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Aging increases the susceptibility to motor memory interference and reduces off-line gains in motor skill learning

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ABSTRACT

Declines in the ability to learn motor skills in older adults are commonly attributed to deficits in the encoding of sensorimotor information during motor practice. We investigated whether aging also impairs motor memory consolidation by assessing the susceptibility to memory interference and off-line gains in motor skill learning after practice in children, young, and older adults. Subjects performed a ballistic task (A) followed by an accuracy-tracking task (B) designed to disrupt the consolidation of A. Retention tests of A were performed immediately and 24 hours after B. Older adults showed greater susceptibility to memory interference and no off-line gains in motor skill learning. Performing B produced memory interference and reduced off-line gains only in the older group. However, older adults also showed deficits in memory consolidation independent of the interfering effects of B. Age-related declines in motor skill learning are not produced exclusively by deficits in the encoding of sensorimotor information during practice. Aging also increases the susceptibility to memory interference and reduces off-line gains in motor skill learning after practice.

1. Introduction

Motor skill learning is the process of improving the spatial and/or temporal accuracy of a motor skill through motor practice. Motor practice is essential for learning motor skills because it is during practice (online learning) that the nervous system encodes both perceptual and procedural information, which is later used for the elaboration of motor memories (Censor et al., 2012). However, the nervous system does not stop processing information with the end of practice. After practicing a motor skill (A), the information encoded during practice is progressively consolidated within the brain as a form of motor memory (McGaugh, 2000). If the consolidation process is successful, the motor memory trace encoded during practice of A becomes more robust, less susceptible to interference, leading to the retention of A or even to further improvements in skill performance between practice sessions without additional training (off-line learning) (Press et al., 2005). During the initial stages of the consolidation process, however, motor memories are still fragile and if, for example, a second motor task (B) is practiced soon after, behavioral interference may occur (Brashers-Krug et al., 1996), especially if both motor skills compete for the same neural circuitries (Lundbye-Jensen et al., 2011). When interference occurs, motor memories do not consolidate properly and the retention of previous learning (A) is compromised. Hence, learning successfully a new motor skill (A) depends not only on improving the encoding of perceptual and procedural information during practice but also on optimizing the consolidation of motor memory while avoiding motor memory interference (B) after practice (Brashers-Krug et al., 1996).

Although age-related differences in the ability to learn new motor skills vary substantially depending on the nature of motor task (Seidler, 2006), the effects that aging has on motor skill learning are well described (Janacsek et al., 2012; Smith et al., 2005; Voelcker-Rehage and Willimczik, 2006). Older adults tend to show either smaller improvements during motor practice or require extended periods of training to achieve skill levels comparable to those obtained by younger counterparts (Coats et al., 2013; Smith et al., 2005). Age-related differences in motor skill learning are usually explained by the developmental changes undergone by the structures and functions of the brain responsible for processing motor memories (Thomas et al., 2004). When the formation of a

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motor memory trace involves brain areas that are either still developing or affected by the aging process, ontogenetic differences in motor skill learning are likely to arise. In contrast, when the brain areas involved show an early maturation and/or resistance to change with the aging process, age-related differences in motor skill learning are less pronounced (Reber, 1993). Indeed, because variations in the structure and function of the brain determine individual differences in motor skill learning (Tomassini et al., 2011), it would be expected that age-related differences would be more pronounced when the formation of the memory involves brain areas susceptible to change with chronological age. However, it is unclear whether specific changes in the ability to either encode, consolidate, or retrieve motor memory emerge during a lifetime period in particular (Janacsek et al., 2012) and if the slowed ability to acquire motor skills in older adults results from deficits during the encoding of perceptual and procedural information during practice, from the consolidation of motor memories after practice, or from both.

The latter is possibly because most of the studies investigating mechanisms underlying age-related changes in motor skill learning have mainly focused on online learning processes involving the encoding of sensorimotor information during motor skill acquisition (Spirduso, 1975). In spite of the relevance that off-line learning mechanisms have to the formation of motor memory (Robertson et al., 2004), only a few studies have investigated whether changes in motor skill learning across the life span could be related to differences in the consolidation of motor memory (Brown et al., 2009; Dorfberger et al., 2007; Nemeth and Janacsek, 2011; Nemeth et al., 2010; Spencer et al., 2007). In general, the results of those investigations indicate that, compared with younger counterparts, older subjects tend to show either smaller (Nemeth and Janacsek, 2011; Nemeth et al., 2010) or no improvements in motor skill learning during consolidation (Brown et al., 2009; Spencer et al., 2007). It is interesting to note that when baseline differences are factorized into the analysis, in almost all the aforementioned studies the rate of motor skill acquisition between age groups during practice is fairly similar. This suggests that, rather than in the encoding of motor memory during motor skill practice, the deficits in motor skill learning commonly observed in older adults lie in the consolidation of motor memory and thus in the processes taking place after memory encoding, once the motor practice session has ended.

