Brief Communication

Early boost and slow consolidation in motor skill learning

Christophe Hotermans,^{1,2} Philippe Peigneux,¹ Alain Maertens de Noordhout,² Gustave Moonen,² and Pierre Maquet^{1,2,3}

¹Cyclotron Research Centre, University of Liège, B-4000 Liège, Belgium; ²Neurology Department, CHU Sart Tilman, University of Liège, B-4000 Liège, Belgium

Motorskill learning is a dynamic process that continues covertly after training has ended and eventually leads to delayed increments in performance. Current theories suggest that this off-line improvement takes time and appears only after several hours. Here we show an early transient and short-lived boost in performance, emerging as early as 5–30 min after training but no longer observed 4 h later. This early boost is predictive of the performance achieved 48 h later, suggesting its functional relevance for memory processes.

Motor learning depends on practice but also continues to develop over time after practice has ended. Over the years, two notions, reminiscence and memory consolidation, were developed to account for the protracted time course of motor learning. Reminiscence, as coined by Ballard (1913), is a general phenomenon denoting the change in the performance of a partially learned act that occurs after the subject has rested. Reminiscence has been observed for both verbal and motor tasks, although more reliably for the latter (Eysenck and Frith 1977). It usually implies an improvement in performance observed after a rest period, although it has also been applied to “the restitution of performance to its previous level, from whence it has dropped during the course of massed practice” (Eysenck and Frith 1977). Reminiscence has been reported after rest periods ranging from a few seconds to several days (Eysenck and Frith 1977) although the term has recently been specifically used for improvements in performance occurring within minutes after the end of practice (Walker 2005). In motor learning, a large body of experimental work using the pursuit rotor task suggested that reminiscence reflects the “consolidation of learning” (Eysenck and Frith 1977), even though early theories related reminiscence to recovery from muscular or mental fatigue (Kraepelin 1985).

Likewise, memory consolidation is a hackneyed expression that can have several meanings. At the behavioral level, consolidation can refer, as does reminiscence, to an improvement in performance observed between practice sessions but also to a reduction in vulnerability of a memory trace after the acquisition of a novel skill (Robertson et al. 2004a). At the physiological level, memory consolidation also pertains to the off-line processes taking place at the molecular, cellular, or systemic levels that underpin these behavioral effects. A current hypothesis proposes that the acquisition of a motor skill is followed by two phases of consolidation, one involving a process of stabilization during wakefulness, by which the memory trace becomes resistant to interference, and one involving a sleep-dependent process of enhancement, characterized by a higher level of performance (Walker 2005). However, this view is still debated (Peigneux et al. 2005) and appears to fit experimental data only when the motor sequence is explicitly known by participants (Robertson et al. 2004b), but not when it is acquired unintentionally (implicit learning) (Robertson et al. 2004b, 2005; Press et al. 2005).

tionally (implicit learning) (Robertson et al. 2004b, 2005; Press et al. 2005).

In this article, we aimed at characterizing the time course of motor learning of an explicitly learned sequence using the finger tapping task (FTT). Our objective was to comprehensively assess motor memory consolidation, from the minutes following training up to 48 h later.

One-hundred-five right-handed healthy participants (61 women and 44 men; range, 18–37 yr) without any history of neurological, psychiatric, or sleep disorder gave their written informed consent to participate in this study approved by the Ethics Committee of the Faculty of Medicine of the University of Liège. Musicians and professional typists were excluded.

