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Mentally Simulated Motor Actions in Children

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The present study investigated the effects of age and arm preference on motor imagery ability. Children (groups: 6.5, 8.3, and 10.1 years) and young adults (22.4 years) physically or mentally performed a drawing motor task with the right or the left arm. Imagery ability, accessed by the timing correspondence between executed and imagined movements, was poor at 6 and 8 years but improved at age 10, and was robust in adults. The arm condition had no influence on imagery ability. We suggest that maturation of parietal and prefrontal cortices during development may contribute to improvement of action representation.

INTRODUCTION

The simulation theory postulates that mental (covert) and executed (overt) actions rely on similar motor representations (Jeannerod, 2001; Jeannerod & Decety, 1995). Internal movement simulation or motor imagery is a state of mental rehearsal during which subjects feel themselves performing a movement (first-person process), without moving the limbs or activating the muscles involved in the execution of the same movement. Several investigations have provided evidence for numerous neurocognitive similarities between mental and sensorimotor states. For instance, mental rehearsal of movement retains the same temporal structure and follows the same motor rules (e.g., speed–accuracy trade-off) or biomechanical constraints as their execution counterpart (Cerritelli, Maruff, Wilson, & Currie, 2000; Decety & Jeannerod, 1995; Decety, Jeannerod, & Prablanc, 1989; Gentili, Cahouet, Ballay, & Papaxanthis, 2004; Maruff, Wilson, De Fazio et al., 1999; Papaxanthis, Pozzo, Kasprinski, & Berthoz, 2003; Papaxanthis, Schieppati, Gentili, & Pozzo, 2002; Sirigu et al., 1996). Likewise, the activation pattern of brain areas occurring during the motor production is broadly shared during the simulation state. Notably, the parietal and prefrontal cortices, the supplementary motor area, the premotor and primary motor cortices, the basal ganglia and the cerebellum are activated during both executed and imagined movements

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(Decety, 1996; Ehrsson, Geyer, & Naito, 2003; Fadiga & Craighero, 2004; Gerardin et al., 2000; Jeannerod, 2001).

The exploration of motor imagery becomes a potential tool to investigate action representation (Jeannerod, 1995). Action representation is generated by internal forward models, that is, neural networks that simulate the dynamic behavior of the body and its interaction with the environment. For example, during an arm reaching movement, the forward model relates the sensory signals of the actual state of the arm (e.g., position, time, velocity) to the motor command and predicts the future states of the arm (forward dynamic model) and the sensory consequences of its motion (forward sensory model). Motor imagery of a movement can be considered as a conscious process equivalent to motor prediction for that movement (Jeannerod, 1995, 2001; Jeannerod & Decety, 1995). The cerebellum and the parietal cortex are neural structures highly involved in mental rehearsal of motor actions (Blakemore & Sirigu, 2003; Decety et al., 1994; Gerardin et al., 2000; Sirigu et al., 1996). Impairment in imagined actions occurs in patients with lesions in the parietal cortex (Danckert, Ferber et al., 2002; Sirigu et al., 1996; Wolpert, Goodbody, & Husain, 1998) and the cerebellum (Kagerer, Bracha, Wunderlich, Stelmach, & Bloedel, 1998) as well as in people with schizophrenia (Danckert, Rossetti, d'Amato, Dalery, & Saoud, 2002; Maruff, Wilson, & Currie, 2003).

However, while the simulation theory is corroborated by several results obtained in adults (Courtine, Papaxanthis, Gentili, & Pozzo, 2004; Decety & Jeannerod, 1995; Gentili et al., 2004; Papaxanthis, Pozzo, Skoura, & Schieppati, 2002; Papaxanthis, Schieppati, et al., 2002; Sirigu et al., 1996) and adolescents (Choudhury, Charman, Bird, & Blakemore, 2006, 2007), little information is available regarding its validity in children. This question is relevant because childhood is a decisive period for the development of internal models (Maruff, Wilson, Trebilcock, & Currie, 1999; Wilson, Maruff, Ives, & Currie, 2001). For instance, a recent study (Molina, Tijus, & Jouen, 2008), in which children had to move, or thinking moving, in order to take a puppet back to its home, has shown that 5-year-old children failed to reveal any motor imagery capacity. However, by age 7, children demonstrated this capacity if the task instructions explicitly forced them to feel their actual or virtual movements. Indeed, significant correlations were found between actual and virtual walking movement durations in these 7-year-old children only when they were told that they were transporting a heavy puppet in their arms (informed condition). Also, grip force did not change significantly between the standard and the informed condition. These two results, movement duration and hand pressure, allowed the authors to propose that the 7-year-olds were able to evoke motor imagery in some conditions. Furthermore, recent neuroimaging findings have shown that the parietal cortex, involved in action prediction, undergoes a particularly extended course of development, compared with sensory and motor regions of the brain (Giedd et al., 1999; Gogtay et al., 2004).

