Journal Club

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Motor Memory Consolidation, Night and Day

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Review of Robertson et al. (<http://www.jneurosci.org/cgi/content/full/25/27/6372>)

In neuroscience, the term consolidation traditionally refers to the processes through which newly acquired, labile memories stabilize. However, in addition to being preserved, performance can be enhanced in the absence of practice (i.e., “off-line”). Improvements in performance beyond practice have been reported for learning sequences of finger movements either explicitly (when subjects are aware of the sequence) or implicitly (when subjects are unaware of the sequence). However, whereas increases in performance for sequences learned explicitly develop exclusively overnight (Walker et al., 2002), off-line learning for sequences learned implicitly also occurs during the day (Robertson et al., 2004). These findings offer the intriguing possibility that consolidation of memories acquired explicitly may be sleep dependent, whereas consolidation of memories acquired implicitly may just depend on time.

In their *Journal of Neuroscience* article, Robertson et al. (<http://www.jneurosci.org/cgi/content/full/25/27/6372>) address this possibility experimentally by interfering with neural activity of the primary motor cortex (M1) after implicit learning on the serial reaction-time task (SRTT). The authors reasoned that, if off-line learning was supported by a unique

mechanism, performance would be similarly affected by disrupting M1 function regardless of the time of interference. They applied repetitive pulses of transcranial magnetic stimulation (rTMS) over M1 immediately after practice either at 8 A.M. or at 8 P.M. and reassessed performance after a 12 h interval [Robertson et al. (2005), their Fig. 1 (<http://www.jneurosci.org/cgi/content/full/25/27/6372/FIG1>)]. The results revealed a distinct impairment of off-line learning when rTMS was applied at 8 A.M., but not at 8 P.M. [Robertson et al. (2005), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/25/27/6372/FIG2>)]. This effect was location and time specific. Interestingly, the application of rTMS at 10 A.M. did not impair performance, suggesting that the contribution of M1 to off-line learning was restricted to a narrow time window of <2 h [Robertson et al. (2005), their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/25/27/6372/FIG3>)].

The study by Robertson et al. (2005) has some important implications for the understanding of memory consolidation. Primarily, it replicates previous findings demonstrating that off-line learning of implicitly acquired skills occurs both during the day and during the night, supporting the hypothesis that memory consolidation is modulated by awareness. Furthermore, it suggests that the consolidation of implicitly acquired skills may be influenced by the time of day at which the skill was learned. This finding contradicts a recent hypothesis stating that memories are stabilized during the day and enhanced during the night (Walker and

Stickgold, 2004). However, neither study was originally designed to address off-line learning during the daytime. By using the implicit version of the SRTT, Robertson et al. (2005) showed that memory enhancement can also occur during the day and can be prevented by interfering with M1 function within a narrow time interval.

In addition, the results of this study offer significant insight into the role of the primary motor cortex in motor skill learning. Increased M1 activity has been consistently reported during the acquisition of motor sequences in the SRTT (Grafton et al., 1995). Yet the fact that learning often transfers to other effectors questions whether M1 contributes directly to the formation of motor memories or simply reflects priming from higher-order cortices that encode the skill at a more abstract level (Grafton et al., 1998). The inhibitory effect of rTMS opens up the possibility that M1 is directly involved in motor memory consolidation, and is consistent with the notion of parallel levels of representation within the nervous system.

The study has some caveats worth noting, however. Based on their findings, the authors conclude that different mechanisms involving M1 may engage during the day and overnight. They propose two possible explanations for the behavioral dissociation induced by TMS, both dependent on sleep. However, overnight changes in memory consolidation do not necessarily reflect sleep-related consolidation. Neither the effect of sleep deprivation nor the effect of sleep induction during the daytime was evaluated here. Moreover, the possibility that improve-

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ments in performance may have occurred while subjects were still awake (on average 3 h before bedtime) was not examined. Thus, the idea that the differential effect of rTMS on performance is based on sleep, rather than time of day, may require additional study.

The authors dismiss a circadian rhythm in cortical excitability as a source for the behavioral dissociation. This interpretation rests on the lack of a statistically significant difference in the resting motor threshold as assessed exclusively before practice. Although the motor threshold is a reliable measure of cortical excitability, it likely reflects axonal excitability rather than synaptic transmission, which can be assessed using other measures (e.g., input–output motor-evoked potential curve, intracortical inhibition/facilitation). Given that the effect of rTMS on cortical excitability was not examined, a

circadian modulation of synaptic transmission cannot be completely excluded.

In addition, one might question whether the similarity in the level of performance observed at test (8 A.M.) and retest (12 h later) supports the proposal that consolidation of off-line learning (memory enhancement) is mechanistically different from that associated with skill acquisition (memory stabilization). The magnitude of the inhibitory effect of rTMS on motor cortical excitability depends on the parameters of choice. Thus, longer exposure times and/or suprathreshold stimulation could potentially influence memory retention through retroactive interference, which would be inconsistent with the authors' proposal.

This paper raises the intriguing possibility that consolidation of procedural motor skills acquired implicitly may be influenced by the time of acquisition. The results offer support for an active role of

the motor cortex in off-line learning and will stimulate additional research in the fields of motor learning and memory consolidation.

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