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## Note

# Decline in motor prediction in elderly subjects: Right versus left arm differences in mentally simulated motor actions

Xanthi Skoura<sup>a</sup>, Pascaline Personnier<sup>b</sup>, Annie Vinter<sup>a</sup>,  
Thierry Pozzo<sup>b</sup> and Charalambos Papaxanthis<sup>b,\*</sup>

<sup>a</sup>Laboratoire d'Etude de l'apprentissage et du développement (LEAD), CNRS, UMR 5022, Université de Bourgogne, Dijon, France

<sup>b</sup>Motricité et Plasticité, INSERM U 887, Université de Bourgogne, Campus Universitaire, BP 27877, 21078 Dijon, France

### ARTICLE INFO

#### Article history:

Received 24 October 2006

Reviewed 4 January 2007

Revised 16 April 2007

Accepted 16 July 2007

Action editor David Carey

Published online 27 December 2007

#### Keywords:

Aging

Human

Motor imagery

Motor prediction

Movement duration

Right and Left arm

### ABSTRACT

This study investigates the effects of age upon the temporal features of executed and imagined movements performed with the dominant (D; right) and nondominant (ND; left) arms. Thirty right-handed subjects were divided into two groups: (i) the young group ( $n = 15$ ; mean age:  $22.5 \pm 2.5$  years) and (ii) the elderly group ( $n = 15$ ; mean age:  $70.2 \pm 2.2$  years). The motor task, involving arm pointing movements among four pairs of targets (.5 cm, 1 cm, 1.5 cm and 2 cm), imposed strong spatiotemporal constraints. During overt performance, young and elderly subjects modulated movement duration according to the size of targets, despite the fact that movement speed decreased with age as well as in the left arm compared with the right. This observation was also valid for the covert performance produced by the young group. However, such a strong relationship between covert movement durations and target size was not as obvious in the elderly group. Young, compared to elderly subjects, showed stronger correlations and smaller absolute differences between executed and imagined movements for both arms. Additionally, the absolute difference between executed and imagined arm movement durations was more pronounced for the left than the right arm in aged subjects. This result suggests a selective decline with age of mental prediction of motor actions, which is more prominent when the ND arm is involved.

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## 1. Introduction

Motor imagery, a concept similar to *internal movement simulation* or *covert movement execution*, is a state of mental rehearsal during which a subject replicates a motor action without moving the limbs or activating the muscles involved in the execution of the same action. Internal simulation of single movements or movement patterns has been shown to recruit neural networks overlapping with those activated during overt

movement performance. For instance, exploration of brain activity during overt or covert movements revealed a common activation of the parietal and prefrontal cortices, the supplementary motor area, the premotor and primary motor cortices, the basal ganglia and the cerebellum (Decety, 1996; Fadiga and Craighero, 2004; Jeannerod, 2001). At the behavioural level, using the mental chronometry paradigm in various motor tasks (arm pointing, writing, and walking), several studies have shown that covert actions preserve the same

\* Corresponding author. INSERM U 887, Université de Bourgogne, Campus Universitaire, BP 27877, Dijon 21078, France.

E-mail address: [charalambos.papaxanthis@u-bourgogne.fr](mailto:charalambos.papaxanthis@u-bourgogne.fr) (C. Papaxanthis).

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doi:10.1016/j.cortex.2007.07.008

spatiotemporal characteristics and obey the same motor rules or biomechanical constraints as their overt counterparts (Courtine et al., 2004; Decety et al., 1989; Gentili et al., 2004; Maruff et al., 1999; Papaxanthis et al., 2002a, 2002b, 2003). These neurocognitive similarities between sensorimotor and mental states highly support the *simulation theory* developed by Jeannerod (2001). This theory postulates that covert actions are part of motor representations and are related to the higher levels of the central nervous system involved in motor planning and prediction.

However, while the simulation theory is corroborated by several results in young individuals, little information is available regarding its validity in normal/healthy aging. This question is relevant because clear differences emerge when performance and brain activation are compared between elderly and young people during cognitive or motor tasks. For example, in 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 is detected in elderly subjects. Intriguingly, when elderly and young people perform equally, an important bilateral activation emerges in elderly people. Thereby, aged subjects engage more brain regions during task execution (Logan et al., 2002; Reuter-Lorenz, 2002; Mattay et al., 2002; Ward and Frackowiak, 2003). Similar investigations, examining motor performance in relatively simple motor tasks, have shown that elderly subjects recruit additional cortical and subcortical areas (Heuninckx et al., 2005).

