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Research report

Mentally represented motor actions in normal aging I. Age effects on the temporal features of overt and covert execution of actions

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Abstract

The present study examines the temporal features of overt and covert actions as a function of normal aging. In the first experiment, we tested three motor tasks (walking, sit–stand–sit, arm pointing) that did not imply any particular spatiotemporal constraints, and we compared the duration of their overt and covert execution in three different groups of age (mean ages: 22.5, 66.2 and 73.4 years). We found that the ability of generating motor images did not differentiate elderly subjects from young subjects. Precisely, regarding overt and covert durations, subjects presented similarities for the walking and pointing tasks and dissimilarities for the stand-sit-stand task. Furthermore, the timing variability of imagined movements was always greater compared to actual movements and was of the same amount in the three groups of age. In the second experiment, we investigated the effect of age (three groups with mean ages: 22, 64.8 and 73.2 years) upon temporal characteristics of covert and overt movements involving strong spatiotemporal constraints (speed/accuracy trade-off paradigm). During overt execution young and elderly subjects respected Fitts's law despite the fact that movement speed progressively decreased with age. Thus, while execution is deteriorated, the motor preparation process is still intact in old age, and follows well-known laws of biological motions. For covert execution, movement speed progressively decreased with age but elderly subjects did not respect Fitts's law. This suggests that the generation and control of motor intentions that consciously do not come to execution, particularly those concerning complex motor actions are progressively perturbed in the aging brain.

Keywords: Aging; Motor imagery; Motor prediction; Movement timing; Human; Locomotion; Sit–stand–sit; Arm movement

1. Introduction

The ability of generating mental images allows humans to carry out cognitive operations on static and moving objects or individuals whilst they are absent from their sensory-perceptual system. This top-down process within the central nervous system (CNS) has a considerable biological significance as it permits humans to recall past- and/or to predict and anticipate future-events and actions. Internal movement simulation, commonly termed as *motor imagery*, is a large part of this mental process and it can be defined as a mental state during which a subject replicates an action without any apparent motion of the limbs involved in the actual execution of the same action. Covert movement execution can be operated on simple and complex movements involving either isolated limbs or the whole body in interaction with the environment (see, for instance, motor tasks performed by athletes or musicians).

Several experimental investigations have been devoted to a description and an understanding of the similarities and dissimilarities existing at the neural and functional level, between executed and internally simulated motor actions.

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Today, most of the neuroscientists suggest that roughly the same neural network in the sensorimotor system is activated when a subject imagines or executes an action. For instance, brain's neuroimaging exploration provided evidences that similar neural structures, including the parietal and prefrontal cortices, the supplementary motor area, the premotor and primary motor cortices, the basal ganglia, the cerebellum, and for some motor tasks the spinal cord, are engaged during both movement execution and internal simulation (for a review see [11,15,21]). Specifically, this overlap has been reported for hand movements [25,31], finger-to-thumb movements [38], toe and tongue movements [14] as well as during walking [29]. It has also been shown that muscular force is enhanced by an 'imagined' training [39,51] and that autonomic activation is increased, compared to rest, when subjects imagine motor actions with large physical effort [8,9,33]. Interestingly, several studies showed that motor images of various motor tasks (arm pointing, writing and walking) preserve the same spatiotemporal characteristics and obey the same motor rules or biomechanical constraints as their actual counterparts [4,7,10,16,27,34–36].

These large neurocognitive similarities between overt and covert stages corroborated and validated the *simulation theory* developed by Jeannerod [19–21]. This theory postulates that covert actions are prepared motor actions, more explicitly, that internal simulation of different kinds of movements should engage their corresponding motor representations in the imaging brain, the only difference being that covert actions are not executed. However, while the simulation theory is confirmed for several motor tasks in young individuals, little information is available regarding its validity/relevance for normal aging. Can elderly people generate accurate motor images of their own actions? Is this ability function of the kind and difficulty of motor task being imagined? It is well known that normal aging influences cognitive functions [2,13,24,40,41] and sensorimotor control of actions [22,43,44]. The state of musculoskeletal system, in particular that of muscular mechanics and structure, is also modified [17,23,26,32,46,47,49]. At the neural level, clear differences emerge when comparing brain's activation between elderly and young people during the performance of motor or cognitive tasks. For instance, there are significant age-related differences in neural activity associated with repetitive movements of the hand [18]. For memory-related tasks (i.e. episodic memory, spatial working memory, etc.), in which old people perform less well than young people do, task-specific underactivation of localised brain regions are detected in elderly subjects. Intriguingly, when elderly and young people perform equally, a prominent bilateral activation emerges in old people. They engage more brain regions during the execution of the task [24,41].

In the current study, using the mental chronometry paradigm, we tried to assess the level of accuracy of motor action simulation as a function of normal aging. Two experiments were conducted. In the first experiment, we compared the temporal features of internal action simulation and execution according to age. In order to generalize our findings, this comparison was carried out in three different motor tasks (walking, sit–stand–sit and arm pointing) that did not imply any particular spatiotemporal constraints. In the second experiment, we investigated the effect of age upon temporal characteristics of covert and overt movements involving strong spatiotemporal constraints (speed/accuracy trade-off paradigm). According to the well-documented decline of sensorimotor and cognitive functions in old adults, we anticipated differences in both executed and simulated actions between elderly and young subjects. Besides, for the old adults, we expected a temporal discrepancy between overt and covert movement execution, in particular for motor tasks involving high spatiotemporal constraints.

2. Experiment 1

The aim of the first experiment was to examine the effects of normal aging on the temporal correspondence of overtly and covertly accomplished motor tasks. For this purpose, we selected from the subject's motor repertoire three movements that are regularly executed in every day life, i.e. walking, stand from – and sit on – a chair and pointing with the dominant arm. The accomplishing of these tasks involves different effectors and therefore it requires different motor strategies from the subjects. By choosing various motor tasks we wanted to enlarge our findings, especially those concerning the temporal features of covert movement execution in elderly people. Since muscular mechanics, sensorimotor control and especially cognitive functions are altered with age, on could expect to find significant differences between young and elderly people, in particular for the timing features of simulated actions.