Subjects were asked to repeat a five-element sequence of key presses on a standard computer keyboard with their left, non-dominant hand, for trial (block) periods of 30 sec, interleaved with 30-sec rest periods. Subjects were instructed to perform the sequence “as fast and as accurately as possible” without interruption. The entire sequence [4–1–3–2–4], numbering from index to little finger, was permanently displayed on screen. Subjects were instructed that they should not correct occasional errors but continue with the task without pause. All subjects were trained to the FTT (12 blocks) and then tested on two further blocks, 5 min, 30 min, 4 h, or 24 h after the end of the training session (groups 1–4) (Fig. 1). In addition, they were retested 48 h later (12 blocks). A further group was submitted to a continuous practice for 26 blocks, corresponding to an absence of delay between training and testing (group 5). Speed performance was computed as the number of three-element chunks generated that belonged to the trained sequence. Analysis was conducted on three-element chunks rather than entire sequences because perceptual chunking constitutes a natural cognitive mechanism in human learning. The chunk length of three elements was used given that humans are sensitive to the temporal context set by previous stimuli up to three elements during motor sequence learning (Cleeremans and McClelland 1991). During learning, a motor sequence is hierarchically organized in chunks acting as single memory units, which are progressively assembled in a complete sequence (Gobet et al. 2001; Sakai et al. 2003). Accuracy score was computed as the percentage of correctly generated three-element chunks (i.e., from the learned sequence) out of the total number of three-element chunks generated, per two 30-sec blocks. No significant change in accuracy was observed in any comparison, because accuracy remained very high throughout the whole experiment in all groups and conditions (see the tables). Similar

³Corresponding author.

E-mail pmaquet@ulg.ac.be; fax 324-366-3687.

Article published online before print. Article and publication date are at <http://www.learnmem.org/cgi/doi/10.1101/lm.239406>.

Figure 1. Experimental design. Subjects were distributed in seven groups of 15 subjects. All subjects were submitted to the FTT for a total of 26 practice blocks. The first 12 blocks were similar in all groups and represent the training session. The other 14 blocks were variously distributed in time during a 48-h period (see text). Each bar represents a 30-sec block of practice separated by 30 sec of rest.

results were obtained computing accuracy on entire five-element sequences (data not shown). In consequence, we report below only analyses conducted on speed performance.

Comparisons within and between experimental groups were performed by using repeated-measures ANOVA with the number of correctly generated sequence triplets as a dependent variable. Between-session effects were computed comparing the average of the last two blocks of the training session (blocks 11–12) against the two retest blocks (blocks 13–14) or the first two blocks of the second training session at 48 h (blocks 15–16). The ANOVA showed that performance improvement was determined by the interval between the end of training and testing, $F_{(4,70)} = 5.09$ and $P < 0.005$ (Table 1). Planned comparisons revealed that performance significantly increased after 5 min, 30 min, and 24 h (P s < 0.005) but not after uninterrupted practice or after a 4-h delay (P s > 0.25) (Fig. 2A). Performance improvement in subjects tested within 30 min after the end of training was similar (5 min, $P > 0.31$) or even better (30 min, $P < 0.05$) than the performance improvement observed in subjects tested 24 h later, and consistently better than during uninterrupted practice or after a 4-h interval (P s < 0.05).

Results in the 4-h and 24-h interval groups confirm studies showing a relative stagnation in performance after several hours of wakefulness and its significant improvement overnight, in the case of motor learning of an explicitly known sequence (Fischer et al. 2002; Walker et al. 2002; Korman et al. 2003). However, we observed a boost in performance 5 and 30 min after FTT training, which is not consistent with a previous report showing no improvement at short post-training delay (Walker et al. 2003b). The discrepancy is possibly related to subtle differences in the task and its instructions. We observe that our subjects were relatively slower but more accurate than those reported by Walker et al. (2003b). This suggests a difference in criterion and possibly in

strategy during task practice. The discrepancy cannot be ascribed to our choice of analyzing three-element chunks since, in all performed analyses, we obtained identical results when computing performance on the entire five-element sequence (data not shown). In any case, our findings suggest a transient gain in performance early after task practice, thereby extending earlier results showing that performance does not improve during post-training wakefulness.

To independently replicate these findings, another group of subjects (group 6) was similarly trained during 12 blocks and then practiced 14 more blocks after a 30-min delay (Fig. 1). Data were compared with group 5 that per-

formed 26 blocks uninterruptedly. Again, the repeated-measures ANOVA indicated that performance changed differently in groups 5 and 6 between training (blocks 11–12) and testing (blocks 13–14), $F_{(1,28)} = 9.7$ and $P < 0.005$ (Table 2). Planned comparisons indicated that performance increased over the 30-min delay ($P < 0.001$) but not after uninterrupted practice ($P > 0.14$). Interestingly, similar levels of performance were eventually achieved in both groups after 26 blocks of practice ($P > 0.31$) (Fig. 2B). This finding shows that after a short rest, performance is improved and, at retest, immediately reaches levels observed much later in case of continued practice.

