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Facteurs influençant la consolidation et l'apprentissage d'une habileté motrice chez l'humain

par
Maxime Trempe

Département de kinésiologie

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présentée par :

Maxime Trempe

a été évaluée par un jury composé des personnes suivantes :

Jean-Marc Lavoie	Président-rapporteur
Luc Proteau	Directeur de recherche
Julie Messier	Membre du jury
Yannick Blandin	Examinateur externe
Guy Doucet	Représentant du Doyen

RÉSUMÉ

La pratique physique a longtemps été perçue comme le déterminant premier de l'apprentissage du mouvement. Souvent exprimée par l'expression « Vingt fois sur le métier remettez votre ouvrage», cette idée se base sur l'observation qu'une grande quantité de pratique est nécessaire pour maîtriser un geste technique complexe. Bien que l'importance de la pratique physique pour l'apprentissage du mouvement demeure indéniable, il a récemment été démontré que les changements neurobiologiques qui constituent les bases de la mémoire prennent place *après* la pratique. Ces changements, regroupés sous le terme « consolidation », sont essentiels à la mise en mémoire des habiletés motrices. L'objectif de cette thèse est de définir les processus de consolidation en identifiant certains facteurs qui influencent la consolidation d'une habileté motrice. À l'aide d'une tâche d'adaptation visuomotrice comportant deux niveaux de difficulté, nous avons démontré qu'une bonne performance doit être atteinte au cours de la séance de pratique pour enclencher certains processus de consolidation. De plus, nos résultats indiquent que l'évaluation subjective que l'apprenant fait de sa propre performance peut moduler la consolidation. Finalement, nous avons démontré que l'apprentissage par observation peut enclencher certains processus de consolidation, indiquant que la consolidation n'est pas exclusive à la pratique physique. Dans l'ensemble, les résultats des études expérimentales présentées dans cette thèse montrent que la consolidation regroupe plusieurs processus distincts jouant chacun un rôle important pour l'apprentissage du mouvement. Les éducateurs physiques, les entraineurs sportifs et les spécialistes de la réadaptation physique devraient donc planifier des entrainements favorisant non seulement l’acquisition de gestes moteurs mais également leur consolidation.

Mots clés : apprentissage moteur, consolidation, observation, adaptation visuomotrice, apprentissage hors-ligne, stabilisation

ABSTRACT

Physical practice has long been regarded as the single most determinant factor of motor skill acquisition. Often expressed by the old adage “practice makes perfect,” this idea easily relates to the common observation that extensive practice is necessary to master complex motor skills. Although the importance of physical practice for motor skill learning is undeniable, recent evidence demonstrates that the neurobiological changes that constitute the foundation of memory occur *after* physical practice. Regrouped under the term “consolidation”, these changes are essential for the memory storage of motor skills. The objective of this thesis was to identify factors that influence motor skill consolidation. Using a visuomotor adaptation task with two levels of difficulty, we showed that a good performance must be attained during practice to trigger certain consolidation processes. In addition, our results indicate that the learner’s subjective evaluation of his/her own performance can also modulate consolidation. Finally, we showed that observation triggers consolidation processes, indicating that consolidation is not exclusive to physical practice. Together, the results presented in this thesis demonstrate that consolidation regroups several distinct processes that each plays an important role for motor skill learning. Physical education teachers, athletic coaches and rehabilitation specialists should therefore plan training schedules favoring not only motor skill acquisition but also motor skill consolidation.

Keywords: motor learning, consolidation, observation, visuomotor adaptation, off-line learning, stabilization

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AE	Absolute error
ANOVA	Analysis of variance
AON	Action observation network
CCW	Counterclockwise
CE	Constant error
CNS	Central nervous system
CW	Clockwise
D	Dimension
EEG	Electroencephalography
M	Mean
M1	Primary motor cortex
NSERC	Natural sciences and engineering research council of Canada
REM	Rapid eye movement
RMSE	Root mean square error
rTMS	Repetitive transcranial magnetic stimulation
SD	Standard deviation of the mean
SE	Standard error of the mean
SRTT	Serial reaction time task
VE	Variable error

[…] when you practice and learn,

you will never be quite the same as you were before.

- Schmidt & Lee (2005)

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CHAPITRE 1

INTRODUCTION

La maîtrise d'un geste technique complexe nécessite de la pratique… beaucoup de pratique. Il n'est donc pas surprenant que la pratique physique soit perçue depuis longtemps comme le déterminant premier de l'apprentissage. Au cours du XX^{e} siècle, cette croyance a guidé les travaux de nombreux chercheurs qui ont voulu identifier les facteurs permettant d'optimiser les séances de pratique et ainsi accélérer l'apprentissage (voir Schmidt & Lee, 2005 pour une revue sur le sujet). Or, des études récentes ont permis de démontrer que des processus importants pour l'apprentissage du mouvement prennent également place <u>après</u> les séances de pratique. Par exemple, Smith et Macneill (1994) ont observé que la simple privation de sommeil suite à la pratique d'une tâche motrice pouvait effacer les gains de performance obtenus lors de la séance de pratique. Similairement, Muellbacher et al. (2002) ont démontré qu'une impulsion magnétique envoyée à répétition vers le cortex moteur primaire, immédiatement après une séance de pratique, peut ramener la performance de l'apprenant au niveau initial, comme si la séance de pratique n'avait jamais eu lieu. Bien que la pratique physique demeure importante pour l'apprentissage, il semble que certains processus prenant place après les séances de pratique le soit tout autant.

La communauté scientifique a regroupé sous le terme « consolidation » l’ensemble des processus prenant place suite à la pratique d’une habileté motrice. Bien que la consolidation ait fait l’objet de nombreuses études au cours des dernières années, plusieurs questions demeurent encore en suspend. Dans cette thèse, nous utiliserons des mesures comportementales pour chercher à mieux définir les différents processus de consolidation en précisant certains facteurs qui influencent la consolidation d’une habileté motrice. Dans un premier temps, nous présenterons au Chapitre 2 une revue de la littérature sur la consolidation. Par la suite, nous présenterons au Chapitre 3 une étude méthodologique décrivant la tâche d’adaptation visuomotrice employée dans nos deux premières études sur la consolidation. Au Chapitre 4, nous nous intéresserons à l’influence du niveau de performance de l’apprenant sur la consolidation, puis, au Chapitre 5, à l’influence de l’évaluation subjective que l’apprenant fait de sa propre performance. Le Chapitre 6 portera sur la nécessité ou non de pratiquer physiquement une tâche motrice pour enclencher les processus de consolidation. Finalement, les résultats présentés dans la thèse seront intégrés les uns aux autres dans une discussion générale au Chapitre 7.

CHAPITRE 2

REVUE DE LA LITTÉRATURE

Motor skill consolidation

Trempe, M., Proteau, L.

Département de kinésiologie, Université de Montréal, Montréal, Qc, Canada

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2.1 Introduction

Physical practice has long been regarded as the single most determinant factor of motor skill acquisition, and early models of motor skill learning advocated this position (Adams, 1971; Crossman, 1959; Fitts, 1964; Schmidt, 1975). Often expressed by the old adage “practice makes perfect,” this idea easily relates to the common observation that extensive practice is necessary to master a complex motor skill. Although the importance of physical practice for motor skill learning is undeniable, recent evidence demonstrates that the neurobiological changes that constitute the foundation of memory do not occur during physical practice. Specifically, the pioneering works of Merzenich (Merzenich, Kaas, Nelson, Sur, & Felleman, 1983; Merzenich et al., 1984) and Taub (1980) on brain plasticity provided clear demonstrations that learning modifies neuronal connections within the adult brain. Since then, physical practice has also been associated with the enlargement of specific cortical motor maps (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Giraux, Sirigu, Schneider, & Dubernard, 2001; Karni et al., 1995; Kleim et al., 2004; Pascual-Leone et al., 1995) and the recruitment of different brain networks (Doyon & Benali, 2005; Floyer-Lea & Matthews, 2005; Halsband & Lange, 2006; Ungerleider, Doyon, & Karni, 2002). However, these changes require significant synaptic reorganization that involves the expression of specific genes and the creation of new proteins (Kandel, 2001; McGaugh, 2000). Just as Rome was not built in a day, this neuronal reorganization requires time to be completed and is therefore likely to extend beyond practice sessions.

The idea that some “learning” processes remain active after physical practice was first demonstrated in animal studies. For example, in an experiment typical of these studies, rodents were administered a protein synthesis inhibitor before acquiring a certain behavior (McGaugh, 2000). Although the animals had no difficulty acquiring the correct behavior, retention was strongly impaired when the animals were retested the following day. This indicates the drug disrupted important processes normally occurring <u>after</u> the acquisition phase. Moreover, the observation that only retention, not acquisition, was impaired provided compelling evidence that the processes responsible for memory retention differ from those serving memory acquisition. This finding suggests a two-stage model in which memories are first acquired and then stored for long-term retention. These post-acquisition processes are essential to memory formation and have been grouped under the term “consolidation” (Krakauer & Shadmehr, 2006; Robertson, Pascual-Leone, & Miall, 2004; Stickgold & Walker, 2007).

A growing body of evidence demonstrates that consolidation processes are crucial for motor skill learning. For example, repetitive transcranial magnetic stimulation (rTMS) applied over the primary motor cortex immediately after participants had practiced a fast ballistic pinch of the index finger and thumb impaired retention of the motor skill (see also Baraduc, Lang, Rothwell, & Wolpert, 2004; Muellbacher et al., 2002). No impairment was observed if the same stimulation was applied to control sites (occipital cortex and dorsolateral prefrontal cortex) or 6 hours after practice ended (see also Kantak, Sullivan, Fisher, Knowlton, & Winstein, 2010; Muellbacher et al., 2002), suggesting that consolidation processes are both localized within specific brain networks and time-dependent. Similar observations have been reported for participants learning to adapt their movements to compensate for a perturbation of visual feedback (visuomotor rotation) or to external forces applied against their hand (dynamic adaptation). Although participants adapted their movements to compensate for such perturbations within one practice session, retention was impaired if a second and opposed perturbation (Task B) was practiced immediately after the first one (Task A). In contrast, retention was hardly affected if Tasks A and B were practiced several hours apart (Brashers-Krug, Shadmehr, & Bizzi, 1996; Krakauer, Ghilardi, & Ghez, 1999). In both these examples, the disruption of the consolidation processes (with rTMS or by practicing a conflicting task) had a significant effect on long-term memory formation. Thus, successful motor skill learning depends not only on the quantity of practice but also on the integrity of post-acquisition processes.

2.2 Performance stabilization

Previous research on memory consolidation has demonstrated that retention can be impaired if an interfering agent (e.g., drugs, electroshock, protein synthesis inhibitor) is administered soon after the acquisition of a new memory (McGaugh, 2000). Similarly, practicing two different tasks successively has also been found to impair retention (Brashers-Krug, et al., 1996; Krakauer, et al., 1999; Walker, Brakefield, Hobson, & Stickgold, 2003), whereas no such interference is observed when the interfering agent or the second task is experienced several hours after initial acquisition. Consolidation therefore plays a protective role for newly developed memory representations by transitioning them from a labile, interference-susceptible state to a more stable, interference-resistant state.

The observation that retention is impaired when two tasks are practiced successively implies that it may be impossible to consolidate two different motor skills simultaneously. However, this conclusion is somewhat difficult to reconcile with the common observation that motor skills are rarely learned in complete isolation from one another. Hence, consolidation may not always be subject to interference. When participants learn to adapt their movements to compensate for a 30° counterclockwise (CCW) rotation of visual feedback, retention is impaired when a second rotation is practiced immediately after the first one (Krakauer, et al., 1999), regardless of the size (in degrees) of the second interfering rotation (Hinder, Walk, Wooley, Riek, & Carson, 2007). Interference has also been reported when participants successively learned two distinct sequences of finger movements (Walker, Brakefield, Hobson, et al., 2003). In contrast, no interference occurred when the second visuomotor rotation was replaced by a dynamic adaptation task in which participants had to adjust their movements to compensate for a force pulling on their arm (Krakauer, et al., 1999). Similarly, (Balas, Roitenberg, Giladi, & Karni, 2007) reported interference when participants wrote a few words in their native language after practicing a sequence of finger movements, whereas no interference was observed when the writing task was performed with the other hand (Balas, Netser, Giladi, & Karni, 2007) or when participants wrote the same words using an unfamiliar script (Balas, Roitenberg, et al., 2007).

One current hypothesis argues that interference between two tasks depends on the degree to which their memory representations conflict in working memory (Bays, Flanagan, & Wolpert, 2005). For instance, Shadmehr and Holcomb (1999) observed interference when two skills activated the same brain network (i.e., when the neuronal representations of the two skills overlapped) as if the memory representation of the second task overwrote the first one and erased the performance gains resulting from practice. This hypothesis leads to the prediction that interchanging the execution of two skills every few trials should produce massive interference between the skills and result in poor learning. However, this prediction finds little experimental support. In contrast, a large body of research on "contextual interference" has shown that random practice (i.e., interchanging the execution of two skills from trial to trial) consistently results in better retention compared to a schedule in which two skills are practiced separately in a blocked manner, one after the other. The beneficial effect of random practice on motor learning has been associated with the increased cognitive effort imposed by this type of schedule (Lee & Magill, 1983; Shea & Morgan, 1979). One possibility to reconcile these two opposite ideas is that by interchanging the tasks constantly during practice (random practice), the learner gains awareness of the different nature of the tasks and is able to form a specific memory representation for each task. Because the two tasks are then clearly dissociated, interference is decreased (Bays, et al., 2005). In contrast, a blocked practice schedule in which the two skills are practiced one after the other may not facilitate such dissociation and the same memory representation may be reactivated during practice of the second skill, thus causing interference and resulting in impaired retention.

In sum, when two different motor skills have to be learned, optimal learning may be achieved by practicing the second skill several hours after the first one, that is, when the first skill has become consolidated. Whenever this schedule is not possible, coaches and instructors should structure the practice session to favor a clear dissociation between the skills (for example, by changing the exercises or the context of the exercises), thus ensuring minimal interference between the two skills.

2.3 The case of off-line learning

In addition to performance stabilization, consolidation has been associated with off-line learning, which is a spontaneous improvement in performance without practice (Robertson, Pascual-Leone, & Miall, 2004; Walker, 2005). This behavioral outcome was first observed using a perceptual learning task in which participants had to identify the orientation of a briefly presented set of bars (Karni & Sagi, 1993; Stickgold, James, & Hobson, 2000). With practice, participants improved their discrimination skill. When retested the following day, participants performed significantly better than at the end of the initial practice session, even though they received no additional training (Karni & Sagi, 1993). This result generated great enthusiasm in the research community as it ran against the old adage “practice makes perfect” and indicated that the simple passage of time could be sufficient to improve one's performance. Since then, other procedural tasks have been used to determine whether the passage of time could also be beneficial to motor skill learning. Among the different tasks used, the finger sequence task and the serial reaction time task (SRTT) have been the two most common.

The finger sequence task consists of producing a sequence of finger movements as fast and accurately as possible. In typical experiments, participants are first taught a 5-element sequence before practicing it for 12 blocks of 30 seconds each, with each block separated by a 30-second pause. This practice session is then followed several hours later by a retention test composed of 3 blocks of 30 seconds. Although the task has a declarative aspect (knowing the order of the elements), its procedural aspect is obviously more challenging. Consolidation intervals ranging from 8 to 24 hours led to significant increases in the number of sequences performed during each block, ranging from 18% (Korman, Raz, Flash, & Karni, 2003; Kuriyama, Stickgold, & Walker, 2004; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) to 34% (Fischer, Hallschmid, Elsner, & Born, 2002). In some instances, these gains were also accompanied by an increase in the number of correct movements per block (Fischer, et al., 2002; Korman, et al., 2003; Kuriyama, et al., 2004). As with the visual discrimination task, these gains occurred although no practice took place between the practice and retest sessions. No significant off-line learning was observed when the consolidation interval was shorter than 5 hours (Korman, et al., 2003; Walker, et al., 2002).

Similar results have also been reported with the SRTT in which participants had to respond as fast and as accurately as possible to one of four stimuli presented on a computer screen. Unknown to the participants, in some conditions the stimuli presentation followed a pre-determined sequence (usually made of 12 elements). After a single practice session, reaction times were shorter when the stimuli were presented in the pre-determined sequence rather than randomly, indicating that the participants had learned the sequence. Because participants were usually unable to explicitly evoke the sequence order, learning was thought to occur implicitly. When retested 12 hours after the initial practice session, with no additional practice between the sessions, the participants' reaction time "spontaneously" decreased (Press, Casement, Pascual-Leone, & Robertson, 2005; Robertson, Pascual-Leone, & Press, 2004; Robertson, Press, & Pascual-Leone, 2005).

These results are spectacular in that they show that motor skill learning progresses even when the learner is not actively practicing the task. Similar observations have also been reported with an auditory discrimination task (Gaab, Paetzold, Becker, Walker, & Schlaug, 2004) and a visuomotor adaptation task (Doyon, et al., 2009; Huber, Ghilardi, Massimini, & Tononi, 2004; Trempe & Proteau, 2010). Although there is no doubt that consolidation is beneficial to memory retention, the question of whether consolidation truly *improves* performance is still open to debate, specifically because it is often difficult to isolate off-line learning from other confounding factors. For example, off-line learning should not be confused with the simple dissipation of the fatigue caused by massed practice. Fatigue impairs performance and can mask the true learning that occurs during a practice session. Therefore, a rest interval sufficiently long for participants to recover would result in a spontaneous increase in performance (see Rickard, Cai, Rieth, Jones, & Colin Ard, 2008 for a discussion). Additionally, one should be particularly cautious with experiments in which learning is assessed by averaging several practice trials together. This procedure is common in the SRTT literature in which as many as 15 repetitions of the learned sequences are used to evaluate retention (180 movements, see for example Press, et al., 2005), as well as in the finger sequence task in which as many as 3 blocks of 30 seconds are averaged (Fischer, et al., 2002; Walker, et al., 2002). In both cases, it is difficult to determine whether the spontaneous increase in performance observed in retention sessions originates from consolidation or is simply due to continued learning *during* the retention test (see also Robertson, Pascual-Leone, & Miall, 2004 for a similar discussion). This pitfall could be avoided by considering only the first few movements of the retest session. However, these trials are often contaminated by a "warm-up decrement" (i.e., a small and short lived decrease in performance at the beginning of a practice session (see Schmidt & Lee, 2005, p448) that potentially masks off-line learning. Alternatively, off- and on-line learning could be dissociated by comparing the performance of a consolidation group with the performance of a control group performing as many trials without a chance to consolidate the new skill. Assuming that control participants did not suffer from fatigue (due to the use of short training sessions, for example), their performance should indicate the amount of improvement that can be expected solely from physical practice. Unfortunately, this control condition is far too often lacking.

This is not to say, however, that off-line learning is impossible or that the between-sessions improvements previously reported were misinterpreted. One idea that is particularly appealing for off-line learning is that the learner may gain an “insight” between practice sessions regarding the execution of the motor task, thus improving his or her performance. Most of us have had the experience of finding the solution to a difficult problem after putting it is aside for a while, giving rise to the popular expression “sleep on it.” In a clever experiment, Wagner et al. (2004) empirically tested this idea by asking participants to find the answer to long sequences of mental calculations. Unknown to the participants, all sequences were governed by a specific rule that provided the final answer without having to do all the calculations. Participants who benefited from a night of sleep between the practice and retest sessions were significantly more likely to discover the rule than those who did not sleep (see also Fischer, Drosopoulos, Tsen, & Born, 2006 for similar results), supporting the popular conception that insight can arise when a problem is left aside. Although this effect may occur when learning a motor skill, experimental evidence is still needed.

2.4 Underlying processes

Extensive work has been done to characterize the processes of consolidation and identify the molecular substrates of memory. James McGaugh (2000) and Nobel laureate Eric Kandel (2000) have led this field of research and demonstrated how memory formation produces long-lasting changes within different neuronal networks. Recently, attention has also been directed at the finding that memories acquired during practice are replayed during subsequent rest intervals, with (Ji & Wilson, 2007; Wilson & McNaughton, 1994) or without sleep (Hoffman & McNaughton, 2002). When a rodent moves within its environment, “place cells” located in the hippocampus fire selectively with the specific positions occupied by the animal (O'Keefe & Nadel, 1978). Each path followed by the animal is associated with a specific activation sequence of hippocampal neuronal ensembles. Wilson and McNaughton (1994) were the first to report that the activation sequence elicited during practice was later reactivated during rest, suggesting that the memory representation was being replayed and further processed after the practice session. A similar reactivation of the hippocampus has also been reported after practice sessions of a route learning task in humans (Peigneux et al., 2004). Brain activity during rest periods is therefore influenced by prior waking experiences, arguing that consolidation may not be limited to a “construction” process based on synaptic modification but may also include further information processing.

This idea is consistent with the results of neuroimaging studies demonstrating consolidation is associated with a shift of the brain networks solicited during practice (Karni et al., 1995; Shadmehr & Holcomb, 1997; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). In their early work on memory consolidation, Shadmehr and Holcomb (1997) reported a reduction in the activation of the prefrontal cortex when participants resumed practice after 5.5 hours of consolidation and an increase in the activation of the contralateral dorsal premotor, contralateral posterior parietal, and ipsilateral anterior cerebellar cortex. Similarly, rodent experiments have demonstrated that memories that were initially hippocampus-dependent gradually evolved to become hippocampus-independent after consolidation, indicating that the memory trace was transferred to different brain structures during consolidation (Tse et al., 2007). These results suggest that consolidation may play an important role in integrating new memories into pre-existing networks (Walker & Stickgold, 2010).

The observation that consolidation has localized (modification of specific synapses) and widespread (interaction between large networks) effects argues that consolidation may comprise two distinct processes: First, a “synaptic consolidation” process involving the formation of new synapses or the modification of existing ones by molecular mechanisms, and second, a “system consolidation” process by which memory representations are further processed and integrated with existing memories (Diekelmann & Born, 2007, 2010). Although it may be tempting to associate these two processes with the two behavioral outcomes presented above (i.e., performance stabilization and off-line learning), experimental evidence is still required.

2.5 The role of sleep in memory consolidation

A large amount of research has been dedicated to the role of sleep in memory consolidation. Because of the brain’s reduced capability to process exteroceptive information during sleep (Rama, Cho, & Kushida, 2006), the sleeping state seems particularly well-suited for large scale reorganization of neuronal connections. Although this hypothesis is both plausible and appealing, conclusions are controversial and subject to ongoing debate (Cai & Rickard, 2009; Rickard et al., 2008; Vertes, 2004; Vertes & Siegel, 2005). For example, off-line learning following an initial practice session of the finger sequence task has been reported to occur with (Fischer et al., 2002; Walker et al., 2002) or without (Fischer et al., 2002) sleep, while some authors reported no off-line learning at all (Cai & Rickard, 2009). When sleep-dependent gains were observed, they could either be correlated with the amount of time spent in slow-wave sleep (Walker et al., 2002) or in REM sleep (Fischer et al., 2002). Moreover, the observation that brain reactivation occurs while awake (Hoffman & McNaughton, 2002) or sleeping (Ji & Wilson, 2007; Wilson & McNaughton, 1994) suggests that some processes could take place regardless of the brain state. This subject is not within the scope of the present chapter, but readers seeking a more in depth discussion of the importance of sleep in memory consolidation are referred to more authoritative reviews on the subject (Diekelmann & Born, 2010; Vassalli & Dijk, 2009; Vertes, 2004; Walker, 2005).

2.6 Consolidation and motor skill learning

There is now ample evidence supporting the position that consolidation is an important process in motor skill learning. Yet, *what* is learned or stabilized during consolidation remains largely speculative. One current view proposes that consolidation leads to the automatization of the new motor skill (Walker & Stickgold, 2006). This hypothesis originates from the results of Kuriyama et al. (2004), who used a finger sequence task to demonstrate that gains in speed after consolidation were larger for the transitions that were performed slowly during acquisition, whereas fast and easy transitions showed only minimal improvement. This finding was interpreted as evidence that participants initially learned the sequence by “chunking” or grouping certain segments together (Rosenbloom & Newell, 1987) and that consolidation allowed participants to incorporate the smaller memory units (chunks) into a larger, single memory representation. Consolidation would therefore promote the “unitization” of distinct memory units into a global schema or motor program (Walker & Stickgold, 2010). Support for this hypothesis was provided by recent results showing that, after extensive practice and consolidation, the elements of a sequence become so firmly linked together that asking participants to modify the last elements of the sequence slowed down performance of the entire sequence (Rozanov, Keren, & Karni, 2010). This “unitization” may therefore free some attentional resources, making the execution of the skill more automatic.

The automatization hypothesis finds support in previous neuroimaging studies. For example, Shadmehr and Holcomb (1997) reported that when participants adapted their movements to a velocity-dependent force field (dynamic adaptation), a consolidation interval resulted in a shift of the brain activation pattern from regions involved in the cognitive processing of information to regions regulating automated movements. Using a finger sequence task, Walker et al. (2005) also reported activation increases in the cerebellum and primary motor cortex following consolidation.

Because consolidation had been linked to the development of a global motor program, we recently conducted an experiment to determine which specific aspects of the motor program are consolidated and stored in long-term memory (Trempe, Mackrous & Proteau, unpublished data). Participants practiced a sequence of back and forth planar movements toward three different targets while the normal dynamics of their movement were modified by the lateral attachment of a 1-kg mass to their forearm. The task required that participants 1) learn the relative timing of the movement sequence to perform each segment in the prescribed intermediate time (the invariant of the motor program), 2) learn to complete the entire movement sequence in a prescribed total movement time (the parameter of the motor program), and 3) reach the targets as accurately as possible. After completing an initial training session in which visual and temporal feedback were provided, participants performed immediate and 24-hour no-feedback retention tests. The precision and the variability of the relative timing were maintained closer to the levels obtained during the immediate retention test in the 24-hour retention test, indicating that the structure of the motor program had been consolidated and stored in memory (see Figure 2.1A). These results support the idea that consolidation promotes the formation of a generalized motor program. Interestingly, participants showed a significant decrease in spatial accuracy when retested 24-hours post-acquisition compared to the immediate retention test (see Figure 2.1B). This observation suggests that the response specification relating to spatial accuracy may not be consolidated between training sessions and may need to be recalibrated at the beginning of each session. This result is in line with many reports showing that performance usually suffers from a short-lived “warm-up decrement” when practice is resumed after a pause

(Schmidt & Lee, 2005). It seems therefore advisable for coaches and instructors to provide their athletes/students with the opportunity to rehearse and recalibrate the consolidated motor skill before a competition event or practice session.

2.7 Time course of motor skill consolidation

Memory consolidation is, by definition, time-dependent. As time passes, the memory trace of the motor skill becomes stable and resistant to interference. Surprisingly, the relationship between time and consolidation remains poorly understood. Brashers-Krug et al. (1996) tested the effects of several between-session time intervals (from no break to 4 hours) on memory consolidation. Although their statistical comparisons were not designed to contrast the different time intervals, their data revealed a trend for better retention following longer consolidation (see Figure 2.2). Similarly, in a study conducted by Press et al. (2005), longer consolidation intervals were associated with greater gains in performance (for 4- and 12-hour interval).

The observation that consolidation progresses with the passage of time raises two important questions: Is there a minimal amount of time required, and is there a maximum time beyond which no more gain will occur? The first question appears particularly important for optimizing motor skill learning as it defines the minimal time window during which memories should be protected from interfering agents. Unfortunately, no clear answer can be found in the current literature, mostly because the statistical comparisons employed rarely have the necessary power to detect the small differences occurring after short consolidation intervals. Nonetheless, a trend for consolidation gain has been observed after 5 minutes (Brashers-Krug et al., 1996), 30 minutes (Hotermans, Peigneux, Maertens de Noordhout, Moonen, & Maquet, 2006) and 2 hours (Walker et al., 2002), although no gain was reported after 1 hour by Press et al. (2005).

A similar difficulty arises when assessing whether there is an upper time limit to memory consolidation. Although higher gains have been observed with longer consolidation intervals, it seems unlikely that these gains would grow indefinitely. For participants learning a finger sequence task, 72 hours of consolidation resulted in greater performance gains compared to 24 hours (Walker, Brakefield, Seidman et al., 2003). Similarly, Korman et al. (2003) reported slightly larger gains for a 48-hour retention interval compared to a 24-hour interval. However, because the authors used a repeated measures design, it is difficult to determine whether these additional gains were related to the prolonged consolidation period or to the additional practice resulting from performing the 24-hour retention test. In contrast, using a visuomotor adaptation task, Krakauer et al. (2005) reported that adaptation assessed 48 hours post-acquisition was slightly lower compared to adaptation assessed 24 hours post-acquisition. Although further work is clearly needed to precisely characterize the time course of consolidation, it seems safe to state that most gains occur within the first 24 hours after acquisition. This being said, it is noteworthy that consolidation gains have been found to persist for 1 month (Penhune & Doyon, 2002), 2 months (Savion-Lemieux & Penhune, 2005) and even three years (Karni & Sagi, 1993). These results concur with the anecdotal observation that motor skills are never really forgotten, even if they are not often practiced. Once consolidated, it seems that a motor skill can be maintained for a long period.

2.8 Factors influencing consolidation

Motor skill expertise requires extensive practice. In favorable circumstances, the more one practices, the better one gets. Yet, does the same relation apply to the consolidation processes? Does more practice result in a better or perhaps deeper reorganization of the memory trace? Using a finger sequence task, Walker et al. (2003) reported that doubling the amount of practice from 12 to 24 blocks of 30 seconds had no significant impact on between-session improvement (see also Wright, Rhee, & Vaculin, 2010), suggesting no relation between the quantity of practice and consolidation. In contrast, Krakauer et al. (2005) reported that although doubling the amount of initial practice in a visuomotor adaptation task (from 264 to 528 trials) did not lead to better performance during acquisition, it did prevent the interfering effect of practicing a second and conflicting rotation 5 minutes after the acquisition of the first rotation. Thus, extensive practice may not result in additional consolidation gains, but it does seem to influence the stability of the new memory representation.

Alternatively, it has been suggested that consolidation may not depend on the amount of practice *per se,* but rather on the attainment of a certain performance level (Hauptmann & Karni, 2002). Using a word-counting task, Hauptmann and Karni (2002) reported that consolidation resulted in performance gains only when asymptotic performance (the leveling off or saturation of within-session improvement) had been reached during the initial practice session (see also Korman, et al., 2003 for a similar discussion), regardless of the amount of initial practice (Hauptmann, Reinhart, Brandt, & Karni, 2005). Using a visuomotor adaptation task, we also observed that participants who attained a performance close to perfect during acquisition had difficulty to de-adapt their movement following consolidation. No such difficulty was observed when participants did not beneficiate from consolidation or did not attain close to perfect performance during acquisition (Trempe & Proteau, 2010). Both rodent (Kleim, et al., 2004) and human (Karni, et al., 1995) experiments have provided evidence that a reorganization of the primary motor cortex occurs when performance reaches an asymptote. These results argue that some consolidation processes are performance-dependent in that a certain level of performance must be attained to trigger the resource and energy consuming process of plasticity.

How is this performance level determined? We recently suggested that the feedback received by the learner during acquisition might act as an important signal to trigger specific consolidation processes (Trempe, Sabourin, & Proteau, 2011, in press). To test this hypothesis, two groups of participants performed an initial practice session of a visuomotor adaption task before being retested the following day. The practice and retest sessions were identical for both groups with the exception of the feedback given to the participants during the first session. One group received positive feedback that led the participants to feel successful while the other group received feedback that led them to believe they did not do very well. Regardless of the feedback, all participants performed similarly during acquisition. However, when retested 24 hours later, participants who were led to feel successful during acquisition showed better retention than those who were led to feel less successful. The “successful” participants even outperformed another group who were also led to feel successful during practice, but were not allowed a consolidation interval, indicating that the increased performance in retention was not simply caused by higher motivation (see Figure 2.3). We concluded that feedback is not only used to modify movements from trial to trial, but also serves an important role in memory formation. Further evidence supporting the role of feedback for memory formation is provided by a recent report (Hadipour-Niktarash, Lee, Desmond, & Shadmehr, 2007) in which a TMS stimulation applied over the primary motor cortex immediately after movement execution (the moment when the learner receives feedback) impaired retention. The same stimulation applied 700 ms after movement completion had no effect on retention. At the neurophysiological level, the feedback treatment is associated with a modulation of the EEG signal over the frontal cortex (Holroyd, Pakzad-Vaezi, & Krigolson, 2008) that is believed to be elicited by the anterior cingulate cortex, a major output of the mesencephalic dopaminergic system (Holroyd & Coles, 2002). Because of the important role of dopamine in memory formation (Jay, 2003), it seems conceivable that positive feedback acts as a reward signal that triggers specific consolidation processes.