2.1. Methods

2.1.1. Participants

We tested 24 (12 of whom were females), right-handed (Edinburgh Inventory of handedness), volunteered subjects. They were divided into three age groups: (i) young (4 male and 4 female), aged between 19 and 23 years (mean age: 22.5 ± 1.4 years), (ii) elderly I (4 male and 4 female), aged between 64 and 68 years (mean age: 66.2 ± 1.6 years), (iii) elderly II (4 male and 4 female), aged between 72 and 75 years (mean age: 73.4 ± 1.3 years). All subjects were in good health, with normal or corrected for normal vision and did not present any nervous, muscular or cognitive disorder. The elderly subjects were all retired, having a regular physical activity (~1.5 h 2 days per week) and a daily cognitive activity (reading newspapers or literature). Cognitive evaluation of elderly subjects has been made using the *mini mental state examination* test (mean score = 28.4 ± 0.9). The young subjects were students from the University of Burgundy. None of the 24 subjects was informed of the aim of the experiment or had explicit knowledge concerning motor imagery processes. The experiment was carried out in agreement with legal requirements and international norms. A local ethics committee approved the experimental protocol.

2.1.2. Experimental protocol

The whole experiment took place in a large room (25 m × 20 m × 10 m). All subjects executed (overt movement) and imagined themselves executing (covert movement) three motor tasks: (i) *walking task*, walking for a distance of 8 m, (ii) *sit–stand–sit task*, stand up from a chair and, immediately after achieving the upright standing position, sit down again and (iii) *pointing task*, pointing with their right-dominant arm between two targets.

The walking task: A black line drawn on the ground indicated the length of the locomotor path. Subjects, standing upright, were asked to walk or to imagine walking along the specified path at a natural self-selected speed. During the imagined trials, the subjects stood also upright with their eyes open.

The sit–stand–sit task: Subjects were seated on an armless chair placed at knee height and they kept their arms folded across the chest. A back support on the chair was used to set their trunk in the vertical position while their feet were placed flat, 10 cm apart at the heels, with the shanks positioned in 10° flexion relative to the vertical. The subjects were asked to perform or to imagine performing the sit–stand–sit task at a natural speed. For the overt execution, we emphasized, especially to the elderly subjects, that they had to maintain their equilibrium. One trial consisted of three repetitive sit–stand–sit movements. During the imagined trials, subjects were seated on the chair with their eyes open and they adopted exactly the same posture as during the actual trials.

The pointing task: Subjects were comfortably seated on a chair in front of a table. In the middle of the table, a block of sheets (A4 format) was placed aligned with the subject's chest in a distance of 20 cm. Each sheet was composed from vertical and horizontal lines drawn every 1 mm. On the middle of each sheet, two targets were printed (black squares 2 cm × 2 cm, inter-target distance 20 cm). The subjects, holding a pencil in their right-dominant hand, were asked to point (the direction of the movement was in the fronto-parallel plane) or to imagine themselves pointing between the targets very accurately at a natural self-selected speed. Overt and covert trials started either from the right (half of the trials) or from the left target. Before each overt trial, the subjects placed the pencil in the center of one of the targets indicated by the experimenter and then they executed the movement. During the imagined trials, the subjects were seated on the chair with their eyes open, they positioned the pencil on the center of the target indicated by the experimenter and then they imagined the movement. The subjects were free to start the movement, overt or covert, when they felt ready. One actual or imagined trial consisted of five cyclical pointing movements between the targets, namely of 10 arm movements. We informed subjects that only one target missing was tolerated per trial and that if they missed more than one target the trial must be performed again. Each trial was accomplished in a separate sheet. For each overt trial, we measured the spatial precision of the pointing movements.

Before the experiment, all subjects actually performed three times each motor task in order to familiarize themselves with the experimental protocol. We gave particular attention to the instructions concerning the mental simulation of the motor tasks. Subjects were asked to feel themselves executing the task (motor or internal imagery) rather than watching themselves performing it (visual or external imagery). All subjects, after four to six mental trials in each motor task, reported being able to generate precise motor images. During the experiment, subjects performed 10 overt and 10 covert trials for each motor task, namely 60 trials. The 60 trials were pseudo-randomly presented to the subjects. The whole protocol lasted ~20 min per subject. A rest period of around 1 m was introduced after each cycle of 12 consecutive trials, in order to prevent physical or mental fatigue.

2.1.3. Data and statistical analysis

For the three motor tasks, the duration of both overt and covert movements was recorded by means of an electronic stopwatch (temporal resolution 1 ms) that the subjects held in their left hand. They started the stopwatch when they actually or mentally initiated the task and they stopped it immediately after they had actually or mentally accomplished it. No subject reported difficulties in measuring the duration of his (her) overt or covert movements.

For each participant, the mean duration and its standard deviation were calculated over all trials for the three motor tasks. The variability of the overt or covert execution was indexed by computing the coefficient of variation (CV) defined as the standard deviation divided by the mean duration and multiplied by 100. The CV provided a relative quantification of the movement duration variability. We checked that all variables were normally distributed (Kolmogorov–Smirnoff test) and that their variance was equivalent (Levene test).

We performed a between group repeated-measures analysis of variance (ANOVA) for each motor task (walking, sit–stand–sit, pointing). The factors included in the ANOVA were Group (young, elderly I, elderly II) and Movement condition (overt or covert). Post hoc differences were assessed by means of Scheffé tests. The software package Statistica® was used.

2.2. Results

2.2.1. Temporal features of overt and covert movements

All subjects found the three motor tasks natural to perform. However, they reported that simulating movements mentally required high levels of concentration. Fig. 1 displays the average values (±S.D.) of overt and covert movement durations; motor tasks and groups are depicted separately.