How do we measure motor memory consolidation? From a behavioral perspective, the effectiveness in which motor memories are consolidated is normally inferred from motor skill performance in a retention test performed at some point after acquisition (Kantak and Winstein, 2012). Similar or higher levels of performance at retention compared with acquisition indicate that the memory trace has undergone successful stabilization or off-line improvement, respectively (Robertson et al., 2004). A second, time-dependent, strategy that can be used to study the effects of aging on motor memory consolidation consists of using behavioral interference between tasks. Given the limited capacity of the brain to simultaneously consolidate a large number of memories (McGaugh, 2000), the introduction of a second motor task (B) immediately or soon after practicing a first motor skill (A) can be used to challenge the robustness of the memory trace encoded during practice of A. A pronounced decline in the performance of A in a retention test performed after B is indicative of an incomplete consolidation of the memory trace. In contrast, if the disruptive effects of B on the performance of A are less pronounced or absent, the memory trace of A is assumed to be consolidated (Brashers-Krug et al., 1996). If aging reduces the effectiveness of the consolidation process, it would be expected that older subjects would also show a greater susceptibility to motor memory interference. However, whether potential age-related deficits in motor memory consolidation are associated to a greater susceptibility to behavioral interference or these are 2 independent processes remains to be elucidated.

The study of the effects of chronological age on motor memory consolidation in general and interference in particular may improve the effectiveness of motor skill learning programs aimed at the acquisition of multiple motor skills in different age groups. It could be useful, for instance, to optimize rehabilitation programs of elderly subjects that need to regain mobility after a cerebrovascular accident such as a stroke. Unfortunately, little is known about the effects of chronological age on the susceptibility to motor memory interference (Stephan et al., 2009). The results of the only study which has specifically investigated age-related patterns in motor memory interference suggest that, certainly, aging could increase the likelihood of recently encoded motor memories being disrupted when a second motor skill is introduced during the first stages of the consolidation process (Dorfberger et al., 2007). However, because this study included only children and adolescents, it is unclear if this age-related pattern for motor memory interference continues to evolve in later life periods. To evaluate changes across the life span in the ability to consolidate motor memory, we investigated the effects of chronological age on the susceptibility to motor memory interference and the ability to obtain off-line gains in motor skill learning in children, young, and older adults. We hypothesized that, compared with children and young adults, older adults would be more prone to show motor memory interference and will display smaller off-line gains in motor skill learning.

2. Methods

2.1. Participants

Sixty-eight healthy subjects from 3 different age groups were recruited to participate in the study. Subjects were naïve to the 2 motor skills used in the experiments before enrollment. Furthermore, they were all right-handed according to their responses on the Edinburgh Handedness Questionnaire (Oldfield, 1971). General exclusion criteria for participation were: self-reported history of neurologic, psychiatric, or medical diseases as well as current intake of medications and/or recreational drugs affecting the central nervous system and/or the ability to learn. In addition, all subjects were specifically asked about noticeable memory impairments that could compromise their participation in the study. The age of the subjects had to be within these ranges: 8–14 years for children, 18–30 years for young adults, and $\geq$60 years for older adults. In addition to a control group including exclusively older subjects, the rest of the participants were allocated into 3 different age groups (children, young, and older adults). Two male and 1 female older subjects as well as 2 female children were excluded because they did not demonstrate learning during the performance of either one of the motor skills. In total, data of 63 subjects were included in the analysis (Table 1). The ethics committee for the Greater Copenhagen area approved the study and subjects, or parents in the case of children, provided written informed consent before participation. The study was performed in accordance with the declaration of Helsinki II.

Table 1
Characteristics of subjects included in the study

	Children	Young	Old	Control
N	17	17	17	12
Sex (M/F)	8/9	5/12	5/12	5/7
Mean age (SD)	11 (1.84)	23.12 (2.17)	69.12 (4.84)	68.24 (5.68)
Handedness score (SD)	92.5 (7.84)	84.5 (13.30)	91.87 (9.29)	92.92 (9.71)

Key: F, female; M, male; SD, standard deviation.