Whether there is a minimal quantity or frequency of successful feedback to trigger these consolidation processes is still an open question. Anecdotal evidence from everyday life indicates that some experiences need only to occur once to be remembered for the rest of our lives, indicating that certain types of memory do not necessitate a critical amount of repetition or reward to be remembered. To our knowledge, no convincing evidence indicates whether there is a minimum frequency or occurrence of successful feedback that must be experienced to consolidate a motor skill. The observation that participants can learn a timed motor sequence with as little as 1 block of trials (2 min and 12 s of practice; Savion-Lemieux & Penhune, 2005) or a visuomotor rotation with only 24 trials (for a total practice time of 6 seconds; Trempe & Proteau, 2010) suggests that if a minimum exists, it seems to be quite low.

Because of the importance of reward for motor skill consolidation, it is advisable for coaches and instructors to avoid rewarding incorrect movements for the sake of increasing the learner's motivation. Such inappropriate reinforcement may lead the learner to consolidate faulty movements that will inevitably have to be corrected in future practice sessions. Establishing with the learner a specific and measurable objective to be achieved during the practice session (Kyllo & Landers, 1995) and providing him/her the opportunities to evaluate his/her own performance in relation with the objective seems to be an excellent method of providing reward. By doing so, only successful movements (i.e., movements that attained the objective) are rewarded and consolidated.

2.9 Observation and consolidation

In most reports, consolidation has been studied using physical practice tasks, thus raising the possibility that physical practice may be a prerequisite for motor skill consolidation. To our knowledge, four reports have investigated the consolidation processes following either observation (Van Der Werf, Van Der

Helm, Schoonheim, Ridderikhoff, & Van Someren, 2009) or motor imagery (Debarnot, Creveaux, Collet, Doyon, & Guillot, 2009; Debarnot, Creveaux, Collet, Gemignani, et al., 2009; Debarnot, Maley, De Rossi, & Guillot, 2010). In all these reports, a consolidation interval that included sleep resulted in significant increases in performance. However, the initial acquisition session also included either physical practice (Debarnot, Creveaux, Collet, Doyon, et al., 2009; Debarnot, Creveaux, Collet, Gemignani, et al., 2009; Debarnot, et al., 2010) or contractions of the muscles used to perform the task (Van Der Werf, et al., 2009), making it difficult to determine whether consolidation was triggered uniquely by observation/motor imagery. To determine whether consolidation takes place in the absence of physical practice, we conducted a series of experiments in which participants observed an expert model perform a sequence of arm movements (Trempe, Sabourin, Rohbanfard, & Proteau, 2011). Participants who were asked to reproduce the sequence 24 hours after observation performed no better than participants who reproduced the sequence 5 minutes after observation, indicating that a prolonged retention interval did not result in off-line learning. However, the results of a second experiment demonstrated that the memory representation of the sequence learned by observation was stabilized during retention and interfered with the learning of a second sequence observed 8 hours later. No such interference occurred when the two sequences were observed 5 minutes apart. This result is opposite to what has been typically reported when tasks are physically practiced (Brashers-Krug, et al., 1996; Krakauer, et al., 1999) and suggests that consolidation processes 1) take place after observation learning and 2) differ from those taking place after physical practice.

Interestingly, observation resulted in better learning when the two tasks were observed 5 minutes apart. Coaches and instructors wishing to demonstrate two different skills during a practice session may optimize their athlete's/student's learning by demonstrating the two skills in close succession. This presentation schedule allows the learner to form a clear representation for each skill and decreases potential interference between the two skills.

2.10 Reconsolidate the consolidated memories

Once consolidated, memories are not forever protected against interference. In a series of experiments, Walker (2003) demonstrated that the memory representation of a finger movement sequence could be disrupted by a second interfering sequence even after it had been consolidated. Specifically, participants learned a first sequence (Sequence A) on day 1 and demonstrated off-line learning when retested on day 2. Then, if participants practiced a second sequence (Sequence B) immediately after recall of Sequence A on day 2, retention of Sequence A was impaired when retested 24 hours later (on day 3). No such impairment was observed if Sequence B was practiced on day 2 without recall of Sequence A. From these results, the authors concluded that the reactivation of Sequence A on day 2 returned its memory representation to a labile state that was susceptible to interference from Sequence B. Without recall, the memory representation remained in a stable form and was not subject to interference. This suggests that once reactivated, memories need to go through another consolidation phase, or "reconsolidation", to regain a stable form (see Alberini, 2005; Nader & Hardt, 2009 for reviews). Learning could then be seen as a cycle of destabilization-reconsolidation. According to Alberini (2005), the stability of a memory representation depends on the number of destabilization-reconsolidation cycles experienced. Every time memories are destabilized and reconsolidated, they become more stable and less susceptible to disruption (see also Suzuki et al., 2004), explaining the notorious difficulty of getting rid of an old habit when performing a motor skill.

Results from reconsolidation experiments thus provide valuable guidance for learners wishing to modify a deeply anchored, incorrect technical execution. Because memory traces become labile once again upon rehearsal, an effective training method may consist of deliberately rehearsing the incorrect execution at the beginning of the practice session before attempting to perform the correct movement. The destabilized memory representation associated with the incorrect execution may then be subject to interference from the correct movement and eventually be overwritten by the desired memory trace. This appealing hypothesis will, however, benefit from experimentations to evaluate its promises.

2.11 Conclusion

Although early models of motor skill learning have traditionally seen physical practice as the most important factor, several recent experiments have highlighted the important role of consolidation processes for motor skill learning. During consolidation, the skill's memory representation undergoes further processing to become integrated into existing brain networks and kept in long-term memory, a dynamic process that is repeated every time the memory representation is rehearsed. While practice still makes perfect, consolidation ensures that perfection is maintained.

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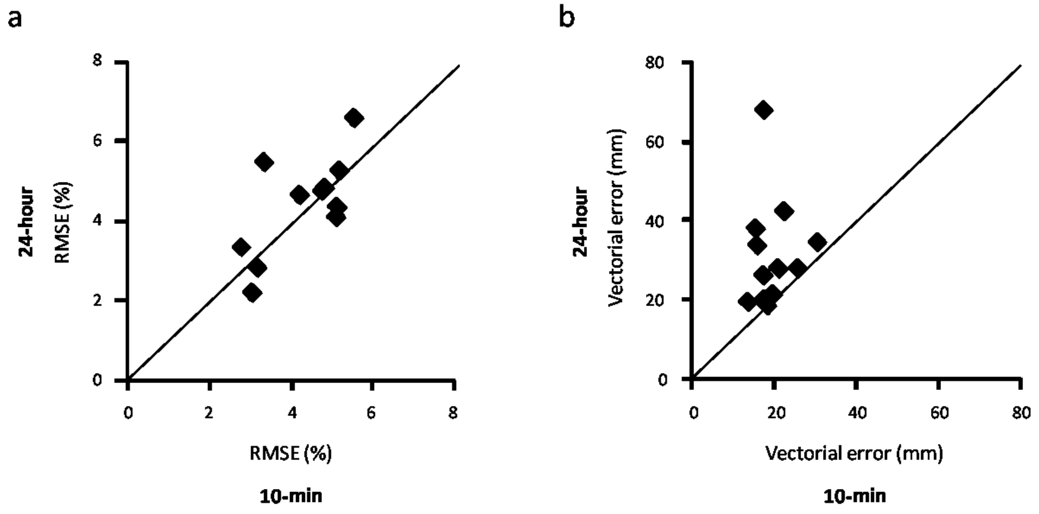

Figure 2.1: Participants practiced a sequence of back and forth planar movements toward three different targets and had to perform each segment in a prescribed movement time while being as spatially accurate as possible. Participants were then retested, without visual feedback, 10 minutes and 24 hours later. Each symbol represents the participants' mean error 10 minutes (*x* axis) and 24 hours (*y* axis) after acquisition. Data illustrated close to the identity line indicates good retention, whereas data illustrated above the identity line indicates impaired retention. Participants demonstrated good retention of the structure of the motor program 24 hours after acquisition, as measured by the *root mean squared error* (RMSE) of the segments' movement time (A). RMSE was calculated by comparing the relative timing of each segment of the sequence (i.e., the movement time of each segment divided by the total movement time) to the prescribed relative timing. However, participants failed to retain the response specification relating to spatial accuracy, as shown by a decrease in the vectorial error 24 hours after acquisition (B).

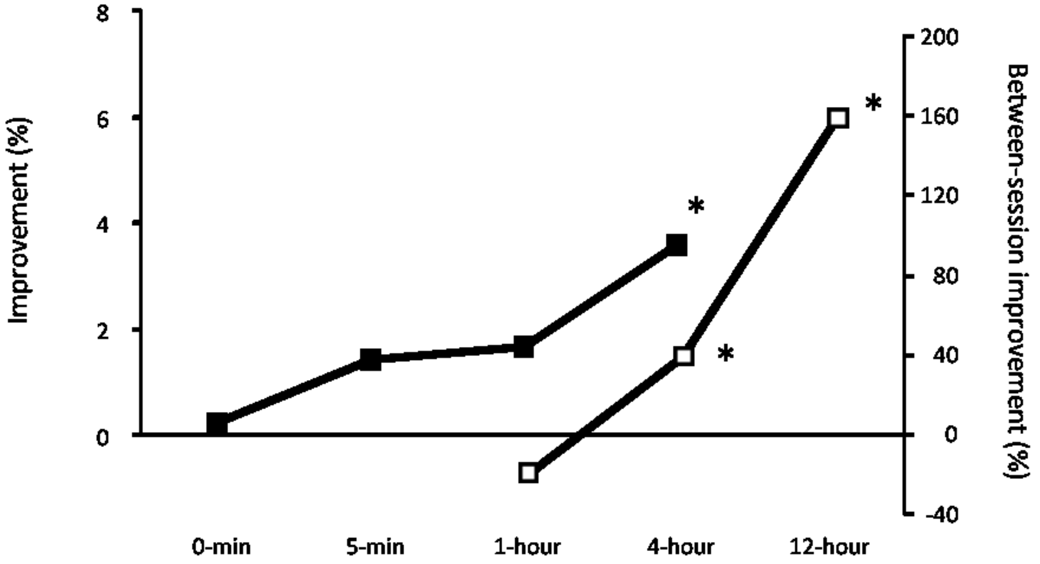

Figure 2.2: When participants had to adapt their movements to two different visuomotor rotations (Tasks A and B), participants demonstrated impaired retention of Task A when the second task (Task B) was experienced immediately after Task A (0-min group). Increasing the between-task interval resulted in progressively better retention. However, only a 4-hour between-task interval allowed participants to perform significantly better in retention compared to acquisition (adapted from Brasher-Krug et al. 1996, filled squares, left *y* axis). When participants learned to produce a sequence of finger movements, longer between-session intervals (4- and 12-hour) resulted in greater performance gains compared to a 1-hour interval (adapted from Press et al., 2005, opened squares, right *y* axis).

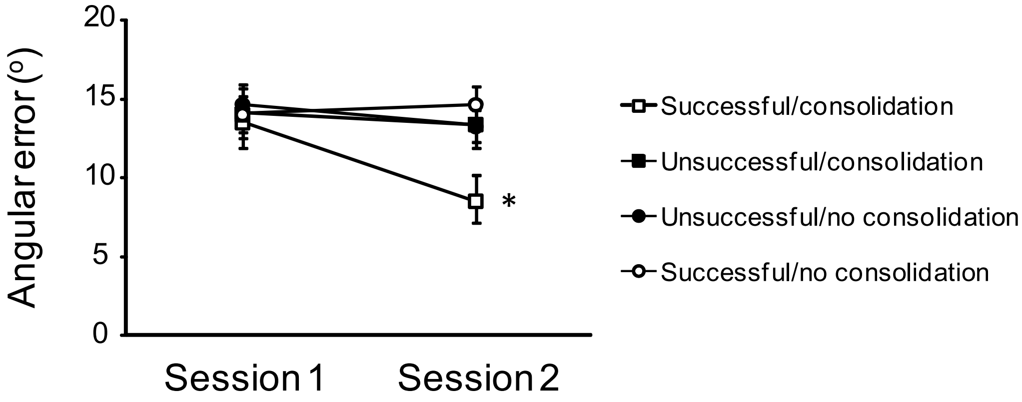

Figure 2.3: Mean angular error of participants who adapted to a rotation of visual feedback. Although the participants' adaptation did not differ during the first practice session, participants who felt successful and benefited from a consolidation interval showed better retention during the second practice session (adapted from Trempe, Sabourin & Proteau, in press).

CHAPITRE 3

ÉTUDE MÉTHODOLOGIQUE

Plusieurs études ont démontré que la consolidation peut entrainer une amélioration spontanée de la performance (voir Robertson, Pascual-Leone, & Miall, 2004; Walker, 2005 pour des revues sur le sujet). Dans ces études, une précision n'a cependant jamais été soulevée : une amélioration de la performance peut être observée que s'il y a encore place à l'amélioration. Il semble en effet peu probable que la consolidation puisse entrainer une amélioration de la performance lorsque l'apprenant devient un expert et que des gains minimes de performance nécessitent de nombreuses heures (voir journées) d'entrainement. Cela signifie-t-il que la consolidation n'est plus importante une fois l'atteinte d'un certain niveau de performance ?

Nous avons voulu déterminer l'influence du niveau d'expertise de l'apprenant sur les processus de consolidation. Pour ce faire, nous avions besoin d'une tâche expérimentale permettant à l'apprenant d'atteindre deux niveaux d'expertise différents avec la même quantité de pratique, condition essentielle pour isoler les effets liés au niveau d'expertise. La tâche d'adaptation visuomotrice, dont les particularités méthodologiques sont présentées dans ce chapitre, répondait à ce besoin.

Straight ahead acts as a reference for visuomotor adaptation

Trempe, M., Proteau, L.

Département de kinésiologie, Université de Montréal, Montréal, Qc, Canada

In

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3.1 Abstract

One can adapt movement planning to compensate for a mismatch between vision and action. Previous research with prismatic lenses has shown this adaptation to be accompanied with a shift in the evaluation of one's body midline, suggesting an important role of this reference for successful adaptation. This interpretation leads to the prediction that rotation adaptation could be more difficult to learn for some directions than others. Specifically, we hypothesised that targets seen to the right of the body midline but for which a rotation imposes a movement to its left would generate a conflict leading to a bias in movement planning. As expected, we observed different movement planning biases across movement directions. The same pattern of biases was observed in a second experiment in which the starting position was translated 15 cm to the right of the participants' midline. This indicates that the "straight ahead" direction, not one's midline, serves as an important reference for movement planning during rotation adaptation.

Keywords: Visuomotor adaptation, Motor learning, Body midline, Straight ahead, Aiming movements

3.2 Experiment 1

3.2.1 Introduction

Manual aiming toward a visual target puts into play a series of processes to identify the target and its location into an allocentric frame of reference and to transform this information into appropriate motor commands in an egocentric frame of reference. The mapping between the object's location and the appropriate motor commands is adaptable. When a mismatch is induced between vision and action, such as when aiming at a target while wearing prismatic lenses, one can recalibrate his/her movement plan to compensate for the prismatic effect. Clear evidence of this remapping is observed when the lenses are removed as movements then become biased toward the direction previously imposed by the prism (Shadmehr & Wise, 2005). Similar aftereffects have been observed when the visual feedback available during an aiming movement (visuomotor adaptation) or the forces acting on the hand (dynamic adaptation) were modified (Brashers-Krug, Shadmehr, & Bizzi, 1996; Shadmehr & Holcomb, 1997; Shadmehr & Mussa-Ivaldi, 1994). This remapping likely takes place at the CNS level because adaptation has been shown to change the brain activation pattern observed during movement execution (Inoue et al., 2000; Shadmehr & Holcomb, 1997).

How the brain performs this remapping remains unclear. In a visuomotor adaptation task (for example, the visual feedback is rotated 30° clockwise relative to the true hand trajectory), it could be that the CNS first plans a movement vector as when no bias was induced and then, through practice, learns to counter-rotate it to compensate for the rotation of the visual feedback. Although possible, this hypothesis is difficult to reconcile with the observation that adaptation for a rotation is local, generalizing poorly to unpracticed directions (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Ghahramani, Wolpert, & Jordan, 1996; Krakauer, Pine, Ghilardi, & Ghez, 2000). Moreover, if remapping occurs through a simple rotation of the original movement vector, adaptation should be a function of the amount of practice, regardless of the number of possible target directions. This is not what has been observed. Rather, Krakauer et al. (2000) reported that the learning rate of a new mapping decreased as the number of target directions increased. This led them to suggest that adaptation for a rotation of visual feedback could require the development of a new directional axis of reference. Similarly, Hatada et al. (2006a, 2006b) proposed that prism adaptation requires a shift of the internal egocentric frame of reference used for movement planning in a natural no-prism context, which is supported by their observation that prism adaptation resulted in a shift in the subjective evaluation of one’s body midline (Hatada et al., 2006a, 2006b). This suggests that the body midline could serve as a reference to encode the position of the target. For successful adaptation, the only necessary transformation would be a shift of the subjective evaluation of this reference, leaving the relation between the target position and the shifted body midline intact.

This proposition leads to the prediction that, in a visuomotor adaptation task, it should be more difficult to aim at some directions than at others. Specifically, if movement direction is initially planned in relation to the body midline, then a visual target located to the right of the body midline but for which the rotation imposes a movement oriented to the left of that line (i.e., a movement that has to cross the reference) would generate a conflict between the perceived location of the target in an allocentric frame of reference and the initial direction of the required movement in an egocentric frame of reference. This conflict would lead, at least early in practice, to lesser adaptation, and thus biased movement planning.

The goal of the present study was to test the hypothesis that the body midline is used as a reference axis for the learning of a new directional mapping between vision and action. To reach our goal, participants performed goal directed movements in a visuomotor rotation adaptation task (30° clockwise rotation). Participants aimed at eleven targets equally spaced between -50° and +50° relative to their midline. If movements requiring a crossing of the body midline show lesser adaptation shortly after movement onset than movements for which such a crossing is not necessary, it would support the hypothesis that the body midline is used as a reference for the planning of movement direction. On the contrary, if movements are equally adapted to the rotation regardless of whether or not they require crossing of the body midline, it would indicate that movement direction is planned relative to something other than the body midline.

3.2.2 Method

Participants

Twelve right-handed undergraduate students from the Département de kinésiologie of the Université de Montréal took part in this experiment. They all gave informed consent to participate in the study, were all naive about our hypothesis 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.

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 Figure 3.1a. 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 16 cm permitting free displacement of the manipulandum on the tabletop. Participants sat on a chair with their head resting at a fixed location on the side of the screen so that by looking at the mirror they could always see what was displayed on the computer screen. Participants could not see the actual displacement of their arm, but the cursor (black, 5 mm in diameter) displayed on the screen and reflected by the mirror provided them 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 face. 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 be easily gripped by the participant. From the participants' perspective, the far end of the manipulandum was located 40 cm to the left of the starting base and 70 cm in the sagittal plane. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the displacement of the stylus on-line and to illustrate it with a 1:1 ratio on the computer screen. The bottom of the stylus and the bottom of the optical encoder located at the junction of the two arms of the manipulandum were covered with a thin piece of Plexiglas. By lubricating the working surface at the beginning of each experimental session, displacement of the stylus was near frictionless.

Procedures.

Participants aimed with their left hand at targets located at a distance of 4.5 cm from the starting base (Krakauer, Ghez, & Ghilardi, 2005; Krakauer, Ghilardi, & Ghez, 1999). Eleven targets were equally spaced between -50° and 50° relatively to the starting base (see Figure 3.1b). The targets (filled circles, 5 mm in diameter; index of difficulty: 4.17 bits, Fitts, 1954) were presented in random order with the restriction that each target appeared once in each consecutive block of eleven trials. Participants were asked to aim at the target in one continuous motion and following a straight path. They were asked to be as accurate as possible while completing their movement in a time bandwidth of 250 ms +/- 50 ms. They were verbally informed to either slow down or speed up if their movement time felt under 200 ms or over 300 ms, respectively. Using a prescribed movement time bandwidth ensured that all participants used a similar speed-accuracy trade-off throughout the experiment. Participants were instructed to initiate their movement as they pleased following target presentation. Participants were informed explicitly that it was not a reaction time task.

Participants were briefed that they would perform manual aiming movements and that at some point in the session they would have to adjust their movements to compensate for a visual perturbation. The exact nature of the perturbation and its moment of occurrence were not mentioned, however. Then, participants performed 15 familiarization trials for which the displacement of the stylus resulted in an identical displacement of the cursor on the computer screen (i.e., no rotation). Following this familiarization phase, participants performed 55 acquisition trials (5 trials per target) for which the displacement of the cursor was rotated 30˚ clockwise in comparison to the displacement of the stylus. A movement progressing directly in line with one's midline was illustrated as progressing in straight line 30° to the right of one's midline.

Data reduction.

To provide a quick feedback to the participant during acquisition, movement initiation was detected once the stylus had been moved by 1 mm, whereas for the main analyses, movement initiation was defined as the moment at which the tangential velocity of the cursor reached 10 mm/s. The difference in procedures used to detect movement initiation during acquisition and in the main analyses explains why the movement times to be reported below are longer than the target movement time used during acquisition.

To obtain the velocity profile of the movements, the displacement data of the stylus over time were filtered using a second order recursive Butterworth filter with a cutting frequency of 10 Hz. We then numerically differentiated the smoothed data once using a central finite technique. Both during acquisition and for the main analyses movement was deemed to be completed when the cursor was not displaced by more than 2 mm in a time frame of 50 ms.

Data analyses.

To determine how participants adapted movement planning to compensate for the rotation, we calculated their angular error (angle between a reference vector joining the starting base and the target and that joining the starting base and the cursor) 100 ms after movement initiation as detected on the velocity profile. Because this delay should not have permitted participants to use sensory information to correct their movement (Carlton, 1992), it is likely that the location of the cursor at this temporal marker mainly reflected movement planning processes. We calculated both the constant direction planning error (i.e., the mean signed error between the rotated target position and the stylus/hand position) and the absolute direction planning error (i.e., the mean of the absolute value of the error between the rotated target position and the stylus/hand position)[1]. The absolute error (AE) was chosen because it is a measure of movement accuracy. The constant error (CE), in addition of being a measure of accuracy, adds to the previous variable by indicating whether movement planning was biased relative to the target. Specifically, a positive constant error indicated a movement planned/initiated too far to the right, whereas a negative constant error indicated that the movement was planned/initiated too far to the left relative to the reference vector.

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[1] The constant error was calculated using $\sum_{i=1}^{n}\frac{(x_i - T)}{n}$ where x_i is the direction of the movement on trial *i*, *T* is the direction of the target, and *n* is the total number of movements executed. The absolute error was calculated using $\sum_{i=1}^{n}\frac{|x_i - T|}{n}$.

Our hypothesis predicts that targets visually displayed to the right of the body midline, for which the rotation imposed a movement to the left of the body midline, should show lesser adaptation than other targets not requiring such a crossing. Because of our choice of target locations, movements toward the targets located at 10˚ and 20˚ to the right of the body midline were expected to show a larger bias to the right than movements toward the remaining targets. To obtain a general idea of movement planning accuracy for all possible targets, we averaged the directional planning error of the last two movements performed toward each target separately.

Because our hypothesis predicts that movement planning should be more difficult for the 10˚ and 20˚ targets (hereafter called crossed targets) than for the remaining targets, we contrasted planning AE and CE for these two targets with that of their mirror targets located at -10˚ and -20˚. Note that the crossed and mirror targets were located at the same distance from the body midline (see Figure 3.1b); however, the mirror targets resulted in movements to be executed in the same hemifield as where the targets were displayed. For each participant, both the planning AE and CE were averaged into blocks of two trials for the crossed targets, each block comprising one movement toward the target located at 10° and one movement toward the target located at 20°. The same operation was repeated for the mirror targets. Data were submitted to an ANOVA contrasting 2 Target directions (crossed vs. mirror) X 5 Blocks of trials with repeated measurements on both factors. Significant interactions were broken down into their simple main effects. Post hoc comparisons of significant main effects and of significant simple main effects were broken down using Dunn's technique. To ensure no inflation of type 1 error, the ANOVA's specific assumptions were verified before its computation. The normality of the distribution was assessed by calculating the z score of the skewness and kurtosis values (Tabachnick & Fidell, 2007). Hartley's F_{max} test was used to assess the homogeneity of variance. To correct for a possible violation of the sphericity assumption, we used the average of the Greenhouse-Geisser and Huyn-Feldt correction (Stevens, 1992). Note that the original degrees of freedom are reported. All significant effects are reported at $p < .05$.

3.2.3 Results

Figure 3.2 illustrates the mean absolute and constant direction planning errors of the last two movements performed toward each target. Clearly, planning bias and accuracy differed as a function of movement direction. Specifically, both constant and absolute planning errors peaked for movements directed at the 10° and 20° targets. In addition, participants showed a larger constant planning error for the targets located to the extreme right of the distribution (30°, 40° and 50°) in comparison to those located to the extreme left (-30°, -40° et -50°). Because no difference was noted for the absolute error, it suggests that planning for movements directed at the extreme right was not less accurate but was systematically biased to the right.

The results of the ANOVA contrasting direction planning performance for the crossed targets and their mirror targets revealed a significant main effect of Direction for both the constant and absolute errors $F(1\ ,\ 11) = 50.9$, $\eta^2 = .82$ and $F(1\ ,\ 11) = 41.5$, $\eta^2 = .79$, respectively, confirming significantly larger biases to the right but also significantly larger planning errors when aiming at the crossed targets than when aiming at their mirror targets. The ANOVA also revealed a significant main effect of Blocks of trials for both the constant and the absolute errors, $F(4, 44) = 10.6$, $\eta^2 = .49$ and $F(4, 44) = 9.9$, $\eta^2 = .48$, respectively. Post hoc comparisons showed that the constant error at the first block was significantly larger than at the following three blocks ($p = .07$ for the last block), whereas the absolute error was significantly larger at the first block than at the remaining blocks ($p < .02$). Figure 3.3 illustrates the adaptation curves for the mirror and crossed targets. Both CE ($r^2 = .74$ for the crossed targets, $r^2 = .79$ for the mirror targets) and AE ($r^2 = .76$ for the crossed targets, $r^2 = .92$ for the mirror targets) were best fitted by a first order exponential function. This differs slightly from the double exponential function reported by Krakauer and colleagues (1999). Note that the difference in CE and AE between the crossed and mirror targets at the first trial does not represent a difference in initial performance. Because eleven targets were presented randomly, the mirror targets were not the first one to appear. As a result, participants could use the information about the rotation obtained from the first few movements toward other targets to reduce the mirror targets' initial error. Importantly, this generalization was not observed for the crossed targets.

Because we calculated the direction error as early as 100 ms after movement initiation, our dependent variables were unlikely to be affected by online control (Carlton, 1992). Nonetheless, we wanted to confirm that the less accurate direction planning observed for the crossed than for their mirror targets could not result from participants performing faster movements, and thus generally less accurate movements (Fitts, 1954; Meyer, Smith, & Wright, 1982; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) for the crossed targets than for their mirror targets. Therefore, we measured the distance travelled by the cursor at 100 ms and submitted the data to the same type of ANOVA as our spatial dependent variables. The main effect of Direction and the Block x Direction interaction were both not significant, F (1, 11) = 2.7, p = .13, η^2 = .2 and F (4, 44) = 1.4, p = .3, η^2 = .1, respectively (Table 3.1), indicating that the differences in planning error observed between the crossed and mirror targets did not result from different speed-accuracy trade-offs.

Although the distance travelled by the cursor at 100 ms suggested no difference in the initial movement impulse between directions, we also contrasted the total movement time data in a 2 Directions X 5 Blocks of trials ANOVA. In general, participants had no difficulty performing their movements in the prescribed movement time. The ANOVA revealed a significant main effect of Direction, F (1, 11) = 5.98, η^2 = .35, revealing significantly longer movement times when aiming at the crossed targets than at their mirror targets (a difference of 37 ms, see Table 3.1). The longer movement times observed for the crossed targets than for their mirror targets might indicate that participants used a strategy based on online corrections to reach the crossed targets. To evaluate this possibility, we computed the angular error at movement endpoint and submitted the data to the same type of ANOVA as previously. The ANOVA revealed a significant main effect of Direction, F (1, 11) = 52.6, η^2 = .8, and F (1, 11) = 49.1,

η^2 = .8 for CE and AE, respectively. Although angular error decreased between the 100 ms marker and the end of the movements for the crossed targets, this last analysis indicates that movements were still more accurate toward the mirror targets than toward the crossed targets (Table 3.1). This finding is further supported by the observation that only 43% of movements aimed at the crossed targets ended on target as opposed to 63% for movements aimed at the mirror targets. The observation that participants took more time to complete their movements toward the crossed targets and that these movements were still less accurate than those toward the mirror targets reinforces our finding that crossing the body midline is difficult.

These results are congruent with the hypothesis that the body midline serves as a reference for movement planning because movements that had to cross this reference showed a lesser adaptation than those for which such a crossing was not required. To further test this hypothesis, we looked at the distribution of planned direction for both the crossed and mirror targets. If the body midline is a reference –or anchor point- difficult to cross, direction planning toward the 10° and 20° targets (which should be directed at -20° and -10°, respectively to compensate for the 30° CW rotation) should be “blocked” at 0°, that is, the participants’ midline. Figure 3.4 illustrates the distribution of planned direction for all movements directed toward the crossed targets as well as their mirror targets. The planned direction of approximately 60% of the movements aimed at the 10° and 20° targets (light grey bars) was blocked to the right of the participants’ midline (0°). Moreover, considering that the light grey bars illustrate the planned direction of movements toward two targets located 10° apart, one could have expected to see two distinct peaks representing each specific target direction. This is not what we observed as the results were fitted by a unimodal distribution (r^2 = .99). On the other hand, the results for the mirror targets (dark grey bars) were best fitted by a bimodal distribution (r^2 = .98 for the bimodal distribution as opposed to r^2 = .92 for the unimodal distribution), showing that participants could plan distinct movements toward each target. Because only one dominant direction was observed when aiming at the 10° and 20° targets and that this dominant direction was oriented to the right of the participants' midline supports the hypothesis that the body midline is a reference difficult to cross.

The results reported above converge to support our initial hypothesis. However, using a video-aiming task without rotation of the visual feedback, Ghez et al. (1995) reported some systematic variations in directional errors for different target directions. They hypothesized that these directional biases represented transformation errors related to distortions in the participants' representation of the location of their hand in peripersonal space. Thus, the difference we reported between the crossed and mirror targets might not have been caused by the crossing of the reference but rather by a transformation error as suggested by Ghez et al. (1995). To test this possibility, we recruited six additional participants (right-handed) who were submitted to the experimental protocol as previously described but without rotation of the visual feedback. If the results reported above resulted from transformation error, we should observe in the no rotation condition planning errors for the -20° and -10° targets that mimic those of the crossed targets in the rotation condition, whereas planning errors for the -50° and -40° targets in the no rotation condition should mimic that of the mirror targets in the rotation condition. The results of interest are summarized in Table 3.2. No significant difference was observed between the two directions for any of the dependent variables ($p > 0.3$). Therefore, because no difference was observed between the two directions in the no rotation condition, movement planning differences observed in Experiment 1 cannot be attributed to a systematic variation of directional error across direction under normal condition but to the difficulty associated with the crossing of the body midline.

3.2.4 Discussion

Results of previous studies suggested that the CNS adapts movement planning to compensate for a rotation of the visual feedback available during movement execution (Krakauer et al., 1999) and that each movement direction must be learned independently of the others (Krakauer et al., 2000). Our results add to these previous findings by showing that some directions are more difficult to learn than others. Specifically, movements toward targets located in the participant's right hemifield for which the rotation imposed a movement in the left hemifield were planned less accurately than movements aimed at other directions for which crossing the body midline was not required. Moreover, movement planning of 60% of the movements performed toward the crossed targets did not cross the body midline which provides strong support to the hypothesis that the body midline could serve as an important axis of reference for movement planning in a visuomotor adaptation task.