Age-related modifications in corticospinal control of upper limb muscles have been observed in transcranial magnetic stimulation experiments. Precisely, these investigations have indicated a decline in the amplitude of motor evoked potentials (MEPs) during simple isometric contractions and a reduction in cortical inhibitory mechanisms in aged people (Sale and Semmler, 2005). Since normal aging strongly influences cognitive functions (Briggs et al., 1999; Dror and Kosslyn, 1994; Logan et al., 2002; Raz et al., 1999; Reuter-Lorenz, 2002) and sensorimotor control of movement (Ketcham et al., 2002; Seidler-Dobrin and Stelmach, 1998; Seidler et al., 2002; Smith et al., 1999), one could expect mental operations related to motor prediction to be altered in elderly individuals. Hence, the general objective of the present study was to delineate internal simulation of motor actions as a function of normal aging. In particular, we investigated the effect of age upon temporal characteristics of covert and overt movements involving strong spatiotemporal constraints. In view of the fact that mental and motor processes become slower with age (Salthouse, 2000; Skoura et al., 2005) we anticipated a general decline of motor prediction in aged subjects. Furthermore, we examined if any deterioration in motor imagery with age could be related to the side of the limb involved in mental operations, i.e., the dominant (D; right) or the nondominant (ND; left) arm. It is not currently well-known if motor control, imagery and prediction are influenced by a lifetime of preferential use of the hand for skilled (D) and unskilled (ND) motor tasks. Such a question is pertinent as neural adaptations in corticospinal control of the left (ND) arm occur with age. For instance, Sale and Semmler (2005) found lower MEPs and shorter silent-period durations in the left hand of elderly compared with young subjects, whereas there was no age

difference in the right hand. In addition, there are significant age-related differences in brain neural activity associated with repetitive movements of the hand, which were more prominent when using the ND hand (Hutchinson et al., 2002). Regarding these findings, we expected a stronger alteration in motor action covert stages when the left (ND) arm is recruited in elderly people.

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## 2. Methods

### 2.1. Participants

Thirty volunteers (informed consent was signed), all right-handed, participated in the present study. Handedness was determined by means of the Edinburgh Handedness inventory (Oldfield, 1971). Subjects also performed multiple behavioural tasks (writing, catching, grasping and throwing), which confirmed right arm dominance. Subjects were divided into two different groups as a function of age: (i) the young group (eight males and seven females; mean age:  $22.5 \pm 2.5$  years), (ii) the elderly group (seven males and eight females; mean age:  $70.2 \pm 2.2$  years). The young subjects were students from the University of Burgundy. The elderly subjects were all retired, had a regular physical activity ( $\sim 1.5$  h two days per week approved by a medical doctor) and at least one daily cognitive activity (reading newspapers, books or crosswords). All subjects were in good health, with normal or corrected vision and without any nervous, muscular or cognitive disorders. Elderly subjects had cognitive evaluation by means of the *Mini Mental State Examination* test (all scores  $\geq 28$ ). Subjects received complete information about the experimental procedures, but none of them was informed of the aim of the experiment. A local ethics committee approved the experimental protocol which was carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 1964).

### 2.2. Experimental protocol

The experiment took place in a small room ( $5 \times 4$  m). The space was sound-attenuated, temperature regulated ( $22 \pm 1.5$  °C) and illuminated with homogeneous white light. Subjects were comfortably seated on an adjustable chair in front of a table whose edge was aligned with their chest at the level of the diaphragm. In the middle of the table, a block of paper (A4 format) was placed at a distance of 20 cm from the subject's chest. Each sheet was composed of vertical and horizontal lines 1 mm apart. In each sheet, two targets were printed (black squares, inter-target distance 20 cm). We used four different sizes of targets ( $.5 \times .5$  cm,  $1 \times 1$  cm,  $1.5 \times 1.5$  cm, and  $2 \times 2$  cm); however, in each trial, only one pair of targets (the two targets had always the same size) was presented to the subjects. Young and elderly adults had to point or to imagine themselves pointing between the targets very accurately and as fast as possible (i.e., adapted Fitts' law motor paradigm, see also Sirigu et al., 1996; Maruff et al., 1999) while holding a pencil either with their right (D) or left (ND) hand.