In the present experiment, our intent was twofold. First, we investigated the age at which children generate accurate motor representations. In the literature, studies using grip force modulation paradigms have shown that age four to age six is a critical time for the development of internal dynamic representations (Blank, Heizer, & von Voss, 1999, 2000; Pare & Dugas, 1999). Furthermore, Piaget and Inhelder (1966) have proposed that children develop complete (anticipatory) mental representations of moving objects at around 8/9 years. The period from 6 to 8 years also constitutes a critical phase for the development of visual mental images (Kosslyn, Margolis, Barrett, Goldknopf, & Daly, 1990). The Molina et al. (2008) study suggests that motor imagery is not completely developed at 7 years of age. Considering these findings, we tested the acquisition of the motor ability in children aged 6, 8, and 10 years.

Regarding previous studies that demonstrated a development of the parietal cortex until adolescence (Blakemore & Choudhury, 2006; Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003; Toga, Thompson, & Sowell, 2006), and considering that this brain region is important for the generation of motor intentions (Blakemore & Sirigu, 2003), we anticipated that action representation would exhibit progressive improvement with age.

We also wondered whether arm preference is integrated in action representation during childhood. Young adults are able to generate accurate motor images with the preferred (P) and the nonpreferred (NP) arm (Maruff, Wilson, De Fazio et al., 1999). However, such information is missing for children. Hand preference for reaching objects is developed early, with right–left side differences in kinematic parameters to be consistent at 6, 9, and 12 months of age (Fagard, 2006; Michel, Tyler, Ferre, & Sheu, 2006; Ronqvist & Domellof, 2006; van Mier, 2006).

Based on these findings, we expected that the P hand should outperform the NP one during movements executed by children of 6, 8, and 10 years. On the contrary, because motor imagery is not well developed in childhood, one could speculate that children would not be able to integrate hand preference in action representation and would imagine P and NP hand movements with similar durations. This would suggest that hand preference in children is related to execution process only, and not to action planning and prediction. On the other hand, one could expect that, because arm preference is rapidly developed and integrated into motor behavior, children should be able to incorporate it into action representation even if this latter is not well developed. Previous studies, exploring hand performance and laterality scores in an unimanual tapping test have shown that older children were faster than younger children, but the differences between the two hands were not related to age (Carrier, Dumont, Beau, & Michel, 1993). To our knowledge, the present study is the first to explore the incorporation of arm preference into action representation in childhood.

METHODS

Participants

Thirty-six children, all right handed, participated in the experiment. Children were divided into three age groups, each group corresponding to one school level: (i) the 6-year-olds (first elementary grade): $N = 12$, 6 females; mean age: 6.5 ± 0.4 years, (ii) the 8-year-olds (third grade): $N = 12$, 6 females; mean age: 8.3 ± 0.5 years, and (iii) the 10-year-olds (fifth grade): $N = 12$, 6 females; mean age: 10.1 ± 0.5 years. Children were essentially from middle socioeconomic status families. They were in good health, with normal or corrected vision and without any nervous, muscular, or cognitive disorders. Informed consents were obtained from parents for each child. A control group of 12 young adults (mean age: 22.4 ± 0.7 years) also participated in our experimental protocol. They were students from the University of Burgundy and all were right handed, with normal or corrected vision and without any nervous, muscular, or cognitive disorders. The experimental protocol was carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 1964).