Nonetheless, before concluding as such, one has to consider that in our experiment, the starting location of the hand was directly in line with the body midline. Thus, apart from being the division between the right and left hemifield, the midline also represented the "straight ahead" direction, that is, the direction perpendicular to the strip of Plexiglas used to defined the starting location and to the side of the computer screen on which participants rested their head (straight ahead is illustrated as a thin black line on Figure 3.1b). Previous work from our laboratory has shown that straight ahead movements were generally more accurate than angled movements (Lhuisset & Proteau, 2004). Movements toward targets located directly in front of the hand starting position were directionally more accurate than movements toward targets located at -40°, -20°, +20° and +40° from the initial hand position. This held true regardless of the starting location of the hand being aligned or not with the body midline. This straight ahead advantage led us to question whether the reference we reported as difficult to cross was restricted only to the body midline or could be extended more generally to the straight ahead direction. We conducted a second experiment to determine whether the results reported in Experiment 1 indicate that it is the body midline or the straight ahead that is an important reference for movement planning.

3.3 Experiment 2

The apparatus and procedures were as in Experiment 1 but with the following modifications. Twenty-four participants took part in this experiment. For twelve participants, the task was exactly as in Experiment 1 (0 cm group). For the remaining twelve participants, the starting base was located 15 cm to the right of the participants' midline (15 cm group). For this second group, the 0° target was located directly in front of the starting base while the remaining 10 targets were located 10° apart on each side of the 0° target. If the body midline represents the reference used for movement planning in the visuomotor adaption task, no accuracy difference should be observed between targets direction for the 15 cm group as no movement would require crossing the body midline. However, if movements aimed at targets located at 10˚ and 20˚ -i.e., that require movements to cross a straight ahead reference (direction defined as 0˚)- are still plan less accurately than their mirror targets, it would suggest that the straight ahead direction, not the body midline, acts as a reference for movement planning.

3.3.1 Results

Without surprise, participants of the "0 cm" group reproduced the same pattern of directional planning error as in Experiment 1. Both the constant and absolute direction planning errors varied as a function of movement direction (see Figure 3.5). Importantly, we observed the same pattern of results for the "15 cm" group (see Figure 3.6). To verify the similarity of the results, the constant and absolute directional errors of the two groups were contrasted for the crossed targets and for their mirror targets. The data were submitted to independent ANOVAs contrasting 2 Groups (0 cm vs. 15 cm) x 2 Target directions (crossed vs. mirror) X 5 Blocks of trials with repeated measurements on the last two factors.

For the constant error, the ANOVA revealed a significant Direction x Block of trials interaction, *F* (4, 84) = 5.4, $\eta^2 = .20$, confirming a larger direction planning bias when aiming toward the crossed targets (*M* = 19.4°, *SE* = 0.8°) than when aiming at the mirror targets (*M* = 5.0°, *SE* = 1.0°). This difference was significant for all five blocks ($p < .003$); the interaction was caused by a larger decrease of error between the first and second block for the mirror than for the crossed targets. In addition, we also observed a significant Direction X Group interaction, F (1, 21) = 4.3, $\eta^2 = .17$. Post hoc comparisons showed no significant difference between the "15 cm" and the "0 cm" groups for the crossed targets (*M* = 19.1°, *SE* = 1.2° and *M* = 19.6°, *SE* = 1.1°, respectively), whereas the "15 cm" group showed a smaller planning bias than the "0 cm" group for the mirror targets (*M* = 2.1°, *SE* = 1.5 and *M* = 7.9°, *SE* = 1.4° for the "15 cm" and "0 cm" groups, respectively).

The ANOVA computed on the absolute error also revealed a significant Direction x Block of trials interaction, F (4, 84) = 2.81, $\eta^2 = .12$, indicating a significantly larger planning error for the crossed targets than for their mirror targets (*M* = 19.4°, *SE* = 0.8° and *M* = 10.6°, *SE* = 0.6°, respectively). This difference was significant for the entire practice session ($p < .005$); the interaction was caused by a larger decrease of error between block 1 and block 2 for the mirror than for the crossed targets. Thus, movement planning toward the crossed targets was not only biased to the right, indicative of lesser adaptation, but it was also less accurate than for the mirror targets.

The ANOVA computed on the distance travelled at 100 ms revealed a significant Direction X Block of trials interaction, F (4,84) = 2.9, $\eta^2 = 0.12$ (see Table 3.3). Post hoc comparisons revealed that the position of the cursor at this landmark was significantly closer to the starting location for the last 3 blocks of the acquisition phase for movements toward the crossed than the mirror targets. This result is opposite to what would have been expected if the difference between the crossed and mirror targets resulted from different speed-accuracy trade-offs.

The ANOVA computed on total movement time revealed a significant Direction X Block of trials interaction, F (4, 84) = 3.6, $\eta^2 = 0.15$ (see Table 3.3). Post hoc comparisons revealed that movements toward the crossed targets took longer than for the mirror targets for the first and third ($p < .022$) blocks of trials. At movement endpoint, the ANOVA computed on the angular error data revealed a significant Direction X Block of trials interaction for CE, F (4, 84) = 6.1, $\eta^2 =$ 0.22, and AE, F (4, 84) = 6.3, $\eta^2 = 0.23$. Post hoc comparison revealed that at the exception of the first block of trials, movements were significantly more accurate when aiming at the mirror targets than at the crossed targets. This finding is further supported by the observation that only 45% of movements aimed at the crossed targets ended on target as opposed to 68% for movements aimed at the mirror targets (averaged over both groups). Thus, although participants did decrease their error as movements progressed toward the crossed targets, this decrease was not sufficient to reach an accuracy equivalent to the one observed for the mirror targets.

Regardless of the position of the starting point, aiming to the left of the <u>straight ahead</u> when the target is visually displayed to its right causes large directional planning errors. Figure 3.7 illustrates for the 15 cm group the planned direction of all movements performed toward the crossed targets (light grey bars) and their mirror targets (dark grey bars). Direction planning for most of the movements aimed at the crossed targets (~ 70 %) did not cross the straight ahead line (0º). Results were fitted by a unimodal distribution (r^2 = .99) with a mode to the right of the straight ahead. In contrast, movements toward the mirror targets were distributed on a wider range of directions, and were best fitted by a bimodal than by a unimodal distribution (r^2 = .95 and .90, respectively), each mode being centered near the target direction.

For the 0 cm group, Figure 3.8 illustrates that the planned direction of most movements performed toward the crossed targets (~ 70 %) did not cross the straight ahead reference. Although the results were best fitted by a bimodal than a unimodal distribution (r^2 = .99 and .92, respectively), the most important observation is that both modes were centered to the right of the reference (1.8° and 13.1°). In contrast, the mirror targets were aimed at more accurately as a large number of movements were directed in their specific direction. Results were best fitted by a bimodal than a unimodal distribution (r^2 = .95 and .92, respectively).

3.3.2 Discussion

The results of this experiment reproduced those obtained in Experiment 1 and add to them by indicating that a strong reference for movement planning is not one's midline but rather what is straight ahead. These observations support previous findings reported by Lhuisset and Proteau (2004).

3.4 General discussion

The results of the present study support the hypothesis that a reference is used for movement planning in a visuomotor adaptation task (Hatada et al., 2006a; Krakauer et al., 2000). Our results add to these previous findings by showing that this reference originates from the hand starting position and defines a straight ahead movement vector. Because our measure of angular error was calculated as early as 100 ms following movement initiation, that is before movement could be amended with visual feedback (Carlton, 1992), this reference is likely used for movement planning.

Our observation that between 60 % to 70 % of movements aimed at the crossed targets did not cross the straight ahead direction (whether it was in line or not with the body midline) is strong evidence supporting the hypothesis that the straight ahead serves to plan movement direction. Because the targets were seen to the right of the hand's starting point, the initial movement impulse was oriented in this direction. The participants' relative inability to cross the straight ahead reference might explain why, with practice, the CNS shifts its straight ahead subjective evaluation (Hatada, et al., 2006a, 2006b). In the latter studies, prolonged practice with 15° prism glasses resulted in participants shifting their subjective evaluation of their midsagittal axis by approximately 6º.

The most important finding of the present report is that participants showed large planning errors for movements aimed at targets located across the straight ahead reference. This result might appear to contradict the results of anti-pointing experiments in which participants looked at a target located 16° to the right of their midline but aimed at a imaginary target located 16° to the left of their midline without considerable loss of accuracy (Carey, Hargreaves, & Goodale, 1996). However, two major differences exist between our visuomotor adaptation task and previous anti-pointing task. First, in the anti-pointing task participants were told that their movements had to be directed in the opposite hemifield, giving them the possibility to elaborate an explicit strategy to compensate for the perturbation. In our task, participants were not briefed about the particularity of the crossed targets. Moreover, only two targets out of eleven required such a crossing of the straight-ahead which might have made it difficult to elaborate a strategy specific for these two targets. Second, because movements were aimed at a symmetrical position in the anti-pointing task, the relation between the target position and the straight ahead could still be used to plan the movement in the opposite hemifield. In our task, this transposition was not possible because the rotation did not result in a movement to a symmetrical position in the opposite hemifield. This second difference adds further support to our hypothesis that the straight ahead is an important reference for movement planning because if the target can be localized relative to the straight ahead reference and that this relation remains unaltered (as in the anti-pointing task), aiming movements are more accurate than when the relation is perturbed (as in our visuomotor adaptation task).

Our observation that even at the end of the acquisition phase the aiming error of movements toward the crossed targets remained more than twice as large as that of the control group (no-rotation) is surprising. Two reasons might explain why aiming error for the crossed targets did not reach baseline values. First, our practice session might have been too short to allow a complete mastery of this difficult task. Second, perhaps movements toward the crossed and mirror targets were based on different strategies. For example, the use of the straight ahead reference was possible for movements toward the mirror targets, whereas another reference was required for movement toward the crossed targets. Because only two targets out of eleven required crossing the reference, perhaps the strategy used for the mirror targets (and the seven other targets not requiring a crossing of the reference) became dominant as it was implemented nearly five times more often than the specific strategy needed for the crossed targets. Therefore, it is conceivable that this dominant strategy interfered with the one required for the crossed targets, slowing down the rate of adaptation and making movements in this direction less accurate.

Figures 3.4, 3.7 and 3.8 (light grey bars), illustrate that although most movements did not cross the straight ahead reference, some did. Thus, it could be argued that movement planning was not blocked at 0º because of the difficulty to cross the straight ahead reference but rather because participants did not have sufficient practice to reduce/eliminate the error. This position would be supported if trials crossing the reference largely occurred near the end of the practice session. This was not the case. Thus, it is likely that the few trials that crossed the straight ahead reference reflects normal variability (i.e., noise) in movement planning.

It has been reported that hand's trajectory curvature varies according to movement direction (Kim, Gabbard, Buchanan, & Ryu, 2007), resulting from a change in the contribution of the upper and lower arm to the movement. Specifically, Kim et al. (2007) reported an increase in the left hand's trajectory curvature for targets located to the left of the body midline because of a decrease in the contribution of the upper-arm to the movement. In the present report, no bias between direction was observed for the control group (no-rotation) which argues against such a biomechanical explanation of the difference in planning accuracy between the crossed and mirror targets. In addition, participants of the 15 cm group should have shown smaller planning errors than participants of the 0 cm group because a displacement of the starting position of the left hand to the right engages more shoulder movement when aiming to the left. This was not the case. Both these results argue against a biomechanical explanation of the planning bias observed for the crossed targets.

Our observation that directional accuracy varied across movement directions, even when the straight ahead reference did not have to be crossed, was unexpected. Nonetheless, it strongly supports the role of straight ahead as a reference for movement planning. The large directional error noted for the 0° target suggests that perceiving a target aligned with the reference but planning a movement away from it might cause a conflict. For targets seen in the left hemifield, the directional error decreased with target eccentricity, indicating a decreasing influence of the straight ahead reference for movement planning. The same basic observation applies to the targets seen in the right hemifield. However, the conflict became more important when the reference needed to be crossed, explaining why the largest directional error was observed for the 10° target. This difficulty arose because this target was seen closest to the reference <u>and</u> the movement needed to cross the reference to the greatest extent. Then, it decreased for the 20° target as it was perceived further away from the reference and because the movement needed to cross the reference to a smaller extent.

Finally, although our results provide clear evidence supporting the role of the straight ahead for the planning of movement direction in a visuomotor adaptation task, it seems unlikely that rotation adaptation is limited only to a shift in the evaluation of a particular reference. Because such a shift would have a central origin, one would expect this adaptation to transfer to the unpracticed arm. However, only incomplete interlimb transfer has been reported with a visuomotor rotation task (Sainburg & Wang, 2002). Therefore, at least part of the adaptation appears effector specific. The relative importance of central versus effector specific adaptation remains to be determined.

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Table 3.1: Mean values for the main dependent variables at the last block of the practice session (standard error). * indicates a significant difference between the mirror and crossed targets.

	100 ms			Movement endpoint		
	CE (˚)	AE (˚)	Distance travelled (mm)	CE (˚)	AE (˚)	Movement time (ms)
Mirror targets	4.3 (1.8)*	9.2 (0.8)*	8.1 (0.4)	2.3 (0.7)*	3.1 (0.5)*	280 (12)*
Crossed targets	16.2 (1.1)*	16.3 (1.1)*	7.4 (0.5)	7.8 (1.0)*	7.6 (1.0)*	317 (19)*

Table 3.2: Mean values for the main dependent variables at the last block of the practice session for the control group (standard error). Note that no significant difference was observed between the directions corresponding to the crossed and mirror targets in Experiment 1.

	100 ms			Movement endpoint		
	CE (˚)	AE (˚)	Distance travelled (mm)	CE (˚)	AE (˚)	Movement time (ms)
Mirror targets (-50° and -40°)	6.1 (1.6)	7.4 (0.8)	8.0 (0.5)	-1.0 (0.8)	2.1 (0.5)	279 (11)
Crossed targets (-20° and -10°)	6.5 (2.7)	7.9 (1.7)	8.0 (0.5)	-0.7 (0.8)	2.2 (0.6)	270 (6)

Table 3.3: Mean values for the main dependent variables at the last block of the practice session for both the 15 cm and 0 cm group (standard error). * indicates a significant difference between the mirror and crossed targets.

		100 ms			Movement endpoint		
		CE (˚)	AE (˚)	Distance travelled (mm)	CE (˚)	AE (˚)	Movement time (ms)
15 cm group	Mirror targets	0.2 (3.1)*	9.9 (1.5)*	8.6 (0.6)	0.7 (0.8)*	2.8 (0.5)*	289 (13)
	Crossed targets	18.2 (1.6)*	18.2 (1.6)*	9.1 (0.4)	10.7 (0.9)*	10.7 (0.9)*	255 (11)
0 cm group	Mirror targets	5.6 (2.2)*	9.4 (1.0)*	7.9 (0.3)	2.8 (0.9)*	3.8 (0.6)*	294 (13)
	Crossed targets	16.6 (1.3)*	16.6 (1.3)*	7.2 (0.3)	6.7 (0.8)*	6.7 (0.8)*	301 (11)

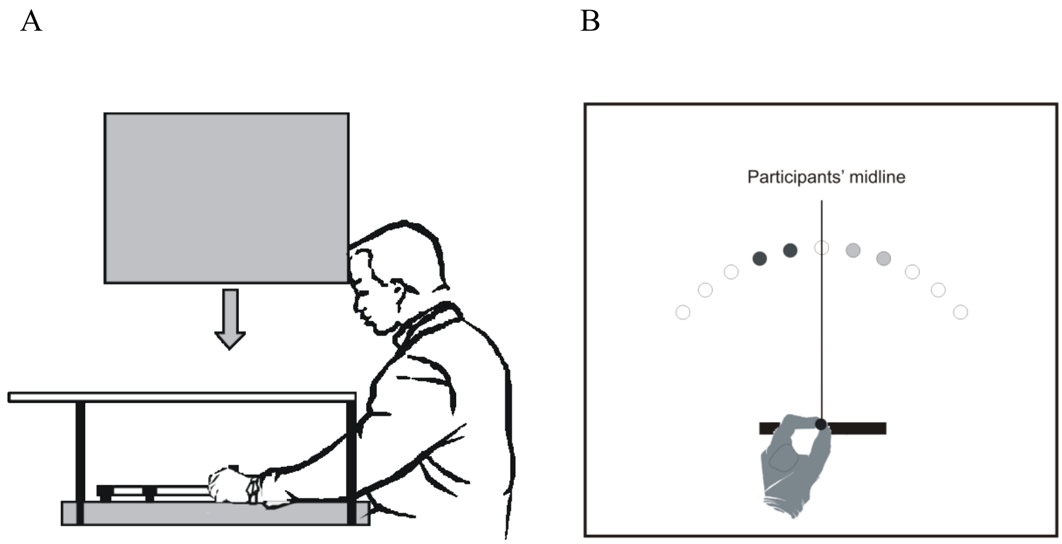

Figure 3.1: (A) View of the apparatus. (B) Because of the 30˚ clockwise rotation, movements performed along one's midline were illustrated as progressing 30° to the right. For the 10° and 20° targets (illustrated as light grey circles), this resulted in the targets being seen in the right hemifield while movements had to be aimed at the left hemifield. The mirror targets (-10° and -20° targets) used in the different analyses are illustrated as dark grey circles.

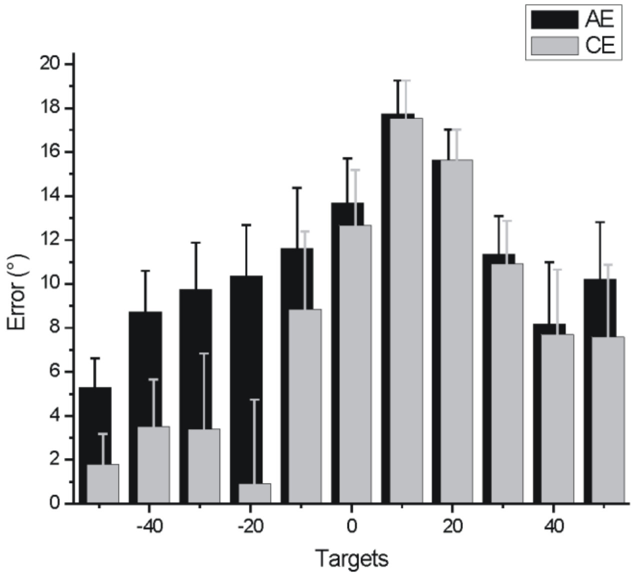

Figure 3.2: Constant error (CE) and absolute error (AE) of the last two movements performed toward each target. The error bars illustrate the standard error. For the constant error, a positive value indicates a movement initiated too far to the right. Note the largest bias for the 10° and 20° targets.

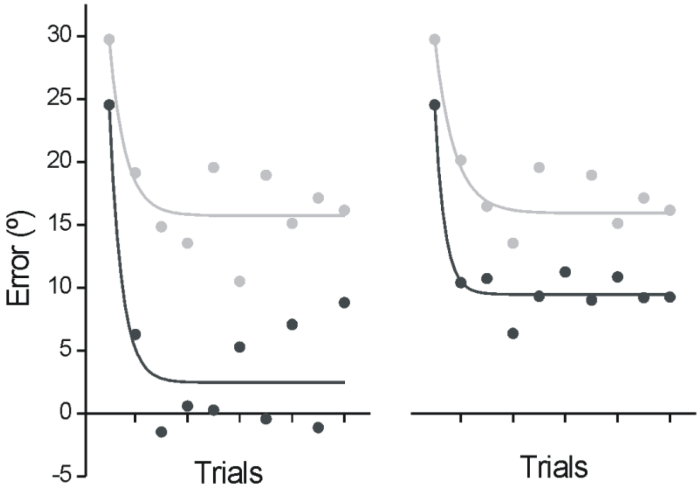

Figure 3.3: Mean errors of movements toward the crossed (light grey) and mirror (dark grey) targets. CE and AE are illustrated on the left and right panels, respectively. Both adaptation curves are best fitted by a first order exponential function.

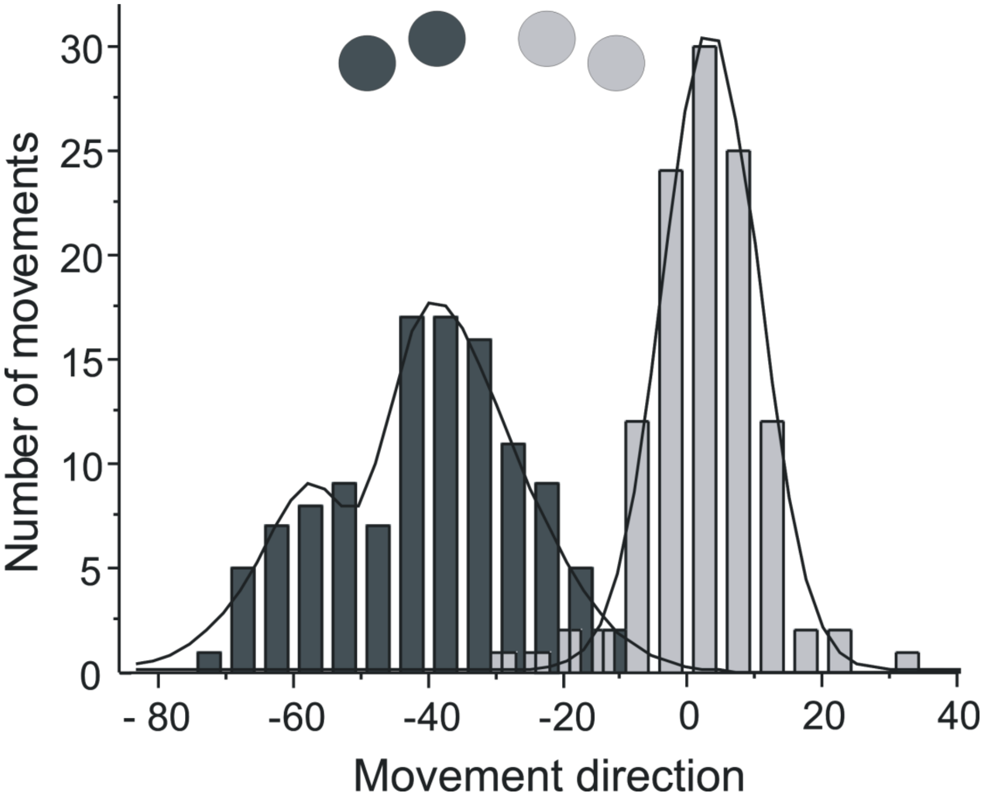

Figure 3.4: Cumulative histogram of the planned direction of all movements performed toward the 10° and 20° targets (light grey bars) and the -10° and -20° targets (dark grey bars). The coloured circles indicate the direction of movements that accurately compensates for the rotation. Thin black line illustrates the best fitting curve for each set of targets. Note the different distributions for the crossed and mirror targets.

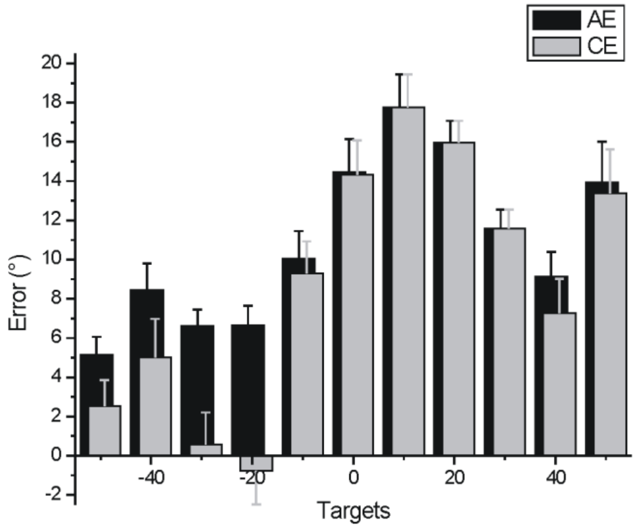

Figure 3.5: Constant error (CE) and absolute error (AE) of the last two movements of participants of the 0 cm group. The error bars illustrate the standard error. For the constant error, a positive value indicates a movement initiated too far to the right. Note the largest bias for the 10° and 20° targets.

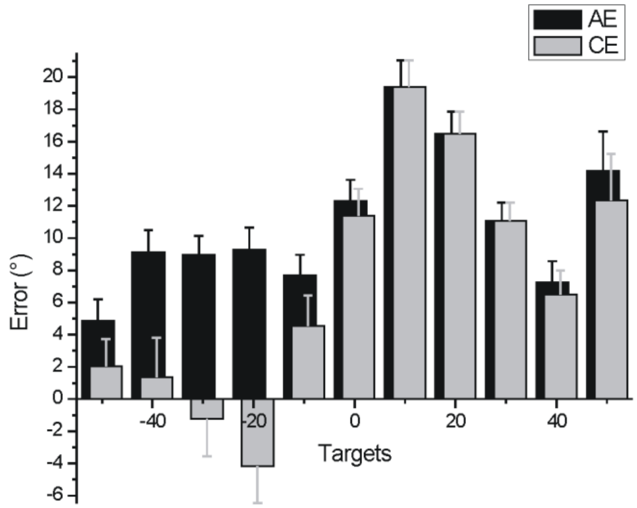

Figure 3.6: Constant error (CE) and absolute error (AE) of the last two movements of participants of the 15 cm group. The error bars illustrate the standard error. For the constant error, a positive value indicates a movement initiated too far to the right. Note the largest bias for the 10° and 20° targets.

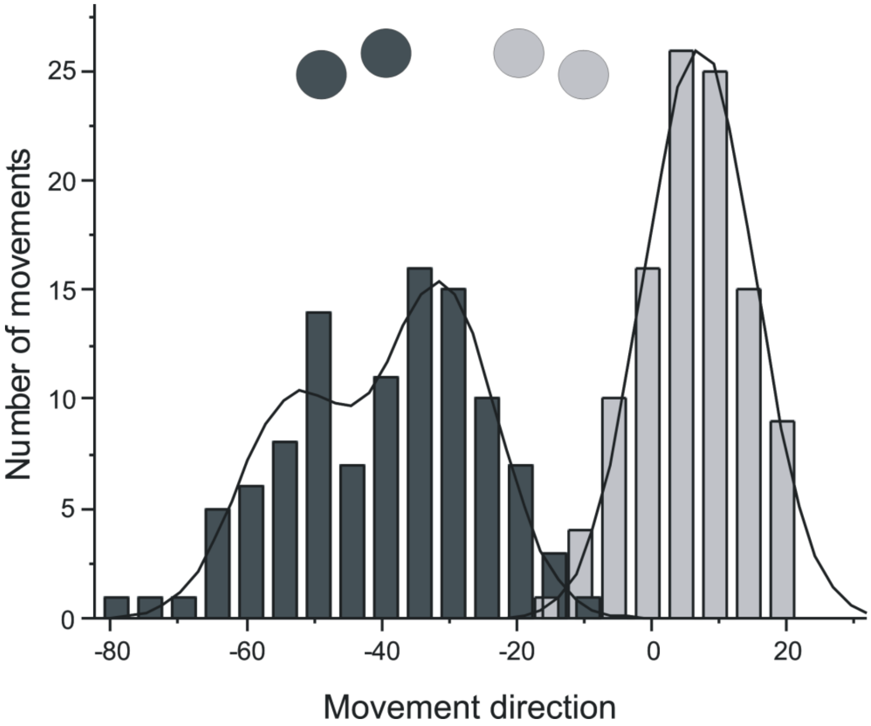

Figure 3.7: Cumulative histogram of the planned direction of all movements performed by participants of the 15 cm group toward the 10° and 20° targets (light grey bars) and the -10° and -20° targets (dark grey bars). The coloured circles indicate the direction of movements that accurately compensates for the rotation. Thin black line illustrates the best fitting curve for each set of targets. Note the different distributions for the crossed and mirror targets.

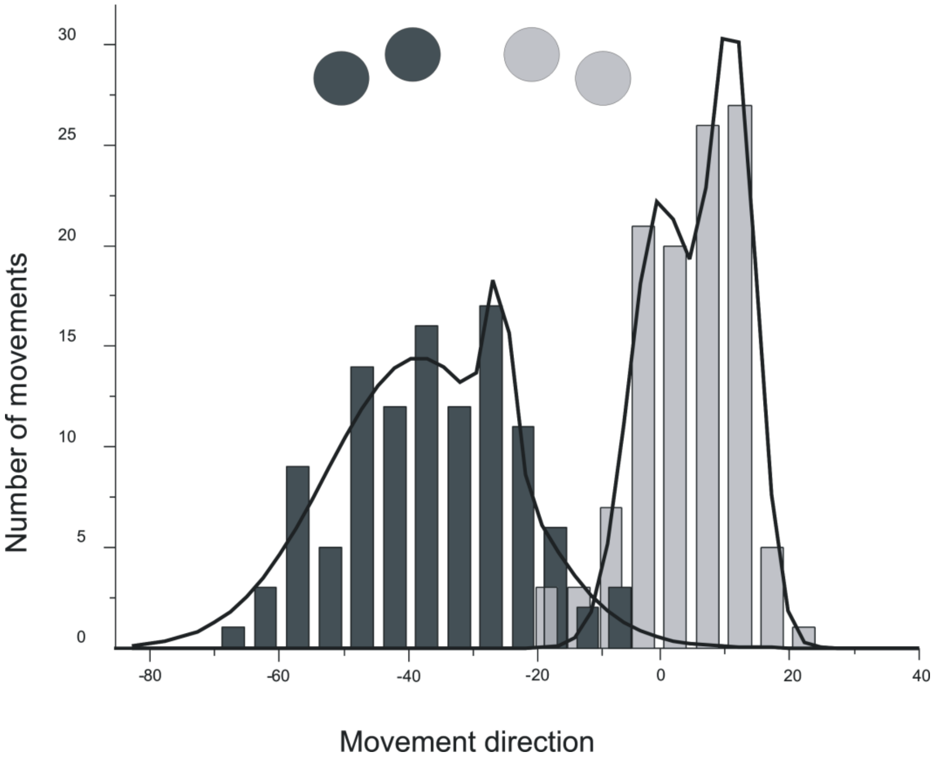

Figure 3.8: Cumulative histogram of the planned direction of all movements performed by participants of the 0 cm group toward the 10° and 20° targets (light grey bars) and the -10° and -20° targets (dark grey bars). The coloured circles indicate the direction of movements that accurately compensates for the rotation. Thin black line illustrates the best fitting curve for each set of targets. Note the different distributions for the crossed and mirror targets.

CHAPITRE 4

PERFORMANCE OBJECTIVE ET CONSOLIDATION

Nous avons mentionné précédemment que la relation entre le niveau d'expertise de l'apprenant et les processus de consolidation demeure encore nébuleuse. Existe-t-il un niveau de performance seuil devant être atteint pour enclencher la consolidation ? Y a-t-il une performance limite au-delà de laquelle la consolidation n'a plus d'effet ? L'apprentissage hors-ligne (*off-line learning*) survient-il uniquement chez le débutant ? Pour répondre à ces questions, nous avons employé la tâche d'adaptation visuomotrice présentée au chapitre précédent. Plus précisément, nous avons cherché à déterminer si l'atteinte de différents niveaux de performance lors de la séance de pratique initiale entraine des changements comportementaux distincts suite à une période de consolidation.

Distinct consolidation outcomes in a visuomotor adaptation task: off-line learning and persistent after-effect

Trempe, M., Proteau, L.

Département de kinésiologie, Université de Montréal, Québec, Canada

In

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4.1 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.

Keywords: consolidation, off-line learning, stabilization, aiming movements, motor learning, video aiming, visuomotor adaptation

4.2 Experiment 1

4.2.1 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 retested 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 & Holcomb (1997) presented a 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 retested 5.5 hours 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-hour groups to maximise any beneficial effects (but see also Doyon et al., 2009).

4.2.2 Method

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 4.1). 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.