In the *walking* task, simulated and executed movement durations were very similar among the three groups of age. The average movement duration was 6.56 ± 0.84 s for the overt ($n = 240$) and 6.59 ± 0.86 s for the covert ($n = 240$) movements. The ANOVA analysis confirmed that Group ($F_{2,21} = 0.44$, $p = 0.65$), Movement condition ($F_{1,21} = 0.32$, $p = 0.85$) and their interaction ($F_{2,21} = 2.73$, $p = 0.12$) did not reach significance.

For the *sit–stand–sit* task, significant differences between durations of overt and covert movements were revealed ($F_{1,21} = 32.98$, $p < 0.0001$). For all the participants, but two subjects from the group elderly I, durations of covert movements (on average 5.82 ± 0.83 s, $n = 240$) were shorter than those of overt movements (on average 6.34 ± 0.79 s, $n = 240$). However, the amount of this discrepancy was similar for all groups. Indeed, the main effect of Group ($F_{2,21} = 0.31$, $p = 0.74$) and the interaction between Group and Movement conditions ($F_{2,21} = 1.53$, $p = 0.24$) did not show significant effects.

For the *pointing* task, the subjects respected the instructions given to them, in particular the requirement concerning the spatial accuracy of the arm movements. Hence, considering all pointing movements toward the targets ($n = 2400$,

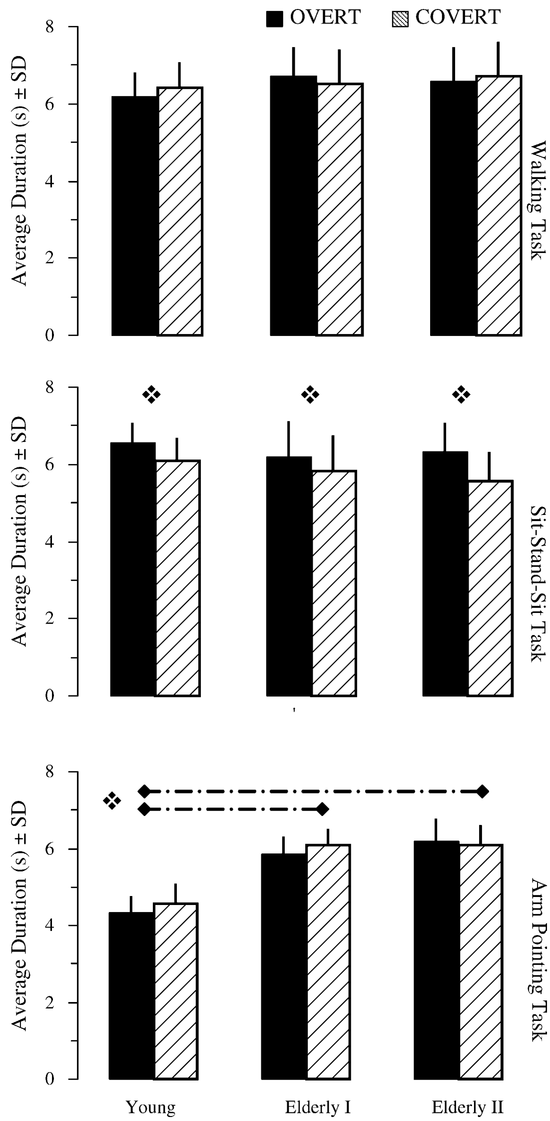

Fig. 1. Histograms showing for the three groups of age the average durations (±S.D.) of overt and covert movements for the walking, sit–stand–sit and pointing tasks. Significant differences ($^{*}p < 0.01$).

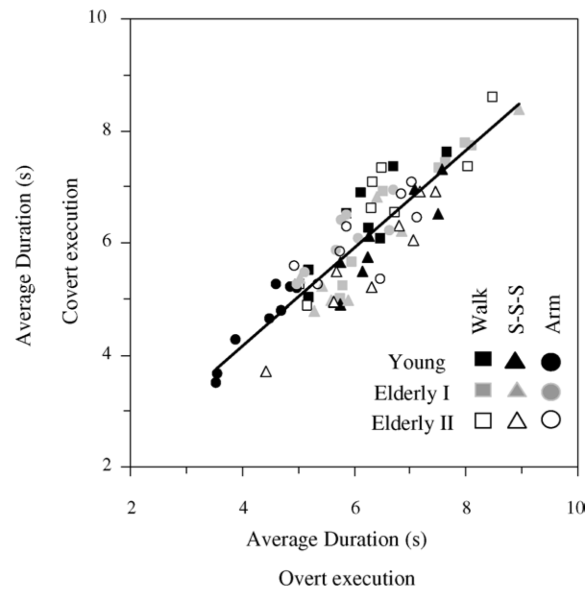

Fig. 2. Average durations of the overt movements are plotted vs. the average durations of the corresponding covert movements for the three motor tasks. Each point is the average of 10 repetitions for each subject. The dark line corresponds to the best fit line ($y = 0.8718x + 0.6747$).

i.e. 24 subjects × 10 trials × 10 movements within each trial) very few targets were missed, and never more than one target per trial. A between-group ANOVA analysis gave no significant effect ($F_{2,21} = 1.02$, $p = 0.28$). More precisely, the young group missed eight times the targets (1%), the *elderly I* group missed them 11 times (1.4%), and the *elderly II* group missed them 10 times (1.3%). Despite this spatial precision, a clear difference was observed between the young and the two elderly groups for both overt and covert durations (group effect, $F_{2,21} = 17.12$, $p < 0.0001$). Specifically, young subjects pointed significantly faster than elderly subjects (young versus elderly I: $p < 0.001$; young versus elderly II: $p < 0.001$). Nevertheless, the temporal similarities between actual (on average 4.60 ± 0.86 s) and imagined (on average 4.77 ± 0.78 s) movements were preserved with age ($F_{1,21} = 1.99$, $p = 0.47$). The interaction between Group and Movement condition did not reach significance ($F_{2,21} = 1.55$, $p = 0.20$).