Overt and covert trials started from the right (half of the trials) or from the left target. Before an overt or covert trial,

the subjects, following the experimenter's instructions, took the pencil with their right or left hand and placed it in the centre of one of the targets before actually performing or imagining the movement. They were free to start the movement, overt or covert, when they felt ready. One executed or imagined trial consisted of five cyclical pointing movements between the targets, namely of 10 arm movements. For each overt trial, we measured the spatial precision of the pointing movements. Subjects were informed that if they missed more than two targets during a trial, this trial must be performed again. Each trial was performed on a distinct sheet. Prior to the experiment, all subjects practiced four times with both hands and with each target size. For the imagined trials, we emphasized to them that they must feel themselves performing the task (motor or internal imagery) rather than watching themselves doing it (visual or external imagery). All subjects verbally stated being able to generate motor images after having practiced 6–10 times with each pair of target. Subjects were requested to execute and to imagine arm movements as fast as possible, preserving, however, the spatial precision.

During the experiment, all subjects performed 10 overt and 10 covert trials for each target size and operating arm (a total of 160 trials). They performed the overt trials first (80), followed by the covert trials (80) after a time interval of 5 min. Within overt or covert trials, the operating arm and the target sizes were randomly presented to the subjects. The whole protocol lasted for ~55 min per subject. When a subject performed 10 consecutive trials, he (she) rested for ~1 min in order to prevent physical or mental fatigue.

### 2.3. Data recording and statistical analysis

The duration of overt and covert pointing movements was recorded by means of an electronic stopwatch (temporal resolution 1 msec) that the subjects held in their left (when pointing with the right arm) or right (when pointing with the left arm) hand. The subjects started the stopwatch when they actually or mentally initiated the movement and they stopped it when they had actually or mentally accomplished it.

We required the subjects to record their actual and mental movement durations because they reportedly felt more comfortable (especially the elderly subjects) manipulating the stopwatch themselves. We had previously validated this method in both young (Papaxanthis et al., 2003) and elderly subjects (Skoura et al., 2005). However, for the current experiment, we reevaluated this method for the D and the ND arm by examining four elderly and four young subjects who participated in the current experiment. Firstly, we estimated the temporal accuracy with which subjects measured their actual movements. Specifically, we compared movement durations (10 trials) recorded simultaneously by a stopwatch (subject measured his/her movement duration) and by a 3D accelerometer ( $\pm 5$  g, Biopac MP 150). The two recording methods gave similar results for both groups. Considering all trials (8 subjects  $\times$  4 targets  $\times$  2 arms  $\times$  10 trials), the average durations were  $5.86 \pm .71$  sec (stopwatch) and  $5.77 \pm .67$  sec (accelerometer) for the elderly group and  $4.52 \pm .59$  sec (stopwatch) and  $4.39 \pm .55$  sec (accelerometer) for the young group. There

were no significant differences within each group between the two recording methods (*paired t-tests*;  $ps > .30$ ). Secondly, we compared the temporal accuracy of executed and imagined movements in two situations: (i) the subject measured the movement himself, (ii) the experimenter measured the subject's movement, indicating the beginning (verbally) while the subject indicated (verbally) the end of the movement. Again, the two recording methods gave similar results in both groups. Considering all trials, the average durations were  $5.15 \pm .55$  sec (duration recording by subjects) and  $5.02 \pm .48$  sec (duration recording by experimenter) for the elderly group and  $4.68 \pm .49$  sec (duration recording by subjects) and  $4.52 \pm .45$  sec (duration recording by experimenter) for the young group. Again, no significant differences as a function of recording method were observed in both groups (*paired samples t-tests*;  $ps > .35$ ).

