Brain and Cognition 73 (2010) 135–145

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Distinct consolidation outcomes in a visuomotor adaptation task: Off-line leaning and persistent after-effect

Maxime Trempe [1], Luc Proteau *

Département de Kinésiologie, Université de Montréal, 2100 boul. Édouard Montpetit, Montréal, Québec, Canada H3T 1J4

ARTICLE INFO

Article history:
Accepted 16 April 2010
Available online 21 May 2010

Keywords:
Consolidation
Off-line learning
Stabilisation
Aiming movements
Motor learning
Video aiming
Visuomotor adaptation

ABSTRACT

Consolidation is a time-dependent process responsible for the storage of information in long-term memory. As such, it plays a crucial role in motor learning. In two experiments, we sought to determine whether one's performance influences the outcome of the consolidation process. We used a visuomotor adaptation task in which the cursor moved by the participants was rotated 30° clockwise. Thus, participants had to learn a new internal model to compensate for the rotation of the visual feedback. The results indicated that when participants showed good adaptation in the first session, consolidation resulted in a persistent after-effect in a no-rotation transfer test; they had difficulty returning to their normal no-rotation internal model. However, when participants showed poor adaptation in the first session, consolidation led to significant off-line learning (between sessions improvement) but labile after-effects. These observations suggest that distinct consolidation outcomes (off-line learning and persistent after-effect) may occur depending on the learner's initial performance.

1. Introduction

Motor learning is a process that extends beyond training sessions. Specifically, physical practice triggers a series of physiological changes in the CNS, from gene expression to protein synthesis, that are regrouped under the term "consolidation" (Stickgold & Walker, 2007). These changes necessitate time to occur and together they lead to the long-term retention of the new skill (McGaugh, 2000).

In recent years, consolidation has been associated with two distinct behavioural outcomes: off-line learning and performance stabilisation. Off-line learning refers to a spontaneous improvement in performance without practice (Walker, 2005) and has often been observed in sequence production tasks (Fischer, Hallschmid, Elsner, & Born, 2002; Kuriyama, Stickgold, & Walker, 2004; Walker, Brakefield, Hobson, & Stickgold, 2003; Walker & Stickgold, 2005). In these studies, participants practiced a sequence of finger movements to produce it as fast and accurately as possible. When re-tested following a night of sleep, participants were typically faster and made fewer errors than during practice, even if no additional practice took place between the practice and retest sessions. These findings provide a clear demonstration that important processes take place between practice sessions. However, it is obvious that to observe off-line learning, something must be left to be learned. When one approaches asymptotic performance such that small refinements are the result of many hours/days of intense practice, it seems illusionary to expect off-line learning between two practice sessions. Thus, off-line learning seems more likely to be observed in beginners who are still learning what the task is and how to do it.

Consolidation has also been associated with performance stabilisation. This outcome has mainly been observed in adaptation studies in which the natural relation between vision and action (visuomotor adaptation) or the mechanical properties of the arm (dynamic adaptation) was distorted. Although these manipulations caused large movement errors early in practice, participants quickly learned to recalibrate their movements to achieve the desired goal. To do so, it is thought that participants developed a new internal model that predicted and compensated the distortion (Shadmehr & Mussa-Ivaldi, 1994). Using this paradigm, consolidation has been associated with a resistance to interference. Specifically, retention of the newly acquired internal model was short-lived when a different distortion was introduced soon after practice of the first adaptation task, whereas retention of the internal model was hardly affected when the two distortions were practiced several hours apart (Brashers-Krug, Shadmehr, & Bizzi, 1996; Krakauer, Ghilardi, & Ghez, 1999). Thus, it seems that a certain time is necessary for the newly developed internal model to become stabile and stored in long-term memory. In a very influent study, Shadmehr and Holcomb (1997) presented a

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* Corresponding author. Fax: +1 514 343 2181.
E-mail addresses: maxime.trempe@umontreal.ca (M. Trempe), luc.proteau@umontreal.ca (L. Proteau).

[1] Fax: +1 514 343 2181.

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doi:10.1016/j.bandc.2010.04.005

neurophysiological explanation of this stabilisation by using a viscous force field to deviate the participants' aiming movements (dynamic adaptation). At first, movements were largely deviated by the force field and participants produced curved trajectories. However, after an extensive training session (400 trials), participants adapted to the force-field and produced almost perfectly straight movements, as if no force was applied on their hand. Because there was little left to be learned at the end of the practice session, it is not surprising that no behavioural evidence of off-line learning was observed when participants were re-tested 5.5 h later. Nevertheless, using regional cerebral blood flow analysis, the authors observed that the structures generally associated with long-term memory storage showed an activation increase during the retest session. Thus, although it had no effect on task performance, the authors argued that consolidation resulted in a change in the neural representation of the internal model (Shadmehr & Holcomb, 1997).