There is a possibility that an early boost in performance only occurs following the initial learning episode. Alternatively, it might take place systematically following the end of each practice, even when the motor memory is deemed consolidated. To solve this issue, subjects of group 7 were trained to the FTT (12 blocks) and then practiced 12 blocks again 48 h later. As expected, performance significantly improved between sessions, $F_{(1,14)} = 6.4$ and $P < 0.05$, demonstrating the consolidation of the motor memory. In this group, an additional testing (two blocks) was performed 30 min after the end of the second session (Fig. 1). Performance was assessed across the 30-min rest period (blocks 23–24 vs. 25–26). These results were compared with the corresponding blocks in groups 1–4, in which these blocks are contiguous. A repeated-measure ANOVA showed that performance improvement over the 30-min period was significantly higher than over uninterrupted practice, $P < 0.0005$ (interaction effect $F_{(4,70)} = 3.7$, $P < 0.01$), demonstrating that a boost in performance also occurs shortly after a consolidated memory has been used (Fig. 2C; Table 2). The amplitude of the performance gain over the 30-min delay in group 7 was similar to the one observed in groups 2 and 6, 30 min after the initial training session (although tending to be smaller, $P = 0.06$).

Table 1. Speed and accuracy scores (blocks 11–16)

Group	Speed			Accuracy		
	I	II	III	I	II	III
Group 1 (5 min)	88 (21)	101 (23)	96 (26)	97 (3)	98 (4)	98 (4)
Group 2 (30 min)	92 (29)	109 (33)	106 (34)	96 (4)	98 (3)	98 (3)
Group 3 (4 h)	82 (20)	85 (30)	98 (31)	96 (5)	95 (8)	98 (3)
Group 4 (24 h)	87 (29)	96 (30)	104 (34)	97 (3)	98 (4)	96 (5)
Group 5 (uninterrupted)	77 (18)	81 (20)	86 (22)	93 (8)	94 (8)	95 (4)
Group 6 (30 min)	83 (22)	95 (22)	100 (24)	96 (5)	98 (3)	98 (2)
Group 7 (48 h)	93 (17)	101 (15)	109 (20)	98 (4)	98 (3)	98 (4)

Speed and accuracy values are mean (SD) scores in each experimental group at the end of the training session (I; averaged over 11–12 blocks), during test (II; 13–14 blocks), and during retest (III; 15–16 blocks).

Figure 2. Result. (A) Performance (average numbers of correct three-element chunks generated per two 30-sec blocks) at the end of training (gray bars) and during testing (black bars) following different intervals in group 1–5. (B) Performance during training and prolonged testing (blocks 1–26) in groups 5 (uninterrupted practice, squares) and 6 (30-min interval, circles). (C) Performance in group 7 at the end of repeated practice 48 h after training (gray bar) and following a further 30-min interval (black bar). (D) Significant correlation in group 2 between early boost (gain in performance over a 30-min interval) and long-term improvement (gain in performance after a 48-h interval).

We also investigated the relationship between the immediate, within-learning session improvement and the delayed, between-sessions improvement of performance to the FTT. In group 1 and 2, within-session gain during training was computed as the percentage of improvement from block 1 to the average of the last two blocks of training (block 11–12); between-session gains, as the percentage of improvement from the end of the