For each subject, the mean duration of movements and its standard deviation (SD) were calculated over all trials. We checked that all variables were normally distributed (*Shapiro-Wilk W test*) and that their variance was equivalent (*Levene's test*). We used three steps in our statistical analysis. First, we tested whether movement duration was modulated as a function of target size. We performed an analysis of variance (ANOVA), with *Target size* (.5 cm, 1 cm, 1.5 cm, and 2 cm) as within-subject factor, for each independent variable separately (i.e., young-right-overt; young-right-covert, young-left-overt; young-left-covert; idem for the elderly group). Subsequently, we examined whether overt movement durations correlated with covert movement durations. For young and for elderly participants, coefficients of correlation have been computed individually between covert and overt movements for the four target sizes, and then compared by means of *t-tests*. We completed this analysis by calculating, for each participant, the absolute difference between the average duration of overt movements ( $n = 10$ ) and the average duration of covert movements ( $n = 10$ ) in each experimental condition. Then, we averaged the absolute difference for the four target sizes and performed an ANOVA with *Group* as a between-subject factor (young, elderly) and *Arm* (right, left) as a within-subject factor. We thought that strong correlations and small absolute differences would suggest good covert movement ability. Finally, we explored the influence of age and operating arm upon the temporal features of overt and covert arm movement performance. In this analysis, we did not consider movement durations for each pair of target separately, but we averaged, for each subject and each condition, the durations corresponding to the four target sizes. Using these average values, we performed an ANOVA, with *Group* as a between-subject factor (young, elderly), *Arm* (right, left) and *Movement* (overt, covert) as within-subject factors. *Post hoc* differences were assessed by means of *Scheffé tests*. Using the same statistical analysis as described above, we also analyzed the temporal variability of overt and covert movements' performance. Variability was indexed by computing the coefficient of variation (CV) defined as the SD divided by the mean duration, multiplied by 100. Lastly, using *independent t-tests* we explored movement precision between young and elderly subjects. We simply recorded if the pen was inside or outside of the target, without detailing further its spatial position.

### 3. Results

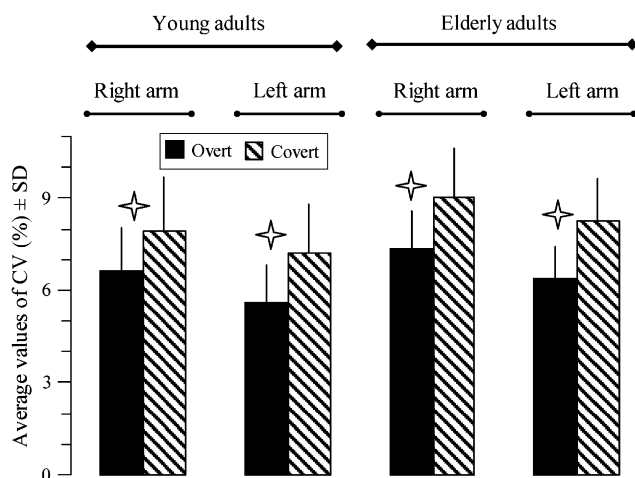
#### 3.1. Movement precision and temporal variability

Young and elderly adults respected our requirements concerning spatial precision since few overt trials were repeated (respectively, 27 and 33 trials for the young and elderly groups). In addition, considering the total number of overt pointing movements between the targets ( $n = 24,000$ ; 30 subjects  $\times$  4 target sizes  $\times$  2 arms  $\times$  10 trials  $\times$  10 movements within each trial), an insignificant number of targets were missed. The young group missed the targets 184 times (1.53%) and the elderly group missed them 201 times (1.68%). Although a tiny difference in missing targets existed between elderly and young groups, the statistical comparison (*independent t-test*) gave no significant effect of age upon spatial precision ( $t = -1.68$ ;  $p = .102$ ).

Fig. 1 shows the average values and the SD of the CV. While temporal variability was significantly greater for the covert compared to overt movement performance (on average 8.09% and 6.45%, respectively;  $F_{1, 28} = 35.78$ ,  $p < .001$ ), we did not find such statistical differences for the Group (on average 7.73% for the elderly and 6.81% for the young group) or for the Arm (on average 7.71% for the right and 6.83% for the left arm) ( $p > .4$  for both comparisons). In addition, we did not detect any interaction effect ( $p > .3$  for all comparisons).

