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BRIEF REPORT

Executed and Imagined Bimanual Movements: A Study Across Different Ages

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Movements with both hands are essential to our everyday life, and it has been shown that performing asymmetric bimanual movements produces an interference effect between hands. There have been many studies—using varying methods—investigating the development of bimanual movements that show that this skill continues to evolve during childhood and adolescence. In the current study we used a spatial bimanual task to delineate the development of bimanual movements not only during different stages of childhood but also during late stages of adulthood. Furthermore, we used the same task as a window to observe the involvement of motor imagery through the same age groups. For this study we recruited participants from 4 different age groups and asked them to perform congruent and noncongruent bimanual movements in a Real condition, where participants moved both hands, and in an Imagery condition, where they had to imagine 1 hand's movements while actually using the other hand. Our results showed that, with actual movement execution, the interference between motor programs of the 2 hands is higher in children (6–10 years old) than in younger adults (20–30 years old), while it tends to increase again in the elderly adults (60–80 years old). Interestingly, in the Imagery condition, the interference was present only among 10-year-old and 20- to 30-year-old participants, suggesting that motor imagery, not yet developed in young children and compromised by age in the elderly subjects, did not modulate motor performance in these last 2 groups.

Keywords: bimanual movements, coordination, motor imagery, development, aging

Bimanual movements are a peculiar feature of the human motor system, and many interactions with the surrounding environment are composed of actions performed with both hands without any visible effort. However, it has been shown that moving each hand in an asymmetric way produces interference effects caused by the reciprocal influence of different motor programs of each hand (Chan & Chan, 1995). A fundamental discovery is that bimanual coordination follows intrinsic dynamics where specific patterns are spontaneously adopted because they are more stable and efficient. An example of these dynamics is represented by in-phase (e.g., flexing both index fingers) or antiphase movements (e.g., extending one index finger and flexing the other). In-phase movements are well

executed at both low and high speed, while antiphase movements are well executed only at low speed and tend to shift to in-phase movements at high speed (Kelso, 1984; Kelso & Schöner, 1988). This interference effect between hands is thought to reflect interactions between two different motor programs (Heuer, 1993; Wolpert & Ghahramani, 2000), but also a conflict between perceptual goals related to each hand rather than intrinsic motor conflicts (Mechsner, Kerzel, Knoblich, & Prinz, 2001). A classic example of this interference effect (also called *coupling*) in the spatial domain is the case in which one subject is asked to draw simultaneously circles with one hand and lines with the other (Franz, 1991; Franz, Zelaznik, & McCabe, 1997). Kinematic components of both programmed movements interfere with each other, and the result is that both hands' trajectories tend to become oval (i.e., the lines tend to become circles and circles tend to become lines). Even if the ability to move both arms with simple symmetric movements is present during the first year of life, more complex bimanual asymmetric movements seem to appear in 24-month-old children (Fagard & Jacquet, 1989). This bimanual skill tends to continuously develop during the teen and adolescence years. Normative data on a classic dexterity test, the Purdue Pegboard, has shown a monotonic increase of bi-

manual coordination from 2-year-old to 11-year-old children (Wilson, Iacoviello, Wilson, & Risucci, 1982). While the Purdue Pegboard focuses on a general index of coordination, other studies have explored selectively spatial aspects of bimanual coordination during development. One of the first studies on drawing tasks in children showed that using both hands simultaneously led to errors in performing specific movements like copying parallel oblique lines (Abercrombie, Lindon, & Tyson, 1968). After this observation, different developmental studies focused on the difference between mirror (i.e., each hand moves toward an opposite “mirrored” direction, for instance one hand toward the left and the other toward the right in respect to the body midline) and parallel (i.e., each hand moves toward the same direction, for instance both hands toward the left) bimanual movements showing that drawing accuracy is higher in mirror versus parallel movements in 7-year-old children but that these differences decrease significantly in 8- to 10-year-old children (Fagard, 1987; Fagard, Hardy, Kervella, & Marks, 2001; Fagard & Pez , 1992; Hauert & Steffen, 1987); furthermore, developmental advancements with mirror movements are earlier obtained than advancements with parallel bimanual movements during childhood (Fagard & Corroyer, 2003). Indeed, mirror movements are most prominent in young children (Utley & Steenbergen, 2006) but tend to disappear during the first decade of life (Lazarus & Todor, 1987). Other studies have used variations of the bimanual coordination task developed by Preilowski (1972, 1975), in which each hand moves a handle linked to a specific coordinate axis (i.e., one hand for the *x*-axis and the other hand for the *y*-axis) to draw pictures. Results with this task showed that bimanual coordination, both in speed and accuracy, significantly increases with age, from 6 to 13 years old and from 6 to 15 years old (Steese-Seda, Brown, & Caetano, 1995, and Marion, Kilian, Naramor, & Brown, 2003, respectively). Furthermore, conditions requiring more asymmetric performance between hands and conditions without visual feedback significantly worsen bimanual performance (Marion et al., 2003). With the same task, it has been found that older adults, between 60 and 85 years old, did not perform as well as the younger adults, between 19 and 29 years old (Moes, Jeeves, & Cook, 1995). In general, bimanual coordination in the elderly population, 60–80 years old, tends to be poorer than in the younger population, 20–30 years old (Serrien et al., 2000; Stelmach, Amrhein, & Goggin, 1988; Swinnen et al., 1998; Temprado, Swinnen, Carson, Tourment, & Laurent, 2009).