Assessment of Arm Preference and Imagery Ability

Arm preference in children was assessed by means of simple tests drawn from Bryden (1977). Eight items were used, 4 were unimanual (drawing, throwing a ball, holding scissors, and brush-

ing one's teeth), and 4 were bimanual (tightening the lid on a bottle, hitting a nail with a hammer, lighting a match, and wiping a plate with a cloth). Only children who obtained a score equal or superior to 6 were selected. Arm preference in young adults (mean laterality 0.87 ± 0.06) was determined by means of the Edinburgh Handedness inventory (Oldfield, 1971) and confirmed via multiple behavioral tasks that the young participants actually performed (writing, catching, grasping, and throwing).

Children's motor imagery ability was evaluated by using an adapted version of the Practise Imagery Questionnaire proposed by Wilson et al. (2001). The questionnaire consisted of 18 questions, 6 in each of three subscales that evaluated different aspects of praxis imagery: kinaesthetic, body position, and action. There were no differences between groups (*t*-tests, $p > .05$) in any of the subscales (*Kinaesthetic*: 6 yrs = 3.8 ± 1.1 , 8 yrs = 4.4 ± 1.2 , 10 yrs = 4.8 ± 1.2 ; *Position*: 6 yrs = 4.1 ± 1.2 , 8 yrs = 4.8 ± 1.3 , 10 yrs = 5.2 ± 1.2 ; *Action*: 6 yrs = 4.5 ± 1.2 , 8 yrs = 5.1 ± 1.0 , 10 yrs = 5.3 ± 1.2). In addition to measuring imagery ability, we asked 12 children (4 per group) to indicate the position of the pencil in the maze (5 trials) when they mentally performed the task with the P arm. This information was requested at 2 sec and 3 sec after the experimenter's go signal. The children first accomplished the experiment and then they participated to the motor imagery control task. The estimated position of the pencil was different at 2 sec and 3 sec for all children. Certainly, this information does not guarantee the quality of the imagined movements; however, it confirms that the participants mentally explored the entire maze.

Adults' motor imagery ability was assessed by means of a French version of the Movement Imagery Questionnaire (MIQr, Hall and Martin, 1997). The MIQr measures the difficulty (from 1 = very difficult to 7 = very easy) of forming visual and kinaesthetic images of movements with a 7-points-scale in 8 items (maximum score = 56; visual modality = 28; kinaesthetic modality = 28). All participants were good imagers, as they reported total scores higher than 19 in both modalities.

Material and Experimental Procedure

The experiment took place inside the school, in a sound-attenuated and temperature regulated ($\sim 22^\circ\text{C}$) room, illuminated by natural and/or homogeneous white light. Participants 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. For each trial, participants were presented with a plain sheet of paper (A4 format, placed at a distance of 10 cm from their chest level), on which we drew a template (maze) of 1.5 cm in width and 54 cm in length. In order to make the task more fun for children, we drew a rabbit at the beginning of the maze and a carrot at the end of it. Participants, holding a pencil in their right (P) or left (NP) hand, were asked to trace or to imagine tracing a line inside the maze as quickly and as accurate (without touching the lines) as possible, *as would the rabbit do for getting to the carrot*. Before an executed or imagined trial, the participants took the pencil with their right or left hand and placed it at the beginning of the maze (just in front of the rabbit). The trial started when the experimenter said "go" and ended when the participant said "stop," as soon as she or he arrived at the carrot. For each executed trial, we measured the spatial precision of the tracing movements, that is, the number of times that participants touched or drew outside the lines of the maze. Prior to the experiment and after receiving a demonstration by the experimenter, all participants practiced 3 times with each hand. The results of these trials were not included in the main experiment. For the imagined trials, we emphasized to them that they had to feel themselves performing the task (motor or internal imagery) rather than watching themselves doing it (visual or external imagery). Imagined practice trials were also performed with both hands. All participants verbally affirmed that they were able to imagine the movement in a first-person perspective