#### 3.2. Temporal features of overt and covert movements in elderly and young individuals

Fig. 2 illustrates the main findings of our study, namely the average durations ( $\pm$ SD) of overt and covert movements for the two groups of age, the D and the ND arm and the four target sizes. Qualitatively, the first interesting result is related to the modulation of overt and covert movement durations according to the size of the targets. Noticeably, whatever the group or the operating arm, durations of overt movements progressively increased as the size of the targets gradually



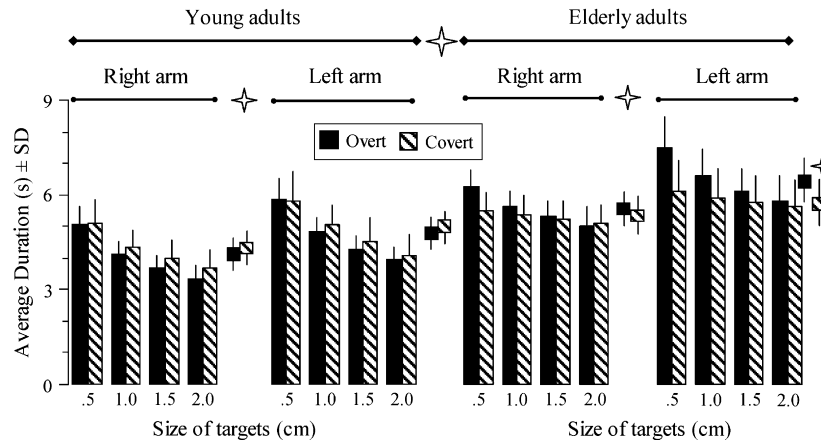
**Fig. 1 – Histograms illustrating the average values and SDs of the CV% for the different experimental conditions. Significant differences between overt and covert movement performance can be observed (stars;  $p < .05$ ).**

decreased ( $p < .001$ ; for the ANOVA). *Post hoc* comparisons showed that movement durations were significantly different between all targets ( $p < .02$ ; for all the *post hoc* comparisons). This observation was also valid for the covert performance produced by the young group (ANOVA,  $p < .0001$ ; *post hoc* comparisons between targets,  $p < .02$ ). However, such a strong relationship between covert movement durations and target size was not as obvious in the elderly group. While the ANOVA revealed a significant effect of target size ( $p < .001$ ), there was not a target-by-target size significant modulation of movement duration. The *post hoc* analysis showed that movement durations were not significantly different ( $p > .05$ ) between the following targets: .5 cm versus 1 cm, 1 cm versus 1.5 cm and 1.5 cm versus 2 cm.

In Fig. 3, the average durations of overt movements are plotted across the average durations of covert movements. The correlations between overt and covert movement durations were significant in both age groups (young group: right arm,  $r = .87$ ; left arm,  $r = .88$ ; for both  $p < .0001$ ); (elderly group: right arm,  $r = .46$ ; left arm,  $r = .51$ , for both  $p < .001$ ). However, the correlation between overt and covert movements for the individuals in the young group was significantly higher than that of individuals in the elderly group ( $p < .0001$  for both arms).

We further explored these findings by comparing average movement durations between Group, Arm and Movement. These values (collapsed across target sizes) are depicted by the squares in Fig. 2. The ANOVA (2 Group  $\times$  2 Movement  $\times$  2 Arm) showed a significant main effect of Group ( $F_{1, 28} = 45.34$ ,  $p < .0001$ ). As could be anticipated, regardless of the operating arm, elderly subjects performed the task more slowly, in physical and imagined conditions (29.8%) than young subjects did (respectively,  $5.80 \pm .83$  sec and  $4.47 \pm .62$  sec). The statistical analysis did not show a main effect of Movement ( $F_{1, 28} = 2.26$ ,  $p > .1$ ). The average durations of overt and covert movements (collapsed across conditions) were, respectively,  $5.21 \pm 1.08$  sec and  $5.07 \pm .93$  sec. However, we found a significant interaction effect between Group and Movement ( $F_{1, 28} = 12.63$ ,  $p < .0001$ ). The *post hoc* analysis revealed a significant difference between elderly and young subjects for both overt ( $p < .0001$ ) and covert ( $p < .002$ ) movements, and also a significant difference between overt and covert movement durations in the elderly ( $p < .012$ ) but not in the young group ( $p > .5$ ).

