Neurobiology of Learning and Memory xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Review

Not only . . . but also: REM sleep creates and NREM Stage 2 instantiates landmark junctions in cortical memory networks

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ARTICLE INFO

Article history:
Received 4 November 2014
Revised 16 April 2015
Accepted 16 April 2015
Available online xxxx

Keywords:
REM
NREM Stage 2
Episodic memory
Sleep
Landmark junctions
Preplay
Dreams
Unconscious

ABSTRACT

This article argues both rapid eye movement (REM) and non-rapid eye movement (NREM) sleep contribute to overnight episodic memory processes but their roles differ. Episodic memory may have evolved from memory for spatial navigation in animals and humans. Equally, mnemonic navigation in world and mental space may rely on fundamentally equivalent processes. Consequently, the basic spatial network characteristics of pathways which meet at omnidirectional nodes or junctions may be conserved in episodic brain networks. A pathway is formally identified with the unidirectional, sequential phases of an episodic memory. In contrast, the function of omnidirectional junctions is not well understood.

In evolutionary terms, both animals and early humans undertook tours to a series of landmark junctions, to take advantage of resources (food, water and shelter), whilst trying to avoid predators. Such tours required memory for emotionally significant landmark resource-place-danger associations and the spatial relationships amongst these landmarks. In consequence, these tours may have driven the evolution of both spatial and episodic memory. The environment is dynamic. Resource-place associations are liable to shift and new resource-rich landmarks may be discovered, these changes may require re-wiring in neural networks. To realise these changes, REM may perform an associative, emotional encoding function between memory networks, engendering an omnidirectional landmark junction which is instantiated in the cortex during NREM Stage 2. In sum, REM may preplay associated elements of past episodes (rather than replay individual episodes), to engender an unconscious representation which can be used by the animal on approach to a landmark junction in wake.

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1. Introduction

The proposal that sleep, as compared to an equivalent time awake, benefits memory in some way (or ways) is of long-standing (Jenkins & Dallenbach, 1924; Marr, 1971; Winson, 1985). More recent work shows this sleep gain is achieved through active memory processing (Diekelmann & Born, 2010; Ellenbogen, Payne, et al., 2006; Gais & Born, 2004; Rasch & Born, 2013; Squire, 2009; Stickgold, 2005, 2006, 2009) rather than, as originally thought, a passive advantage conveyed by a period of non-interference (Jenkins & Dallenbach, 1924). Over the past twenty years, data on sleep-memory relationships has proliferated but findings have been somewhat contradictory and the precise nature of active memory processing during sleep is still not well characterised, indicating the need for new models which can account for the divergent empirical data (Ackermann & Rasch, 2014; Conte & Ficca, 2013; Genzel, Kroes, et al., 2014; Schabus, 2009). The role of REM in memory processing has remained particularly obscure (Ackermann & Rasch, 2014; Rasch & Born, 2007). This article concentrates on REM memory processing but argues this cannot be considered in isolation from the role of NREM, which is, briefly, considered also.

Since Müller and Pilzecker (1900) the dominant conceptual view has been that sleep benefits memory stabilization or "consolidation". Recent work, however, suggests dynamic modification through memory organisation and reorganisation as memory traces are redistributed and memories evolve (Born & Wilhelm, 2012; Stickgold & Walker, 2005, 2013). Through being spatially reorganized and anatomically relocated in the brain (Ribeiro & Nicolelis, 2009; Sterpenich, Albouy, et al., 2009; Walker & Stickgold, 2004) – as memory traces are propagated away from their initial encoding sites during sleep (Ribeiro & Nicolelis, 2004).

Throughout this paper we try to avoid the "consolidation" concept, the term is hypothetical (Dudai, 2012; Inostroza & Born, 2013), indeed metaphorical (Llewellyn, 2013a), and rarely clearly

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http://dx.doi.org/10.1016/j.nlm.2015.04.005
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Please cite this article in press as: Llewellyn, S., & Hobson, J. A. Not only . . . but also: REM sleep creates and NREM Stage 2 instantiates landmark junctions in cortical memory networks. *Neurobiology of Learning and Memory* (2015), http://dx.doi.org/10.1016/j.nlm.2015.04.005

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defined before use (Payne & Nadel, 2004). No consensus now exists over what processes should be included under "consolidation" (Stickgold & Walker, 2007) and at least some of these processes may be distinct (Walker, 2005). Hence, through theorising REM-mediated "landmark junction creation", NREM-mediated "landmark junction instantiation" and "indexation" in the hippocampus, we strive for more theoretical specificity about dynamic sleep memory processes than can be achieved under the "umbrella" (Llewellyn, 2013a) concept of consolidation.

1.1. Episodic memory networks and memory for spatial navigation

This paper is primarily concerned with episodic memory networks. Episodic memory is understood here as involving higher-order, associational binding of what, where and when into a flexible memory representation within which 'when' is identified as the moment by moment sequential order (micro-time) within which events are played out rather than a subjective timeline (macro-time) e.g. it happened at Christmas two years ago, see, for example, Davachi (2006), Hassabis and Maguire (2007) and Fouquet, Tobin, et al. (2010). In episodic memory networks, a connection (or pathway) can be formally identified with the sequentially occurring phases of an episodic memory, associated through Hebbian plasticity (Buzsáki, 2005, 2006). In contrast, the possible significance and function of nodes/junctions in episodic networks is not well understood and is our focus here.