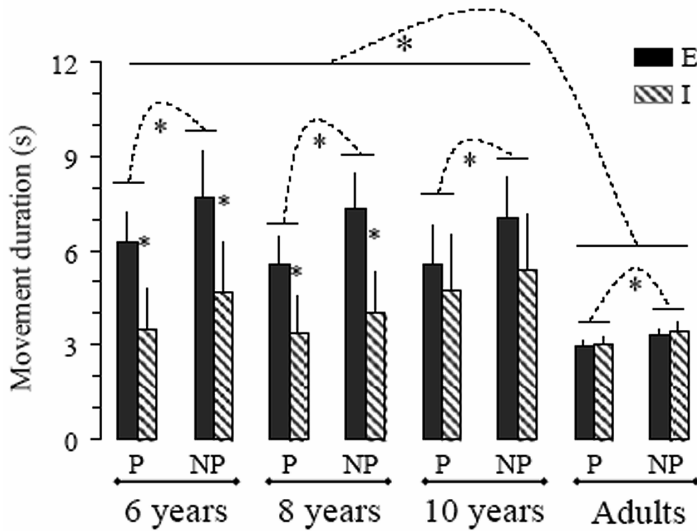


FIGURE 1 Histograms showing the average durations ($\pm SD$) of executed (E) and imagined (I) movements for the preferred (P) and the nonpreferred (NP) hand in the four age groups. Stars (*) indicate significant differences.

after having practiced 3 to 6 times with each hand. During the experiment, each participant performed a block of 9 executed and a block of 9 imagined trials for each hand (a total of 36 trials). *Hand* (P, NP) and *Movement* (Executed, Imagined) conditions were contra-balanced between the participants. A time interval of 5 minutes separated the block of executed and imagined movements. The experiment lasted ~15–20 minutes per participant.

Data Recording and Statistical Analysis

We used the mental chronometry paradigm as an indicator of the development of action representation. Specifically, we compared the timing correspondences between executed and imagined actions. Their temporal invariance, well documented in young adults, argues in favor of similar motor representations (internal model) between covert and overt actions. In our experiments, we considered that isochrony between executed and imagined movements should be an indicator of the childrens' ability to internally represent their motor actions. The duration of executed and imagined tracing movements was recorded by means of an electronic stopwatch (temporal resolution 1 msec). The time interval between the experimenter's go signal and the participant's stop signal was measured. We excluded 3 children aged 6 years, because they were unable to respect the task's instructions, mainly because of a too high level of motor agitation. Consequently, their imagined movements were very inconsistent, ranging from 2 sec to 11 sec. The children included in the study did not show such motor agitation.

For each participant, the mean duration and its standard deviation were calculated over all trials ($N = 9$) for each experimental condition separately. Variability of executed and imagined movement durations was indexed by computing the coefficient of variation (CV) defined as the standard deviation divided by the mean duration, multiplied by 100. We checked that these variables

were normally distributed (*Shapiro-Wilk W test*) and that their variance was equivalent (*Levene's test*). We explored the effects of age and arm preference on the temporal features (average durations and CV) of executed and imagined hand movements by performing an ANOVA, with *Age* as a between-subject factor (6 years, 8 years, 10 years, Adults), *Hand* (P, NP) and *Movement* (Executed, Imagined) as within-subject factors. Post-hoc differences were assessed by means of *Scheffé* tests.

In order to further examine participants' imagery ability, we computed an Index of Performance. We calculated, for each participant, the absolute difference (IE-II) between the average duration of executed movements ($N = 9$) and the average duration of imagined movements ($N = 9$) for the right and the left hand separately. In order to account for inter-individual differences in movement duration, we calculated, for each participant, the ratio between the absolute difference IE-II and the average executed movement duration $((IE-II/E)*100)$. A ratio near to zero indicates good imagery ability. We checked that these variables were normally distributed and that their variance was equivalent. Statistical differences for the Index of Performance were tested using ANOVA with *Age* as a between-subject factor, and *Hand* as within-subject factors, with post-hoc differences assessed by means of *Scheffé* tests.

We examined the influence of hand preference in executed and imagined movements by computing an Index of Laterality. We calculated, for each participant, the ratio $((NP-P)/P)*100$ between the average duration of NP hand movements ($N = 9$) and the average duration of P hand movements ($N = 9$) for the executed and the imagined movements separately. A ratio near to zero indicates no hand differences. We checked that these variables were normally distributed and that their variance was equivalent. Statistical differences for the Index of Laterality were tested using ANOVA with *Age* as a between-subject factor and *Hand* as within-subject factors, with post-hoc differences assessed by means of *Scheffé* tests.