The previous results are further illustrated in Fig. 2. Average durations of overt movements are plotted versus the average durations of covert movements for each subject individually; groups and motor tasks are shown separately. Notably, it can be observed that durations of actual movements are greater compared to those of imagined movements during the sit–stand–sit task (triangles). Furthermore, pointing movements of young subjects (black circles) are faster compared to those of the elderly subjects and for the walking and pointing tasks, overt and covert durations are almost similar for most of the subjects (respectively squares and circles). Considering all data points ($n = 72$), the correlation coefficient between overt and covert movements was high ($r = 0.90$, $p < 0.0001$).

2.2.2. *Temporal variability differed between overt and covert movements*

Fig. 3 shows, for the different experimental conditions, the average values of intra-subject temporal variability evaluated using the coefficient of variability (CV). Regardless of age or motor task, the CV was greater for the covert (on average 9.07 ± 0.76%, $n = 720$) than for the overt (on average 5.48 ± 0.59%, $n = 720$) execution. The ANOVA analysis confirmed this observation, revealing a significant effect of movement execution for the walking ($F_{1,21} = 95.45$, $p < 0.0001$), the sit–stand–sit ($F_{1,21} = 18.01$, $p < 0.001$) and the pointing ($F_{1,21} = 8.06$, $p < 0.01$) tasks. No other effect was significant ($p > 0.2$).

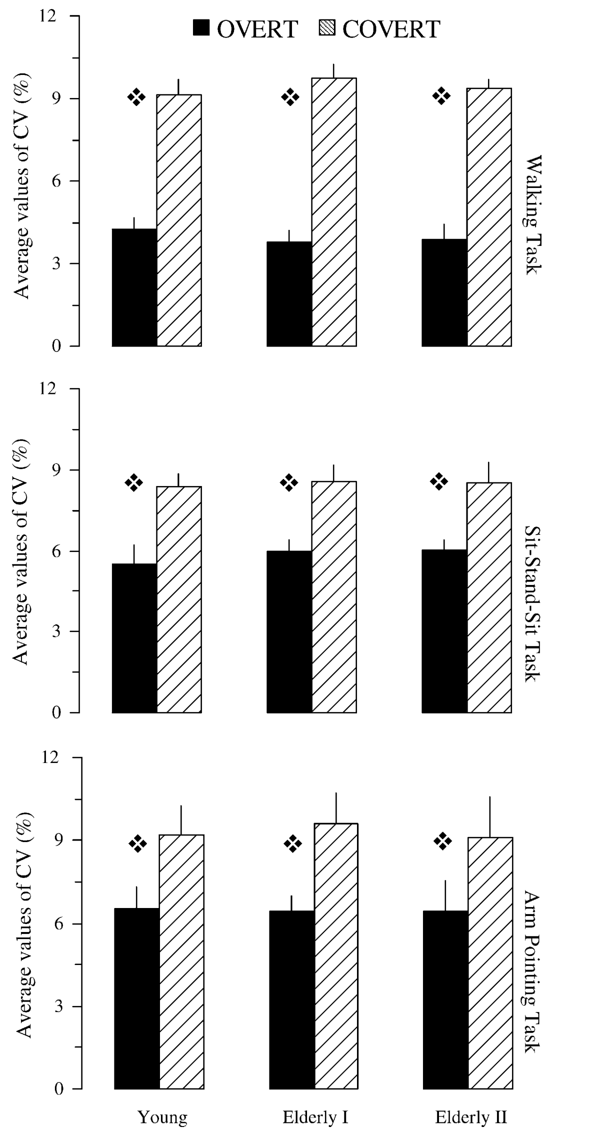

Fig. 3. Average values (±S.D.) of the coefficient of variation (CV) representing for the three groups of age and the three motor tasks the timing variability of overt and covert movement execution. Significant differences ($^*p < 0.01$).

These results are further illustrated in Fig. 4. Average CV values of overt movements are plotted versus the average CV values of covert movements for each subject individually; age groups and motor tasks are depicted separately. It can be observed that CV values of imagined movements are greater than those of actual movements for most of the subjects in the three motor tasks. Considering all data points ($n = 72$), the correlation coefficient between overt and covert movements was very low ($r = -0.009$, $p = 0.94$).

3. Experiment 2

The results of the first experiment showed that the ability of generating motor images did not differentiate elderly subjects from young subjects. Elderly subjects performed similarly to young subjects with regard to the matching between actual and imagined movement duration, displaying *timing similarities* for the walking and pointing tasks and *timing dissimilarities* for the stand-sit-stand task. Furthermore, the timing variability of imagined movements was always greater compared to actual movements and was of the same amount in the three groups of age.

However, it is worth pointing out that, in the present experiment, the motor tasks involved did not require high spatiotemporal control for their achievement. We can wonder whether an effect of normal aging on mentally executed motor actions could not appear if motor tasks imposing high spatiotemporal constraints were involved. Fast arm movement execution combined with end-point precision requires high levels of sensorimotor control and attention, and therefore it is very demanding, in particular for elderly people. Internal movement simulation may accentuate the cognitive demands of the task, in particular in old adults, since sensory information about movement, that could be use for movement regulation, is lacking.

The next experiment investigated whether age could affect mentally executed actions requiring a progressive difficulty in the control of spatiotemporal movement parameters. In this second experiment, subjects were requested to perform a motor task implying a speed/accuracy trade off (Fitts's law paradigm). In order to prevent elderly people from any physical risk due to increasing task constraints, especially the loss of equilibrium, all subjects performed exclusively pointing movements with their right-dominant arm.