Fig. 2 reveals a difference between the right and the left arm in both age groups. This qualitative observation was confirmed by the ANOVA (2 Group  $\times$  2 Movement  $\times$  2 Arm) which revealed a main effect of Arm ( $F_{1, 28} = 67.93$ ,  $p < .0001$ ). Subjects executed the task faster (14.42%) with the right than the left arm (respectively,  $4.79 \pm .82$  sec and  $5.49 \pm 1.03$  sec). Young and elderly subjects showed similar levels of lateralisation; the interaction between Group and Arm was not significant ( $F_{1, 28} = .45$ ,  $p > .5$ ). The average laterality index (left arm durations/right arm durations) was 1.16 in the young group (overt: 1.17; covert: 1.14) and 1.14 in the elderly group (overt: 1.17; covert: 1.10). We also found a significant interaction effect between Movement and Arm ( $F_{1, 28} = 7.81$ ,  $p < .001$ ). A *post hoc* analysis revealed a significant difference between the right and the left arm for both overt ( $p < .0001$ ) and covert ( $p < .0001$ ) movements. Furthermore, a significant difference



**Fig. 2 – Histograms showing, for the two groups and arms, the average durations and SDs of the overt and covert movements according to the size of the targets. The squares among the histograms depict the *grand average* (values of all target sizes intermingled) and SDs of the overt and covert movements durations. Significant differences are indicated by stars ( $p < .05$ ).**

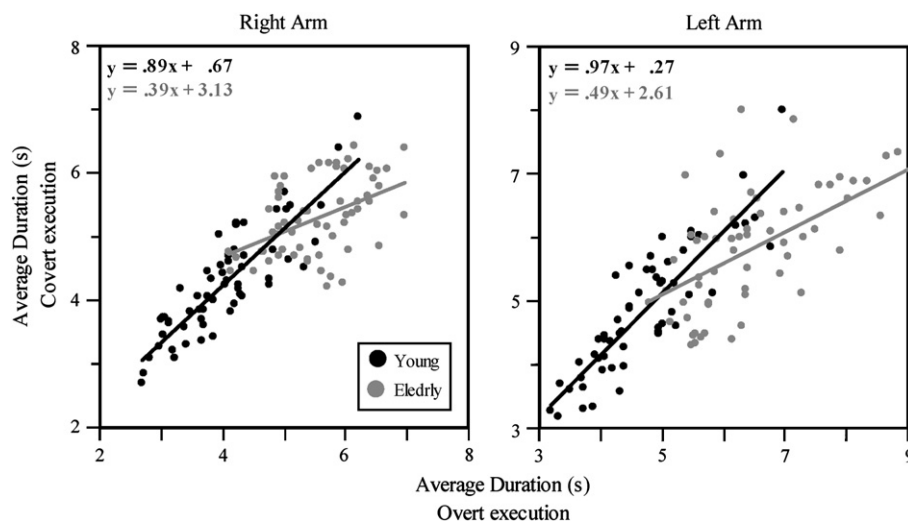
appeared between overt and covert movement durations for the left ( $p = .003$ ) but not for the right ( $p = .99$ ) arm.

More appealing, however, was the significant interaction between the three factors ( $F_{1, 28} = 6.50, p < .05$ ). A *post hoc* analysis confirmed the previous statistical results (main and interaction effects) and additionally showed that overt and covert movement durations were significantly different in the elderly group for the left ( $p < .0001$ ) but not for the right ( $p = .35$ ) arm. In order to further explore these findings, we calculated the absolute difference between overt and covert movement durations, an index that provides good information about motor imagery ability. These differences, illustrated in Fig. 4, were significantly larger in the elderly than in the young group. The ANOVA (2 Group  $\times$  2 Arm) performed upon these absolute

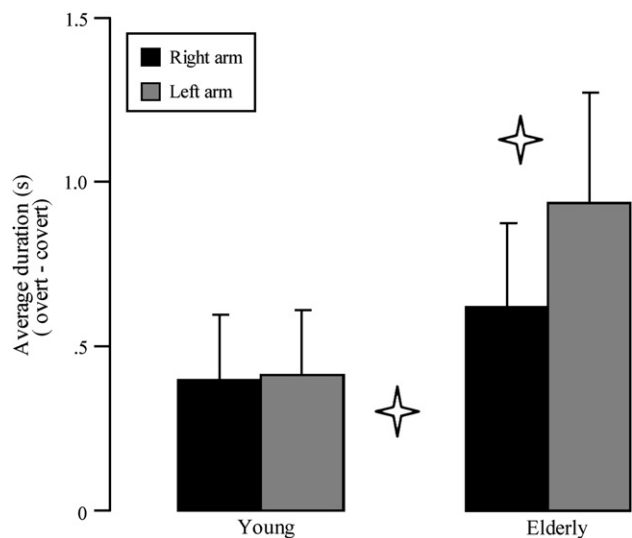
differences revealed a main effect of Group ( $F_{1, 28} = 13.55, p < .0001$ ) and Arm ( $F_{1, 28} = 7.28, p < .02$ ) and an interaction effect between Group and Arm ( $F_{1, 28} = 6.55, p < .02$ ). The *post hoc* analysis showed significant differences between the right and the left arm in the elderly group only ( $p < .002$ ).