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 Figure 4.1. 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 (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the displacement of the stylus on-line and to illustrate it with a 1:1 ratio on the computer screen. The bottom of the stylus and the bottom of the optical encoder located at the junction of the two arms of the manipulandum were covered with a thin piece of Plexiglas. By lubricating the working surface at the beginning of each experimental session, displacement of the stylus was near frictionless.

Procedures

Participants aimed with their left hand at one of 2 targets located at 10° and 20° to the right of their body midline and 4.5 cm away from the hand starting location (Huber, Ghilardi, Massimini, & Tononi, 2004; Krakauer et al., 1999; Krakauer, Pine, Ghilardi, & Ghez, 2000; Trempe & Proteau, 2008). These targets (filled circles, 5 mm in diameter) were presented in alternation, starting with the 10° target. Participants were told to initiate their movements as they pleased, to reach the target in one continuous motion and to follow a straight path (Krakauer et al., 1999). Vision of the cursor and target was permitted at all time. Participants were asked to be as accurate as possible while completing their movement in a time bandwidth of 250 ms +/- 50 ms. They were verbally informed to either slow down or speed up if their movement time fell under 200 ms or over 300 ms, respectively. Using a prescribed movement time ensured that participants used similar speed-accuracy trade-off through the experiment (Fitts, 1954).

Participants performed two practice sessions. The first practice session began with 15 familiarization trials for which the displacement of the stylus resulted in an identical displacement of the cursor on the computer screen (i.e., no rotation). Following this familiarization phase, participants performed either 24 (limited practice condition) or 144 acquisition trials (extensive practice condition, see Table 4.1 for details) for which displacement of the cursor was rotated 30° clockwise in comparison to the displacement of the stylus. Specifically, a movement progressing directly in line with one's midline was illustrated as progressing in straight line 30° to the right of one's midline. A second training session took place after a retention delay of either 10 min (10-min groups) or 24 hours (24-hour groups), allowing us to dissociate the effects related to consolidation from those related to physical practice. This second training session was followed by a transfer test with no rotation (Table 4.1).

Testing sessions were schedule between 8 and 10 am. Participants in the 24-hour group were invited to pursue their usual occupation between the sessions. They were asked to sleep a minimum of 7 hours and to avoid the consumption of alcoholic beverage or the of use recreational drugs. Compliance to the instructions was confirmed verbally by the participants at the beginning of the second session.

In addition, a fifth group of participants performed 144 trials without rotation of the visual feedback. Their performance served as baseline measure of movement planning accuracy. Note that the position of the targets they aimed at was rotated 30° to the left to correspond to the direction aimed at by the participants of the experimental conditions.

Data reduction

To determine how participants adapted their movement planning to compensate for the rotation, we calculated their angular error (angle between the reference vector joining the starting base and the target and that joining the starting base and the cursor) 100 ms after movement initiation (Hinder, Walk, Wooley, Riek, & Carson, 2007; Trempe & Proteau, 2008). Because this delay should not have permitted participants to use sensory information to correct their movement (Carlton, 1992), it is likely that the location of the cursor at this temporal marker mainly reflects movement planning process. A positive angular error indicates a movement initiated too far to the right, whereas a negative value indicates that the movement was initiated too far to the left.

Data were inspected to remove outliers for which the angular error 100 ms after movement onset deviated considerably from the participant's learning curve. Less than 3% of the trials were removed, with no difference between groups. Note that outliers could not be detected on the basis of the standard deviation or the *z* score because the amount of learning from trial to trial was too large to provide a sensitive criteria.

Adaptation was assessed by calculating the mean constant angular error for each session:

$$\sum_{i=1}^{n} \frac{(x_i - T)}{n}$$

where x_i is the direction of the movement on trial i, T is the direction of the target, and n is the total number of movements executed. Importantly, when two practice sessions are separated by even a short retention delay, it is common to observe, at the beginning of the second session, a transient and short-lived decrease in performance called "warm-up decrement" (Schmidt & Lee, 2005). To control for this effect, the first few trials of the second practice session are often excluded from the analyses (Krakauer et al., 2005; Krakauer et al., 1999). In the present report, the first trial of the second session was excluded.

Statistical analyses

To facilitate reading of this article, details concerning the statistical analyses computed are defined in the results section. For all analyses, to ensure no inflation of type 1 error, we assessed the normality of the distribution by looking at the detrended and the expected normal probability plots provided by SPSS (Tabachnick & Fidell, 2007). Hartley's F_{max} test was used to assess the homogeneity of variance of the ANOVAs. Post hoc comparisons were made using Dunn's technique. All significant effects are reported at $p < .05$ and corrected for the number of comparisons (Bonferroni's technique: Cardinal & Aitken, 2006).

4.2.3 Results

Baseline comparison

As reported previously, participants adapted their movements to compensate for the rotation of the visual feedback (Krakauer et al., 2005; Krakauer et al., 1999; Trempe & Proteau, 2008). Their angular error decreased rapidly within the first few trials and more slowly thereafter (Figure 4.2). To evaluate whether participants reached baseline level during the first practice session, we first averaged the angular error of the last 6 trials of the first session for each participant and then computed a 5 Groups one-way ANOVA (limited practice: 10-min and 24-hour groups, extensive practice: 10-min and 24-hour groups, no-rotation control group). Participants of the limited practice groups (10-min and 24-hour) were significantly less accurate than those performing the same task without rotation (i.e., the control group), $F(4, 54) = 4.8$, $\eta^2 = 0.28$, $p < 0.001$ for both *post hoc* comparisons (mean angular error of 11.3° (*SE* = 1.6) and 4.4° (*SE* = 0.9) for the limited practice and control groups, respectively). In contrast, the angular error of the two extensive practice groups did not differ significantly from that of the no-rotation control group (mean angular error of 8.9°, *SE* = 0.9, for the extensive practice groups).

Movement time

Participants had no difficulty performing the task in the prescribed movement time (*M* = 269 ms, *SE* = 13). To ensure that participants did not use different speed-accuracy trade-offs (Fitts, 1954) during the rotation adaptation phase, we contrasted the movement time data in a 4 Groups (limited practice: 10-min and 24-hour groups, extensive practice: 10-min and 24-hour groups) X 2 Sessions ANOVA. The ANOVA revealed no significant difference between the groups, $F(3, 40) = 0.5$, $p = 0.6$, $\eta^2 = 0.39$, and no significant interaction involving the Group factor.

Off-line learning

Prior reports have shown that consolidation results in significant off-line learning of a new internal model (Doyon et al., 2009; Huber et al., 2004).To measure this effect, we calculated the between-session improvement of the 4 rotation groups by averaging the mean angular error of the second session and subtracted it to the mean angular error of the first and last 12 trials of the first practice session. We chose this procedure to ensure that the results would not be biased by random fluctuations in the participants' performance. If consolidation results in off-line learning, participants of the 24-hour groups should demonstrate a larger improvement than those of the 10-min groups. The data were compared using contrasts defined *a priori*.

Figure 4.2C illustrates that a 24-hour break did not systemically result in off-line learning. Specifically, the performance gain between the first and second session of practice was minimal and statistically equivalent for the 10-min and 24-hour extensive practice groups (M = 1.9, SE = 0.9 and M = 2.8, SE = 1.2, respectively). This increase in performance was significantly smaller than that of participants who practiced a limited number of trials in session 1 and had a 24-hour break (p = 0.002). Moreover, concerning the limited practice groups, participants who had a 24-hour break showed a significantly larger improvement between sessions 1 and 2 than those who had only a 10-min break (p = 0.036, M = 6.85, SE = 0.9 and M = 3.35, SE = 0.9, respectively). Thus, consolidation resulted in off-line learning but only for the limited practice group.[2]

Our main dependent variable revealed that consolidation did not improve movement planning accuracy off-line when participants initially performed an

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[2] Note that we also computed the same contrasts using the mean angular error at movement endpoint. Results were similar to those observed at 100 ms. Specifically, from the first to the second experimental session, participants of the limited practice groups reduced their error by 3.4° (0.5) and 2.4° (0.6) (24-hour and 10-min groups, respectively), whereas participants of the extensive practice groups reduced their error by 1.7° (0.6) and 1.2° (0.7) (24-hour and 10-min groups, respectively). However, the contrasts failed to reveal a significant difference between the 10-min and 24-hour groups. This was to be expected because participants had sufficient time to correct their movements online (Carlton, 1992). Consequently, the terminal error was relatively low at the end of session 1, leaving little room for further improvement.

extensive practice session. It is however possible that consolidation led to more efficient and less variable movement planning instead. For instance, learning a new movement results in changes in muscles synergy and intersegmental torques leading to a decrease in the end-effector (i.e., the stylus in the present study) variability (Corcos, Jaric, Agarwal, & Gottlieb, 1993; Hong & Newell, 2006). To test for this possibility, we compared the decrease in variability from the first to the second session of participants of the extensive practice groups. We used a principle component analysis to compute the 2D variability of the last 11 trials performed in both sessions.[3] Specifically, we calculated a confidence interval ($\alpha = 0.05$) around each participant mean angular position 100 ms after movement onset. We then represented this interval with an ellipse and used the surface of the ellipse to quantify the 2D variability (Sokal & Rohlf, 1981). Participants of the 10-min and 24-hour groups decreased their variability from the first session to the second by 0.2 ($SE = 0.5$) and 0.3 ($SE = 0.3$) mm^2, respectively. A two-tailed T-test did not reveal any difference between the groups, $t(20) = -0.2$, $p = 0.86$, $d = 0.08$, suggesting that consolidation did not increase the “efficiency” of movement planning.

After-effect

To determine the stability of the newly developed internal model, we removed the rotation at the end of the second session and measured the persistence of the after-effect. At first, movements were biased in the direction

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[3] We used only the data of the last 11 trials because of the large inter-trial variability at the beginning of session 1 that resulted from the adaptation to the rotation.

previously imposed by the rotation, showing that participants had learned to some extent a new internal model. Then, with practice and visual feedback, the leftward bias decreased as participants gradually returned to their normal no-rotation model. To measure the persistence of the after-effect, we average the angular error of the last 6 trials of the no-rotation test for each participant. The data were compared using orthogonal contrasts defined *a priori*. (Note that the first 6 trials of the no-rotation test were not included in the analysis because they reflected the amplitude of the after-effect rather than its persistence.) Following limited practice in the first practice session, the 10-min and 24-hour groups similarly returned to their normal no-rotation internal model. No between-group difference in the after-effect was detectable at the end of the no-rotation transfer-test, $p = 0.76$, $d = 0.01$ (Figure 4.3A). However, when participants were given extensive practice during the initial session, those who had a 24-hour break showed a significantly more persistent after-effect than those of the 10-min break group, $p = 0.036$, $d = 0.4$ (Figure 4.3B). That is, at the end of the transfer test, their movements were more biased in the direction previously imposed by the rotation. Thus, consolidation resulted in different after-effects according to the amount of initial practice.

4.2.4 Discussion

The objective of this first experiment was to determine whether distinct consolidation outcomes are observed depending on the learner's initial performance. To answer this question, participants practiced either 24 or 144 trials of a visuomotor adaptation task and were retested 10 minutes or 24 hours later. The most interesting and innovative result of Experiment 1 is the finding that different initial training led to different bias in the no-rotation transfer test following a consolidation interval. Specifically, when the initial session consisted of 144 trials, participants of the 24-hour break showed more persistent after-effects than those of the 10-min group. In contrast, when the initial session consisted of 24 trials, persistency of the after-effect did not differ significantly between the 10-min and 24-hour groups. Thus, a certain amount of training (or the attainment of a certain performance) seems to be a pre-requisite to observe persistent after-effects.

Consolidation also resulted in off-line learning but only for the limited practice group, that is when the initial performance was inaccurate. The observation that consolidation did not result in persistent after-effect for the limited practice group with a 24-hour break strongly suggests that consolidation of the visuomotor adaptation task produces at least two distinct outcomes (we will come back to this point in section 4.4).

The results of Experiment 1 do not enable us to determine whether the persistent after-effect exhibited by participants of the extensive practice group with a 24-hour break was triggered by the larger amount of initial practice or by the level of performance they had reached during session 1. Specifically, is this outcome practice dependent or performance dependent?

4.3 Experiment 2

To answer the previous question, we used a modified version of the visuomotor adaptation task. We have previously reported that the ease with which one can adapt to a rotation of the visual feedback depends on the direction of the target to reach at (Trempe & Proteau, 2008). Specifically, when a target is visually perceived to the right of the hand's starting location but requires a movement to the left to compensate for the rotation of the visual feedback, participants showed a large bias to the right. It seems that participants have difficulty crossing the direction that is "straight ahead" of their starting location. However, when movements are aimed at targets for which crossing of the straight-ahead is not necessary, adaptation is easier and quicker. Thus, after an equal amount of practice trials, participants can plan their movements accurately for some targets (i.e., no-crossing targets) but not for others (crossing targets). If persistent after-effect is practice dependent, for the same amount of practice we should observe similar after-effect for all the targets, regardless of the initial accuracy of the participants. On the contrary, if this consolidation outcome is performance dependent, we should observe more persistent after-effect only for the targets for which the participants show good performance, i.e. that do not require a crossing of the straight ahead.

4.3.1 Method

Participants

Thirty-one new right-handed participants took part (mean age 23; 19 female) in this experiment. They all gave inform written consent and the same inclusion criteria as in Experiment 1 were used.

Procedures

Figure 4.4 illustrates the location of the targets used in Experiment 2. Participants aimed with their left hand at one of eleven targets equally spaced between -50° and 50° relative to the starting base and located at a distance of 4.5 cm. Because of the 30° rotation, 2 targets were perceived to the right of the starting base but required a movement aimed to the left of the starting base. These targets, located at 10° and 20° to the right of the starting base, corresponded to those used in Experiment 1 and were expected to be the most difficult to aim at (Trempe & Proteau, 2008). Hereafter, they will be referred to as the "crossed targets." In contrast, the two targets located at the same visual angle but to the left of the starting base did not require a crossing of the straight ahead reference. These two "mirror targets" were therefore easier to aim at.

As in Experiment 1, participants performed two practice sessions that could be separated by either 10-min (10-min group) or 24-hour (24-hour group). For both groups, the first session began with 15 familiarization trials followed by a limited amount of practice trials with 30° CW rotation of the visual feedback (55 trials, 5 trials toward each target). During the familiarization phase, the targets were selected randomly with the restriction that 3 trials were directed at the crossed and mirror targets, respectively, whereas during the practice phase, the targets were presented in random order with the restriction that each target appeared once in each consecutive block of eleven trials. Pilot studies showed that this limited amount of practice was sufficient for the participants to reach baseline level when aiming at the mirror targets while their performance remained poor when aiming at the crossed targets. Thus, if persistent after-effect depends on the amount of practice, a 24-hour break should not result in more persistent after-effect for any type of targets. However, if this outcome is performance dependent, the 24-hour group should show a more persistent after-effect than the 10-min group but only when aiming at the mirror (easy) targets.

Details concerning the experimental sessions are provided in Table 4.1. Unless stated otherwise, the remaining procedures and analyses were identical to those described in Experiment 1.

4.3.2 Results

Baseline comparison

As expected, the participants' performance varied depending on the target location. Specifically, participants compensated for about half of the 30° rotation when aiming at the crossed targets while their error was 0.8° larger than baseline when aiming at the mirror targets (Figure 4.5).

We first compared the performance of the 10-min and 24-hour groups at the end of the first session (last four trials per type of target) with that of a control group performing the same task but without rotation in a 3 Groups (control, 10-min, 24-hour) X 2 Types of target (crossed vs. mirror) ANOVA. The ANOVA revealed a significant Group X Type of target interaction, $F(2, 28) = 6.8$, $p = 0.004$, $\eta^2_p = 0.33$. Post hoc comparisons revealed that both the 10-min and 24-hour groups performed as accurately as the control group when aiming at the mirror targets (both $p > 0.6$) but showed a significantly larger bias when aiming at the crossed targets (both $p < 0.001$). Therefore, as reported previously (Trempe & Proteau, 2008), rotation adaptation differed between the types of target (see Figure 4.5A and B). No difference was observed between the 10-min and 24-hour groups (both $p > 0.6$), however, indicating that participants of both groups adapted identically to the rotation of the visual feedback.[4]

Movement time

Participants had no difficulty performing the task in the prescribed movement time ($M = 240$ ms, $SE = 12$). To ensure that participants did not use different speed-accuracy trade-offs (Fitts, 1954) during the rotation adaptation phase, we contrasted the movement time data of the 10-min and 24-hour groups in a 2 Groups X 2 Types of target (crossed vs. mirror) X 2 Sessions ANOVA. The ANOVA revealed no significant difference between the groups, $F(1, 22) = 0.02$, $p = 0.6$, $\eta^2_p = 0.001$, and no significant interaction involving this factor.

Off-line learning

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[4] Movements directed at the crossed targets appear less variable than those directed at the easier mirror targets. We believe that this results from participants having difficulty to plan a movement that crosses the straight ahead direction (see Trempe & Proteau, 2008). As a consequence, their movements are initiated as if they were “blocked” by this reference, which may explain why participants are less variable, at least early in practice.

To determine whether consolidation resulted in off-line learning, we compared the performance improvement from session 1 to session 2 in a 2 Groups (10-min vs. 24-hour) x 2 Types of target (crossed vs. mirror) ANOVA. The ANOVA revealed a significant Group X Type of target interaction, $F(1, 22) = 4.2$, $p = 0.05$, $\eta^2_p = 0.16$. Post hoc comparisons revealed that participants of the 24-hour group reduced their movement planning error significantly more than those of the 10-min group when aiming at the crossed targets ($p = 0.007$) but not when aiming at the mirror targets ($p = 0.98$). Thus, consolidation resulted in significant off-line learning only when the initial performance was inaccurate (see Figure 4.5C). [5]

After-effect

Finally, to determine whether the persistent after-effects observed in Experiment 1 were caused by the amount of practice or by the performance level, we compared the mean angular error of the second half of the no-rotation transfer test (last 2 movements for each type of target) with a 2 Groups (10-min vs. 24-hour) X 2 Types of target (crossed vs. mirror) ANOVA. The ANOVA revealed a significant Group X Type of target interaction, $F(1, 21) = 7.0$, $p = 0.015$, $\eta^2_p =$

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[5] As in Experiment 1, we computed the same ANOVA using the angular error at movement endpoint. Again, the results were similar to those observed at 100 ms. When aiming at the crossed targets, participants of the 24-hour and 10-min groups reduced their error by 5.0° (1.4) and 2.3° (0.4), respectively. In contrast, when aiming at the mirror targets, participants of the 24-hour and 10-min groups reduced their error by 3.3° (0.9) and 3.8° (0.8), respectively. The ANOVA failed to reveal a significant difference between the groups, $F(1, 22) = 2.2$, $p = 0.15$.

0.25. Post hoc comparisons revealed that when aiming at the crossed targets (Figure 4.3C), participants of both the 10-min and the 24-hour groups showed similar after-effect ($p = 0.54$). However, as illustrated on Figure 4.3D, participants of the 24-hour groups showed a more persistent after-effect than those of the 10-min group when aiming at the mirror targets ($p = 0.03$). Thus, consolidation resulted in persistent after-effect, but only when the initial performance was good.

4.3.3 Discussion

The objective of Experiment 2 was to determine whether the persistent after-effects observed in Experiment 1 after a consolidation interval were practice dependent or performance dependent. To reach our goal, participants performed a visuomotor adaptation task and aimed for a limited number of trials at different targets. These targets were either easy or difficult to reach. Two important findings emerged from the results. First, consolidation resulted in off-line learning of the new internal model but only when the initial adaptation was incomplete, that is for movements directed at the crossed (difficult) targets. Second, and more importantly, we observed a persistent after-effect only for movements directed at the mirror (easy) targets, that is for the targets for which the initial adaptation was good. Note that this after-effect was observed although participants practiced almost three times less than the extensive practice groups of Experiment 1. Therefore, persistent after-effect is a consolidation outcome that seems to occur when the task is initially well performed, regardless of the amount of practice.

4.4 General discussion

Our objective was to determine whether the skill level attained by the learner during practice leads to different consolidation outcomes. In the visuomotor adaptation task, participants had to modify their movement planning to compensate for a rotation of the visual feedback. Two distinct behavioural outcomes of consolidation emerged from our results. When participants showed poor adaptation at the end of initial practice (after limited practice in Experiment 1 and when aiming at the crossed targets in Experiment 2), consolidation led to off-line learning. However, following an extensive practice session (Experiment 1) and when the initial adaptation reached baseline level (Experiment 2), consolidation resulted in a persistent after-effect.

4.4.1 Persistent after-effect

Previous studies using a visuomotor adaptation task have reported that successful adaptation leads to the development of a new internal kinematic model, that is a new association between vision and action (Krakauer et al., 1999). This new model is initially labile and time is required for it to become stabile. For example, practicing an opposite rotation immediately after the formation of a new model leads to a performance decrease in retention, but has no effect if the two tasks are separated by four hours (Brashers-Krug et al., 1996). Thus, consolidation plays a crucial role in the stabilisation and the storage of the new internal model in long-term memory. Our results add to these findings by showing for the first time that consolidation can also lead to more persistent after-effect. One key finding of the present study was that this persistent after-effect occurred only following an extensive practice session (Experiment 1) and when aiming at the mirror targets (Experiment 2), that is for the group/target showing the highest initial adaptation. This difference was particularly evident in Experiment 2 in which the initial adaptation differed by more than 10° between the targets. These results therefore suggest that a certain level of performance must be attained before persistent after-effect may be observed.

It is important to mention that the initial after-effect (i.e., the movement's bias observed immediately after the removal of the rotation) did not differ between the extensive practice groups of Experiment 1 and when participants aimed at the mirror targets in Experiment 2. This is not surprising because the initial amplitude of the after-effect reflects the performance at the end of the practice phase: in the two experiments, the 10-min and the 24-hour groups had showed similar adaptation by the end of the second session with the rotation. Thus, similar initial after-effects were expected. To assess the persistence of the new internal model, we therefore needed to look at the last trials of the no-rotation transfer test. Interestingly, whereas participants of the 10-min groups could "de-adapt" their movements within just a few trials, participants of the 24-hour groups showed a more persistent leftward bias, indicating that they had more difficulty returning to their normal no-rotation internal model. This suggests that once good performance is attained, consolidation "crystallized" the new internal model in the CNS, that is, made it more salient in the context of our task.

The persistent after-effect we observed might be closely related to the stabilisation process previously described (Walker, 2005). If one thinks of the no-rotation transfer test as an interfering task, a persistent after-effect might reveal a stabilized internal model that resists to interference. Thus, the attainment of a certain level of performance might have triggered long-term memory storage processes. This idea is congruent with the results of Karni et al. (1995) who reported that three weeks of daily practice of a fingers sequence task induced an increase in the activation of the primary motor cortex. Interestingly, this increase was observed only when participants had reached asymptotic performance. Similarly, using microstimulation in the motor cortex of rats that were learning to produce reaching movement, Kleim et al. (2004) observed a reorganisation of the motor map and the formation of new synapses after a minimum of 7 or 10 days of training. In both these studies, the reorganisation became apparent when performance plateaued. Thus, it appears that a certain level of performance must be attained before the CNS stores the acquired skill and engages the resources and energy consuming process of plasticity.

This hypothesis is also supported by the results of Shadmehr & Holcomb (1997). In their study, participants performed a practice session in which they adapted their movements almost completely to an imposed force field. The authors reported that consolidation led to a reorganisation of the neural representation of a new internal model, although this reorganisation had no effect on performance. It is important to note, however, that in the dynamic adaptation paradigm, consolidation was associated with a performance stabilization that became behaviorally apparent only when participants faced a different force field. This is very similar to our persistent after-effects that are observed only when the rotation is removed, or put differently, when participants are experiencing a "different" task. Therefore, when a learner attains a good level of performance, consolidation incurs changes in brain activity that may have no effect on performance if re-tested using the same task.

An important aspect of the present study is the dissociation of the effects of the performance reached through practice from those related to the amount of practice; in Experiment 2, participants performed the same number of movements toward the mirror and the crossed targets. Thus, the difference in performance noted for the mirror and the crossed targets resulted only from the inherent difficulty of the task. One could argue that movements toward the mirror targets benefited from trials directed at the seven other directions as they too did not require a crossing of the straight ahead axis. This is unlikely because it has been shown that rotation adaptation does not transfer well to unpractised directions (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Ghahramani, Wolpert, & Jordan, 1996; Trempe & Proteau, 2008). Moreover, Krakauer et al. (2000) reported that an increase in the number of target directions caused a decrease in the rate of adaptation. This suggests that information gained from movements performed to a specific target direction is not used to plan movements toward other target directions. Thus, adaptation is specific to the trained directions.

4.4.2 Off-line learning

Numerous studies using sequence learning tasks have shown the capacity of individuals to improve their performance in a motor skill between practice sessions (Fischer et al., 2002; Kuriyama et al., 2004; Walker & Stickgold, 2006).

In these studies, off-line learning resulted in spontaneous gains observable right from the beginning of the second session. Moreover, off-line learning has also been reported in a visuomotor adaptation task (Doyon et al., 2009; Huber et al., 2004), showing that this outcome is not restricted to the sequence learning tasks. In the present study, we observed off-line learning gains but only when participants practiced only a limited amount of trials (Experiment 1) or when aiming at the difficult targets (Experiment 2). Specifically, participants of the 24-hour group decreased their movement planning error by 20% and 24% between practice sessions (Experiments 1 and 2, respectively). These decreases correspond to the size of off-line learning reported previously (Fischer et al., 2002; Kuriyama et al., 2004). Not finding such a spontaneous decrease for the 10-min groups indicates that this effect was not simply caused by physical practice but resulted from the consolidation that took place between the practice sessions.

It is also interesting to note that off-line learning was observed only for the conditions in which the initial adaptation was the weakest. Not finding off-line learning for movements toward the mirror targets is not surprising as the initial error was already reduced at baseline level but one could have expected participants of the extensive practice groups to improve slightly between-session. One interpretation of these findings is that consolidation may improve performance up to a certain point. As performance increases and additional gains become more difficult to achieve, it is likely that only physical practice will result in further improvement. Thus, it is seems plausible that consolidation will produce off-line learning gains when the initial performance is modest. This interpretation is supported by the results of Kuriyama et al. (2004) whose participants had to perform as quickly and accurately as possible a sequence of finger movements. By measuring the speed of the transitions between the sub-movements of the sequence, they observed that only the slow transitions (i.e., problem points) improved off-line. Importantly, this occurred despite the fast transitions (easy parts of the sequence) could still improve furthermore. Thus, only the modestly performed aspects of the task beneficiated from off-line learning.

This is not to say however that off-line learning "process" does not take place when the initial performance is good. But just as networks activated during learning change as performance improves (Doyon & Benali, 2005), consolidation might also take place in different networks as the learner progresses, leading to different behavioural outcomes. This hypothesis is in line with the results of Walker, Stickgold, Alsop, Gaab, & Schlaug's (2005) imaging study in which a night of sleep following the initial acquisition of a finger sequence task led to off-line learning gains. Interestingly, these gains were concomitant with an activation increase in the prefrontal cortex and the hippocampus, two structures known to be involved in the early phase of learning (Doyon & Benali, 2005). In contrast, Shadmehr & Holcomb (1997) reported an activation decrease of the prefrontal cortex when consolidation led to a performance stabilisation, and more importantly an activation increase of the premotor cortex and of the cerebellum, two structures associated with long-term motor memory.

Together, the results of Experiment 1 and 2 demonstrate that consolidation results in two distinct behavioural outcomes: off-line learning and persistent after-effect. Importantly, these outcomes seem to be closely linked to the learner's performance during the initial practice session. However, it is still too early to determine whether these two outcomes represent two different expressions of a unique consolidation process or indicate that different processes take place during consolidation.

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4.5 References

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Table 4.1: Experimental conditions

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

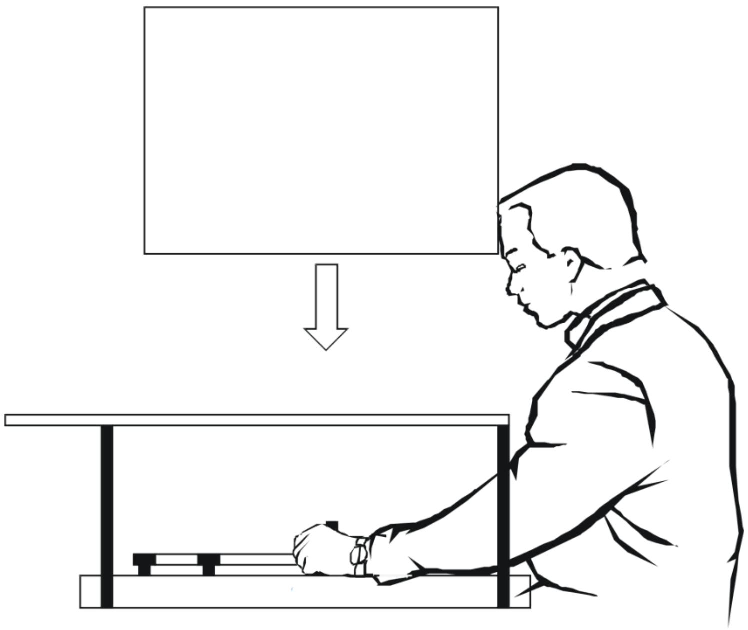

Figure 4.1: View of the apparatus.

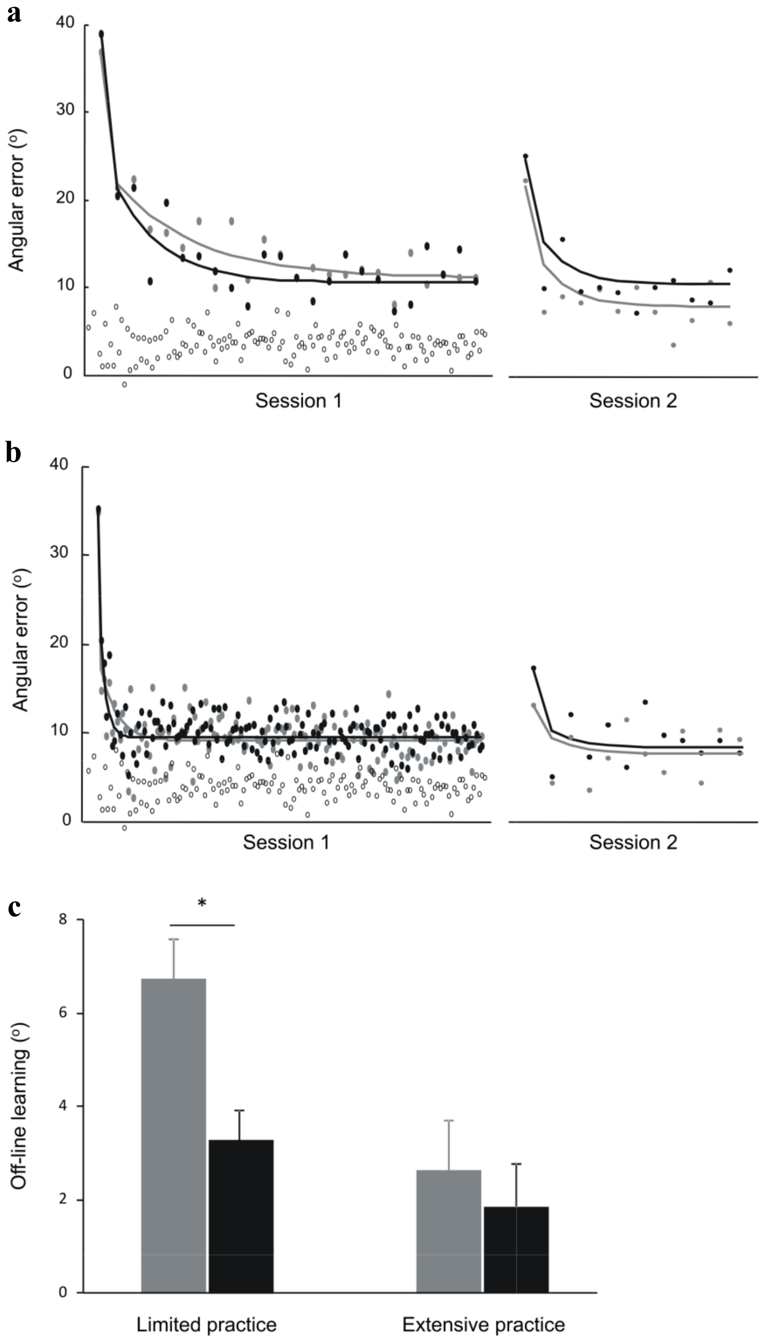

Figure 4.2: Adaptation curves of the limited (A) and extensive (B) practice groups with a 10-min (black) or 24-hour (grey) rest interval between practice sessions. As in Krakauer et al. (1999), data were fitted by a double exponential function. The black opened circles illustrate the angular error of a control group performing 144 practice trials with no-rotation of the visual feedback. (C) Off-line learning between sessions 1 and 2 for the 10-min (black) and 24-hour (grey) groups. The error bars represent the standard error of the mean and the symbol * indicates a significant difference.