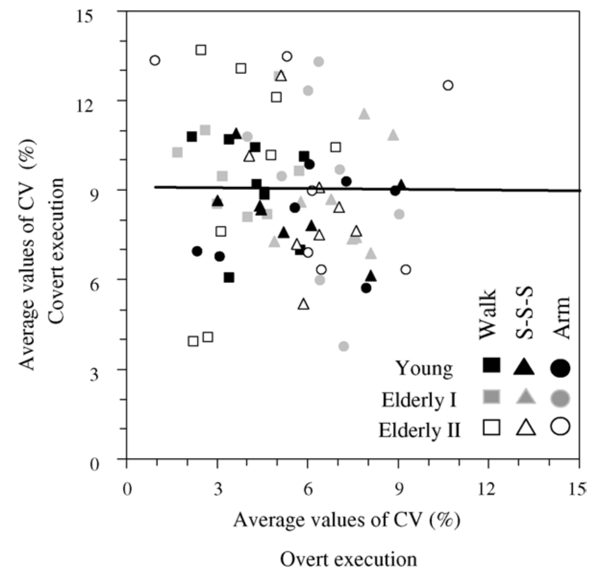

Fig. 4. Average values of the coefficient of variation (CV) of the overt movements are plotted vs. the average values of CV of the corresponding covert movements for the three motor tasks. Each point is the average of 10 repetitions for each subject. The dark line corresponds to the best fit line ($y = -0.0087x + 9.116$).

3.1. Methods

3.1.1. Participants

The second experiment involved 24 volunteers who were divided into three age groups: (i) young (4 male and 4 female), aged between 19 and 25 years (mean age: 22 ± 1.9 years), (ii) elderly I (3 male and 5 female), aged between 62 and 67 years (mean age: 64.8 ± 2 years), (iii) elderly II (3 male and 5 female), aged between 71 and 75 years (mean age: 73.2 ± 1.7 years). None of them participated in the first experiment. All subjects were in good health, right-handed (Edinburgh Inventory of handedness) with normal or corrected for normal vision and without any nervous, muscular or cognitive disorders. The young subjects were students from the University of Burgundy. The elderly subjects were all retired, having a regular physical activity (∼1.5 h 2 days per week) and a daily cognitive activity (reading newspapers or literature). Cognitive evaluation of elderly subjects have been made using the *mini mental state examination* test (mean score = 28.6 ± 0.7). None of the subjects was informed of the aim of the experiment or had explicit knowledge concerning motor imagery processes.

3.1.2. Experimental protocol

A local ethics committee approved the experimental protocol which was carried out in agreement with legal requirements and international norms. The experimental procedure was strictly similar to that of the pointing task of the first experiment. The only difference was that, in the second experiment, we used four different sizes of targets (squares 0.5 cm × 0.5 cm, 1 cm × 1 cm, 1.5 cm × 1.5 cm, 2 cm × 2 cm). For each trial, only one pair of targets (the two targets had always the same size) was presented to the subjects who had to point or to imagine themselves pointing between them very accurately and as fast as possible while holding a pencil in their right-dominant hand. According to the Fitts's law, the changing target's width (*W*: 0.5, 1, 1.5, 2 cm) and the fixed inter-target distance (*A*: 20 cm) lead to four indices of difficulty [$ID = \log_2(2A/W)$]: respectively 6.3, 5.3, 4.7 and 4.3. Overt and covert trials started either from the right (half of the trials) or from the left target. Before each overt or covert trial, the subjects placed the pencil in the center of one of the targets indicated by the experimenter and then they actually performed or imagined the movement. The subjects were free to start the movement, overt or covert, when they felt ready. One actual or imagined trial consisted of five cyclical pointing movements between the targets, namely of 10 arm movements. Subjects were informed that only two target missings were permitted per trial and that if they missed more than two targets the trial must be performed again. Each trial was accomplished in a separate sheet. For each overt trial, we measured the spatial precision of the pointing movements.

As for the first experiment, all subjects practiced three times with each pair of targets before the experiment started. For the imagined trials, we emphasized to them that they must feel themselves executing the task (motor or internal imagery) rather than watching themselves performing it (visual or external imagery). All subjects were able to generate motor images after having practised four to six times with each pair of targets. During the protocol, all subjects performed 10 overt and 10 covert trials for each target's size, namely 80 trials, the overt trials first (40) and, after a time interval of 5 m, the covert trials (40). Within overt or covert trials, target's sizes were pseudo-randomly presented to the subjects. The whole protocol lasted ∼30 min per subject. When the subject performed 10 consecutive trials, he (she) rested for ∼1 min in order to prevent physical or mental fatigue.

3.1.3. Data and statistical analysis

The duration of overt and covert pointing movements was recorded by means of an electronic stopwatch (temporal resolution 1 ms), that the subjects held in their left hand. The subjects started the stopwatch when they actually or mentally initiated the task and they stopped it when they had actually or mentally accomplished it. For each subject, the mean duration and its standard deviation were calculated over all trials. We checked that all variables were normally distributed (Kolmogorov–Smirnoff test) and that their variance was equivalent (Levene test). We performed a between group repeated-measures analysis of variance (ANOVA), with Group (young, elderly I, elderly II) as a between-subject factor, Size of the target (5, 10, 15, 20 mm), and Movement condition (overt or covert) as within-subject factors. Post hoc differences were assessed by means of Scheffé tests. We also calculated linear regression equations for each subject separately: (a) between movement durations (imagined or actual) and index of difficulty, (b) between actual and imagined movements (all targets' width intermingled). Statistical analysis (*t*-tests, both for independent and dependent samples) was performed on both correlation coefficients and slopes of regression equations. The software package Statistica® was used.

3.2. Results

All subjects found the overt and covert performance of the motor task challenging and none of them, especially elderly people, experienced any physical or mental fatigue during the protocol. Considering all pointing movements ($n = 9600$; 24 subjects × 4 target size's × 10 trials × 10 movements within each trial) very few targets were missed. A very small number of trials was repeated due to the fact that one subject missed more than twice the targets per trial, respectively, 4, 7, 8 trials for the young, elderly I and elderly II groups. Regarding the total number of pointing movements, the *young* group missed 49 times the targets ($n = 3200$; on average 1.6%), the *elderly I* group missed them 56 times ($n = 3200$; on average 1.8%), and the *elderly II* group missed them 59 times ($n = 3200$; on average 1.9%). A between-group ANOVA analysis gave no significant effect ($F_{2,21} = 0.14$, $p = 0.26$).