training session (blocks 11–12) to the two-block retest after, respectively, 5 and 30 min (blocks 13–14) or the beginning of the second practice session at 48 h (blocks 15–16). The within-session improvement during training was significantly correlated neither with 5 and 30-min gain in performance (group 1: Pearson correlation coefficient $r = -0.24$, $P > 0.38$; group 2: $r = 0.21$, $P > 0.4$) nor, as reported by Walker et al. (2003b), with the 48-h gain (group 1: $r = -0.29$, $P > 0.28$; group 2: $r = -0.17$, $P > 0.5$). In contrast, the performance gain following the 5- and 30-min rest periods was significantly related to the enhancement in performance observed 48 h after initial practice (group 1: $r = 0.72$, $P < 0.005$; group 2: $r = 0.52$, $P < 0.05$) (Fig. 2D). This finding suggests that the short-lived improvement in performance observed after 5 and 30 min of off-line processing actually reflects the extent to which performance will improve over extended periods, which are thought to allow for memory consolidation (Fischer et al. 2002; Walker et al. 2002; Korman et al. 2003).

The present findings extend our understanding of the off-line processing of complex motor memories in man, in teasing apart an enduring consolidation process that requires extended periods of time and a temporary early boost in performance that occurs shortly after task practice. Presently, it has been hypothesized that consolidation is a two-step process. In a first step, the motor memory is stabilized: Performance does not improve for several hours of wakefulness but is resistant to interference (Walker et al. 2003a). In a second step, memory representation seems to be qualitatively modified during sleep (not explicitly studied here), in such a way that motor performance improves overnight (Fischer et al. 2002; Walker et al. 2002, 2003a,b; Korman et al. 2003), especially in terms of the goal of the motor act (Cohen et al. 2005), and generalizes to the untrained hand (Korman et al. 2003). Data gained using the serial reaction time (SRT) task yielded evidence for a similar sleep-dependent consolidation step when learning was explicit but not when it was implicit (Robertson et al. 2004b).

In the present study, we additionally identified a transient and short-lived boost in performance that occurs if a rest period intervenes at short delay between task practice and retest. Similar transient enhancements in performance were previously observed following practice of the pursuit rotor task in the general framework of reminiscence (Eysenck and Frith 1977), but the generality of this phenomenon has hitherto been underestimated. In the SRT task, when the sequence is learned implicitly, a boost has been incidentally reported after a 3-min interval (see Fig. 3 in Heuer and Klein 2003). However, others failed to detect a similar improvement in performance when subjects were tested 15 min (Robertson et al. 2004b) or 1 h (Press et al. 2005) after training. We also found that the performance advantage provided by the boost is transient and attenuates after several blocks (Fig. 2B). This finding has profound consequences on future experimental designs. Indeed, retest sessions in studies exploring motor memory consolidation should allow for enough continu-

Table 2. Speed and accuracy scores (blocks 23–26)

Group	Speed		Accuracy	
	I	II	I	II
Group 1 (5 min)	104 (26)	106 (23)	96 (6)	97 (3)
Group 2 (30 min)	110 (28)	113 (29)	97 (4)	97 (3)
Group 3 (4 h)	103 (27)	104 (24)	95 (6)	95 (5)
Group 4 (24 h)	107 (32)	112 (32)	95 (6)	95 (6)
Group 7 (48 h)	113 (16)	123 (19)	97 (4)	97 (5)

Speed and accuracy values are mean (SD) scores in experimental groups during continued practice (groups 1–4) or after a 30-min delay (group 7) over the 23–24 (I) and 25–26 (II) blocks.

ous practice to properly estimate consolidated performance and rule out the potential confound due to the boost. Finally, the boost is also short-lived and no longer observed 4 h after practice. At this post-training time, performance would only reflect the core stabilized memory, uncontaminated by the boost.

The significant correlation observed between the boost and the overnight enhancement in performance suggests that the early boost represents a particular state of motor memory. We argue that the structuring of the motor memory taking place during training would lead to an early but temporary readiness for action that heralds the long-term consolidation process. From our present data, however, it cannot be known if the latter is triggered by training, by the early boost, or by the ordered succession of both phases.