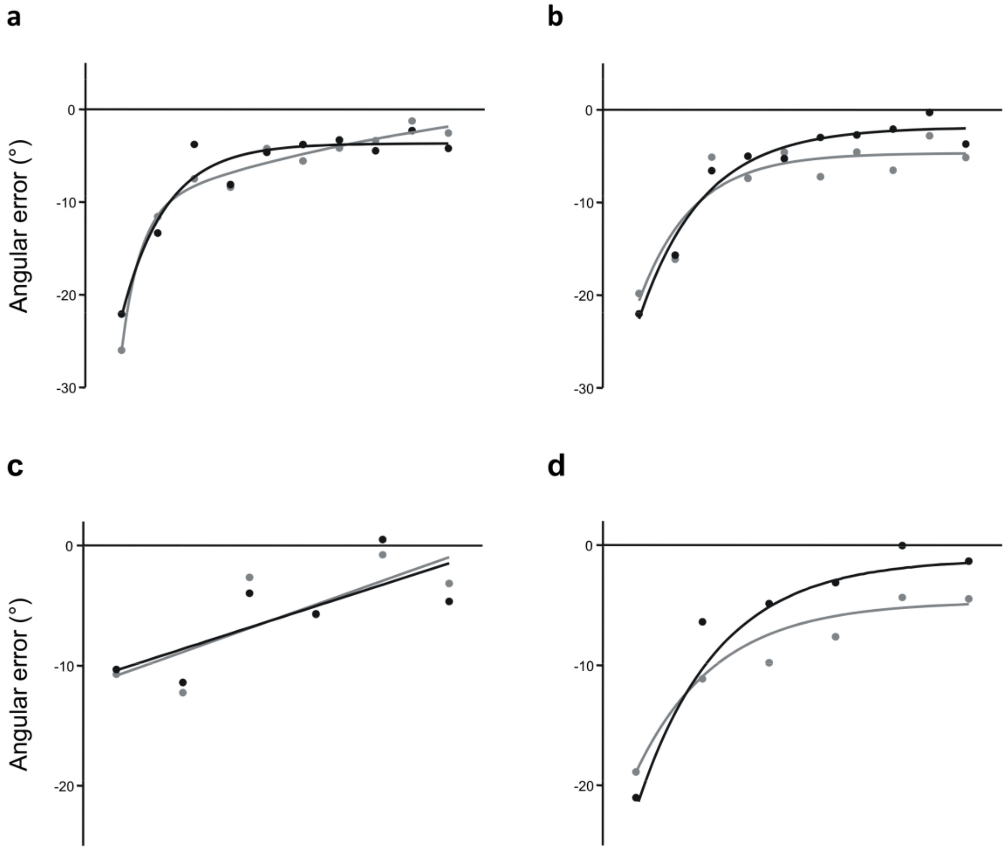

Figure 4.3: No-rotation transfer data of the limited (A) and extensive (B) practice groups with a 10-min (black) or 24-hour (grey) rest interval between practice sessions. A negative value indicates a bias in the direction previously imposed by the rotation, whereas a value of 0° indicates that participants have returned to baseline. Experiment 2: No-rotation transfer data of the 10-min (black) and 24-hour (grey) groups for the crossed (C) and mirror (D) targets.

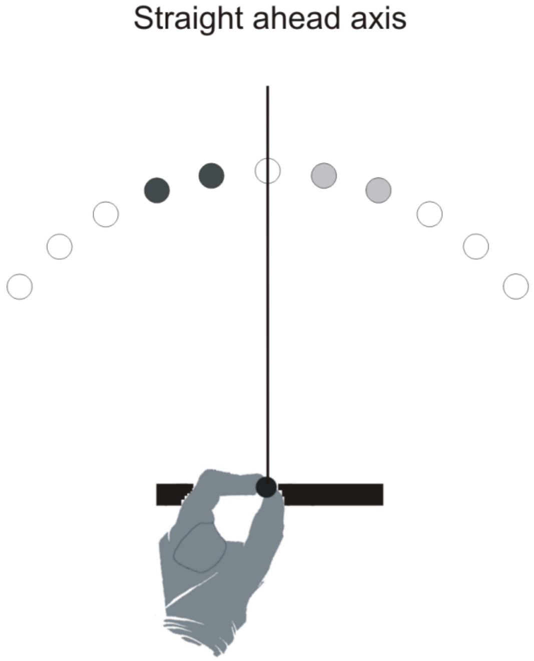

Figure 4.4: Because of the 30˚ clockwise rotation, movements performed along one’s midline were illustrated as progressing 30° to the right. For the 10° and 20° targets (“crossed targets”: illustrated as light grey circles), this resulted in the targets being seen to the right of the hand’s starting location while the movements had to be directed to the left of the hand’s starting location. The “mirror targets” (-10° and -20° targets) used in the different analyses are illustrated as dark grey circles.

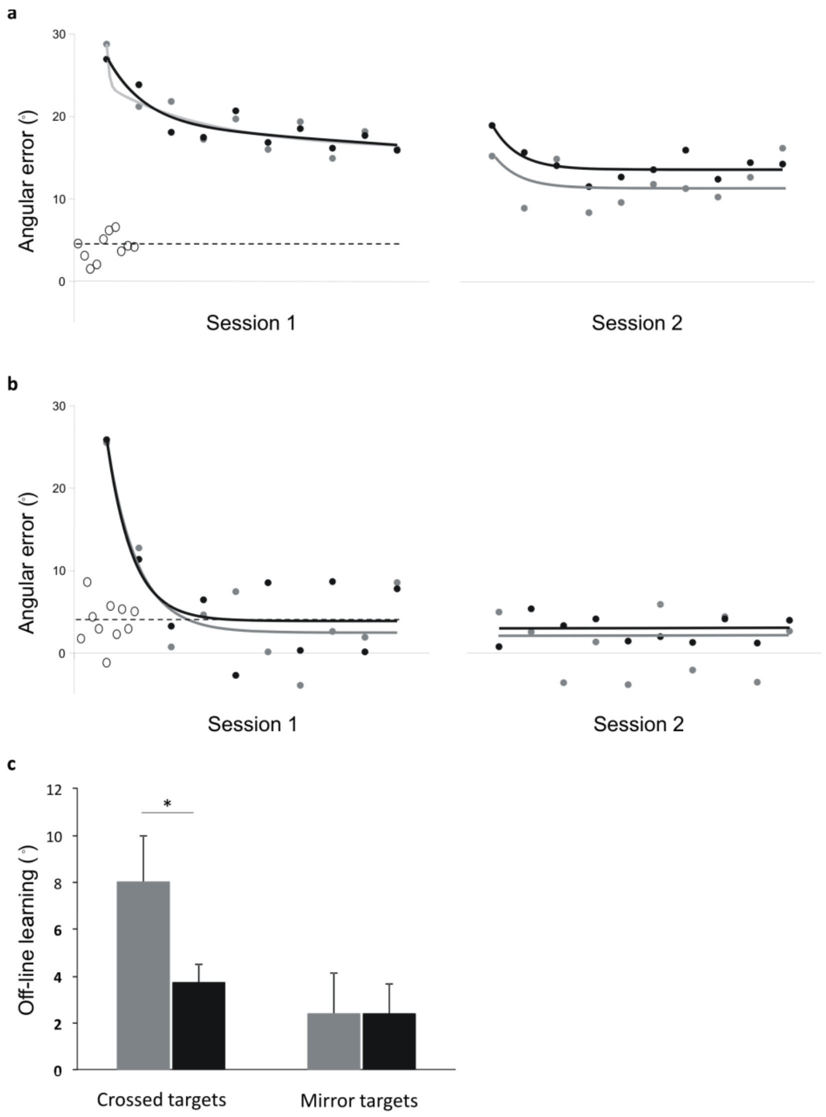

Figure 4.5: Adaptation curves of the 10-min (black) and 24-hour (grey) groups for the crossed (A) and mirror (B) targets. As in Krakauer et al. (1999), data were fitted by a double exponential function. The black opened circles illustrate the angular error of a control group performing 55 practice trials with no-rotation of the visual feedback. (C) Off-line learning between sessions 1 and 2 for the 10-min (black) and 24-hour (grey) groups. The error bars represent the standard error of the mean and the symbol * indicates a significant difference.

CHAPITRE 5

PERFORMANCE SUBJECTIVE ET CONSOLIDATION

Les résultats de Trempe et Proteau (2010) démontrent clairement que le niveau de performance de l'apprenant influence les processus de consolidation. Il demeure toutefois difficile de déterminer comment le système moteur parvient à discriminer une bonne performance d'une mauvaise. Cette tâche est d'autant plus difficile lorsque l'on considère des tâches motrices complexes pour lesquelles un apprenant nécessite plusieurs séances de pratique avant de produire un seul « bon » mouvement. Dans une telle situation, cela signifie-t-il qu'il n'y a pas de consolidation suite aux premières séances de pratique ? Cette position est difficile à concilier avec la multitude des résultats montrant des effets positifs de la consolidation après une seule séance de pratique (voir Robertson, Pascual-Leone, & Miall, 2004; Walker, 2005 pour des revues sur le sujet). Alternativement, il est possible que la consolidation ne soit pas influencée par la performance objective de l'apprenant, mais plutôt par sa performance subjective. En d'autres mots, peut-être consolidons-nous uniquement ce que nous pensons bien réussir ?

Success modulates consolidation of a visuomotor adaptation task

Trempe, M., Sabourin, M., Proteau, L.

Département de kinésiologie, Université de Montréal, Québec, Canada

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5.1 Abstract

Consolidation is a time-dependent process that is responsible for the storage of information in long-term memory. As such, it plays a crucial role in motor learning. Prior research suggests that some consolidation processes are triggered only when the learner experiences some success during practice. In the present study, we tested whether consolidation processes depend on the objective performance of the learner or on the learner's subjective evaluation of his/her own performance (i.e., how successful the learner believes he/she is). Four groups of participants performed two sessions of a visuomotor adaptation task for which they had to learn a new internal model of limb kinematics; these sessions were either 5 minutes or 24 hours apart. The task was identical for all participants, but each group was given a difficult or an easy objective that affected the participants' evaluation of their own performance during the initial practice session. All groups adapted their movements similarly to the rotation of the visual feedback during the first session. However, when retested the following day, participants who had a 24-hour rest interval and had initially experienced success performed significantly better than those who did not feel successful or who were given a 5-min rest interval. Our results indicate that a certain level of subjective success must be experienced to trigger certain consolidation processes.

Keywords: consolidation, aiming movements, motor learning, off-line learning, visuomotor adaptation

5.2 Introduction

Learning is a process that extends beyond training sessions. Since the pioneering works of McGaugh (see Gold & Greenough, 2001 for a review), numerous reports have shown the importance of post-encoding processes for memory formation. Regrouped under the term "consolidation," these processes lead to a series of long-lasting changes, from gene expression to protein synthesis, in the central nervous system (CNS) and constitute the foundation of long-term memory (McGaugh, 2000; Stickgold & Walker, 2007).

Consolidation plays an important role in motor skill learning. When a new motor skill is learned, its memory trace is initially kept in a labile form that is susceptible to interference (Krakauer & Shadmehr, 2006; Robertson, Pascual-Leone, & Miall, 2004). For example, when participants learned to produce a fast ballistic pinch of the index finger and thumb, transcranial magnetic stimulation (TMS) applied over the primary motor cortex immediately after the practice session impaired retention but had no effect if it was applied six hours later (Muellbacher et al., 2002). Thus, post-encoding processes seem to be time-dependent and necessary to stabilize the new memory trace.

Consolidation also results in a reorganization of the information within the CNS, leading to the activation of different brain networks when the newly learned motor skill is retested following a consolidation interval (Karni et al., 1995; Shadmehr & Holcomb, 1997; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). Behaviorally, this reorganization has often been associated with a spontaneous improvement in performance (also known as off-line learning), even though no additional practice had taken place between the practice and retesting sessions (Press, Casement, Pascual-Leone, & Robertson, 2005; Robertson, Pascual-Leone, & Miall, 2004; Trempe & Proteau, 2010; Walker & Stickgold, 2005; Walker et al., 2005). In addition, consolidation has been associated with performance stabilization. This outcome has mainly been observed in visuomotor adaptation studies in which participants adapted their reaching movements to compensate for either a rotation of the visual feedback or external forces applied to the hand (Task A). Although adaptation occurred during initial training, poor retention was observed if a second and opposed perturbation (rotation or force-field; Task B) was practiced immediately following Task A, whereas retention was minimally affected if Tasks A and B were practiced several hours apart (Brashers-Krug, Shadmehr, & Bizzi, 1996; Krakauer, Ghilardi, & Ghez, 1999).

A reorganization of the CNS, however, does not occur every time a new situation is encountered. Using a word-counting task, Hauptmann and Karni (2002) reported that consolidation resulted in performance gains only when asymptotic performance (the saturation of within-session improvement) had been reached during the initial practice session (see also Korman, Raz, Flash, & Karni, 2003 for a similar discussion), regardless of the amount of initial practice (Hauptmann, Reinhart, Brandt, & Karni, 2005). Using a visuomotor adaptation task, we also observed persistent after-effects following consolidation only when participants initially reached a performance level close to baseline during acquisition (Trempe & Proteau, 2010). Both rodent (Kleim et al., 2004) and human (Karni et al., 1995) experiments have provided evidence that a reorganization of the primary motor cortex occurs when performance reaches an asymptote. Together, these results indicate that certain consolidation processes are triggered only when a certain level of performance is attained during practice.

How this performance threshold is determined and evaluated remains unknown. When learning a complex motor task, several weeks of practice may be needed to reach asymptotic or baseline performance, therefore delaying the initiation of the consolidation processes. This idea is difficult to reconcile with the many reports showing consolidation after a single training session (Press et al., 2005; Trempe & Proteau, 2010; Walker et al., 2005). An alternative possibility is that consolidation may not depend on performance *per se* but rather on the learner's subjective evaluation of his or her own performance. Specifically, a motor skill may be consolidated only when the movement outcome reaches an objective set by the learner (the expected outcome), that is, when the learner subjectively perceives that he/she is successful or that he/she is getting better. Subjective success, not objective performance, would therefore be the key factor modulating memory consolidation.

To test this hypothesis, participants performed two sessions of a visuomotor adaptation task in which they needed to modify their movement planning to compensate for a 30° rotation of the visual feedback (Huber, Ghilardi, Massimini, & Tononi, 2004; Krakauer et al., 1999). In this task, it is thought that participants develop a new internal model (i.e., a new association between what is perceived and the movement to be performed) that predicts and compensates for the rotation of visual feedback (Shadmehr & Mussa-Ivaldi, 1994). Although the task was identical for all participants (i.e., to compensate for the rotation), participants were given a different objective to bias their evaluation of their own performance during the initial practice session. Specifically, participants were either given an objective that they could achieve repeatedly and thus be successful or given an objective that could not be met in most trials. Importantly, the participant's adaptation to the rotation of the visual feedback during the first session was not affected by the different objectives, allowing us to dissociate the effects of success from those associated with the performance level. If success modulates the consolidation processes, participants who were given the easy objective during the first session should demonstrate better performance in a second session 24 hours later as compared with participants subjected to the difficult objective. In addition, this retention difference between the easy- and difficult-objective groups should not be observed if the two sessions are performed 5 minutes apart, that is, without a consolidation interval.

5.3 Method

Participants

Forty-six undergraduate students [mean age 22 ± 0.6 (SE); 21 females] from the Département de kinésiologie of the Université de Montréal took part in the experiment. Participants were all naïve as to the purpose of the study, had no prior experience with the task, and were all self-declared right-handed. None reported neurological disorders, and all had normal or corrected to normal vision.

The study was approved by the Health Sciences Research Ethic Committee of the Université de Montréal.

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 two possible targets. The apparatus is illustrated in Figure 5.1A; 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 (Sony KDL-46XBR4) 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, and the distance between the mirror and the tabletop was 20 cm, permitting free displacement of the manipulandum on the tabletop. Participants sat on a chair with their head resting on the side of the screen so that they could continuously see what was displayed on the computer screen by looking at the mirror. Participants could not see the actual displacement of their arm, but the cursor reflected by the mirror provided them 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, parallel to the leading edge of the table and with 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 participant's midline and 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 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 (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the 2D (frontal and sagittal) displacement of the stylus online and to illustrate it at a 1:1 ratio on the computer screen. The bottom of the stylus and the bottom of the optical encoder located at the junction of the two arms of the manipulandum were covered with a thin piece of Plexiglas. By lubricating the working surface at the beginning of each experimental session, displacement of the stylus was nearly frictionless.

Procedures

Participants aimed with their left hand at one of two targets located at 10° and 20° to the right of their body midline (see Figure 5.1B). The targets (filled circles, 10 mm in diameter) were presented in alternating order starting with the 10° target, and the center of the targets was located 4.5 cm from the starting location (Huber et al., 2004; Krakauer et al., 1999; Trempe & Proteau, 2008).

Participants were told to initiate their movements as they pleased, to reach the target in one continuous motion (i.e., not "stop-and-go"), and to follow a straight path (Krakauer et al., 1999; Trempe & Proteau, 2008). Visual tracking of the cursor (filled square, 10 mm wide) and target was permitted at all times during the reaching movement. Movement was deemed to be initiated when the cursor was displaced by 1 mm and to be completed when the cursor was not displaced by more than 2 mm in a time frame of 100 ms. From the end of the movement, the target and the final position of the cursor remained visible until the manipulandum was returned to the starting base, allowing participants to visually evaluate the success of their movements. Thus, participants did not see the cursor returning to the starting position and, consequently, did not practice the rotation during the return movement. The new target appeared one second after the manipulandum had been stabilized on the starting base. Participants were asked to be as accurate as possible while completing their movement in a time bandwidth of 250 ms ± 50 ms. Participants were verbally informed by the experimenter to either slow down or speed up if their movement time fell under 200 ms or over 300 ms, respectively. Using a short movement time made it more difficult for participants to voluntarily use visual feedback to correct their movements online and thus encouraged them to learn a new internal model. Using a prescribed movement time ensured that participants used similar speed-accuracy trade-off strategies throughout the experiment (Fitts, 1954).

Participants were randomly separated into four groups, and all performed two sessions of the exact same adaptation task. The first practice session began with 15 familiarization trials for which the displacement of the stylus resulted in an identical displacement of the cursor on the computer screen (i.e., no rotation). Following this familiarization phase, participants performed 24 trials for which the displacement of the cursor was rotated 30° clockwise in comparison with the displacement of the stylus. Specifically, a movement progressing directly in line with one's midline was illustrated as progressing in a straight line 30° to the right of one's midline. Participants were instructed that they should modify their movements to compensate for the deviation of the visual feedback and were told that they were going to experience the same deviation during the second session. However, the exact nature of the deviation as well as its moment of occurrence was not disclosed. In addition, participants were given either an easy or difficult objective during the first session. Participants who received the easy objective were told that touching the target with the cursor would be considered a successful trial. Because the targets and the cursor were relatively large, this was relatively easy to do. In contrast, participants who received the difficult objective were told that a trial would be considered successful if the cursor covered and hid the target completely. A prior pilot study had shown this to be very difficult to accomplish. Thus, participants of the easy-objective group were expected to feel more successful than those in the difficult-objective group during the first session.[6] A second training session, identical to the first one (24 trials), took place

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[6] We also tried to manipulate the participant's subjective evaluation by changing the amount of positive feedback/reinforcement offered by the experimenter. However, this procedure was unsuccessful because it was particularly difficult to convince participants of the strength of their performance when they could see for themselves that their movements did not fully compensate

after a retention delay of either 5 minutes or 24 hours. To avoid a performance ceiling during the second session, all participants were asked to meet the difficult objective when they resumed practice the second day. Hereafter, the four groups will be referred to as the 5-min easy-objective (*n* = 12), 5-min difficult-objective (*n* = 12), 24-hour easy-objective (*n* = 11), and 24-hour difficult-objective (*n* = 11) groups. The inclusion of two groups with a 5-minute between-session interval allowed us to isolate the effect related to consolidation.

Testing sessions were scheduled between 10 a.m. and 4 p.m. The various testing times were evenly distributed within all groups, and participants were invited to pursue their usual occupation between the sessions. They were asked to avoid consuming alcoholic beverages or using recreational drugs. Compliance with the instructions was confirmed verbally by the participants at the beginning of the second session. In addition, participants in the 24-hour groups filled out a written questionnaire to report how many hours they had slept and how many times they had woken during the night between the two practice sessions. Although the importance of sleep for the consolidation of a visuomotor adaptation task remains controversial (Doyon et al., 2009; Huber et al., 2004), all participants in the 24-hour groups were asked to sleep at least 7 hours between the sessions.

During each trial, participants could see both the target they had to aim at and the cursor they had to displace. Thus, at the end of each trial, participants could see and evaluate for themselves whether they had achieved the objective.

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for the rotation. Giving participants an objective that they could evaluate by themselves was the only way in which we could successfully influence their perception of their own performance.

Moreover, the experimenter never commented or judged the participants' performance; the experimenter only repeated the instructions regularly during the first session. Participants were not aware that the objective set for them was considered either easy or difficult.

Data reduction

To determine how participants adapted movement planning to compensate for the rotation, we calculated their angular error (angle between the reference vector joining the starting base and the target, and the reference vector joining the starting base and the cursor) 100 ms after movement initiation (Hinder, Walk, Wooley, Riek, & Carson, 2007; Trempe & Proteau, 2008, 2010). Because this delay should not have permitted participants to use sensory information to correct their movements (Carlton, 1992), it is likely that the location of the cursor at this temporal marker mainly reflects the movement planning process. A positive angular error indicates a movement initiated too far to the right, whereas a negative value indicates that the movement was initiated too far to the left.

Data were inspected to remove outliers for which the angular error 100 ms after movement onset deviated considerably from the participant's learning curve. Less than 2.5% of the trials were removed, with no difference between groups. Note that outliers could not be detected based on the standard deviation or the *z*-score because the amount of learning from trial to trial was too large to provide a sensitive criterion

To assess the participants' adaptation to the rotation, we calculated the mean constant angular error[7] of each participant for each session. To verify that all participants used a similar speed-accuracy trade-off, we calculated the participants' movement time for each session. In addition, to determine whether the different objectives led the participants to use a different strategy during the first session, we calculated the within-participant inter-trial variability[8] and the participants' mean latency. Finally, at the end of the first practice session, participants were informally debriefed by the experimenter and evaluated qualitatively as to how they perceived their own performance using a 5-point Likert-type scale (1 = mediocre, 5 = excellent).

Statistical analyses

To facilitate the reading of this article, details concerning the computed statistical analyses are defined in the Results section. For all analyses, to ensure no inflation of type 1 error, we assessed the normality of the distribution by calculating the *z*-score of the skewness and kurtosis values (Tabachnick & Fidell, 2007). Hartley's F_{max} test was used to assess the homogeneity of variance of the ANOVAs. Post hoc comparisons were made using Dunn's technique with Bonferroni adjustment for the repeated-measures ANOVAs (Cardinal & Aitken,

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[7] $\sum \frac{(x_i - T)}{n}$, where x_i is the direction of the movement on trial i, T is the direction of the target and n is the total number of movements performed.

[8] $\sqrt{\sum \frac{(x_i - M)^2}{n}}$, where x_i is the angular error on trial i, M is the mean angular error of Session 1 and n is the total number of movements performed.

2006) and Scheffe's test for the one-way ANOVAs. All significant effects are reported at $p < .05$.

5.4 Results

Sleep data

Total sleep time reported by the participants in the 24-hour groups did not differ significantly, $t(20) = 0.35$, $p = 0.7$, $d = 0.15$. Participants in the easy- and difficult-objective groups slept, on average, 6.9 (0.7) and 6.6 (0.4) hours (*SE*), respectively.

Movement time

To ensure that participants did not use different speed-accuracy trade-offs (Fitts, 1954), we compared the movement time data in a 4 Groups X 2 Sessions ANOVA. Movement time was slightly longer than the prescribed movement time ($M = 311$ ms, $SD = 45$). Although the ANOVA revealed a significant Group X Session interaction, $F(3, 42) = 2.9$, $p = 0.046$, $\eta^2_p = 0.17$, post hoc comparisons revealed no consistent difference between the groups' movement time; participants in the 5-min easy-objective group were significantly faster than participants in the 24-hour difficult-objective group during the first session ($p = 0.036$), and participants in the 5-min difficult-objective group were significantly faster than participants in the 24-hour easy-objective group during the second session ($p = 0.024$). As illustrated in Figure 5.2, the different objectives did not result in a consistent difference between the participants' movement times during the first session.

Success rate and subjective performance

Because of the different objectives, the success rate during the first session differed between the four groups. Specifically, the easy-objective groups touched the target in 58% (*SE* = 7) and 66% (*SE* = 5) of the trials during the first session (5-min and 24-hour groups, respectively), as opposed to the two difficult-objective groups, each of which covered the target completely in only 3% (*SE* = 1) of the trials. The ANOVA comparing the success rates revealed a significant main group effect [$F(3, 45) = 66$, $p < 0.001$, $\eta^2 = 0.8$]. Scheffe's test revealed that the proportion of successful trials was significantly higher for the participants who received the easy objective during the first session compared with participants who received the difficult objective ($p < 0.001$ for all four comparisons). Finally, there was no significant difference between the success rate of either the two easy- ($p = 0.55$) or the two difficult- ($p = 0.9$) objective groups.

At the end of the first practice session, participants were informally debriefed to determine how they evaluated their own performance. Participants who received the easy objective during the first session rated their performance significantly higher than those who received the difficult objective [$F(3, 45) = 51$, $p < 0.001$, $\eta^2 = 0.8$, $p < 0.001$ for the four post hoc comparisons between the easy and difficult-objective groups; $M = 3.5$ (0.2), $M = 4.2$ (0.2), $M = 2.3$ (0.1), and $M = 1.6$ (0.2) for the 5-min, 24-hour easy-objective groups and 5-min, 24-hour difficult-objective groups, respectively (*SE*)]. This outcome indicates that participants who received the easy objective felt more successful than participants who received the difficult objective. It is noteworthy that participants in the 24-hour easy-objective group also rated their performance significantly higher than participants in the 5-min easy-objective group (p = 0.03; this difference is addressed in the following section).

Rotation adaptation

Although the objective differed between the groups, the task remained the same, i.e., to compensate for the rotation of the visual feedback. As illustrated in Figure 5.3, participants in the four groups showed similar adaptation during the first session: their angular error decreased rapidly within the first few trials and more slowly thereafter. The 4 Groups X 2 Sessions ANOVA comparing the mean angular error revealed a significant Group X Session interaction [$F(3, 42) = 4.7$, $p = 0.007$, $\eta^2 = 0.25$]. As expected, post hoc comparisons revealed no significant difference between the groups during the first session ($p > 0.5$). However, the adaptation performance of the four groups differed markedly when participants resumed practice during the second session. Participants in the 24-hour easy-objective group decreased their angular error immediately from the first few trials of the second session and significantly outperformed participants in the other three groups ($p < 0.02$ for all three comparisons). The performance of the two difficult-objective groups and that of the 5-min easy-objective group did not differ significantly from one another ($p > 0.4$ for all three comparisons). However, the objective success rate (i.e., the percentage of trials that completely covered the target) during the second session did not differ significantly between the groups

[*F* (3, 45) = 1.03, $p = 0.4$, $\eta^2 = 0.07$]. On average, participants covered the target completely in 2.1% of the trials (*SD* = 3).

As mentioned above, participants in the 24-hour easy-objective group rated their performance better than participants in the 5-min easy-objective group (although the first practice session was identical for both groups). Because the purpose of the 5-min easy-objective group was to determine whether success alone (i.e., without consolidation) could result in better learning, one can question whether participants in the 5-min easy-objective group were sufficiently motivated by the easy objective to show an increase in performance during the second session. To control for this possibility, we selected the data for the participants who scored "4" in the subjective evaluation test and then contrasted their rotation adaptation using a 2 Groups (5-min and 24-hour easy objective) X 2 Sessions ANOVA. If participants in the 5-min easy-objective group demonstrated less learning than participants in the 24-hour easy-objective group because they felt, on average, less successful, this new subset of participants having exactly the same subjective evaluation of their performance as the 24-hour easy-objective group should show similar learning. In total, six and seven participants from the 5-min and 24-hour easy-objective groups, respectively, were included in this supplementary analysis. The ANOVA revealed a significant Group X Session interaction, [$F(1, 11) = 8.9$, $p = 0.012$, $\eta^2 = 0.45$]. Post hoc comparisons revealed no significant between-group difference during the first session ($p = 0.6$). However, participants in the 24-hour easy-objective group significantly outperformed participants in the 5-min group during the second session ($p =$

0.035), thus supporting our claim that success and consolidation are necessary to observe a performance increase.

In direct support of our hypothesis, the 24-hour easy-objective group outperformed the 24-hour difficult-objective group in the second session, even though both groups had a consolidation interval (see Figure 5.3). This result argues that the consolidation processes taking place between the practice sessions are influenced by the participants' evaluation of their own performance. To further test this idea, we aggregated the data from the two 24-hour groups and correlated the participants' subjective evaluation of their performance with the amount of improvement they demonstrated from the first to the second session. The more successful the participants felt, the more they improved from the first to the second session ($r = 0.48$, $p = 0.005$, see Figure 5.4).

Adaptation strategy

One could argue that the different objectives not only influenced the participants' perception of their own performance but also the adaptation strategy they used during the first session. To test this possibility, we first compared the participants' mean latency during the first session (note that participants were free to initiate their movements as they pleased). Because the data from two groups showed a significant positive skewness, a logarithmic transformation was applied to the data. The 4 Groups one-way ANOVA revealed a significant main effect [$F(3, 45) = 3.2$, $p = 0.03$, $\eta^2 = 0.19$ ($M = 2.8(0.5)$, $2.7(0.5)$, $2.7(0.6)$ and $2.9(0.7)$ for the 5-min easy-objective, 5-min difficult-objective, 24-hour easy-objective, and 24-hour difficult-objective groups (standard error), respectively]. However, Scheffe's test failed to reveal any significant difference between the groups ($p > 0.08$), suggesting that the four groups used a similar adaptation strategy during the first session, regardless of the objective they received.[9]

In addition, we also compared the within-participant inter-trial variability of the angular error during the first session. The ANOVA did not reveal any significant difference between the groups [$F\,(3, 45) = 1.2$, $p = 0.3$, $\eta^2 = 0.07$].

5.5 Control experiment

To rule out the possibility that the reduced retention demonstrated by participants practicing the difficult objective twice was caused by discouragement, we tested an additional group that received the difficult objective during the first session and the easy (thus, not demotivating) objective during the second session 24 hours later. If the effect on retention reported above was caused by discouragement, participants of this additional group should show identical retention compared to the 24-hour easy-objective group. Eleven new participants, naïve to the purpose of the study, took part in this control experiment [mean age 26 ± 0.9 (SE); 6 females]. Participants underwent the exact same protocol as described in the "Method" section.

Results

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[9] Importantly, the latency of the 24-hour easy-objective group did not differ from that of the other three groups ($p = 0.11$, $p = 1$, $p = 0.99$, for the comparisons with the 24-hour difficult-objective, 5-min easy-objective, and 5-min difficult-objective groups, respectively).

Participants in this control group reported sleeping, on average, 7.25 hours (*SE* = 0.4) between the two practice sessions. As in the main experiment, movement time was slightly longer than the prescribed movement time (*M* = 308 ± 7 ms and 297 ± 7 ms for the first and second sessions, respectively). Because participants received the difficult objective during the first session, they were not expected to be successful; they covered the target completely in only 3% of the trials (*SE* = 1.7), and their subjective evaluation of their own performance was low [*M* = 1.6 (0.2)].