Fig. 5 displays the average values (±S.D.) of overt and covert movement durations for the four pair of targets and the three age groups. The ANOVA analysis (3

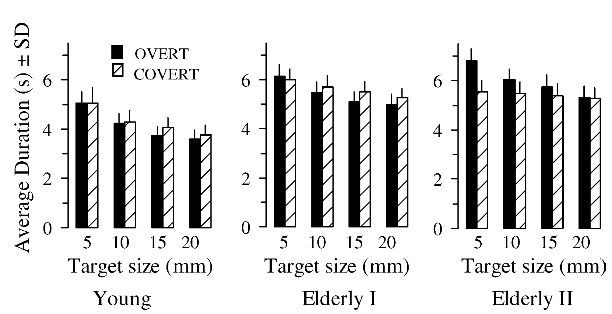

Fig. 5. Histograms showing for the three groups of age the average durations (±S.D.) of overt and covert movements as a function of target's size.

Groups × 4 Target's sizes × 2 Movement conditions) showed several main and interaction effects. We observed significant main effects for Group ($F_{2,21} = 12.06$, $p < 0.001$) and Size of target ($F_{3,63} = 89.02$, $p < 0.0001$). The post hoc analyses revealed a significant difference ($p < 0.001$) between the young (on average 4.21 ± 0.85 s) and the two elderly groups (on average 5.54 ± 0.81 s for the elderly I and 5.70 ± 0.86 s for the elderly II), but not between the two elderly groups ($p = 0.88$). Besides, movement durations progressively decreased when target's sizes gradually increased ($p < 0.001$; on average 5.77 ± 1.02, 5.21 ± 0.97, 4.93 ± 1.00 and 4.69 ± 0.99 s for the targets of 0.5, 1, 1.5 and 2 cm, respectively). Conversely, we did not find a main effect of Movement execution ($F_{1,2} = 0.38$, $p = 0.54$; on average 5.18 ± 1.01 and 5.12 ± 0.98 for the overt and covert movements, respectively).

The two-way interactions showed a significant effect between Group and Movement execution ($F_{2,21} = 7.57$, $p < 0.001$). The post hoc analysis revealed a significant difference between overt and covert movement durations only for the elderly group II ($p < 0.05$). There was also a significant two-way interaction between Group and Size of target ($F_{6,63} = 2.84$, $p < 0.02$). For the young group, movement duration significantly increased when target's size decreased ($p < 0.05$), while for the two elderly groups, such effects were found only when comparing the target of 0.5 cm with the targets of 1.5 and 2 cm ($p < 0.05$).

The ANOVA analysis also revealed a significant interaction between the three factors ($F_{6,63} = 4.96$, $p < 0.001$). Post hoc comparisons showed that overt movement durations progressively increased when target's size gradually decreased. For the young and the elderly II groups, all comparisons between targets were significant ($p < 0.05$). For the elderly group I, significant differences were found for all the comparisons ($p < 0.05$), except when comparing the targets 1.5 and 2 cm ($p = 0.65$). Interestingly, we did not find such a strong relationship between movement durations and target's size for the imagined movements. Precisely, the subjects of the elderly group II did not modulate the durations of simulated movements according to target's size ($p > 0.5$). For the elderly group I, significant differences in durations of simulated movements were found when comparing the target of 0.5 cm with all the others ($p < 0.05$) and the target of 1 cm with the target of 2 cm ($p < 0.05$). However, for the young group, all the durations of simulated movements were significantly modulated by target's size ($p < 0.05$). Table 1 depicts linear regression equations for the three groups and the overt and overt movements. It is noticeable that all groups presented a strong correlation between actual movement duration and index of difficulty, namely movement duration increased linearly as index of difficult increased. For the imagined movements, the same strong correlation was observed for the young group and the elderly group I, but not for the elderly group II. The comparison of r-values between overt and covert movements showed a significant difference only for the elderly group II ($t = 2.67$; $p < 0.05$). The comparison of r-values between groups revealed a significant difference between the elderly group II and the two other groups for the imagined movements only ($t = 2.69$ and 2.38, $p < 0.05$; for the comparisons with the young and the elderly I groups, respectively).

At least, we compared the actual and imagined movement durations for each target size separately. For the young and for the elderly I groups, we did not find any significant differences ($p > 0.1$). For the elderly group II, significant differences emerged for the 0.5 and 1 cm target sizes ($p < 0.001$) but not for the two others ($p > 0.1$). These results are illustrated in Fig. 6. Average durations of overt movements are plotted versus the average durations of covert movements for each subject individually. Overt and covert movement durations of young subjects (black spheres) were smaller than those of the two elderly groups. Furthermore, for the young and elderly I groups, overt and covert durations were almost similar for the majority of subjects (respectively black and grey spheres).

Table 1
Linear regression equations calculated between average movement durations and index of difficulty for the three groups of age and the actual and imagined movements separately

Group	Execution	Linear regression	R^2
Young	Overt	$y = 0.7551x + 0.2465$	0.99*
	Covert	$y = 0.6393x + 0.9854$	0.99*
Elderly I	Overt	$y = 0.5930x + 2.3578$	0.98*
	Covert	$y = 0.3442x + 3.8429$	0.98*
Elderly II	Overt	$y = 0.7136x + 2.2799$	0.99*
	Covert	$y = 0.1310x + 4.744$	0.89

* Significant correlation ($p < 0.01$).