The significance of junctions in episodic memory networks may be deduced from considering spatial networks. Concomitant with both network function and the centrality of place to episodic memory, spatial memory is thought to be a simple form of episodic memory (Deiana, Platt, et al., 2011). Episodic memory may have evolved from memory for spatial navigation in animals and humans (Buzsáki, 2005, 2006; Buzsáki & Moser, 2013; O'Keefe and Nadel, 1978; Winson, 1985). Consequently, the spatial "scaffold", which served animal navigation, may be conserved in human episodic networks (Burgess, Maguire, et al., 2002). This scaffold may be a basic spatial network which comprises nodes/junctions and connections/edges, the former link the latter (for reviews see (Sporns, 2011a, 2011b).

Enabling functional integration and segregation is an important network function (Friston, 2002; Tononi, Edelman, et al., 1998). These principles characterise spatial networks where unidirectional paths are segregated to ensure unambiguous routes but integrated at omnidirectional landmark/junctions which enable orientation and changes in direction. At these omnidirectional landmarks/junctions, individually experienced pathways are 'tied together', superimposed and, therefore, associated (O'Keefe and Burgess, 1996) in both world and mental space. This spatial network characteristic may have evolved to enable REM-mediated associative encoding to create omnidirectional landmarks/junctions which are instantiated in episodic networks during NREM Stage 2.

Despite the likely evolution of episodic memory from spatial memory, the significance of spatial navigation for episodic memory networks has not received much attention in sleep research. Although some sleep research does focus on spatial tasks, see (Peigneux, Laureys, et al., 2004; Rauchs, Orban, et al., 2008; Wamsley, Tucker, et al., 2010).

1.2. Spatial navigation and episodic memories in naturalistic settings

Few animals are nomadic (Powell, 2000). Most vertebrate and some invertebrate animals occupy temporally stable, spatially heterogeneous habitats, the space used on a regular basis is the 'home range' (Burt, 1943), this concept can be traced back to Darwin (Börger, Dalziel, et al., 2008). Home range familiarity has several benefits, feeding efficiency and learned motor programs for the environment (Stamps, 1995), along with speed when fleeing predators because of experience with escape routes (Clarke, da Silva, et al., 1993). In consequence, animals are willing to incur costs to stay in a familiar home range (Powell, 2000). Therefore, if a modified route becomes necessary, an animal will be likely to take a different route within the home range rather than adopt a new home range.

Most natural resources are clumped rather than evenly or randomly distributed (Pielou, 1977). Indeed, consuming foods from clumped, patchy sites, requiring memory for site locations, may have driven the evolution of spatial memory (Cunningham & Janson, 2013). Unsurprisingly, within the home range, animals return to locations with rewards (i.e. food, water, refuge, mates) whilst, if possible, avoiding those where they have encountered aggression, for review, see Stamps and Krishnan (1999).

Consequently, for any animal, there are core areas of intense use, for example, reliable food sources and natural refuges from predators (Benhamou & Riotte-Lambert, 2012; Charnov, 1976; Kaufmann, 1962; Samuel, Pierce, et al., 1985). Intense use is expressed through regular, sometimes daily, tours of these places followed by a straight return to the home base, such tours indicate the use of what–where associations and landmark navigation – at least of a simple form – through a cognitive map (Gallistel, 1990; Janzen, 1971; Noser & Byrne, 2007; Spencer, 2012; Wallace, Hamilton, et al., 2006).

Navigation in world and mental space may be fundamentally the same (Buzsáki & Moser, 2013), implying that spatial networks in the world and the neural networks which represent them take equivalent forms. Retention of a spatial scaffold (regular path navigation which connects a series of landmark places) suggests that two sets of associations are conserved and embedded within episodic memory networks. The first, are the associations that characterise the pathways (or routes) to the series of landmark places, these, as described above, have evolved within episodic networks to become sequential, unidirectional episodic memories. The second set of associations is to the omnidirectional landmark places which are visited via the pathways. Within spatial memory, these associations may have expressed the cumulative significance of the frequently visited landmark place. For example, after several visits to a landmark refuge, the animal would have had multiple experiences at this place, some experiences would be likely to be repeated at each visit (e.g. the place always offered shelter) but other events would be sporadic (e.g. on some occasions mates could be found, on others not; equally, sometimes competitors were present, on other occasions not). See Fig. 1.

Anticipating likely events at the landmark enables the animal to take advantage of possible rewards, whilst avoiding risky confrontations (Valeix, Fritz, et al., 2009). If the animal could discern a pattern in events, this knowledge would confer evolutionary advantage. For example, if the animal could predict when mates would be present but competitors would be absent. Neurons comprising an omnidirectional landmark junction collectively convey its meaning or significance (Buzsáki, 2005). Contemporarily, 'meaning' has assumed abstract definition, the expression of an idea in language but, 'meaning' can imply concrete significance for needs, desires or goals (Clore & Ortony, 2000), i.e. what does this mean for me? To an animal, the meaning or significance of a landmark/junction would lie in the ways that the place met its needs and wants. In evolutionary terms, meaning at an omnidirectional landmark junction in world and mental space may have conveyed the pattern in the risks and rewards associated with the place.

For example, Fig. 2, "Day 1" (below) is a schematic representation of a regular tour (shown in green[1]) to visit five landmark places

[1] For interpretation of colour in Fig. 2, the reader is referred to the web version of this article.

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