To determine whether the performance of the 24-hour easy-objective group during the second session was influenced by increased motivation, the mean angular error of the control group was compared to that of the 24-hour easy-objective group using a 2 Groups X 2 Sessions ANOVA. If the effect reported in the main experiment was simply caused by an increased motivation during the second session, participants in this control group (who received a motivating objective during the second session) should demonstrate a performance similar to that of the 24-hour easy-objective group. The ANOVA revealed a significant Group X Session interaction [F (1, 20) = 9.3, p = 0.006, η^2 = 0.3]. Post hoc comparisons revealed that although both groups adapted similarly during the first session (p = 0.8), the 24-hour easy-objective group significantly outperformed the control group during the second session (p = 0.017). Therefore, this supplementary experiment does not support the idea that the reduced retention may have been caused by discouragement.

5.6 Discussion

The objective of the present study was to determine whether subjective success experienced during practice modulates consolidation processes. Four groups of participants performed two practice sessions of the same visuomotor adaptation task, either 5 minutes or 24 hours apart. Each group was given a different objective that modified how the participants evaluated their own performance. During the initial practice session, all groups similarly adapted their movement planning to counteract the rotation. This suggests that they had all learned a new internal model (Krakauer et al., 1999; Shadmehr & Mussa-Ivaldi, 1994) to the same extent. However, participants who received the easy objective during the first session saw the cursor touch the target in an average of 62% of the trials, whereas those who received the difficult objective covered the target completely in only 3% of the trials. As expected, although explicit success information was not provided by the experimenter, the participants who received the easy objective rated their performance as significantly better than those who received the difficult objective.

Participants who experienced success during the first practice session and had a 24-hour rest interval demonstrated better retention of the new internal model compared with participants who 1) did not have a consolidation interval, and 2) did not experience success during the first session. This better retention of the new internal model significantly reduced the movement planning error resulting from the cursor rotation. The improvement of the 24-hour easy-objective group is consistent with prior results using a visuomotor adaptation task (Doyon et al., 2009; Huber et al., 2004; Trempe & Proteau, 2010) and a sequence learning task (Press et al., 2005; Robertson, Pascual-Leone, & Press, 2004; Walker, 2005; Walker & Stickgold, 2005). However, it is important to note that participants in the 24-hour difficult-objective group did not demonstrate such improvement, although they also had a 24-hour rest interval to consolidate the new internal model. Thus, a simple change in the objective altered what participants retained from their practice session. Considering that there was no difference in the initial adaptation and that participants were tested at the same time of the day and had slept for the same amount of time, our results indicate that the subjective success experienced by the participants in the easy-objective group enhanced retention of the new internal model. In addition, the observation that participants in the 5-min easy-objective group demonstrated lower retention compared with participants in the 24-hour easy-objective group suggests that subjective success modulated the consolidation processes taking place between the practice sessions[10].

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[10] The smaller movement planning error of the 24-hour easy objective group would have permitted participants to increase the proportion of trials that met the easy objective criterion from 66% in Session 1 to 82% in Session 2. However, all participants were given the difficult objective during the second session. Participants in the 24-hour easy objective group did not achieve this objective more successfully than the three other groups. This last observation was expected because completely covering the target with the cursor (the difficult objective) demands near-perfect adaptation that could only have resulted from extensive practice.

The different objectives may have modified not only the success experienced by the participants, but also how the task was learned during the first session. Specifically, one could argue that the difficult objective may have incited participants to explicitly control their movements instead of adapting implicitly to the rotation. Because explicit and implicit memories consolidate differently (Born & Wagner, 2004; Robertson & Cohen, 2006), this could explain the retention difference observed in Session 2. Although it is difficult to assess this possibility directly, our behavioral measures indicate no difference in the way the task was acquired. Specifically, Mazzoni and Krakauer (2006) reported that learning explicitly to compensate for a rotation of the visual feedback leads to less adaptation during the initial acquisition than does learning the same task implicitly. In our study, no such difference was observed between the groups during the first session. In addition, if participants were trying to implement an explicit strategy to compensate for the rotation, this strategy should have affected either or both of the movement times (Kagerer, Contreras-Vidal, & Stelmach, 1997) and the inter-trial variability of the movements (Mazzoni & Krakauer, 2006) during the first session. Again, no such difference was observed. In addition, we observed no difference between the participants' latency. Thus, it seems likely that the participants all used the same strategy during the first session.

The observation that the movement planning error for the difficult-objective groups did not decrease during the second session may suggest that the participants were unmotivated and did not perform at their best. Numerous facts argue against this possibility. First, the practice sessions were short, making it unlikely for participants to become discouraged. Second, the participants who received the difficult objective during the first session decreased their movement planning error within the first few trials of the second session. If they were not thoroughly engaged in the task, we should have expected them to produce movements with the same error throughout the entire second session. Third, participants in the additional group who received the difficult objective during the first session and the easy, and thus motivational, objective during the second session demonstrated reduced retention compared with participants in the 24-hour easy-objective group. Finally, and more importantly, participants in the 5-min easy-objective group received the same objectives as the 24-hour easy-objective group (and were thus equally motivated) and still demonstrated reduced retention.

Although the points presented above argue against an effect of motivation during the second session, it is nevertheless possible that motivation may have influenced the movement planning consolidation processes between the sessions. Specifically, the different objectives may not only have affected the success experienced by the participants during the first practice session, but also their motivation and emotional state. In previous research, arousal (Jensen, 2001) and stress hormones (McGaugh, 2004) have both been found to influence consolidation, making the modulation of emotions a potential mechanism by which success could influence consolidation. In the same vein, Lewthwaite and Wulf (2010) reported that participants who were led to believe that their performance was superior to the average performance of others demonstrated better learning than those who were led to believe that their performance was inferior to the average. In their experiment, however, the feedback provided to the participants in the “superior group” actually improved their performance during the first practice session, therefore making it impossible to dissociate whether the better learning was caused by higher motivation or by the better performance achieved during the first session (see also Hutchinson, Sherman, & Martinovic, 2008 for a discussion on self-efficacy and performance). In the present study, the different objectives did not influence the level of performance achieved by the participants during the first session, thus demonstrating for the first time, to our knowledge, that success and/or motivation influences the consolidation processes taking place between the practice sessions.

An alternative, but not exclusive, possibility is that the different objectives may have modified some reward signals within the brain. Specifically, Holroyd and Coles (2002) proposed that the mesencephalic system may send an increased dopaminergic signal when a positive outcome is detected and a decreased signal when the movement outcome is not as expected. This raises the possibility that the error signals received during practice may inhibit, via the dopaminergic system, some post-encoding processes until a sufficient number of successful trials have been experienced (see Jay, 2003 for a discussion on the role of dopamine in memory formation). In the present study, participants who practiced the easy objective may have received sufficient reward signals during the first practice session to trigger the consolidation processes.

In conclusion, our findings support the hypothesis that the subjective success experienced by the learner modulates the consolidation processes. Moreover, our findings suggest that the objectives given to a learner should be scaled to his or her proficiency level to optimize the learning process. Further work will be necessary to identify the mechanisms by which success influences consolidation processes.

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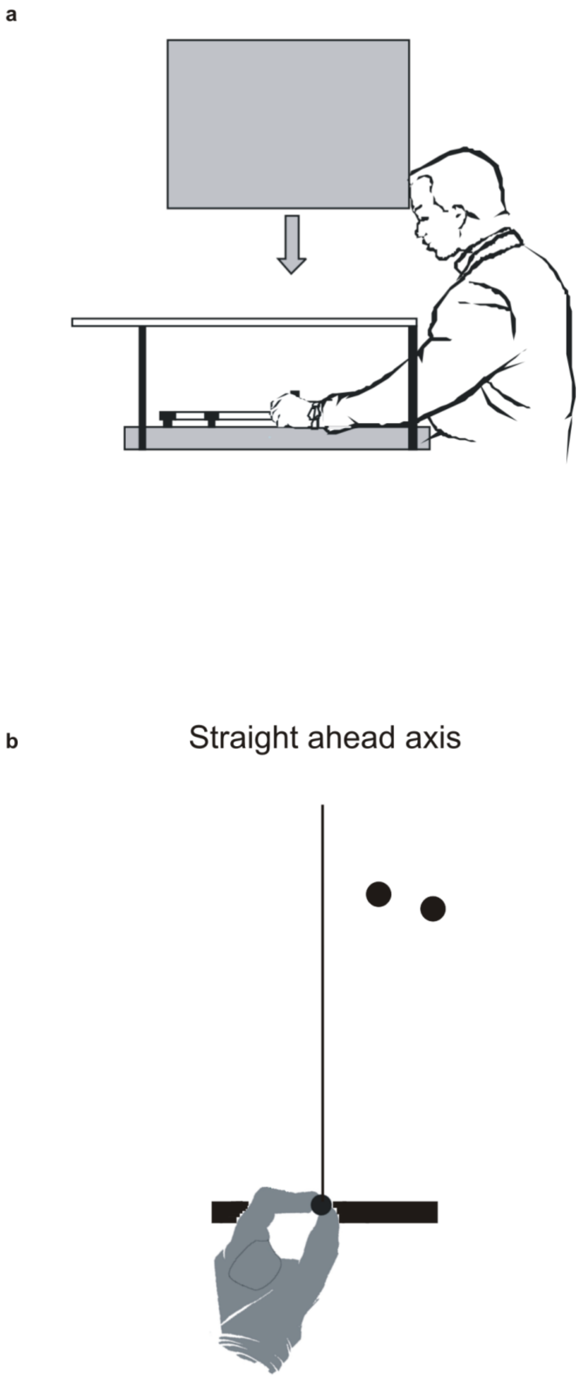

Figure 5.1: A. View of the apparatus. B. Location of the targets.

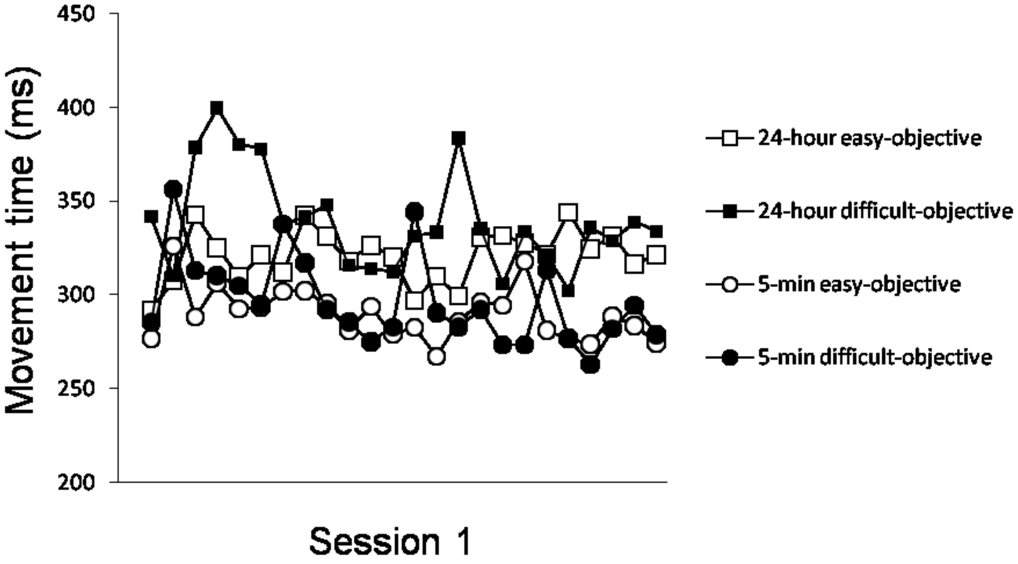

Figure 5.2: Mean movement time (ms) in each of the 24 trials of each group during the first session. Error bars illustrate the standard error of the mean. Although post hoc comparisons revealed that participants of the 5-min easy objective group were significantly faster than participants of the 24-hour difficult objective group during the first session, we found no evidence of a systematic movement time bias caused by the different objectives.

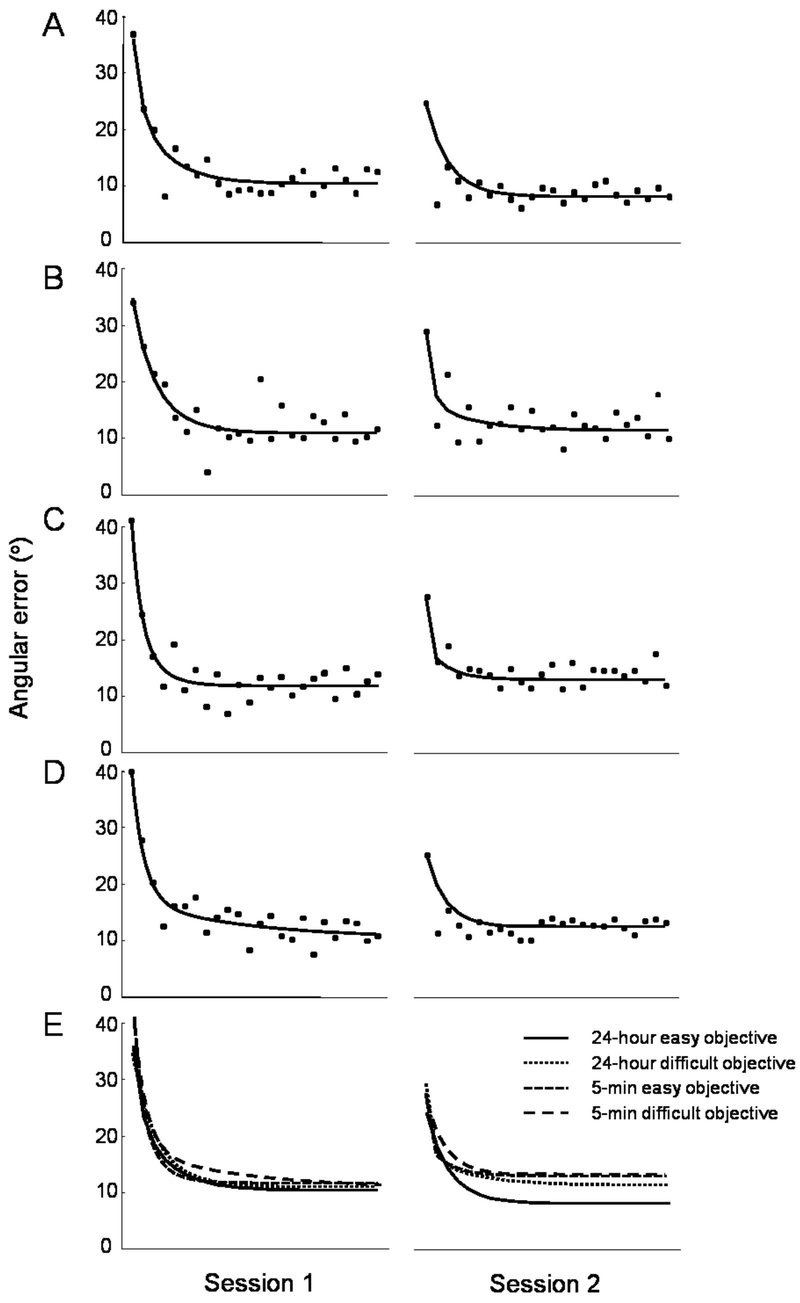

Figure 5.3: Angular error in each of the 24 trials of the 24-hour easy objective (A), 24-hour difficult objective (B), 5-min easy objective (C), and 5-min difficult objective groups, 100 ms after movement onset. For illustration purposes, data were fitted with a double exponential function ($y = y_0 + a_1 * e^{\frac{-(x-x_0)}{t_1}} + a_2 * e^{\frac{-(x-x_0)}{t_2}}$). E. Adaptation curves of the 4 groups. Although participants of all groups demonstrated similar adaptation during the first session, participants of the 24-hour easy objective group outperformed participants of the three other groups during the second session.

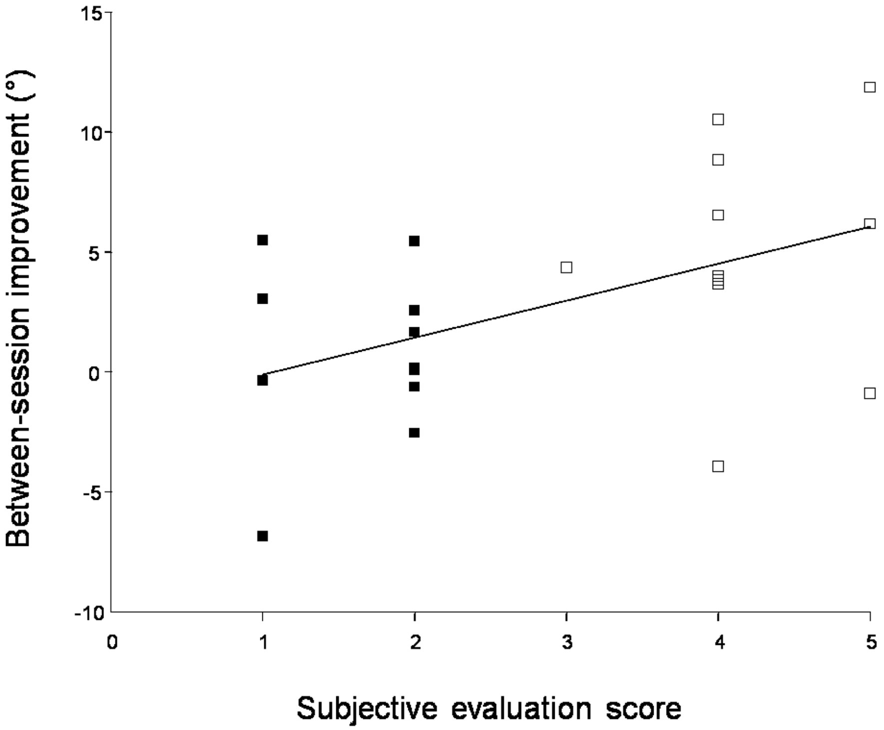

Figure 5.4: Data of the 24-hour easy-objective group (opened squares) and 24-hour difficult-objective group (filled squared) were used to correlate the participants' subjective evaluation of their own performance and their between-session improvement. The more successful the participants felt, the more they improved from the first to the second session

CHAPITRE 6

OBSERVATION, PRATIQUE PHYSIQUE, ET CONSOLIDATION

Les résultats des deux études précédentes démontrent que la performance objective et subjective de l'apprenant influence les processus de consolidation. Qu'arrive-t-il toutefois lorsque le système moteur ne dispose d'aucune information pour juger de la performance et lorsque l'apprenant ne détient aucune information concernant sa propre performance ? Peut-il y avoir consolidation ? Dans ce cas, peut-on consolider une habileté motrice apprise uniquement par observation ? Au contraire, la pratique physique est-elle un pré-requis pour enclencher les processus de consolidation ?

Observation learning versus physical practice leads to different consolidation outcomes in a movement timing task

Trempe, M., Sabourin, M., Rohbanfard, H., Proteau, L.

Département de kinésiologie, Université de Montréal, Québec, Canada

In

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6.1 Abstract

Motor learning is a process that extends beyond training sessions. Specifically, physical practice triggers a series of physiological changes in the CNS that are regrouped under the term “consolidation” (Stickgold & Walker, 2007). These changes can result in between-session improvement or performance stabilization (Walker, 2005). In a series of three experiments, we tested whether consolidation also occurs following observation. In Experiment 1, participants observed an expert model perform a sequence of arm movements. Although we found evidence of observation learning, no significant difference was revealed between participants asked to reproduce the observed sequence either 5 minutes or 24 hours later (no between-session improvement). In Experiment 2, two groups of participants observed an expert model perform two distinct movement sequences (A and B) either 10 minutes or 8 hours apart; participants then physically performed both sequences after a 24-hour break. Participants in the 8-h group performed Sequence B less accurately compared to participants in the 5-min group, suggesting that the memory representation of the first sequence had been stabilized and that it interfered with the learning of the second sequence. Finally, in Experiment 3, the initial observation phase was replaced by a physical practice phase. In contrast with the results of Experiment 2, participants in the 8-h group performed Sequence B significantly more accurately compared to participants in the 5-min group. Together, our results suggest that the memory representation of a skill learned through observation undergoes consolidation.

However, consolidation of an observed motor skill leads to distinct behavioural outcomes in comparison to physical practice.

Keywords: motor learning, consolidation, observation, off-line learning, stabilization

6.2 Introduction

Physical practice has long been regarded as the single most important determinant of motor skill acquisition. This belief was often expressed by the old adage “practice makes perfect,” as advocated by early models of motor skill learning (Adams, 1971; Crossman, 1959; Fitts, 1964; Schmidt, 1975; Shea & Morgan, 1979). Although the importance of physical practice for motor skill learning is undeniable, recent evidence demonstrates that important processes take place between practice sessions. Specifically, physical practice triggers a series of physiological changes in the brain, from protein synthesis to the formation of new synapses (McGaugh, 2000), leading to the long-term retention of the new skill. Regrouped under the term “consolidation” (Stickgold & Walker, 2007), these changes require time to occur and constitute the foundation of motor skill learning.

Current hypothesis states that brain networks activated during physical practice are reactivated during rest (Hoffman & McNaughton, 2002) and/or a sleep interval (Ji & Wilson, 2007; Wilson & McNaughton, 1994). This reactivation is thought to favour a reorganization of the information in the CNS (see however Tononi & Cirelli, 2003; Hill, Tononi, & Ghilardi, 2008 for a different view), leading to the activation of different brain networks when the newly practiced motor skill is retested following a consolidation interval (Karni et al., 1995; Shadmehr & Holcomb, 1997; Walker et al., 2005).

Although this reorganization of the CNS does not necessarily result in a behaviourally observable change in performance (Karni et al., 1995; Shadmehr &

Holcomb, 1997), consolidation has often been associated with a stabilization of the participant's performance (Krakauer & Shadmehr, 2006; Walker, 2005). This outcome has mainly been observed in visuomanual adaptation studies in which participants adapted their reaching movements to compensate for either a rotation of the visual feedback or new forces applied to the hand (Task A). Although adaptation occurred during initial training, poor retention was observed if a second and opposed perturbation (rotation or force-field; Task B) was practiced immediately following Task A, whereas retention was hardly affected if Tasks A and B were practiced several hours apart (Brashers-Krug et al., 1996; Krakauer et al., 1999). Thus, the memory representation acquired through practice is initially kept in a labile form until it is stabilized by the consolidation processes and becomes resistant to different sources of interference.

In addition, consolidation has also been associated with a spontaneous performance increase (i.e., off-line learning) without additional training between the practice and retest sessions (Robertson et al., 2004; Press et al. 2005; Walker & Stickgold, 2005; Walker et al., 2005). For example, when participants practiced a sequence of finger movements to reproduce it as quickly and accurately as possible, they were typically faster and made fewer errors when retested following a night of sleep, even if no additional training took place between the practice and retest sessions.

In the past, consolidation has been studied using mainly physical practice tasks. However, is physical practice a prerequisite for motor skill consolidation? To our knowledge, only four reports have investigated the consolidation processes following either observation (Van Der Werf et al., 2009) or motor imagery (Debarnot, et al., 2009a, 2009b, 2010). In all these reports, a consolidation interval including sleep resulted in a significant increase in performance. However, the initial acquisition session also included either physical practice (Debarnot et al., 2009a, 2009b, 2010) or contractions of the muscles used to perform the task (Van Der Werf et al., 2009), therefore making it difficult to determine whether consolidation was triggered uniquely by observation/motor imagery. Therefore, whether physical practice is a prerequisite for obtaining behavioural evidence of motor skill consolidation remains an open question. In a series of three experiments, we investigated whether the CNS consolidates a motor skill learned solely through observation, without any form of physical practice. To reach our goal, we sought evidence of the two most common behavioural outcomes resulting from consolidation: off-line learning (Experiment 1) and performance stabilization (Experiment 2). Observing off-line learning and/or performance stabilization would indicate that the memory representation learned through observation has been consolidated. In a third experiment, we contrasted our results with those obtained with physical practice tasks.

6.3 Experiment 1

Experiment 1 was designed to determine whether a rest interval following an observation session can result in off-line learning. To do so, we used a timing task that consisted in producing a sequence of arm movements to knock down a series of wooden barriers in a prescribed movement time. This task was chosen because its small accuracy requirements place the focus of what has to be learned on its timing demands, and previous reports have shown that participants can learn the correct movement time simply by observing a model performing the task (Blandin et al., 1999; Blandin & Proteau, 2000). In the present experiment, two groups of participants first observed a video of an expert model performing 40 near-perfect trials; participants then physically performed the task either 5 minutes (5-min group) or 24 hours (24-h group) after observation. If the memory representation acquired through observation is sufficiently improved by consolidation to result in an observable behavioural outcome, participants of the 24-h group should demonstrate better performance during the physical practice phase compared to participants of the 5-min group; they should also perform better compared to participants of a control group performing the task without prior observation.

6.3.1 Method

Participants

Thirty-nine undergraduate students (mean age = 20.5, SE = 0.4; 29 females) from the Département de kinésiologie at the Université de Montréal took part in the experiment. All subjects were 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. The study was approved by the Health Sciences Research Ethic Committee of the Université de Montréal.

Task and apparatus

The apparatus was similar to that used by Blandin et al. (1999) and is illustrated in Figure 6.1. It was placed on a table (74 cm high) and was composed of a wooden base (46 X 53 cm), a start-stop assembly, and three wooden barriers (11.5 X 8.25 cm). Participants sat in front of the apparatus. Aligned with their body midline was a microswitch that served as a starting position. At the beginning of each trial, the wooden barriers were placed perpendicular (vertical) to the wooden base. Participants had to press the microswitch, knock down the three barriers in a clockwise motion with their right hand, and then push down on a metal plate (11.5 X 8.25 cm) surrounding the microswitch (see Figure 6.1). The movements' mean index of difficulty was 2.4 (Fitts, 1954). The start/stop assembly and the barriers were connected to a computer via the I/O port of an A-D converter (National Instrument). A millisecond timer, which was activated when the participants pressed the start microswitch, recorded the time at which each barrier was knocked down, and stopped when the metal plate was pushed down. This enabled us to record the total movement time, i.e., the time elapsed from the pressing of the microswitch to the pushing down of the metal plate, as well as the time needed to complete each of the four segments of the task.

During the observation phase, participants sat on a chair and watched a video displayed on a 46-inch LCD monitor (Sony KDL-46XBR4). The monitor was located two metres in front of the participants.

Procedures

In the retention phase, participants had to complete the entire movement sequence in 1200 ms. As well, each segment of the sequence had to be completed in 300 ms. The experimental movement pattern, the total movement time, and the time to complete each segment of the task were illustrated on a poster located directly in front of the apparatus (see Figure 6.1), which was present during all experimental phases. Participants were instructed to use their right hand to perform the task.

Participants first observed a video of an expert model performing 40 near-perfect trials of the movements sequence (absolute error = 13.0 ms, SE = 1.4; root mean square error = 0.5, SE = 0.03; see below for details concerning the calculations). They were asked to observe the video attentively to learn the correct timing of the sequence. They were explicitly informed that they would have to physically perform the sequence after the observation session. After each trial performed by the model, the time taken to produce the entire sequence (total movement time) as well as the time taken to complete each segment of the sequence were displayed on the monitor to provide feedback to the participants. To ensure that participants remained attentive, the experimenter frequently asked the participant to comment on the performance of the model before the feedback was displayed (through questions such as “Was the previous trial performed too slowly? Too quickly?”). Importantly, participants were asked to keep their hands on their thighs during observation and to avoid moving their arms. They were clearly instructed not to try to reproduce the movements while watching the model. Thereafter, participants performed a retention test (20 trials without feedback) either 5 minutes (5-min group, *n* = 13) or 24 hours (24-h group, *n* = 13) after the observation phase. In addition, a third group performed the retention test without prior observation (control group, *n* = 13).

Testing sessions were schedule between 8 a.m. and 5 p.m. Participants of the 24-h group were instructed to continue with their usual activities between the sessions. They were asked to maintain their normal sleep schedule and to avoid consuming alcoholic beverages or recreational drugs. Compliance with the instructions was confirmed verbally by the participants at the beginning of the second session. Participants also completed a written questionnaire to report how many hours they slept during the night between the observation session and the retention test. In average, participants of the 24-h group slept 7.7 hours (SE = 0.3).

Data reduction

To determine whether participants produced the sequence in the prescribed movement time, we measured the total movement time (i.e., the time elapsed from pressing the start microswitch to pushing down on the metal plate) of all trials performed in the retention test and computed the mean absolute error (AE)[11] and the variable error (VE)[12] for each participant. These measures indicate,

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[11] $AE = \sum \frac{|x_i - 1200|}{n}$ where x_i is the total movement time on trial *i* and *n* is the total number of sequences executed.

respectively, the accuracy and the consistency of the participants' responses. Then, to determine whether participants learned the relative timing of the sequence (i.e., produced all four segments of the sequence in equal time), the time taken to complete each segment of the sequence was expressed as a percentage of the total movement time; this value was used to compute the participants' root mean square error (RMSE; Blandin et al., 1999)[13] and its variability. Trials deviating more than two standard deviations from each participant's mean (for AE and RMSE) were removed from all analyses. Less than 4% of the trials were removed. The low spatial accuracy demands of the task resulted in participants failing to knock down one barrier on less than 1% of the trials. These trials were rejected during the experimental session and immediately re-conducted.

Statistical analyses

Unless mentioned otherwise, data were submitted to 3 Groups one-way ANOVAs. Post hoc comparisons were made using Dunnett's test to compare the performance of the 24-h with the performances of the 5-min and control groups. To ensure no inflation of type 1 error, we assessed the normality of the distribution by calculating the *z* score of the skewness and kurtosis values

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[12] $VE = \sqrt{\sum \frac{(x_i - M)^2}{n}}$ where x_i is the total movement time on trial i, M is the mean total movement time, and n is the total number of sequences executed.

[13] $RMSE = \sqrt{\frac{\Sigma(\frac{y_i}{TMT} - 0.25)}{4}}$ where y_i is the movement time of segment i and TMT is the total movement time of the trial.

(Tabachnick & Fidell, 2007). Hartley's F_{max} test was used to assess the homogeneity of variance of the ANOVAs. When necessary, we used the average of the Greenhouse-Geisser and Huyn-Feldt correction to correct for a possible violation of the sphericity assumption (Stevens, 1992). All significant effects are reported at $p < 0.05$.

6.3.2 Results

Total movement time

To determine whether participants learned the total movement time, we first calculated the mean absolute error and contrasted the data using a one-way ANOVA. The ANOVA revealed a significant difference between the groups, F (2, 38) = 7.2, $p = 0.002$, $\eta^2 = 0.29$. As illustrated in Figure 6.2a, participants of the 24-hour group were significantly more accurate than participants of the control group were ($p = 0.004$) but did not do better than participants of the 5-min group ($p = 0.98$). Furthermore, a second ANOVA contrasting the variable error revealed a significant difference between the groups, F (2, 38) = 5.1, $p = 0.01$, $\eta^2 = 0.22$. As illustrated in Figure 6.2b, participants of the 24-hour group were significantly less variable compared to participants of the control group ($p = 0.007$), whereas no difference between the 24-hour and 5-min groups was observed ($p = 0.65$).

Relative timing

The RMSE and the variability of the RMSE were used to assess whether participants learned the relative timing of the sequence. The ANOVAs revealed no significant difference between the groups, $F(2, 38) = 1.3$, $p = 0.3$, $\eta^2 = 0.07$

and $F(2, 38) = 0.96$, $p = 0.4$, $\eta^2 = 0.05$, respectively (see Figure 6.2c and d). Thus, observation alone was not sufficient for participants to learn the relative timing of the new sequence.

Movement time of the segments

Recent reports have demonstrated that off-line learning occurs when the initial performance is relatively modest (Kuriyama et al., 2004; Trempe & Proteau, 2010). In the present experiment, it is possible that consolidation led to off-line learning but only for the most difficult segment(s) of the sequence. To assess this possibility, we compared the absolute error of each segment of the sequence using a 3 Groups x 4 Segments ANOVA with repeated measurements on the second factor (see Figure 6.3). Although the ANOVA revealed a significant main effect of segment, $F(3, 108) = 6.5$, $p = 0.004$, $\eta^2_p = 0.15$, indicating that some segments were more difficult than others, the Group X Segment interaction did not reach significance, $F(6, 108) = 1.2$, $p = 0.32$, $\eta^2_p = 0.06$. The ANOVA also revealed a significant main effect of Group, $F(2, 36) = 7.1$, $p = 0.002$, $\eta^2_p = 028$; participants of the 24-h and 5-min groups outperformed those of the control group but did not differ significantly from one another.