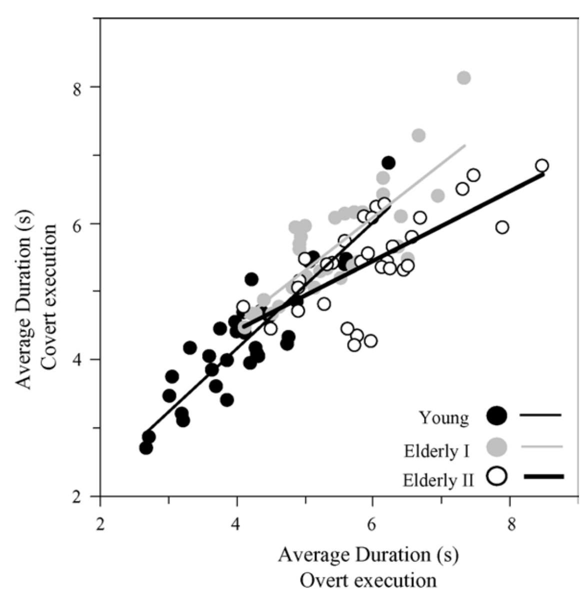

Fig. 6. Average durations of the overt movements are plotted vs. the average duration of the corresponding covert movements for the four target's size. Each point is the average of 10 repetitions for each subject. The lines correspond to the best fit lines: young ($y = 0.9289x + 0.4602$); elderly I ($y = 0.7817x + 1.402$); elderly II ($y = 0.5105x + 2.392$).

Considering the data points of the young ($n = 32$) and elderly I ($n = 32$) groups, the correlation coefficient between overt and covert movements was high, respectively $r = 0.90$, $p < 0.0001$ and $r = 0.82$, $p < 0.001$. For the elderly group II, a clear difference between overt and covert movement duration was observed (white spheres). Considering the data points of this group ($n = 32$), the correlation coefficient between overt and covert movements was lower ($r = 0.63$, $p < 0.001$) than those found in the other age groups. A t-test analysis showed that the slopes of the regression lines describing the relationship between movement duration and item difficulty in young and elderly II groups were significantly different between them ($t = 5.13$, $p < 0.01$).

4. Discussion

In the present study, we explored the temporal features of executed and internally simulated motor actions in young and elderly adults. We mainly found that, for various motor tasks which did not impose high spatiotemporal constraints, elderly subjects showed similar capacities of generating motor images as young subjects. Conversely, when the spatiotemporal constraints of the motor task increased, the generation and manipulation of motor images was perturbed in elderly but not in young subjects.

4.1. Young and elderly subjects presented similar behaviour regarding overt and covert execution of relatively simple motor actions

Normal aging did not affect the ability of internally simulating motor actions whose successful execution does not require high spatiotemporal planning and control. Indeed, old adults showed the same performance as young adults regarding the matching between actual and imagined movement durations, that is, temporal similarities for the walking and pointing tasks and temporal dissimilarities for the stand-sit-stand task. These results are appealing and suggest that motor intentions, executed or simulated, are comparable in young and elderly individuals. High temporal correspondence between overt and covert execution in elderly subjects constitutes a novel result, which expands the well-documented idea, up to now established in young individuals, of a similar cognitive substrate between overt and covert movement execution [4,7,10,16,27,34–36].

However, peculiar is the finding concerned with the temporal differences between executed and imagined movements during the stand-sit-stand task in both old and young adults. Generally, young and elderly subjects actually execute the sit-to-stand phase faster than the stand-to-sit phase [30,37]. This is most likely due to the lack of visual information for the control of the backward motion during stand-to-sit. Consequently, the temporal underestimation of the motor task during internal simulation may be explained by the fact that subjects, during motor imagery, do not need to visually control the stand-to-sit phase, since movement does not occur, and as a consequence they reduce the duration of this phase and thus the duration of the whole movement. It must be noted that temporal dissimilarities between actual and imagined movements has been already observed in both young [3,7,27] and elderly people [42]. However, further studies are certainly needed to determine the functional significance of this temporal dissociation.

Temporal variability of actual and imagined movements gives also valuable information concerning the motor imagery process in elderly people. Specifically, variability of imagined movements was greater compared to actual movements for the three motor tasks, whatever the age of the participants. Greater variability for simulated movements has also been reported in previous studies carried out in young individuals [4,35]. However, the replication of the same effect in elderly subjects is novel and further reinforces the idea of similar behaviour of elderly and young people during actual and imagined movement execution. We have previously proposed that the increased variability in the imagined movement is due to the absence of the peripheral feedback normally generated during the overt execution [4,35]. The lacking of sensory information about movement during covert execution prevents subjects from verifying whether the simulated movement is similar to its actual counterpart.

Thus, elderly, like young subjects, can simulate a specific movement throughout the motor imagery process in all its spatiotemporal aspects. That, in turn, may put forward the idea that motor prediction, more precisely the spatiotemporal and sensory anticipation of motor commands, is preserved through aging, at least for relatively simple movements. Motor prediction can be considered on the basis of the concept of internal models [12,28,50]. This concept stipulates that specialized neural networks would relate motor commands to sensory signals of body motion (forward models), and desired movements to appropriate motor commands (inverse model). Accordingly, during internal movement simulation, accurate timing information for the replicated movement would be provided by the forward model, which predicts the timing features and the sensory consequences of the movement on the basis of the correctly prepared (inverse model) but blocked motor commands [4,16,34–36].

4.2. Dissimilarities between young and elderly subjects during overt and covert execution of arm movements requiring high spatiotemporal control

In the second experiment, the increasing spatiotemporal constraints of the pointing task induced significant variations in temporal features of simulated and executed movements in elderly subjects. Generally, duration of overt and covert arm pointing movements progressively increased, and therefore movement speed progressively decreased, as a function of age.