Statistical differences for the spatial errors (i.e., the number of times that participants touched or drew outside the lines of the maze) were tested by performing ANOVA (normal distribution and equivalence of variance were verified) with *Age* as a between-subject factor, and *Hand* as within-subject factors, with post-hoc differences assessed by means of *Scheffé* tests.

RESULTS

Temporal Features of Executed and Imagined Movements

The average durations ($\pm SD$) of executed and imagined movements, performed either with the P or the NP hand, are illustrated in Figure 1 for the four groups separately. The ANOVA revealed main effects of *Age* ($F(3, 44) = 10.18, p < .001$), *Hand* ($F(1, 44) = 58.04, p < .0001$) and *Movement* ($F(1, 44) = 93.61, p < .0001$). Post-hoc analyses showed that movement duration was significantly different between adults and children ($p < .001$ for all comparisons), but not different between the three groups of children ($p > .05$ for all comparisons). Duration was higher when children used the NP hand (on average: 5.37 ± 2.31 sec) than their P hand (on average: 4.33 ± 1.70 sec), and when they executed (on average: 5.75 ± 2.05 sec) rather than imagined (on average: 4.02 ± 1.75 sec) the movements. As shown by Figure 1, the interaction between *Age* and *Movement* ($F(3, 44) = 8.10, p < .05$) yielded also significance. The *post-hoc* analysis revealed a significant difference between executed and imagined movement durations at 6 ($p < .001$), 8 ($p < .001$), and

10 years ($p < .05$) but not in adults ($p > .05$). In general, all children imagined their arm movements with shorter durations than they executed them. One child from the group of 6 years and 2 children from the group of 10 years did the opposite, namely their imagined movements were slightly longer than their executed ones.

For the coefficient of variation (CV), ANOVA revealed a significant effect of age ($F(3, 44) = 28.02, p < .0001$). Post-hoc analyses revealed that temporal variability was different between adults and children ($p < .001$ for all comparisons), but not different between the three groups of children ($p > .05$ for all comparisons). CV was significantly greater for the imagined compared to the executed movements (on average 11.68% and 17.39%, respectively; $F(1, 44) = 56.67, p < .0001$). We did not find significant statistical differences for the Hand ($p > .05$) or any interaction effect ($p > .05$). The average values of CV (%) were, respectively: 6 yrs = 12.78 ± 5.23 (P executed), 22.92 ± 6.82 (P imagined), 13.47 ± 4.27 (NP executed), and 23.35 ± 7.09 (NP imagined); 8 yrs = 13.60 ± 3.96 (P executed), 17.74 ± 5.56 (P imagined), 12.82 ± 4.98 (NP executed), and 19.67 ± 6.55 (NP imagined); 10 yrs = 15.16 ± 5.84 (P executed), 18.30 ± 5.47 (P imagined), 11.99 ± 4.18 (NP executed), and 19.18 ± 5.71 (NP imagined); adults = 6.97 ± 1.06 (P executed), 9.45 ± 1.56 (P imagined), 6.69 ± 1.34 (NP executed), and 8.54 ± 1.57 (NP imagined).

We further investigated the isochrony between executed and imagined movements as a function of age and hand preference. ANOVA revealed a significant effect of Age ($F(3, 44) = 16.22, p < .0001$), but no significant effect of Hand ($p > .05$) or interaction effects between Age and Hand ($p > .05$). The *post-hoc* analysis showed that Index of Performance did not change from 6 to 8 years ($p > .05$), but it was improved significantly from 8 to 10 years and from 10 years to adulthood (for both $p < .05$). The average values of the Index of Performance (%) were, respectively: 6 yrs = 46.60 ± 11.63 (P) and 46.07 ± 13.73 (NP); 8 yrs = 40.77 ± 10.71 (P), and 44.44 ± 10.23 (NP); 10 yrs = 23.33 ± 10.51 (P) and 23.16 ± 12.80 (NP); adults = 8.92 ± 2.91 (P) and 7.97 ± 2.87 (NP).