6.3.2 Discussion

The objective of the present report was to determine whether the CNS consolidates a motor skill learned through observation. In the present experiment, we sought evidence of off-line learning by comparing the performance of participants who had either a 5-min or a 24-h break between an observation session and a physical practice session. A third group also performed a physical practice session without prior observation. Two main findings emerged from our results.

First, observation alone (i.e., without physical practice) is sufficient to learn a prescribed movement time. Specifically, participants of the 24-hour group were temporally more accurate and less variable compared to participants of the control group. This better performance was noted 24 hours after the initial observation phase, suggesting that the memory representation of the correct movement time was stored in long-term memory. This finding is in line with numerous reports showing that observation is beneficial to motor learning (see Ashford, Bennett, & Davids, 2006 for a meta-analysis). In contrast, observation did not allow participants to learn the relative timing of the new sequence. Specifically, both observation groups (5-min and 24-h) did no better than the control group at producing the four segments of the sequence in equal movement time. As previously reported, physical practice seems to be essential to learn the spatiotemporal structure of a new sequence (Blandin et al., 1999).

Second, and more importantly, our data failed to reveal any difference between the 5-min and 24-h groups. Regardless of the interval between the observation session and the physical practice session, participants were equally accurate and variable when they physically performed the sequence. This finding markedly contrasts with prior reports showing off-line learning when the task was physically practiced (Robertson et al., 2004; Press et al., 2005; Trempe & Proteau, 2010; Walker & Stickgold, 2005; Walker et al., 2005); it also differs from the results of a recent study reporting off-line learning following observation (Van Der Werf et al., 2009; this discrepency will be discussed in section 6.5). In the present experiment, the absence of off-line learning could not be explained by a floor effect because the participants' performance could clearly improve further. Specifically, the mean absolute error of the 24-h group was about 130 ms, whereas errors around 50 ms have been reported when participants physically practiced the task with feedback (Blandin et al., 1999; see also the results of Experiment 3 of the present paper). Furthermore, off-line learning has commonly been associated with a large effect size (with Cohen's *d* ranging from 1 to 2, Fischer et al., 2002; Walker et al., 2002). In our experiment, the post hoc comparisons had a power of 0.8 (considering an expected effect size of 1, Cohen, 1988), which should have been sufficient to detect any significant difference. Also, off-line learning has been associated with performance increase of 20 to 30% (Fischer et al., 2002; Kuriyama et al., 2004); thus, one could have expected the 24-h group to decrease their absolute error to around 100 – 110 ms. This was clearly not the case as the 24-h group had a mean absolute error of 130 ms when tested the second day. In addition, all participants of the 24-h group had sufficient time (including a night of sleep) to consolidate the new sequence, and they all slept within the first 12-h interval after the video presentation, thus decreasing the possible interference from other daily activities (Van Der Werf et al., 2009).

The observation that a 24-hour rest interval did not result in behavioural evidence of off-line learning does not indicate, however, that the memory representation of the movement time was not consolidated. The finding that there was no performance decay 24 hours after acquisition suggests that changes did occur in the CNS to store the new memory representation in long-term memory. Thus, it is possible that following observation, consolidation results in performance stabilization.

6.4 Experiment 2

The objective of the second experiment was to test the hypothesis that a rest interval following an observation session results in a stabilization of the memory representation learned through observation. Two groups of participants observed videos of an expert model performing two distinct sequences (A and B) either 5 minutes or 8 hours apart (Brashers-Krug et al., 1996). Retention was tested the following day. If consolidation stabilizes the memory representation learned through observation, retention should be better if the two sequences are observed 8 hours apart since the memory representation of Sequence A would have become more stable and resistant to the interference of Sequence B (Brashers-Krug et al., 1996; Krakauer et al., 2005).

6.4.1 Method

Participants

Twenty-six undergraduate students (mean age 21.3, *SD* = 1.6; 17 females) from the Département de kinésiologie at the Université de Montréal took part in the experiment. All subjects were naive to the purpose of the study and had no prior experience with the task. None of the subjects reported neurological disorders, and all had normal or corrected to normal vision. The study was approved by the Health Sciences Research Ethic Committee of the Université de Montréal.

Task and apparatus

Sequence A was identical to the sequence used in Experiment 1, whereas Sequence B had the same number of segments (4) but required a different timing (see Figure 6.4). Specifically, Sequence B had to be completed in a total movement time of 1600 ms separated into four segments of 450, 350, 450, and 350 ms, respectively. Thus, Sequences A and B shared no timing characteristics. The movements' mean index of difficulty of Sequence B was 2.2 (Fitts, 1954).

Procedures

Testing sessions were scheduled between 8 a.m. and 5 p.m. Participants observed a video of an expert model performing 40 near-perfect trials of Sequence A (same video as in Experiment 1), then of Sequence B, either 5 minutes (5-min group, n = 13) or 8 hours apart (8-h group, n = 13). The mean absolute error of the model performing Sequence B was 11.9 ms (SE = 1.3) and his mean RMSE was 0.44 (SE = 0.02). Participants returned to the laboratory 24 hours after the observation of the first sequence and physically performed 20 trials of each sequence without feedback (starting with Sequence A). To reduce possible interference effects between Sequence A and B during the retention test, all participants performed a metronome task at the beginning of the retention test and before switching to the second sequence. The task consisted in pressing a button (1 mm) at regular intervals during a period of 2 minutes to match the audible beats (1 beat per 3 seconds) generated by a computer. The rhythm produced by the metronome was completely different from the correct rhythm of both sequences. The remaining procedures were identical to those used in Experiment 1.

6.4.2 Results

Sleep data

Participants slept an average of 7.1 hours (*SE* = 0.29) during the night between the practice sessions and the retention test. There was no significant difference between the groups, $t(24) = 0.30$, $p = 0.77$, $d = 0.12$.

Total movement time

As in Experiment 1, we computed the mean absolute error and the variable error of the total movement time for each participant. In addition, we also computed the constant error (CE) to determine whether movement times were biased in a specific way (i.e., too fast or too slow). Data were submitted to three separate ANOVAs contrasting 2 Groups X 2 Sequences with repeated measurements on the second factor.

The ANOVA contrasting the absolute error revealed a significant Group X Sequence interaction, $F(1, 24) = 4.4$, $p = 0.046$, $\eta^2_p = 0.16$. As illustrated in Figure 6.5a, both groups were equally accurate when performing Sequence A ($p = 0.7$), whereas the 8-h group made larger errors compared to the 5-min group when performing Sequence B ($p = 0.049$). The ANOVA contrasting the CE revealed no difference between the groups, $F(1, 24) = 3.2$, $p = 0.09$, $\eta^2_p = 0.12$, nor a Group X

Sequence interaction, $F(1, 24) = 1$, $p = 0.32$, $\eta^2_p = 0.04$ (see Figure 6.5b). Finally, participants of the 8-h group were significantly less variable compared to participants of the 5-min group, regardless of the sequence, $F(1, 24) = 16.9$, $p < 0.001$, $\eta^2_p = 0.4$ (see Figure 6.5c).

Relative timing

As in Experiment 1, we computed the RMSE of relative timing and its variability to determine whether participants learned the relative timing of the movement sequences. For the RMSE, the ANOVA revealed neither a significant difference between the groups, $F(1, 24) = 0.02$, $p = 0.9$, $\eta^2_p = 0.001$, nor a Group X Sequence interaction, $F(1, 24) = 1.3$, $p = 0.95$, $\eta^2_p = 0.04$. Similar results were obtained when contrasting the variability of the RMSE, $F(1, 24) = 0.008$, $p = 0.93$, $\eta^2_p < 0.001$ and $F(1, 24) = 0.5$, $p = 0.48$, $\eta^2_p = 0.02$ for the main effect of Group and the Group X Sequence interaction, respectively.

6.4.3 Discussion

The objective of Experiment 2 was to determine whether we could find behavioural evidence that a memory representation learned through observation can be stabilized by consolidation. Based on previous reports (Brashers-Krug et al., 1996; Muellbacher et al., 2002; Walker et al., 2003), we hypothesised that a 8-hour rest interval between the observation sessions would lead to improved learning since the memory representation of the first sequence (Sequence A) would have had sufficient time to become stable and resistant to the interference of the second sequence (Sequence B).

Interestingly, the results did not support our hypothesis. First, there was no accuracy difference between the groups when participants performed Sequence A. Thus, regardless of the interval between the observation sessions, Sequence B did not interfere with the learning of Sequence A (i.e., no retrograde interference). This result diverges from previous reports using physical practice showing interference when two tasks are practiced successively (Brashers-Krug et al., 1996; Krakauer et al., 1999).

Participants of the 8-h group performed Sequence B less accurately compared to participants of the 5-min group: a longer between-sessions interval impaired learning of Sequence B. Noteworthy is that participants of the 8-h group performed Sequence B in around 1300 ms, i.e., in a movement time closer to the 1200 ms of Sequence A than to the required 1600 ms for Sequence B. This suggests that the memory representation of Sequence A caused anterograde interference on the learning of Sequence B. Because the two groups differed only by the length of time between the observation sessions, this anterograde interference observed only for the 8-hour break group suggests that consolidation processes took place between the observation sessions and stabilized the memory representation of Sequence A. As a result, participants failed to learn the second sequence and simply reproduced both sequences the following day using the stable memory representation of Sequence A. This explanation is further supported by the finding that participants of the 8-h group performed both sequences with less variability (they kept reproducing the same stable movement time). Thus, our results argue that observation triggered consolidation processes that stabilized the memory representation of the new motor skill.

The finding that an 8-hour interval resulted in anterograde interference (impaired learning of Sequence B) differs from the retrograde interference previously reported using a physical practice protocol (Brashers-Krug et al., 1996; Walker et al., 2003). However, because our sequence production task was also quite different from the adaptation and finger sequence tasks used in these reports, it is difficult to conclude that observation and physical practice trigger different consolidation processes. Experiment 3 was therefore conducted to determine whether the results of Experiment 2 were specific to observation learning or to our sequence production task.

6.5 Experiment 3

To determine whether the results of Experiment 2 were specific to our task, the observation session was replaced by a physical practice session. Participants performed 40 trials with feedback of Sequences A and B either 5 minutes (5-min group, *n* = 12) or 8 hours (8-h group, *n* = 12) apart and were retested the following day. If the results of Experiment 2 were specific to our task, participants of the 8-h group should again demonstrate weaker retention for Sequence B. In contrast, if the results of Experiment 2 were specific to the consolidation processes taking place after observation, participants of the 8-h group should outperform those of the 5-min group in the retention test (as in previous reports using physical practice tasks Brashers-Krug et al., 1996; Walker et al., 2003). None of the participants recruited took part in the previous two experiments. All remaining procedures were identical to those described in Experiment 2.

6.5.1 Results

Acquisition

Acquisition data for AE and RMSE are illustrated in Figure 6.6. To assess whether the 5-min and 8-h groups performed differently during acquisition, we averaged the last 20 trials of each sequence and calculated AE, CE, VE, RMSE, and the variability of RMSE. Data of all dependent variables were then submitted to separate ANOVAs contrasting 2 Groups X 2 Sequences. There was no significant difference between the groups ($p > 0.13$) with the exception that the 8-h group was significantly less variable (VE) compared to the 5-min group when practicing Sequence A ($p < 0.001$, $F(1, 22) = 6.7$, $p = 0.017$, $\eta^2_p = 0.23$ for the Group X Sequence interaction).

Sleep data

Participants slept on average 7.9 hours ($SE = 0.22$) during the night between the practice sessions and the retention test. There was no significant difference between the groups, $t(22) = 0.35$, $p = 0.73$, $d = 0.14$.

Retention

As in Experiment 2, all 20 trials performed during the retention test were used to calculate AE, CE, VE, RMSE, and the variability of RMSE for each participant. Data were then submitted to separate 2 Groups X 2 Sequences

ANOVAs. The ANOVA contrasting the AE revealed a significant Group X Sequence interaction, *F*(1, 22) = 7.5, $p = 0.012$, $\eta^2_p = 0.25$. As illustrated in Figure 6.7a, although both groups performed Sequence A equally accurately ($p = 0.32$), participants of the 8-h group were significantly more accurate compared to participants of the 5-min group when performing Sequence B ($p = 0.016$). This difference was not caused by a specific bias since the ANOVA contrasting the CE revealed no significant difference between the groups, *F*(1, 22) = 0.01, $p = 0.92$, $\eta^2_p < 0.001$, nor a Group X Sequence interaction, *F*(1, 22) < 0.001, $p = 0.99$, $\eta^2_p < 0.001$ (see Figure 6.7b). The variability also did not differ between the groups, *F*(1, 22) = 0.25, $p = 0.6$, $\eta^2_p = 0.01$ and *F*(1, 22) = 0.97, $p = 0.34$, $\eta^2_p = 0.04$ for the main effect of Group and the Group X Sequence interaction, respectively ($p > 0.34$; see Figure 6.7c).

The ANOVAs contrasting RMSE and its variability did not reveal any significant difference between the groups (see Figures 6.7d and e).

6.5.2 Discussion

The objective of Experiment 3 was to determine whether the anterograde interference observed in Experiment 2 was specific to the consolidation processes taking place following observation or to the nature of our task. To answer this question, participants physically practiced two distinct sequences of arm movements (A and B) either 5 minutes or 8 hours apart before being retested the following day. As in Experiment 2, participants of both groups showed equal retention of Sequence A. However, participants of the 8-h group performed Sequence B significantly more accurately compared to participants of the 5-min group. Thus, an 8-hour rest interval between the physical practice sessions led to better learning. Taken together, the results of Experiment 2 and 3 indicate that the consolidation processes taking place after observation lead to different behavioural outcomes than those taking place after physical practice.

6.6 General Discussion

The objective of the present report was to determine whether we could find behavioural evidence that a motor skill learned through observation can be consolidated. To do so, we conducted a series of three experiments in which we sought evidence of off-line learning and stabilization, the two most common behavioural outcomes of the consolidation processes (Krakauer & Shadmehr, 2006; Walker, 2005). In Experiment 1, no off-line learning was observed. This was the case even when the observation and retention sessions were separated by sufficient time (including a night of sleep) and when the participants' performance could improve still further. Although it could be argued that subtle kinematic differences could have resulted from consolidation (for example, smoother and less variable bell-shape velocity profiles to perform each segment of the task), they clearly had no significant impact on what the participants were asked to do, which makes them secondary to the findings of the present study. In Experiment 1, the observers outperformed the control group in the 24-hour retention test, indicating that observation resulted in a lasting representation of the task in the CNS. This proposition is supported by the results of Experiment 2, in which an 8-hour break between the observation of two distinct movement sequences resulted in anterograde interference, suggesting that the memory representation of the first sequence (Sequence A) had been stabilized and kept in memory during the inter-session interval. Together, the results of Experiments 1 and 2 indicate that specific consolidation processes do occur following an observation session. To our knowledge, this is the first time that it is unequivocally shown that physical practice is not a pre-requisite for motor skill consolidation.

Furthermore, the results of all three experiments demonstrate that the behavioural outcomes of the consolidation processes taking place after observation differ from those taking place after physical practice. This is particularly evident when comparing the results of Experiments 2 and 3, in which the same consolidation interval led to opposite results depending on whether the new sequence of movements was initially observed or physically practiced. In addition, the absence of off-line learning in Experiment 1 also differs from the results obtained with physical practice tasks. This new finding suggests that observation may trigger different consolidation processes than those triggered by physical practice.

Although speculative, this hypothesis could explain the contradiction between our results and those of Van Der Werf et al. (2009), who reported off-line learning following observation. In their experiment, participants were asked to press two computer keys with two fingers (corresponding to the fingers used in the sequence production task) during observation. This procedure was employed to ensure that participants did not attempt to physically practice the sequence during observation. However, by doing so, networks involved in the muscle contraction were activated during observation. Although participants were not physically practicing the sequence, this activation may have been sufficient to trigger off-line learning processes associated with physical practice. In contrast, participants in our experiment were instructed to sit still with their hands resting on their thighs during the observation phase. Thus, participants produced no muscle contraction. Similarly, this hypothesis could account for the off-line learning reported by Debarnot et al. (2009a; 2009b) following mental imagery. Because participants physically practiced the sequence before the mental imagery session, the spontaneous improvement observed during the re-test session may have reflected consolidation of the short physical practice phase or the joint effects of imagery and physical practice (see Stefan et al., 2008).

Although observation and physical practice are known to share many similarities (Jeannerod, 1999), these two acquisition modalities are not identical, thus providing hints to explain the different consolidation outcomes. First, while several neuroimaging studies have shown large overlap in the brain regions activated during observation and physical practice, certain brain regions are nevertheless activated more intensely (Cross et al., 2009), or even exclusively (see Grèzes & Decety, 2001 for a meta-analysis) during physical practice. In addition, observation is thought to involve the mirror neuron system (also called the action observation network [AON]), i.e., a subset of neurons that are activated whether the action is produced or observed. Located mainly within the premotor and parietal cortex, these neurons are believed to play a crucial role for our understanding of others' actions (Iacoboni & Dapretto, 2006; Rizzolatti &

Craighero, 2004). However, the primary motor cortex (M1), a key structure for motor skill learning (Sanes & Donoghue, 2000), is not known for being part of the AON and may therefore not be engaged in the long-term retention of skills learned by observation. Although M1 has been reported to be important for the short-term retention of a new internal model learned by observation (Brown et al., 2009), both rodent (Kleim et al., 2004) and human (Karni et al., 1995) experiments have reported that long-lasting plastic changes in M1 occur only when the learner's performance reaches an asymptote. Because no movement is produced during observation, no asymptote can be reached; observation may therefore not provide sufficient stimulation to drive a plastic reorganization of M1. A second, but not exclusive, possibility is that feedback provided to participants during physical practice may be crucial for off-line learning. Specifically, Holroyd and Coles (2002) suggested that the mesencephalic system may modulate its dopaminergic signal in response to the outcome of a movement, thus making this system likely to modulate memory consolidation (Jay, 2003). Again, because observers produce no movement, they obviously receive no feedback about their own performance. Consequently, the dopaminergic signal may remain silent during acquisition and fail to trigger specific consolidation processes.

As mentioned in Experiment 2, the finding that an 8-hour interval between the observation sessions impaired learning of the second sequence is counterintuitive. One could argue that participants of the 8-h group were simply more tired than participants of the 5-min group were when observing Sequence B (around 4 p.m. for the 8-h group vs. 8:30 a.m. for the 5-min group) and therefore encoded the sequence less efficiently. Two lines of evidence argue against this explanation, however. First, no participant reported excessive fatigue at the time of the second observation session. Moreover, when asked by the experimenter at various points during the observation session to comment on the performance of the model (e.g., “Was the previous movement too fast? Too slow?”), participants of the 8-h group provided answers clearly indicating that they remained attentive to the video. Second, and more importantly, participants of the 8-h group in Experiment 3 also practiced Sequence B around 4 p.m. and still demonstrated better learning compared to participants of the 5-min group. Thus, if the larger error observed in Experiment 2 was caused by fatigue, Experiment 3 should have led to similar results.

Nevertheless, it remains difficult to explain why an 8-hour consolidation interval led to opposite results when the sequences were observed or physically practiced. Possibly, information may have been encoded by distinct memory systems (declarative and procedural) depending on the acquisition protocol (see also Kelly et al., 2003 for a similar discussion). Declarative and procedural memories are known to recruit different neural networks and to be consolidated differently (Walker, 2005; Robertson & Cohen, 2006). In the present report, observation learning most likely relied on declarative memory since participants were consciously trying to identify the correct timing of each sequence. It is therefore possible that the two memory representations did not compete for the same resources when learned successively, that is, when the differences between the two sequences were most salient. As a result, no interference was observed in retention for the 5-min group in Experiment 2. This hypothesis is in line with the results of Debarnot et al. (2010), who reported no interference when two sequences were successively practiced by mental imagery. However, when the two sequences were observed 8 hours apart, the stabilized memory representation of the first sequence could have been used as a reference for the acquisition of the second sequence, which would explain why we observed anterograde interference. In contrast, physical practice in Experiment 3 most likely recruited the procedural memory system since the correct rhythm developed through practice can be more easily felt than verbalized. As reported previously (Shadmehr & Holcomb, 1999), two procedural skills learned successively seem to compete for the same resources and are therefore particularly subject to interference. This would explain why, in Experiment 3, a 5-minute pause impaired learning of the second sequence.

This hypothesis is in line with the results of Kelly et al. (2003), suggesting that observational learning is subject to interference from a secondary task engaging the declarative memory system. Using a sequence-learning task, the authors reported that observers failed to learn the sequence when they were concurrently engaged in a tone-counting task, whereas learning occurred when the observers could devote all their attention to the primary task (sequence learning). In contrast, the secondary task did not prevent sequence learning when the primary task was performed physically. Further work is still necessary, however, to determine whether physical practice following observation (and vice versa) interferes with the consolidation processes.

In conclusion, our results indicate that observation does trigger consolidation processes that lead to a stabilization of the new motor skill and its long-term retention. Although observation and physical practice are known to share many similarities, our results indicate that they are consolidated differently.

Acknowledgements

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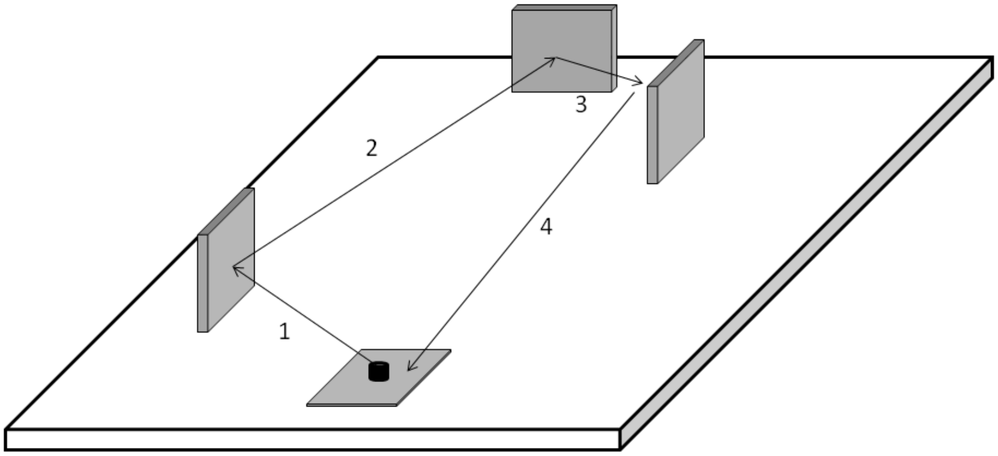

Figure 6.1: Movement pattern used in all three experiments (Sequence A). Participants had to press the start microswitch and then hit the first, second, and third wooden barriers with their right hand before ending their movement by pushing down on the metal plate surrounding the microswitch. Each segment had to be completed in 300 ms.

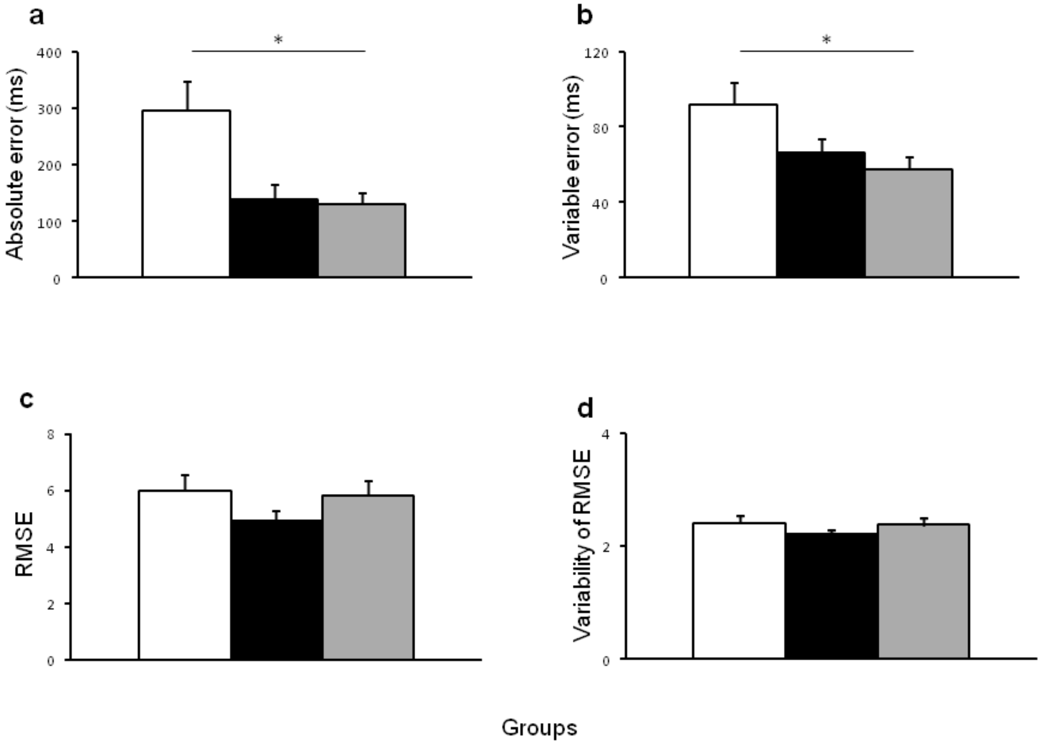

Figure 6.2: Experiment 1. Retention data of the control (white), 5-min (black), and 24-h (grey) groups. The symbol * indicates a significant difference between the groups, and the error bars illustrate the standard error of the mean.

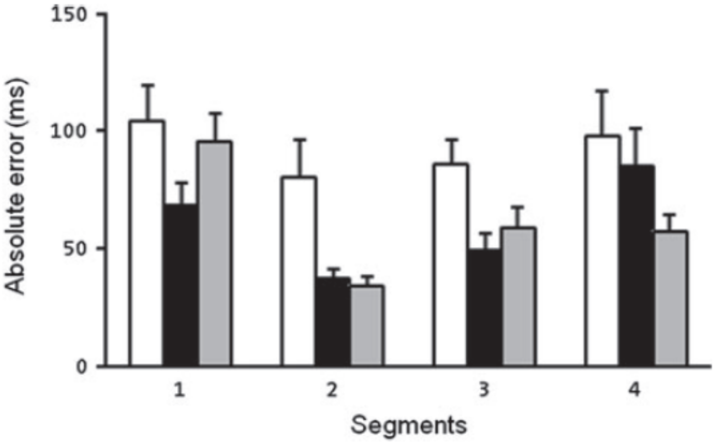

Figure 6.3: Experiment 1. Absolute error of the control (white), 5-min (black), and 24-h (grey) groups for each segment of the sequence. The Segment X Group interaction was not significant (p = 0.32). The error bars illustrate the standard error of the mean.

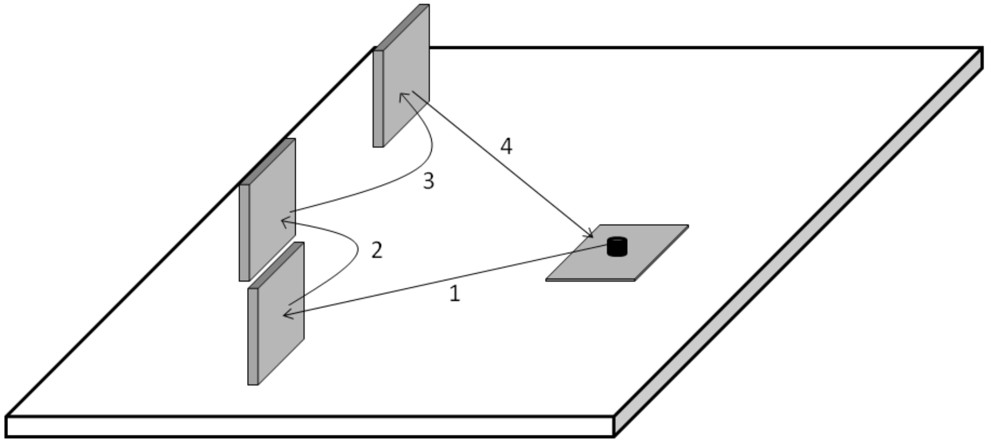

Figure 6.4: Movement pattern of Sequence B (Experiments 2 and 3). Participants had to press the starting microswitch and hit the first, second, and third wooden barriers with their right hand before ending their movement by pushing down on the metal plate surrounding the microswitch. The four segments had to be completed in 450, 350, 450, and 350 ms, respectively.

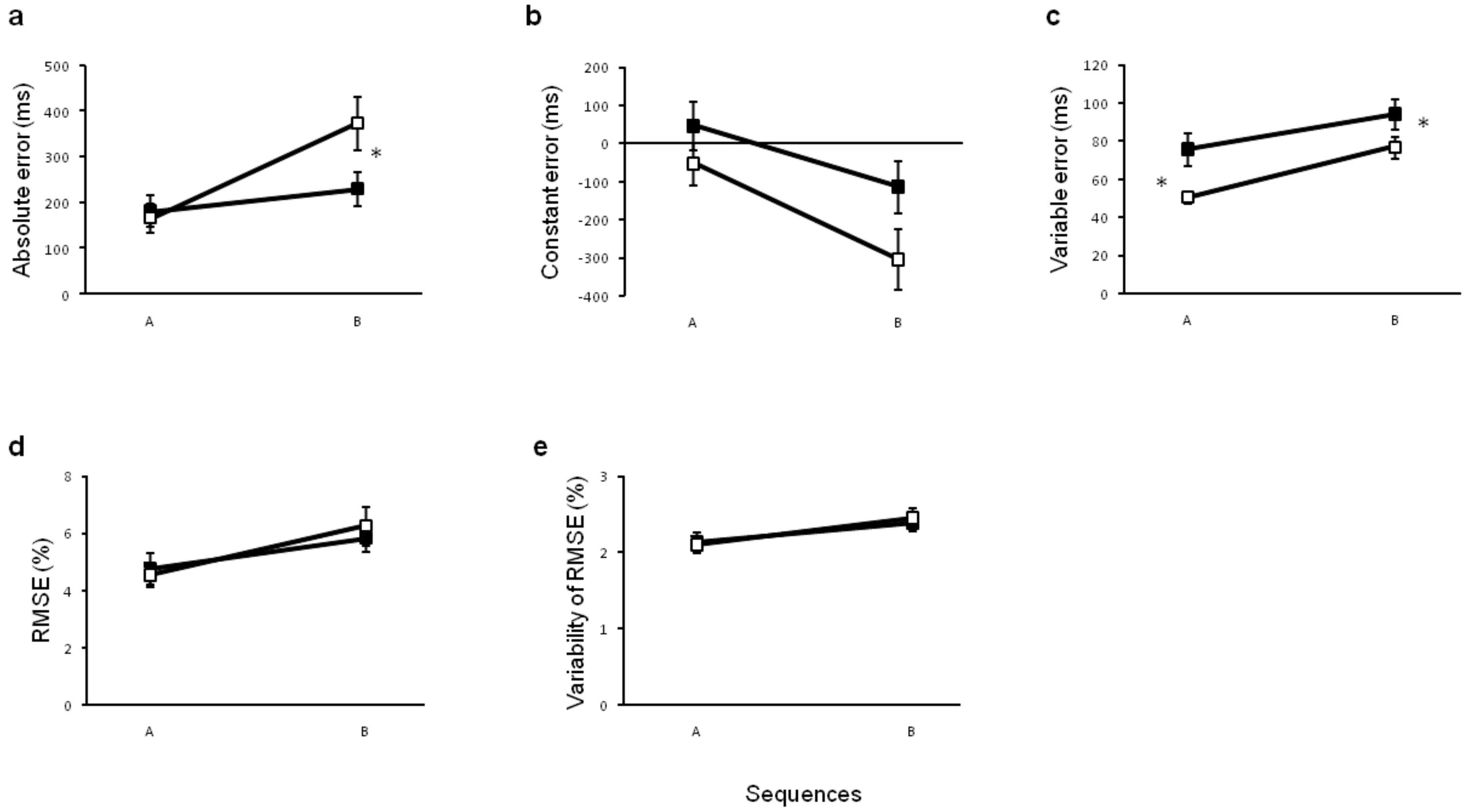

Figure 6.5: Experiment 2. Retention data of the 5-min (filled) and 8-h (opened) groups. The symbol * indicates a significant difference between the groups, and the error bars illustrate the standard error of the mean.