Taken together, these findings raise the possibility that the performance level attained before the rest interval may influence the outcomes of the consolidation processes. To test this hypothesis, we used a visuomotor adaptation task in which participants had to adapt their movement planning to compensate for a 30° rotation of the visual feedback (Krakauer, Ghez, & Ghilardi, 2005; Krakauer et al., 1999; Trempe & Proteau, 2008). Successful adaptation results from the development of a new internal kinematic model: the formation of a new association between the position of the target and the movement required to reach it (Krakauer et al., 1999). Following adaptation, it is common to observe strong and persistent after-effects when the rotation is unexpectedly removed (i.e., a movement bias in the direction opposite to the previously imposed rotation), indicating that a new internal model of movement kinematic has been learned and stabilised (Shadmehr & Mussa-Ivaldi, 1994). In Experiment 1, four groups of participants performed a visuomotor adaptation task with or without consolidation, after either a limited or an extensive initial practice session. If the outcomes of the consolidation process depend on the performance level of the learner, we should expect the extensive and limited practice groups to behave differently during the second practice session. Specifically, if performance stabilisation occurs once a good performance has been reached, persistent after-effect should be observed only after extensive initial practice followed by a consolidation interval. In contrast, participants undergoing limited initial practice followed by a consolidation interval should benefit from off-line learning, but should not show persistent after-effect. Because the amount of practice and the performance level attained by the participants covaried in Experiment 1, we conducted a second experiment to dissociate these two effects.

Finally, because sleep has been found to play a major role for memory consolidation (see Walker (2005) for a review), a night of sleep was included for all 24-h groups to maximise any beneficial effects (but see also Doyon et al., 2009).

2. Experiment 1

2.1. Method

2.1.1. Participants

Fifty-four right-handed undergraduate students (mean age 23; 34 females) from the Département de kinésiologie at the Université de Montréal took part in the experiment (see Table 1). They were all naive to the purpose of the study and had no prior experience with the task. None of them reported neurological disorders and they all had normal or corrected to normal vision. This study was approved by the Health Sciences Research Ethic Committee of the Université de Montréal.

2.1.2. Task and apparatus

Participants performed a manual video-aiming task in which they had to move a computer mouse-like device on a horizontal surface from a fixed starting point toward one of many possible targets. The apparatus is illustrated in Fig. 1. It consisted of a table, a computer screen, a mirror, and a two-degrees of freedom manipulandum.

Participants sat in front of the table. The computer screen (Mitsubishi, Color Pro Diamond 37 inches; 60 Hz refresh rate) was mounted on a ceiling-support positioned directly over the table; the computer screen was oriented parallel to the surface of the table. Its image was reflected on a mirror placed directly beneath it and also parallel to the tabletop. The distance between the computer screen and the mirror was 20 cm, while the distance between the mirror and the tabletop was 20 cm, which permitted free displacement of the manipulandum on the tabletop. Participants sat on a chair with their head resting on the leading edge of the screen so that they could always see what was displayed on the computer screen by looking down at the mirror. Participants could not see the actual displacement of their arm, but the cursor displayed on the screen and reflected by the mirror provided them with online visual feedback about their movement.

The tabletop was covered by a piece of Plexiglas over which a starting base and the manipulandum were affixed. The starting base consisted of a thin strip of Plexiglas glued to the tabletop. It was parallel to the leading edge of the table and had a small indentation on one of its faces. This indentation was located directly in line with the lateral center of the computer screen and the participants' midline. It served as the starting base for the stylus (see below). This indentation made it easy for the participants to position the stylus at the beginning of each trial.

The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined together at one end by an axle. One free end of the manipulandum was fitted with a second axle encased in a stationary base. The other free end of the manipulandum was fitted with a small vertical shaft (length: 3 cm, radius: 1 cm), i.e., the stylus, which could easily be gripped by the participant. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder

Table 1
Experimental conditions.

	Conditions	Break	n	Targets	Session 1		Session 2	
					No rotation	30° CW rotation	30° CW rotation	No rotation
Experiment 1	Limited practice	24-h	11	2	15 trials	24 trials	12 trials	10 trials
		10-min	11					
	Extensive practice	10-min	11		15 trials	144 trials	12 trials	10 trials
		24-h	11					
	Control		10		144 trials	–	–	–
Experiment 2	Limited practice	24-h	12	11	15 trials	55 trials	55 trials	22 trials
		10-min	12					
	No-rotation		7		55 trials	–	–	–