A link between the boost and memory processes is also suggested by the systematic occurrence of the boost after practice, even when motor memory is deemed consolidated. It has been proposed that consolidated memories, when retrieved, are in an active state where they are labile and susceptible to disruption by amnesic agents (Sara 2000). In particular, in the context of the FTT, a consolidated motor memory becomes sensitive to interference after renewed practice of the task, in such a way that no further gain in speed is observed 24 h later (Walker et al. 2003a). Our data suggest that the boost might represent the temporary "activated" state of motor memory. However, we did not formally test for this hypothesis, which should be evaluated in future experiments. It also remains to be tested whether the boost persists when motor memory is more deeply consolidated, for instance, after several weeks of daily practice (Karni et al. 1995).

Alternatively, the boost might be attributed, as it has been argued for the SRT (Heuer and Klein 2003) tasks, to the dissipation of fatigue that would accumulate during prolonged training and gradually would counteract further improvement. However, several elements suggest that fatigue is not likely to explain our results. First, the study design that alternates practice and rest periods every 30 sec limits the accumulation of fatigue during the training session, although it could be argued that the complete dissipation of fatigue might take >30 sec of rest. Second, subjects in group 5 who performed 26 contiguous blocks continue to steadily improve after the first 12 blocks. Their final performance is similar to the performance of the subjects of group 6 who benefit from a 30-min rest between blocks 12 and 13 (Fig. 2B). Third and more importantly, if we assume the dissipation of fatigue to be the main cause of off-line improvement, it would follow that the longer the resting interval, the larger the behavioral improvement, as fatigue would have more time to fade away. Contrary to this prediction, in group 3, performance does not improve between the end of training and the testing session despite 4 h of rest (Fig. 2A). Collectively, these arguments speak against the dissipation of fatigue as an explanation for the observed early boost in performance.

Finally, although the cellular and molecular underpinnings of the boost are still unknown, it is worth noticing the similarity of time course between the motor memory of an explicitly known sequence (our study) and the neural bases of memory, as shown by some animal experiments conducted on the hippocampal formation. Indeed, we have observed that the boost appears within 30 min after the end of training but is no longer observed 4 h after practice. Several processes such as early LTP (Frey et al. 2001), dendritic redistribution of glutamate receptors (Shi et al. 1999) or dendrite morphogenesis (Maletic-Savatic et al. 1999) develop in 30 min after focal synaptic stimulation. Moreover, some of these phenomena wane within a few hours (Frey et al. 2001). The speculation that the boost is underpinned by such cellular mechanisms should be further evaluated in future experiments.

Acknowledgments

This study was supported by the Belgian Fonds National de la Recherche Scientifique (FNRS), the Fondation Médicale Reine Elisabeth, the Research Fund of ULG, the FIRS Research Fund of CHU Sart Tilman, and PAI/IAP Interuniversity Pole of Attraction P5/04. C.H. and P.M. are supported by FNRS.

