

dreams referred to waking thoughts rather than to actual perceptions, representing one-third of the final episodic candidates scored by the subjects. These were not included, however, as episodic memory candidates (Step 7 in Fig. 1). This is because our incessant thoughts, explicit expectancies, and other mental representations do not fit the conventional definition of life episodes. Is this restrictive definition really justified? In particular, the high frequency of remembered mental activities as opposed to events brings to question whether thoughts should be in fact considered as part of life episodes. This point stresses the need for a more articulated account of waking experiences. Whilst future dream studies will require a new appraisal of the information actually extracted and processed by our brains when awake, it is also clear that dreams exhibit functional dissociations that might help to identify the neurocognitive constituents of waking experience and of memory [25].

Acknowledgements

S.S. is supported by the Swiss National Science Foundation (grant 8210-061240). The author thanks Pierre Maquet and Patrik Vuilleumier for helpful discussions.

References

- Epstein, A.W. (1985) The waking event-dream interval. *Am. J. Psychiatry* 142, 123–124
- Marquardt, C.J.G. et al. (1996) An empirical investigation into the day-residue and dream-lag effects. *Dreaming* 6, 57–65
- Cavallero, C. et al. (1990) Memory sources of REM and NREM dreams. *Sleep* 13, 449–455
- Fosse, M.J. et al. (2003) Dreaming and episodic memory: a functional dissociation? *J. Cogn. Neurosci.* 15, 1–9
- Gais, S. et al. (2000) Early sleep triggers memory for early visual discrimination skills. *Nat. Neurosci.* 3, 1335–1339
- Stickgold, R. et al. (2000) Visual discrimination learning requires sleep after training. *Nat. Neurosci.* 3, 1237–1238
- Plihal, W. and Born, R.T. (1997) Effects of early and late nocturnal sleep on declarative and nondeclarative memory. *J. Cogn. Neurosci.* 9, 534–547
- Smith, C. (1995) Sleep states and memory processes. *Behav. Brain Res.* 69, 137–145
- Maquet, P. et al. (2003) Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *J. Neurosci.* 23, 1432–1440
- Wilson, M.A. and McNaughton, B.L. (1994) Reactivation of hippocampal ensemble memories during sleep. *Science* 265, 676–679
- Louie, K. and Wilson, M.A. (2001) Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep. *Neuron* 29, 145–156
- Nadasdy, Z. et al. (1999) Replay and time compression of recurring spike sequences in the hippocampus. *J. Neurosci.* 19, 9497–9507
- Maquet, P. et al. (2000) Experience-dependent changes in cerebral activation during human REM sleep. *Nat. Neurosci.* 3, 831–836
- Eichenbaum, H. et al. (1996) Functional organization of the hippocampal memory system. *Proc. Natl. Acad. Sci. U. S. A.* 93, 13500–13507
- Peigneux, P. et al. (2001) Sleeping brain, learning brain. The role of sleep for memory systems. *Neuroreport* 12, A111–A124
- Tulving, E. (1987) Multiple memory systems and consciousness. *Hum. Neurobiol.* 6, 67–80
- Squire, L.R. (1992) Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol. Rev.* 99, 195–231
- Cicogna, P. et al. (1991) Cognitive aspects of mental activity during sleep. *Am. J. Psychol.* 104, 413–425
- Cicogna, P. et al. (2000) Slow wave and REM sleep mentation. *Sleep Res. Online* 3, 67–72
- Baylor, G.W. and Cavallero, C. (2001) Memory sources associated with REM and NREM dream reports throughout the night: a new look at the data. *Sleep* 24, 165–170
- Buzsaki, G. (1996) The hippocampo–neocortical dialogue. *Cereb. Cortex* 6, 81–92
- McClelland, J.L. et al. (1995) Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* 102, 419–437
- Maquet, P. et al. (1996) Functional neuroanatomy of human rapid-eye-movement sleep and dreaming. *Nature* 383, 163–166
- Braun, A.R. et al. (1997) Regional cerebral blood flow throughout the sleep–wake cycle: an H₂¹⁵O PET study. *Brain* 120, 1173–1197
- Schwartz, S. and Maquet, P. (2002) Sleep imaging and the neuropsychological assessment of dreams. *Trends Cogn. Sci.* 6, 23–30

1364-6613/\$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/S1364-6613(03)00162-1

Research Focus Response

Response to Schwartz: Dreaming and episodic memory

Roar Fosse, Magdalena J. Fosse and Robert Stickgold

Harvard Medical School, Boston, USA

In Schwartz's review [1] of our recent paper on episodic memory replay in dreams [2], Schwartz asks 'why the authors concluded that sleep has no role in episodic memory consolidation', pointing out that 'when studying the role of sleep in memory reorganization and consolidation, one should keep in mind that memory is not a unitary

phenomenon'. We fully agree with Schwartz on this latter issue and clarify our view on the former.

Central to the question of episodic memory consolidation in sleep is the hippocampus formation and the entorhinal cortex. This system plays a critical role in both the encoding and retrieval of recent episodes and events [3,4]. During episodic recall, information is typically thought to flow from the hippocampus into the cortex via the parahippocampal region [5].