The values of the Index of Laterality were largely positive, indicating clearly right-hand dominance. The statistical analysis revealed a significant effect of Age ($F(3, 44) = 4.54, p < .05$) but no significant effect of Hand ($p > .05$) or interaction effects between Age and Hand ($p > .05$). The *post-hoc* analysis showed that the Index of Laterality was of the same magnitude in all the groups of children ($p > .05$); however, it diminished significantly in adults ($p < .05$). The average values of the Index of Laterality (%) were, respectively: 6 yrs = 21.67 ± 11.00 (Executed) and 21.94 ± 13.10 (Imagined); 8 yrs = 24.09 ± 10.78 (E) and 21.93 ± 11.12 (I); 10 yrs = 24.67 ± 10.06 (E) and 22.52 ± 11.70 (I); adults = 10.78 ± 2.61 (E) and 11.92 ± 3.31 (I).

Movement Precision

The average errors (i.e., the number of times that participants touched or drew outside the lines of the maze) were, respectively: 6 yrs = 2.8 ± 2.2 (P) and 8.7 ± 2.9 (NP); 8 yrs = 1.6 ± 1.1 (P) and 4.1 ± 2.5 (NP); 10 yrs = 1.2 ± 1.6 (P) and 3.8 ± 2.8 (NP); adults = 0.8 ± 0.8 (P) and 2.0 ± 1.0 (NP). The ANOVA revealed a main effect of Age ($F(3, 44) = 10.18; p < .003$) and Hand ($F(1, 44) = 78.79, p < .0001$). The *post-hoc* analysis confirmed that spatial errors significantly decreased from 6 years to 8 years and then remained almost constant ($p < .02$, for the comparison of the 6-year-olds with the other groups). In addition, errors were more frequent when the NP hand was used (on average: 4.6 errors) than the P hand (on average: 1.6 errors). There was also a significant interaction between Age and Hand ($F(3, 44) = 8.22, p < .001$). The *post-hoc* analysis revealed that the number of spatial errors: (i) was significantly different between the P and the NP hand in all groups ($p < .05$),

except in adults ($p > .05$), (ii) was not significantly different between the different groups for the P hand ($p > .05$), (iii) was significantly different ($p < .05$) between the 6-year-olds and the other age groups for the NP hand.

DISCUSSION

In the present study, we investigated the temporal features of executed and imagined hand movements in childhood. We found that motor imagery processes are not completely developed in children of 6, 8, and 10 years. Specifically, children imagined hand movements faster than they executed them. This finding suggests that internal models of action are not mature in children and are therefore less accurate in children than in adolescents (Choudhury et al., 2006, 2007) and young adults (Decety & Jeannerod, 1995; Maruff, Wilson, De Fazio et al., 1999; Papaxanthis, Pozzo, et al., 2002; Papaxanthis, Schieppati et al., 2002; Skoura, Papaxanthis, Vinter, & Pozzo, 2005). However, temporal correspondences between imagined and executed movements increased progressively during this age period, which indicates that the ability to generate accurate action representations improves. In addition, we found superior motor performance, that is, better spatial accuracy and faster execution, for the P (right) than the NP (left) hand. The right-hand dominance was also observed in imagined movements. This finding suggests that hand preference is rapidly integrated into action representation (at 6 years in our experiment), although this latter is not yet completely developed during childhood.

Motor Performance and Handedness in Childhood

Our results showed that the P hand clearly outperformed the NP hand and that motor performance, in terms of spatial accuracy and speed, of both hands improved with age. This is not a surprising result, as laterality effects are present very early in the development, that is, before six months (Fagard, 2006; Michel et al., 2006; Ronnqvist & Domellof, 2006; van Mier, 2006). The age-related increase in the general level of motor performance with both hands reflects one of the well-known characteristics of motor development related to a more proficient planning and programming in older children. This improvement has also structural origins that are related to the bilateral maturation of corticospinal pathways and to the development of the frontal, pre-frontal, and parietal cortices during childhood (Gogtay et al., 2004; Paus et al., 1999). However, handedness effects in motor performance as a function of age suggest that sensorimotor control of movement does not mature in a similar manner for the D and the ND hand during development. Anatomical and structural asymmetries in the primary motor cortex (M1) of humans could explain why motor performance of the D hand is superior to that of the ND hand. For instance, research suggests that the area of hand representation is greater in the D left hemisphere than in the ND right hemisphere (Amunts et al., 1996; Hammond, 2002) and that motor representation in M1 undergoes continuous reorganization as an effect of training and experience (Sanes & Donoghue, 2000). Functional causes, like differences in motor planning and motor control, could also explain D and ND hand motor asymmetries. (Sainburg, 2002) has proposed that handedness is strongly related to the control of arm dynamics. According to this hypothesis, in right-handed subjects the D hand is highly proficient in accounting for muscle and inter-joint dynamics. Arm asymmetries during sen-

sorimotor development in young children can be attributed to partial and not stable internal representations of arm dynamics that are used for movement planning, prediction, and control.