4.2.1. Overt movement execution

The age-related decrease in movement speed during actual movement execution could initially be attributed to biomechanical factors. It is well known that aging affects human skeletal muscle structure, which, in turn, may influence muscle contraction properties in elderly people [32,46,47]. This sarcopenia, associated to neural factors, notably to the reduction in motor unit activation capacity [17,49] and to the coactivation of antagonist muscles [23,43], may account for the loss of muscle strength and power in elderly people. However, these structural and neural factors alone cannot fully explain the decline of movement speed which accompanies normal aging. Additional factors related to central mechanisms operating during visuomotor information processing may also be responsible for the reduction of movement speed in old age. For instance, age-related declines in the speed of processing of visual stimuli in simple perception tasks have been reported in the literature [2]. In addition, a progressive slowing of arm movement speed according to task complexity has also been observed for older compared to young adults [22,44]. Finally, during aging, a decline in several aspects of proprioceptive sensitivity occurs [48] which certainly influences movement control.

Although it seems that, apart peripheral, central mechanisms also are actively involved in the weakening of movement execution with age, we estimate that these central operations do not concern action planning, that is the recall of well-known laws of biological motions. For instance, it is of interest that whatever the differences in arm movement velocity between young and old adults, the accomplishment of pointing task obeyed Fitts's law. Ketcham et al. [22], comparing arm movement kinematics between elderly and young subjects in a Fitts's law task, found that older and young adults' motor performance was affected differently by task constraints. They proposed that movement slowing in older subjects is a consequence of multiple factors affecting the execution but not the central planning process.

4.2.2. Covert movement execution

Yet, the most salient finding in the second experiment was that covert arm movements were more influenced by aging than overt movements were. The general observation that durations of imagined arm movements were longer in old compared to young adults suggests that cognitive mechanisms, responsible for the mental representation of motor actions, decline with age. Specific age-effects have also been reported in previous investigations for the generation and manipulation of mental images. In general, older adults are slower in mental rotation of visual stimuli and experienced progressively greater slowing as a function of the angle of rotation [13]. At the level of neural processes, the overall loss of neural connectivity or decreased levels of neurotransmitters in the aging brain are potential causes for proportional slowing of basic processing steps.

An additional appealing observation was that internal movement simulation in elderly adults did not respect the Fitts's law. In elderly I group (mean age 64.8 years) durations of simulated movements generally increased when target's size reduced; however, this phenomenon was not completely comparable with that observed in young group, for which duration was progressively modulated by each target's size. Surprisingly, elderly subjects of group II (mean age 73.2 years) internally simulated arm movements with similar durations whatever the size of the targets.

These findings point out that during motor imagery of fine arm movements, elderly people do not accurately integrate task constraints (for the current study, the combination of movement speed and precision), which may suggest that motor prediction process progressively declines with aging. However, this age-related deterioration of internal movement simulation is dependent on the complexity of the motor task, since elderly subjects presented similar durations for imagined and actual arm movements when the spatiotemporal constraints of the motor task were not important (see Section 2).

Several hypotheses could be proposed to account for the present findings. One could relate age-specific effects on internal action simulation to the way that forward models operate for the prediction of motor actions, when no overt movement accompanies this prediction. Intentions to move and therefore generation of predictions of the upcoming movements involve the activation of the parietal cortex [1,45]. Our results are congruent with previous studies which demonstrated a significant decline of imagined but not of actually executed movements in patients with parietal lobe damage. For instance, patients with left parietal lesions that extended into the inferior parietal lobule modulated the duration of executed arm movements with target's size (Fitts's law paradigm), however, they were not able to modulate in the same way the durations of simulated movements [45]. Comparable results were also obtained in a patient with a right temporoparietal lesion presenting visual neglect [5] and in patients with schizophrenia [6]. The alteration of the temporal processing of imagined actions in elderly adults might suggest a progressive decline on the generation and control of intended but not executed actions in the aging parietal cortex.

On the other hand, one cannot attribute age-specific effects on internal movement simulation to a default in motor prediction process only. Motor imagery is a cognitive process during which the brain, retrieving information from long term memory, monitors intentions and actions plans but consciously retains them from overt execution. This necessitates a high temporal organisation of the sequences of simulated actions, i.e. triggering and retention, which highly requires subject's attention and further loads their working memory. This must be particularly true in elderly adults and in the case of complex motor actions. As working memory and attentional control decline in the aging brain [2,24,41], motor imagination of an action could be specifically deteriorated in elderly people. At the neural level, the frontal and prefrontal cortices, that play an important role on working memory and on timing of motor and cognitive events, are activated during both movement execution and imagination [11,21]. Interestingly, during memory-related cognitive tasks, elderly people under-recruit and non-selectively recruit these brain regions, which may explain why internal movement simulation is altered in elderly adults [24,41]. In a mental rotation visual task, Briggs et al. [2] proposed that age-related slowing of information processing and accuracy were mediated by a decline in working memory but not by a decrease of sensorimotor speed. In a complementary study [40], the authors reported evidences that reduction in the volume of dorsolateral prefrontal cortex mediated age-related decline in performance on mental imagery tasks.

It remains of great interest, however, that elderly people during actual movement execution preserve their capacity of preparing arm movements that respect laws of biological motion, such as Fitts's law, while they loose this capacity when they internally simulate the same motor actions. These dissimilarities may be related to the fact that sensory information from the periphery is not available to the motor system during internal movement simulation. This prevents subjects from verifying whether the simulated movement is similar to its actual counterpart and therefore it precludes the calibration of simulated actions on the basis of sensorimotor information provided from their actual execution. On the contrary, when elderly subjects actually execute a movement, they take advantage, perhaps more than young adults do, from the peripheral sensory feedback in order to control the movement and to better prepare the same action in the future by recalling precise information from their long term motor memory.

As a conclusion, we propose that some aspects of action representations, such as intentions to move or motor predictions, become progressively fragile with age, therefore allocating to sensory feedback a more important role for movement execution and control. This proposition must be further explored because it may help to understand why efficient control of equilibrium and movement decreases with age, and may suggest novel tools for neurological and motor rehabilitation.

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