References

- Ballard, P.B. 1913. *Obliviscence and reminiscence*. Cambridge University Press, Cambridge, UK.
- Cleeremans, A. and McClelland, J.L. 1991. Learning the structure of event sequences. *J. Exp. Psychol. Gen.* **120**: 235–253.
- Cohen, D.A., Pascual-Leone, A., Press, D.Z., and Robertson, E.M. 2005. Off-line learning of motor skill memory: A double dissociation of goal and movement. *Proc. Natl. Acad. Sci.* **102**: 18237–18241.
- Eysenck, H.J. and Frith, C.D. 1977. *Reminiscence, motivation, and personality: A case study in experimental psychology*. Plenum Press, New York.
- Fischer, S., Hallschmid, M., Elsner, A.L., and Born, J. 2002. Sleep forms memory for finger skills. *Proc. Natl. Acad. Sci.* **99**: 11987–11991.
- Frey, S., Bergado-Rosado, J., Seidenbecher, T., Pape, H.C., and Frey, J.U. 2001. Reinforcement of early long-term potentiation (early-LTP) in dentate gyrus by stimulation of the basolateral amygdala: Heterosynaptic induction mechanisms of late-LTP. *J. Neurosci.* **21**: 3697–3703.
- Gobet, F., Lane, P.C., Croker, S., Cheng, P.C., Jones, G., Oliver, I., and Pine, J.M. 2001. Chunking mechanisms in human learning. *Trends Cogn. Sci.* **5**: 236–243.
- Heuer, H. and Klein, W. 2003. One night of total sleep deprivation impairs implicit learning in the serial reaction task, but not the behavioral expression of knowledge. *Neuropsychology* **17**: 507–516.
- Karni, A., Meyer, G., Jezzard, P., Adams, M.M., Turner, R., and Ungerleider, L.G. 1995. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* **377**: 155–158.
- Korman, M., Raz, N., Flash, T., and Karni, A. 2003. Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proc. Natl. Acad. Sci.* **100**: 12492–12497.
- Kraepelin, E. 1985. Der psychologische versuch in der psychiatrie. *Psychologische Arbeiten* **1**: 1–91.
- Maletic-Savatic, M., Malinow, R., and Svoboda, K. 1999. Rapid dendritic morphogenesis in CA1 hippocampal dendrites induced by synaptic activity. *Science* **283**: 1923–1927.
- Peigneux, P., Destrebecqz, A., Hotermans, C., and Cleeremans, A. 2005. Filling one gap by creating another one: Memory stabilization is not all-or-nothing either: Commentary on Walker MP, A refined model of sleep and the time course of memory formation. *Behav. Brain Sci.* **28**: 78.
- Press, D.Z., Casement, M.D., Pascual-Leone, A., and Robertson, E.M. 2005. The time course of off-line motor sequence learning. *Brain Res. Cogn. Brain Res.* **25**: 375–378.
- Robertson, E.M., Pascual-Leone, A., and Miall, R.C. 2004a. Current concepts in procedural consolidation. *Nat. Rev. Neurosci.* **5**: 576–582.
- Robertson, E.M., Pascual-Leone, A., and Press, D.Z. 2004b. Awareness modifies the skill-learning benefits of sleep. *Curr. Biol.* **14**: 208–212.
- Robertson, E.M., Press, D.Z., and Pascual-Leone, A. 2005. Off-line learning and the primary motor cortex. *J. Neurosci.* **25**: 6372–6378.
- Sakai, K., Kitaguchi, K., and Hikosaka, O. 2003. Chunking during human visuomotor sequence learning. *Exp. Brain Res.* **152**: 229–242.
- Sara, S.J. 2000. Retrieval and reconsolidation: Toward a neurobiology of remembering. *Learn. Mem.* **7**: 73–84.
- Shi, S.H., Hayashi, Y., Petralia, R.S., Zaman, S.H., Wenthold, R.J., Svoboda, K., and Malinow, R. 1999. Rapid spine delivery and redistribution of AMPA receptors after synaptic NMDA receptor activation. *Science* **284**: 1811–1816.
- Walker, M.P. 2005. A refined model of sleep and the time course of memory formation. *Behav. Brain Sci.* **28**: 51–104.
- Walker, M.P., Brakefield, T., Morgan, A., Hobson, J.A., and Stickgold, R. 2002. Practice with sleep makes perfect: Sleep-dependent motor skill learning. *Neuron* **35**: 205–211.
- Walker, M.P., Brakefield, T., Hobson, J.A., and Stickgold, R. 2003a. Dissociable stages of human memory consolidation and reconsolidation. *Nature* **425**: 616–620.
- Walker, M.P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J.A., and Stickgold, R. 2003b. Sleep and the time course of motor skill learning. *Learn. Mem.* **10**: 275–284.

Received March 2, 2006; accepted in revised form June 22, 2006.

Early boost and slow consolidation in motor skill learning

Christophe Hotermans, Philippe Peigneux, Alain Maertens de Noordhout, et al.

Learn. Mem. 2006, **13**:

Access the most recent version at doi:[10.1101/lm.239406](https://doi.org/10.1101/lm.239406)

References

This article cites 21 articles, 9 of which can be accessed free at:
<http://learnmem.cshlp.org/content/13/5/580.full.html#ref-list-1>

License

Email Alerting Service

Receive free email alerts when new articles cite this article - sign up in the box at the top right corner of the article or [click here](#).