Motor Imagery, Handedness, and Internal Models in Childhood

Our findings revealed that action representation is not completely developed in children. Notably, the duration of imagined actions were significantly shorter than their executed counterparts. However, temporal differences were greater for the youngest compared to oldest children. It is appealing that temporal similarities between imagined and executed movements improved progressively from 6 years to 10 years, indicating that action representation is progressively developing in this period, even if it remained less accurate than action representation in adults. The improvement of performance we observed between 6 and 8 years corroborates the findings coming from the Molina et al. (2008) study, which showed that the emergence of motor imagery appeared at 7 years, when the experimental conditions obliges children to explicitly think about what they feel when they imagine an action.

Our findings corroborate and extend previous results that showed that the ability to represent accurately actions is in place in adolescents (Choudhury et al., 2006, 2007) and adults (Decety & Jeannerod, 1995; Papaxanthis, Pozzo, et al., 2002; Papaxanthis, Schieppati, et al., 2002; Sirigu et al., 1996; Skoura et al., 2005). It is also of interest and novel that hand preference is integrated into action representation early during development, at 6 years in our study. Notably, hand asymmetries observed in the temporal features of executed actions were also present in the temporal features of imagined actions. This suggests that asymmetries in action selection and planning strongly contribute to manual asymmetries. With advance in age, timing differences between executed and imagined movements decreased for both P and NP hands, suggesting that the ability to formulate action representation improves during childhood, independently of hand preference.

We suggest that improvement in action representation in childhood may be due to refinement of internal models. Action representation is generated by an internal forward model, which is a neural network that simulates the dynamic behavior of the body and its interaction with the environment. We have previously proposed that the use of an inverse and a forward internal model of arm could explain the temporal equivalence between executed and imagined arm movements in elderly (Skoura et al., 2005) and young adults (Courtine et al., 2004; Gentili et al., 2004; Gentili, Papaxanthis, & Pozzo, 2006). Briefly, when subjects execute arm movements, the inverse internal model, integrating the context of the action, generates 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, velocity) to the neural commands (efference copy), initially predicts 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. Children have not completely acquired this ability as they exhibited temporal differences between executed and imagined arm movements. However, our findings clearly showed that imagined actions of both arms progressively improve with age. This indicates that internal forward models become more robust with experience and practice, providing thus accurate motor predictions. Considering also that internal models and feedforward control of arm dynamics are superior for the right than the left arm in

right-handed subjects (Sainburg, 2002), one could understand why the right hand outperforms the left hand during development in both executed and predicted actions.

Development of the Brain and Action Representation in Childhood

While action representation engages several brain regions, it appears that parietal cortex plays a major role in mental rehearsal of motor actions (Blakemore & Sirigu, 2003; Decety, 1996; Decety et al., 1994; Gerardin et al., 2000; Jeannerod, 2001; Sirigu et al., 1996). For instance, impairment in imagined actions occurs in patients with lesions in the parietal cortex. One could speculate that inaccuracy in action representation in children (6–8 yrs) is related to the maturational processes, that is, grey and white matter development, in the parietal cortex (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003; Toga et al., 2006). With advance in age, the maturational processes in parietal cortex increases neural efficiency and may help oldest children (10 yrs) and adolescents (Choudhury et al., 2006, 2007) to progressively improve their ability to generate accurate motor predictions. However, we cannot rule out that other factors, such as, for instance, the attentional span, or the capacity to follow the task's instructions, or more general cognitive aspects, may have at least indirect effects on children's performance in the imagined motor task.

From a more psychological point of view, internally simulating one's own movements may require to plan movements in a virtual space (absence of movement) combined with an actual time. In this sense, it requires the capacity to plan events with flexible relationships between space and time. (Diamond, 2002) has rightly shown that important reorganizations occurred within the parietal and prefrontal cortices during childhood, allowing this capacity to emerge.

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