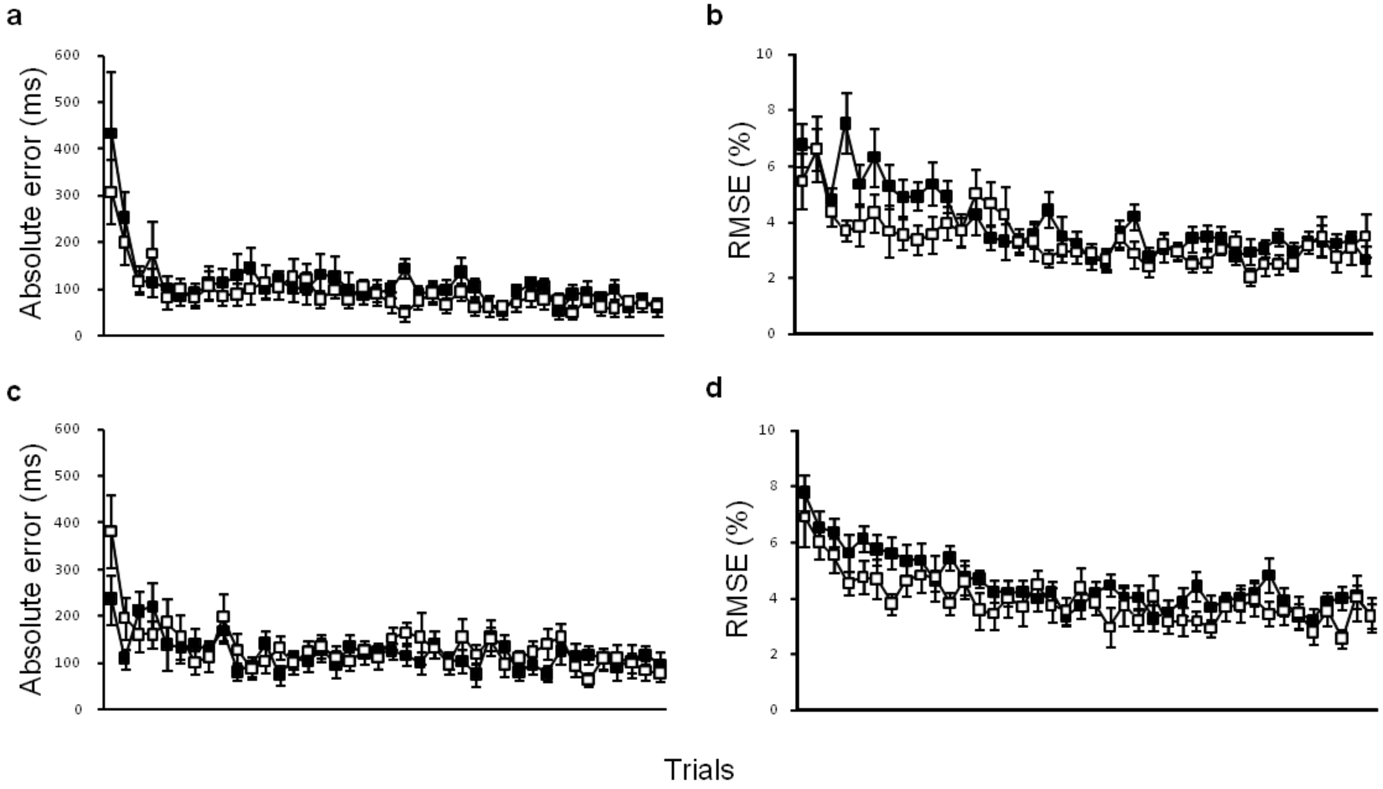

Figure 6.6: Experiment 3. Acquisition data of the 5-min (filled) and 8-h (opened) groups when practicing Sequence A (A and B) and Sequence B (C and D). The error bars illustrate the standard error of the mean.

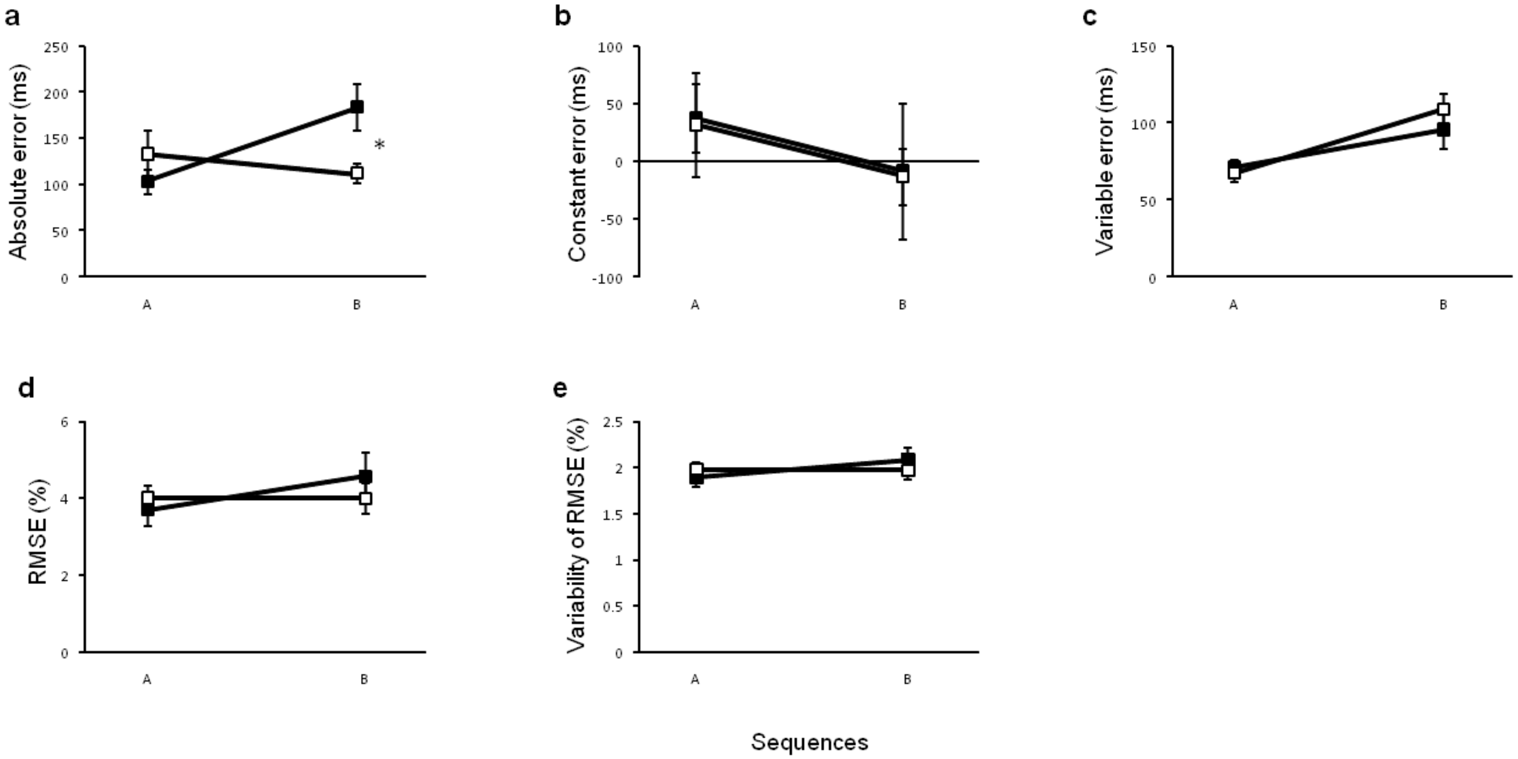

Figure 6.7: Experiment 3. Retention data of the 5-min (filled) and 8-h (opened) groups. The symbol * indicates a significant difference between the groups and the error bars illustrate the standard error of the mean.

CHAPITRE 7

DISCUSSION GÉNÉRALE

La consolidation regroupe une série de processus prenant place suite à une séance de pratique et permettant la mise en mémoire de l'habileté motrice pratiquée (Krakauer & Shadmehr, 2006; Walker, 2005). Bien que différents modèles conceptuels aient été proposés pour expliquer les effets positifs de la consolidation pour l'apprentissage d'une nouvelle habileté (Diekelmann & Born, 2010; Walker & Stickgold, 2010), la nature exacte des processus prenant place suite à une séance de pratique demeure nébuleuse. L'objectif principal de cette thèse consistait à mieux définir les processus de consolidation en précisant certains facteurs qui influencent la consolidation d'une habileté motrice. Plus spécifiquement, nous nous sommes intéressés à l'influence du niveau de performance de l'apprenant ainsi qu'à l'influence de la modalité d'acquisition (pratique physique vs. apprentissage par observation) sur la consolidation. À l'aide d'une tâche d'adaptation visuomotrice comportant deux niveaux de difficulté (Trempe & Proteau, 2008), nous avons démontré qu'une bonne performance doit être atteinte au cours de la séance de pratique pour enclencher certains processus de consolidation (Trempe & Proteau, 2010). De plus, nos résultats indiquent que l'évaluation subjective que l'apprenant fait de sa propre performance peut moduler la consolidation d'un nouveau modèle interne (Trempe, Sabourin & Proteau, soumis). Finalement, nous avons démontré que l'apprentissage par observation peut enclencher certains processus de consolidation, indiquant que la consolidation n'est pas exclusive à la pratique physique (Trempe, Sabourin, Rohbanfard, & Proteau, 2011). Bien que plusieurs questions aient été discutées dans les chapitres précédents, certains aspects nécessitent de plus amples considérations. Dans ce chapitre, nous contrasterons les résultats des études présentées dans la thèse pour en tirer des points de discussion plus généraux.

7.1 Performance et consolidation

Nous avons démontré que la performance objective de l'apprenant au cours d'une séance de pratique influence la consolidation d'un nouveau modèle interne (Trempe & Proteau, 2010). Plus précisément, nous avons observé deux manifestations comportementales de la consolidation : 1) des effets-consécutifs (*after-effects*) persistants lorsque la performance initiale des participants se rapprochait du niveau de base (performance asymptotique), et 2) une diminution de l'erreur angulaire lorsque la performance initiale était modeste (apprentissage hors-ligne). Suite à cette étude, nous avons émis l'hypothèse que la consolidation soit modulée par l'évaluation subjective que l'apprenant fait de sa propre performance, et non par sa performance objective. Cette proposition novatrice diffère des études antérieures dans lesquelles la quantité de pratique (Savion-Lemieux & Penhune, 2005; Walker, Brakefield, Seidman et al., 2003; Wright et al., 2010) et la performance objective de l'apprenant (Karni et al., 1995; Kuriyama et al., 2004) étaient considérées.

Pour évaluer cette hypothèse, nous avons biaisé l'évaluation subjective des participants en leur donnant un objectif facile ou difficile lors de la première séance de pratique (Trempe, Sabourin & Proteau, soumis). Si la consolidation est modulée par l'évaluation subjective que l'apprenant fait de sa propre performance, les participants ayant reçu un objectif facile et ayant connu du succès lors de la première séance de pratique devraient démontrer des effets-consécutifs persistants similaires à ceux observés suite à l'atteinte d'une performance asymptotique dans Trempe et Proteau (2010). Or, les participants ayant connu du succès lors de la première séance de pratique, alors que leur performance initiale était en réalité modeste, n'ont pas démontré d'effets-consécutifs persistants lors de la deuxième séance mais plutôt une diminution de l'erreur angulaire (apprentissage hors-ligne), c'est-à-dire la manifestation comportementale observée dans Trempe et Proteau (2010) lorsque la performance initiale était modeste. Cette observation ne supporte donc pas l'hypothèse que les effets-consécutifs persistants de Trempe et Proteau (2010) aient été causés par l'atteinte d'une bonne performance subjective. Plus précisément, les participants ayant reçu un objectif facile ont démontré un effet-consécutif plus prononcé à la fin de la deuxième session comparativement aux participants ayant reçu un objectif difficile, reflétant la meilleure adaptation des participants ayant reçu un objectif facile (données non-publiées). Cet effet-consécutif plus prononcé ne s'est toutefois pas avéré plus persistant puisque les participants des deux groupes sont retournés à leur modèle interne normal (sans rotation) au même rythme. Ensemble, ces résultats suggèrent que les processus de consolidation menant à des effets-consécutifs persistants prennent place uniquement lorsque l'apprenant atteint un certain seuil de performance objective, quelle que soit l'évaluation subjective que l'apprenant fait de sa propre performance. Bien que cette évaluation subjective puisse influencer la consolidation d'un nouveau modèle interne, certains processus semblent nécessiter l'atteinte d'une bonne performance objective pour être enclenchés.

À titre comparatif, la Figure 7.1 illustre la performance des participants ayant reçu un objectif facile ou difficile lors de la première séance de pratique (Trempe, Sabourin, & Proteau, soumis) ainsi que la performance des participants du groupe « limited practice » ayant réalisé le même protocole expérimental, sans toutefois recevoir d'objectif (Trempe & Proteau, 2010). Il est particulièrement frappant de constater que les participants ayant reçu un objectif facile ont démontré un apprentissage similaire à ceux n'ayant reçu aucun objectif, contrairement aux participants ayant reçu un objectif difficile qui ont démontré un apprentissage nettement inférieur lors de la deuxième séance. Nous proposons deux interprétations pour expliquer ces résultats. Premièrement, il est possible que l'insuccès vécu par les participants ayant reçu l'objectif difficile ait inhibé les processus de consolidation prenant normalement place suite à une séance de pratique et menant à une amélioration/maintien de la performance.

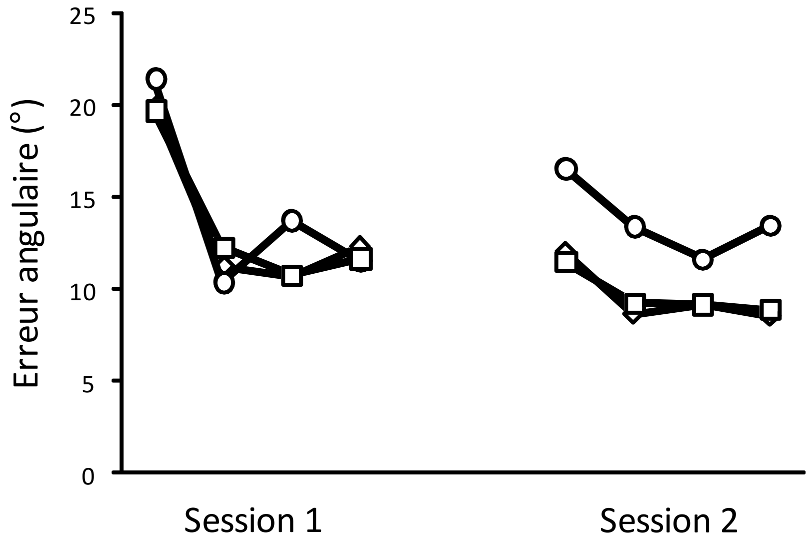

Figure 7.1 : Erreur angulaire moyenne des participants ayant reçu un objectif facile (losanges), difficile (cercles) ou aucun objectif (carrés) lors de la première séance de pratique. Chaque marqueur illustre l'erreur angulaire moyenne pour un bloc de 6 essais.

Ce mécanisme d’inhibition protégerait l’apprenant contre la consolidation d’un modèle interne erroné qui nécessiterait inévitablement des corrections lors des séances de pratique subséquentes. Intuitivement, il semble peu efficace pour le système moteur d’investir énergie et ressources dans la consolidation d’un geste erroné. Deuxièmement, il est possible que les participants n’ayant reçu aucun objectif de la part de l’expérimentateur (groupe "limited practice"; Trempe & Proteau, 2010) se soient eux-mêmes fixés un objectif réaliste et atteignable, facilitant ainsi le maintien de la motivation et de l’intérêt tout au long de la séance de pratique (Lewthwaite & Wulf, 2010). Dans un tel cas, les participants ont vraisemblablement terminé la première séance de pratique en étant satisfaits de leur performance, tout comme les participants ayant reçu un objectif facile, ce qui a eu pour effet d’enclencher les mécanismes de consolidation. Des études supplémentaires seront nécessaires pour dissocier ces deux possibilités.

7.2 L’apprentissage hors-ligne (partie II)

Nous avons émis dans le Chapitre 2 certaines réserves à propos des résultats démontrant que le sommeil, ou le simple passage du temps, puisse entrainer une amélioration spontanée de la performance. Parmi les considérations soulevées, nous avons souligné que l’inclusion de plusieurs essais dans le calcul de la performance lors du test de rétention rendait difficile la dissociation entre l’apprentissage prenant place entre les séances de pratique (appelé apprentissage hors-ligne) et l’apprentissage prenant place durant le test de rétention. Suite aux trois études portant sur la consolidation présentées dans cette thèse, nous désirons réitérer l'influence que peut avoir la méthode employée pour analyser les données sur l'apprentissage hors-ligne.

Nous avons rapporté qu'une pause de 24 heures pouvait mener à l'apprentissage hors-ligne d'un nouveau modèle interne (Trempe & Proteau, 2010). Pour diminuer l'influence de la grande variabilité inter-essais, nous avons calculé l'apprentissage hors-ligne en comparant la performance des 12 essais du test de rétention aux 12 derniers essais de la première séance de pratique. Bien que nous n'éprouvions aucun doute sur l'effet positif de la consolidation sur la rétention du nouveau modèle interne, un lecteur attentif pourra toutefois constater que la consolidation n'a pas entrainé une amélioration de la performance dès le début de la deuxième session. Telle qu'illustrée sur la Figure 4.2A (panneau de droite), la performance du premier essai de la deuxième session était largement inférieure à la performance moyenne observée à la fin de la première séance de pratique (voir également Trempe, Sabourin & Proteau, soumis, pour une observation semblable). L'affirmation que la consolidation puisse entrainer une amélioration spontanée de la performance (Doyon et al., 2009; Robertson & Cohen, 2006; Walker, 2005; Walker, Brakefield, Hobson et al., 2003) doit donc être qualifiée davantage.

La diminution de la performance observée au début de la deuxième séance peut être associée à un « warm-up decrement », c'est-à-dire une diminution temporaire de la performance survenant lorsque l'habileté motrice n'est pas répétée durant un certain temps (Schmidt & Lee, 2005). Il est bien évident que plus le nombre d'essais inclus dans l'analyse augmente, moins grande est l'influence du « warm-up decrement » sur la performance moyenne de la deuxième séance. Nous avons utilisé les données des groupes « limited practice » (Trempe & Proteau, 2010) et « 24-hour easy objective » (Trempe, Sabourin & Proteau, soumis) pour quantifier l'effet du nombre d'essais considérés sur l'apprentissage hors-ligne. Plus précisément, nous avons recalculé l'apprentissage hors-ligne en variant le nombre d'essais de la deuxième séance inclus dans l'analyse. Ces deux groupes ont été choisis puisque les participants ont été soumis au même protocole expérimental (à l'exception de l'objectif donné aux participants du groupe « 24-hour easy objective ») incluant un intervalle de consolidation. La Figure 7.2A illustre la différence, en pourcentage, entre l'erreur angulaire au dernier essai de la Session 1 et l'erreur angulaire moyenne au début de la Session 2. Une valeur négative indique que la consolidation a entrainé une diminution de la performance, alors qu'une valeur positive indique que la consolidation a entrainé une amélioration de la performance (apprentissage hors-ligne). Les différentes colonnes illustrent l'effet d'augmenter le nombre d'essais de la deuxième séance inclus dans le calcul de la performance moyenne. Deux conclusions importantes émanent de cette analyse supplémentaire : 1) plusieurs essais doivent être inclus dans l'analyse pour observer une amélioration hors-ligne de la performance, et 2) plus le nombre d'essais inclus dans l'analyse augmente, plus la taille de l'effet augmente. L'apprentissage hors-ligne ainsi que la taille de l'effet sont donc tributaires des choix arbitraires réalisés lors de l'analyse des données (voir également Rickard et al., 2008 pour une observation semblable).

Nos résultats suggèrent donc qu'une amélioration de la performance requière à la fois une période de consolidation et une séance de pratique physique avec feedback. La combinaison de pratique physique avec feedback et consolidation, présente dans les études de séquence de mouvements, peut donc expliquer au moins en partie l'amélioration « hors-ligne » fréquemment rapportée (Doyon et al., 2009; Kuriyama et al., 2004; Walker, Brakefield, Hobson et al., 2003). Ce constat concorde également avec les résultats d'études d'apprentissage par observation démontrant qu'une séance de pratique physique est essentielle pour que s'exprime les effets

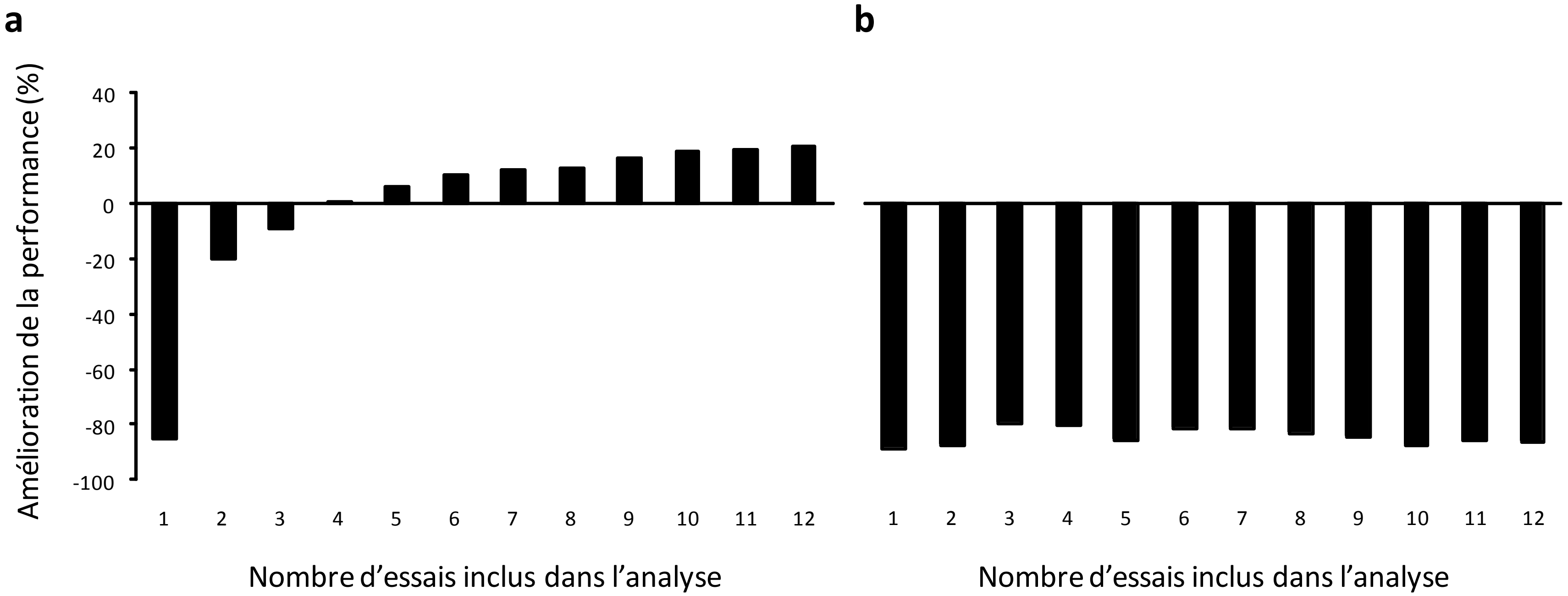

Figure 7.2 : Différence, en pourcentage, entre l'erreur du dernier essai de la Session 1 et l'erreur moyenne au début de la Session 2. L'erreur moyenne au début de la deuxième séance a été calculée en utilisant le premier essai (colonne 1), les deux premiers essais (colonne 2), et ainsi de suite. A) Données des groupes « limited practice » (Trempe & Proteau, 2010) et « 24-hour easy objective » (Trempe, Sabourin & Proteau, soumis). B) Données des groupes « 5-min » et « 24-hour » ayant pratiqué physiquement la Séquence A (Expérience 3; Trempe et al., 2011).

bénéfiques d’une séance d’observation (Blandin et al., 1999; Deakin & Proteau, 2000). Cette idée est d’ailleurs supportée par les résultats de l’Expérience 3 présentée au Chapitre 6 dans laquelle aucune amélioration de la performance n’a été observée suite à une période de consolidation lors d’un test de rétention effectué sans feedback. À des fins de comparaison, nous avons utilisé les données des groupes « 5-min » et « 8-hour » pour calculer la différence, en pourcentage, entre l’erreur mesurée lors du dernier essai de la Session 1 et l’erreur moyenne de la Session 2 (voir plus haut pour le détail des calculs). Comme l’illustre la Figure 7.2B, les participants de ces deux groupes ont démontré une diminution moyenne de la performance de 80% lors du premier essai de la Session 2, diminution similaire à celle obtenue avec la tâche d’adaptation visuomotrice. L’inclusion d’un nombre grandissant d’essais dans l’analyse n’a toutefois pas fait apparaître une amélioration de la performance. Sans feedback, les participants n’ont pu diminuer le « warm-up decrement » (Schmidt & Lee, 2005) présent au début du test de rétention et n’ont ainsi démontré aucun signe d’« apprentissage hors-ligne ».

Quelle que soit la méthode d’analyse choisie, nos résultats sont sans équivoque à un égard : l’apprentissage des groupes ayant bénéficié d’une période de consolidation est supérieur à l’apprentissage des groupes n’en ayant pas bénéficié. Cet effet est d’ailleurs observable dès le tout premier essai de la Session 2 (voir les Figures 4.2A, 4.2B, 4.5B et 5.3E). Nos résultats supportent donc l’idée que la consolidation puisse jouer un rôle important pour la stabilisation et la mise en mémoire des habiletés motrices (Krakauer & Shadmehr, 2006; Walker, 2005).

Bien qu'il soit possible que l'apprenant puisse bénéficier d'une forme d'intuition lors de la consolidation pour découvrir une nouvelle stratégie et améliorer sa performance (Fischer et al., 2006; Wagner et al., 2004), il semble qu'une séance de pratique physique avec feedback soit nécessaire pour valider et mettre en application la nouvelle stratégie.

7.3 Caractérisation des processus de consolidation

Nous avons présenté dans cette thèse trois manifestations comportementales distinctes de la consolidation : 1) des effets-consécutifs persistants (Trempe & Proteau, 2010), 2) une amélioration de la performance (ou un maintien de la performance, selon la méthode d'analyse choisie; Trempe & Proteau, 2010; Trempe, Sabourin & Proteau, soumis), et 3) une interférence antérograde suite à l'apprentissage par observation (Trempe et al., 2011). De par leur spécificité, ces trois différentes manifestations supportent l'hypothèse que la consolidation regroupe plusieurs processus distincts (Stickgold & Walker, 2007) ayant chacun leur propre mécanisme d'action.

Plus précisément, il est plausible que la différence entre les effets-consécutifs persistants et l'amélioration hors-ligne de la performance soit le reflet d'un changement des structures impliquées dans la mise en mémoire du nouveau modèle interne. Cette possibilité est supportée par le modèle de Doyon et Benali (2005) ainsi que par les résultats de Steele et Penhune (2010) montrant qu'une amélioration de la performance est associée à des changements d'activation de certaines structures du cerveau. Similairement, Karni et al. (1995) ont rapporté une réorganisation du cortex moteur primaire (M1) suite à l'atteinte d'une performance asymptotique, c'est-à-dire après plusieurs séances de pratique (voir également Kleim et al., 2004). Il est toutefois important de noter que les participants de Karni et al. (1995) ont démontré une rétention de la séquence de mouvements bien avant qu'il y ait une réorganisation de M1, indiquant qu'une réorganisation de M1 ne soit pas l'unique mécanisme permettant la mise en mémoire d'une nouvelle séquence de mouvements. Dans notre première étude, nous avons observé des effets-consécutifs persistants suite à l'atteinte d'une bonne performance, reflet d'une difficulté des participants à désadapter leurs mouvements et revenir à un modèle interne normal, sans rotation. Ces effets-consécutifs persistants n'ont toutefois pas été observés lorsque la performance initiale était modeste, bien que les participants aient néanmoins démontré une excellente rétention du nouveau modèle interne. Ces résultats suggèrent que l'apprentissage puisse tout d'abord nécessiter une première phase de consolidation, assurant le maintien du nouveau modèle interne dans un état flexible et facilement modifiable lors des séances de pratique subséquentes, suivi d'une deuxième phase de consolidation assurant une mémorisation plus permanente suite à l'atteinte d'une bonne performance. Le maintien de la performance démontré lorsque la performance est initialement modeste serait ainsi le reflet d'une première phase de consolidation, alors que les effets-consécutifs persistants révèleraient une mémorisation plus permanente. Bien que spéculative, cette hypothèse pourrait être mise à l'épreuve expérimentalement en vérifiant si une séquence mémorisée de mouvements dans M1 (Karni et al., 1995) est plus résistante à l'interférence qu'une séquence nouvellement apprise.

Finalement, les résultats de Trempe et al. (2011) démontrant une interférence antérograde suite à l'apprentissage par observation, contrairement à une interférence rétrograde suite à la pratique physique, suggèrent qu'il existe un processus de consolidation spécifique à l'apprentissage par observation. Nous avons souligné précédemment que l'apprentissage par observation puisse faire appel davantage à la mémoire explicite, contrairement à la pratique physique qui utiliserait davantage la mémoire implicite. Bien que ces deux systèmes aient la possibilité d'interagir l'un avec l'autre (Fischer et al., 2006), des différences en ce qui a trait à leur consolidation ont été démontrées (Robertson & Cohen, 2006; Robertson, Pascual-Leone, & Press, 2004; Walker, 2005). Par exemple, Fischer et al. (2006) ont rapporté qu'une nuit de sommeil permet d'améliorer l'identification explicite d'une séquence, sans toutefois en améliorer son exécution implicite. Similairement, Robertson et al. (2004) ont démontré que la consolidation d'une séquence de mouvements apprise de façon explicite nécessite une période de sommeil alors que la consolidation de la même séquence apprise de façon implicite n'en nécessite pas. Il semble donc plausible que la disparité entre l'interférence antérograde rapportée suite à l'observation et l'interférence rétrograde rapportée suite à la pratique physique reflète la différence entre les processus de consolidation associés à la mémoire explicite et ceux associés à la mémoire implicite. Des études supplémentaires seront toutefois nécessaires pour déterminer si les habiletés apprises par observation sont consolidées dans des structures différentes comparativement à celles apprises par pratique physique - par exemple dans l'« action observation network »- ou si leur consolidation met en jeu différents mécanismes moléculaires. Bien qu'il semble improbable que la consolidation des habiletés apprises par observation soit influencée par la performance de l'apprenant (puisqu'aucun mouvement n'est effectué durant l'acquisition), il demeure toutefois possible que les expériences antérieures de l'apprenant (Spilka, Steele, & Penhune, 2010) ainsi que sa croyance en sa capacité à reproduire le mouvement observé influence ce processus de consolidation.

7.4 Conclusion

La pratique physique ne garantit pas à elle seule l'apprentissage d'une habileté motrice. Pour être mémorisée et accessible dans le futur, l'habileté motrice doit être consolidée une fois la séance de pratique terminée. Dans cette thèse, nous avons démontré en utilisant uniquement des mesures comportementales que les processus de consolidation sont influencés par plusieurs facteurs dont la performance de l'apprenant (objective et subjective) ainsi que la modalité d'acquisition de l'habileté motrice. Les éducateurs physiques, les entraineurs sportifs, et les spécialistes de la réadaptation physique soucieux du développement de leurs élèves/athlètes/patients devraient donc planifier des entrainements qui favorisent non seulement l'acquisition de gestes moteurs mais également leur consolidation.

7.5 Références

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