Corresponding author: Magdalena J. Fosse (roar_fosse@hms.harvard.edu).

We found that dreams are not typically characterized by the re-experience of episodic events from recent waking life. This is consonant with the finding that during REM sleep, when dreaming is reported to be most frequent, intense and bizarre, the hippocampal–neocortical dialogue is opposite to that found during waking episodic recall [5]. Noting that information flows from the cortex into the hippocampus during REM, we nonetheless speculated that ‘hippocampal activation during REM might contribute to consolidation or modification of the hippocampal aspect of episodic memories without reactivating those memories via the entorhinal cortex’. ([2], p. 7). As noted by Tulving [3], episodic memory is a hypothetical construct, with the actual memory system assumed to include and organize more elementary operating components. Brain activity associated with each separate component part or process may contribute to the overall consolidation of an episodic memory, and some of these processes may be engaged in dreaming.

Our cognitive data did not allow us to speculate about episodic memory consolidation in NREM. Recent evidence indicates that slow-wave sleep might contribute to episodic memory consolidation in humans, in particular during the early part of the night [6]. During NREM, information typically flows from the hippocampus to the entorhinal cortex [5], which is the pattern seen during episodic recall. Likewise, NREM sleep is associated with replay of hippocampal place-cell firing patterns seen during waking

exploratory behavior [7]. NREM could thus reasonably contribute to the consolidation of hippocampus-dependent memory traces, including those that support episodic recall, as well as their cortical components. Because the hippocampal–cortical dialogue is organized by slow waves (0.5–4 Hz) in NREM, where large groups of neurons fire in a synchronized fashion, it is possible that this processing proceeds without conscious awareness [8].

References

- 1 Schwartz, S. (2003) Are life episodes replayed during dreaming? *Trends Cogn. Sci.* 7, 325–327
- 2 Fosse, M.J. *et al.* (2003) Dreaming and episodic memory: a functional dissociation? *J. Cogn. Neurosci.* 15, 1–9
- 3 Tulving, E. (2002) Episodic memory: from mind to brain. *Annu. Rev. Psychol.* 53, 1–25
- 4 Greicius, M.D. *et al.* (2003) Regional analysis of hippocampal activation during memory encoding and retrieval: fMRI study. *Hippocampus* 13, 164–174
- 5 Buzsáki, G. (1996) The hippocampo–neocortical dialogue. *Cereb. Cortex* 6, 81–92
- 6 Plihal, W. and Born, J. (1997) Effects of early and late nocturnal sleep on declarative and procedural memory. *J. Cogn. Neurosci.* 9, 534–547
- 7 Wilson, M.A. and McNaughton, B.L. (1994) Reactivation of hippocampal ensemble memories during sleep. *Science* 265, 676–679
- 8 Gray, C.M. (1994) Synchronous oscillations in neuronal systems: mechanisms and function. *J. Comput. Neurosci.* 1, 11–38

1364-6613/\$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/S1364-6613(03)00163-3

Research Focus

Visual dreams in the congenitally blind?

Fernando H. Lopes da Silva

Neurobiology Section, Swammerdam Institute for Life Sciences, University of Amsterdam, The Netherlands

An EEG study of sleep in congenitally blind persons revealed a significant correlation between the visual activity reported during dreaming and the decrease of alpha strength recorded from the central and occipital regions of the scalp. This provides the first objective evidence that subjects who have never had visual experiences can have dreams with virtual images that are probably mediated by the activation of the cortical areas responsible for visual representations.

Whether the congenitally blind have dreams with visual content has been a controversial subject for a long time, and is still open to question [1–3]. A fundamental problem of this inquiry is that most studies have been limited to subjective assessments.

Dreams with visual content are expressions of visual imagery. Therefore if dreams with visual content could be demonstrated in congenitally blind persons, this would imply that visual imagery is possible in subjects who have been prevented from having visual experiences. Further-

more, this would allow one to infer that visual imagery does not depend on specific visual perception, but can emerge from activation of visual cortex by non-visual inputs.

This issue was recently raised again by an intriguing finding reported by Bertolo *et al.* [4]. These authors used an indirect method to assess whether dreams with visual content occur in the congenitally blind, namely EEG recordings obtained during sleep. Bertolo *et al.* [4] based their analysis on the assumption that the pattern of cortical activation during dreams with visual content would be similar to that during visual imagery, and that this pattern would be reflected in a change of the scalp EEG alpha-rhythm. Indeed, visual imagery in normal subjects is generally accompanied by a decrease of alpha activity (8–12 Hz) recorded from the scalp [5]. They therefore recorded the EEG from the occipital and central scalp areas of blind subjects whose sleep was continuously monitored. The subjects were awakened every 90 minutes to be questioned about their dream recall, and the authors carried out a spectral analysis of the EEG preceding the moment of awakening.

Corresponding author: Fernando H. Lopes da Silva (silva@science.uva.nl).