#### 4. Discussion

The present study was devoted to the exploration of the temporal features of executed and imagined arm movements in young and elderly adults. By using arm movements requiring high spatiotemporal constraints, we found significant differences in imagery ability between elderly and young subjects.



**Fig. 3 – Average duration of overt movements is plotted versus the average duration of covert movements. Each mark is the average value of 10 overt and 10 covert trials, and shows the temporal regularities between overt and covert arm movements performed either with the right or the left arm between each pair of targets. The total number of marks for each panel is 120 (15 subjects, 2 movement executions, 4 target's sizes). A temporal dissociation between overt and covert arm movements is noticeable for the elderly group.**



**Fig. 4 – Average values and SDs of the absolute difference between overt and covert movements. Significant differences between the young and the age groups as well as between the right and left arm for the elderly group can be observed (stars;  $p < .05$ ).**

Notably, for both the D and the ND arm, young adults showed stronger correlations and smaller absolute differences between executed and imagined movements than elderly subjects did. Furthermore, we observed greater absolute differences between imagined and executed movements for the ND (left) than the D (right) arm in aged individuals. This finding suggests that internal models of action in elderly adults are not as accurate as in young adults, in particular when imagined actions engage the ND arm.

#### 4.1. Slowness of actual and imagined movements in elderly subjects

In the present study, we found that elderly subjects executed arm movements significantly slower than young subjects. This observation could be anticipated from previous findings. In fact, with normal aging emerges sarcopenia (Narici et al., 2003), reduction in motor unit activation capacity (Winegard et al., 1996), coactivation of antagonist muscles (Klein et al., 2001; Seidler et al., 2002), decline in several aspects of proprioceptive sensitivity (Verschueren et al., 2002) and reduction in the central mechanisms operating during visuomotor information processing (Briggs et al., 1999; Ketcham et al., 2002; Seidler-Dobrin and Stelmach, 1998; Smith et al., 1999). These modifications, within the musculo-skeletal apparatus and the central nervous system (CNS), influence movement execution and control in elderly individuals. In most cases, elderly adults compared to young adults, show lengthened deceleration curves, lower peak velocities and secondary corrective sub-movements during movements involving the D arm (Bellgrove et al., 1998; Ketcham et al., 2002; Seidler-Dobrin and Stelmach, 1998).

On the other hand, the general observation that imagined movement durations, as those of executed movements, were

longer in aged, compared to young, individuals constitutes a novel result. This finding may suggest that alterations in cognitive mechanisms responsible for the mental representation of motor actions parallel to those observed in movement execution. This finding builds on previous observations which suggest that aging influences the generation and manipulation of mental-visual images. In general, older adults are slower in mental rotation of visual stimuli and experience progressively greater slowing as a function of the angle of rotation (Dror and Kosslyn, 1994). Similar findings have been also observed during the generation of motor images of finger movements (Sabaté et al., 2004). As a general remark, 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.

#### 4.2. Motor imagery and internal models of action in elderly subjects

Our findings revealed that elderly adults did not show strong relationships between covert movement durations and target size as young adults did. Thereby, one could assume that when elderly subjects internally simulated arm movements between visual targets, they did not fully integrate task constraints (i.e., target size and movement speed). More appealing, the fact that elderly subjects showed poorer correlations and greater absolute differences between executed and imagined movements than young subjects did, indicates a specific weakness of internal movement simulation in aged individuals. It is also of interest that the temporal dissociation between executed and imagined movements was higher for the left than the right arm in elderly adults. These findings suggest that mental prediction of motor actions (Wolpert and Flanagan, 2001; Miall and Wolpert, 1996) via forward internal models, is not well preserved with age.

