statistical patterns (Fischer, Drosopoulos, Tsen, & Born 2006) and the generalisation of information (Tamminen et al., 2010). Durrant, Taylor, Cairney, and Lewis et al. (2011); and Durrant, Cairney, and Lewis, (2012), for instance, showed that sleep-dependent and, less strongly, sleep-independent consolidation promoted the abstraction of an implicit probabilistic structure in sequential auditory stimuli. Given that both the integration of information as well as the abstraction of statistical patterns seem to present fundamental mechanisms in the formation of conceptual representations, a key target of the current study was to explore how memory consolidation, possibly dependent on sleep, facilitates these aspects of concept formation.

A study by Maddox et al. (2009) partially tackled this question by investigating the effect of sleep deprivation on information-integration category learning. The information-integration category learning task has been extensively studied in category learning (Ashby & Maddox, 2005). Key features of this task are that: the category structure cannot be easily verbalised; categorisation accuracy is only maximised when information from two or more stimulus dimensions is integrated at some predecisional stage (Ashby & Gott, 1988); and, categories can display strong within-category variation along different dimensions. The information-integration category learning task, therefore, nicely mimics the basic mechanisms involved in the formation of many natural concepts, as described above. The study conducted by Maddox et al. showed that sleep deprivation led to an overall performance deficit in the information integration category learning task. In the context of the current study more importantly, they also found a significant performance increase in the information-integration category learning task over a 24-hour off-line consolidation period, in which participants received a normal night of sleep. This performance increase cannot be directly attributed to a consolidation benefit as there was no control group, which performed the task without a consolidation break, but it does suggest that sleep may benefit this type of category-learning.

The current study investigated the effect of consolidation on the emergence of cross-modal category representations in more detail. The formation of conceptual representations in real life is usually unintentional - fostered by the incidental exposure to category members. This type of category learning is assumed to be mediated by an implicit, procedural system (Ashby & Maddox 2005; Smith et al., 2012). By modifying the information-integration category learning task (Ashby & Gott 1988), we attempted to mimic the emergence of natural concepts, reduced to its two key mechanisms: the integration of cross-modal information and the abstraction of statistical regularities. We developed a paradigm in which an information-integration structure, across two different sensory modalities (auditory and spatial), was learned through a simple rule-based categorisation task. The abstract nature of this task prevented participants from drawing on prior knowledge and allowed us to track category learning from its very early stages. We conducted two experiments to investigate the effect of time-dependent consolidation (Experiment A) and the effect of sleep-dependent consolidation (Experiment B) on category learning. We predicted that the underlying information-integration category structure would be picked up implicitly during the training and enhanced by time- and sleep-dependent consolidation.

2. Methods

2.1. Participants

Experiments A and B involved 26 participants each. Informed consent was obtained from all participants prior to the study, approved by the University of Manchester Research Ethics Committee. Participants were not familiar with Asian orthographic characters, had normal or corrected-to-normal vision and hearing, and no prior history of psychiatric, learning or sleep disorders. Participants were required to be free of psychological drugs, alcohol and caffeine, and to refrain from daytime napping for 24 h preceding and throughout the study period. In Experiment A participants were randomly assigned to either a 15 min consolidation group (15 min group, $n=13$, mean age: 24.00, S.D. $\pm$ 4.51, 6 F) or a 24 h consolidation group (24 h group, $n=13$, mean age: 24.14, S.D. $\pm$ 3.59, 5 F). In Experiment B participants were randomly assigned to either a 12 h day consolidation group (12 h day, $n=13$, mean age: 19.50, S.D. $\pm$ 1.22, 11 F) or a 12 h night consolidation group (12 h night, $n=13$, mean age: 20.00, S.D. $\pm$ 1.30, 11 F).

2.2. Stimuli and stimulus generation

Each stimulus was defined by a combination of spatial, auditory and visual information, and belonged to one of two categories. In the spatial dimension, each stimulus was characterised by a specific location along the horizontal screen axis, in the auditory dimension by a particular pitch (between 200 and 1000 Hz) and in the visual dimension by an image of an Asian orthographic character. Category assignment was predefined based on obvious image characteristics. However, the same category assignment could be achieved by integrating the information about location and pitch.

Stimuli were first created in spatial and auditory dimensions, in which the category structure was based in terms of an information-integration structure (Ashby & Gott 1988). The visual dimension was added to each stimulus in a second step. Stimuli were generated by drawing 72 random samples from each of two bivariate normal distributions, forming the two stimulus categories. Distribution parameters are shown in Table 1. Transformations of the original values (x,y) into the two stimulus dimensions, space (x', min: -400 pixels, max: 400 pixels from the centre) and tone (y', min: 200 $\log_2$Hz, max: 1000 $\log_2$HZ), were performed according to Formulas (1) and (2).

$$x' = \frac{(x+400)(x'_{max} - x'_{min})}{800} + x'_{min} \quad (1)$$

$$y' = y'_{\min} \times 2^{(y-200)/(800)\times \log_2(y'_{\max}/y'_{\min})} \quad (2)$$

To visualise the category structure, each stimulus can be

Table 1
Parameters of bivariate normal distributions used for the stimulus generation.

Parameter	Category 1	Category 2
μ_x	−0.8	0.8
μ_y	0.8	−0.8
σ_x	2	2
σ_y	2	2
P_{xy}	1.92	1.92