These behavioural findings could be attributed to structural and functional changes that occur with age at the level of the CNS and influence cognitive and motor abilities in latter life (for review see Reuter-Lorenz, 2002; Reuter-Lorenz and Lusting, 2005). For instance, shrinkage of gray matter volume, pervasive loss of white matter and cholinergic and dopaminergic declines have been observed at the structural level. On the other hand, underactivation and overactivation of brain areas are the most prominent functional changes, suggesting non-selective brain activation, compensation or dedifferentiation processes within the aging brain. For example, investigations exploring motor performance have shown that elderly subjects recruit additional cortical and subcortical areas (Heuninckx et al., 2005; Mattay et al., 2002; Ward and Frackowiak, 2003). Likewise, during memory-related cognitive tasks, elderly people under-recruit and non-selectively recruit frontal brain regions (Logan et al., 2002; Reuter-Lorenz, 2002). These modifications compromise memory and attentional control (Briggs et al., 1999; Logan et al., 2002; Raz et al., 1999; Reuter-Lorenz, 2002; Rypma and D'Esposito, 2000), as well as motor abilities (Ketcham et al., 2002; Seidler-Dobrin and Stelmach, 1998; Seidler et al., 2002; Smith et al., 1999) in elderly adults. During motor imagery, the brain monitors intentions and actions' plans but consciously retains them from overt execution. This involves a high temporal organisation of the

sequences of simulated actions, i.e., triggering and retention, which engage the activation of several brain areas and especially the frontal, prefrontal and parietal cortices (Decety, 1996; Jeannerod, 2001; Sirigu et al., 1996; Danckert et al., 2002). The alteration of the temporal processing of imagined actions in elderly adults observed in the present study is in congruence with the current vision of the aging mind and further proposes a progressive decline on the generation and control of intended but not executed actions in the aging brain.

Differences in brain activation between young and aged adults during motor actions are more prominent when using the ND hand (Sale and Semmler, 2005; Hutchinson et al., 2002). This is, for instance, the case in repetitive movements of the hand (index finger abduction/adduction and wrist extension/flexion) during which contralateral primary sensorimotor cortex and premotor cortex had significantly greater activation in the young subjects while caudal supplementary motor area and ipsilateral sensorimotor cortex had significantly greater activation in the older subjects (Hutchinson et al., 2002). This functional differentiation associated, at the behavioural level, to the preferential use of the D arm may also explain why in the current study we found greater temporal differences between actual and imagined movements for the left hand.

At the behavioural level, the concept of internal models may account for our findings. We previously proposed how the use of an inverse and a forward internal model of arm could explain the temporal equivalence between overt and covert arm movements in young adults (Papaxanthis et al., 2002a; Gentili et al., 2004, 2006). Briefly, when subjects executed arm movements, the inverse internal model, integrating the context of the action, generated the appropriate neural commands for the motion of the arm. The forward model, relating the sensory signals of the actual state of the arm (e.g., position, time, and velocity) to the neural commands, initially predicted the future states of the arm (forward dynamics model) and then the sensory consequences of the action (forward sensory model). During motor imagery, accurate timing information for the simulated movement, and thus isochrony between executed and imagined movements, is provided by the forward model, which predicts the sensory consequences of the movement on the basis of the correctly prepared (inverse model) but blocked neural commands.

However, elderly subjects did not completely preserve this ability as they exhibited temporal dissimilarities between executed and imagined arm movements. Age-related decline in imagined actions, which are more prominent for the left hand, may be related to the fact that sensory information from the periphery is not available to the motor system during internal movement simulation as it is during movement execution. The lack of sensory information prevents subjects from verifying whether the simulated movement is similar to its actual counterpart and therefore precludes the calibration of simulated actions on the basis of sensorimotor information provided from their actual execution. Considering that internal models and feedforward control of arm dynamics are superior for the right than the left arm in right-handed young adults (Sainburg, 2002), it is likely that a decline in the

accuracy of internal models in aged subjects would affect the left arm more than the right arm.

The finding that motor imagery deteriorates with age may have clinical implications. We propose that through motor prediction/simulation, one can directly question motor representations and eventually motor imagery could be an interesting tool for an early detection of impairments at the level of motor cognition in elderly subjects.

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## Acknowledgements

This work was supported by the Conseil Regional de Bourgogne, the INSERM and the CNRS.

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