Functional imaging studies have shown that asymmetric bimanual movements, compared to symmetric ones, correspond to a greater activation in a right frontoparietal circuit including the supplementary motor area, premotor cortex, and inferior and superior parietal lobules (Sadato, Yonekura, Waki, Yamada, & Ishii, 1997; Wenderoth, Debaere, Sunaert, Van Hecke, & Swinnen, 2004). These areas seem to be involved in motor intention and planning (Fried, Mukamel, & Kreiman, 2011; Lau, Rogers, Haggard, & Passingham, 2004) as well as in motor control and awareness (Berti et al., 2005). From a developmental point of view, it is important to update this motor control system taking into account the height, weight, and musculoskeletal changes, especially during childhood and adolescence (Caeyenberghs, Wilson, van Roon, Swinnen, & Smits-Engelsman, 2009). Indeed, different imaging studies have found that the primary sensory-motor cortex develops

early, within the first year after birth, while frontoparietal areas involved in motor control continue to mature between 6 and 10 years of age, reaching their peak after puberty (Gogtay et al., 2004; for a review see Casey, Galvan, & Hare, 2005). On the other hand, frontal and parietal regions tend to deteriorate with age in terms of gray and white matter loss (Seidler et al., 2010), and it has been found that these areas show a greater decline compared to temporal and occipital regions even in healthy elderly adults (Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003).

Bimanual movement tasks are not only important tools to evaluate the maturity of motor coordination at different ages but can also be used to evaluate the development of other fundamental aspects of motor system function, such as the ability to imagine an action.

Motor imagery is defined as an active cognitive process in which movements are mentally represented without any overt body movements (Decety & Grezes, 1999), and it has been shown to be an important way for learning a new motor skill or improving motor abilities (Guillot et al., 2009; Reiser et al., 2011). Over the past decade, psychophysical and neuroimaging research on motor control have shown that there are striking similarities between real and imagined movement processes. For instance, in the behavioral domain, the time to complete an imagined movement is known to be similar to the time needed for the actual execution of that movement (Decety et al., 1989; Frak et al., 2001; Sirigu et al., 1995), a phenomenon known as mental isochrony (for a review, see Parsons, 2001). According to the proposal that imagined movements obey the same biomechanical laws as real movements, many neuroimaging studies have reported substantial overlap of brain regions activated during both motor imagery and motor execution (Ehrsson, Geyer, & Naito, 2003; Gerardin et al., 2000; Jeannerod, 1994, 1997). Recently, using radial pointing and mental rotation tasks in a group of 7- to 12-year-old children, it has been shown that the relationship between motor imagery and motor skill becomes stronger with age (Caeyenberghs et al., 2009). Moreover, while timing correspondence between executed and imagined movements is poor in 6- and 8-year-old children, it improves around the age of 10 and tends to be robust in 22-year-old adults (Skoura, Vinter, & Papaxanthis, 2009). The skill to imagine body movements becomes weaker in older adults, after 64 years old, in particular for first-person (i.e., from the same point of view from which we see our performed movements) imagined movements (Mulder, Hochstenbach, van Heuvelen, & den Otter, 2007).

Although many studies have evaluated the development of motor imagery ability when unimanual action was requested, to the best of our knowledge, the effect of imaging movement of one hand on the motor execution of the other hand has never been explored in child populations. Therefore the question is how bimanual coupling develops through age and in particular when it becomes observable in imagery condition.

In the present study we addressed different experimental questions about the development of both execution and imagery ability in bimanual actions, using a specific task in which subjects through different age groups (between 6 and 80 years old) were asked to draw (or imagine drawing) circles with their left hand while simultaneously drawing lines with their right hand. Our assumption was that if we observed a coupling effect in the imagery condition, then the amount of interference could be considered a direct indicator of imaging abilities. First, since the frontoparietal

network underlying motor control completely develops during adolescence and seems to deteriorate in elderly populations, we hypothesized that a bimanual coupling effect would be higher during childhood and old age while decreasing during adulthood. Second, if motor imagery triggers the same motor intention/programming cascade of events as motor execution, we also expected to find a bimanual coupling effect when bimanual movements were characterized by an actual movement with the right hand and an imagined movement with the left hand. If this proved to be true, we also wanted to know whether the same development found in bimanual actual performance through different ages would be present in the Imagery condition.

Method

Participants

Child participants were recruited from a primary school in a middle-class area in Turin, Italy. Adult participants were recruited from undergraduate and postgraduate students, with a middle socioeconomic status, at the University of Turin. Elderly participants were recruited from families of undergraduate and postgraduate students, with a middle socioeconomic status, in Turin. All groups' populations were represented by white Caucasian people and were native Italian speakers. All participants had no history of psychiatric or neurological illness, and all were right-handed. From these populations four groups were formed: 6 years old group ($n = 20$; mean age = 5.45; $SD = 0.5$; males = 10; females = 10), 10 years old group ($n = 20$; mean age = 9.45; $SD = 0.49$; males = 10; females = 10), 20–30 years old group ($n = 20$; mean age = 24.5; $SD = 3$; males = 10; females = 10), and the 60–80 years old group ($n = 20$; mean age = 75.5; $SD = 6.5$; males = 10; females = 10).

Where possible, participants completed an explicit test for motor imagery skills. In order to assess the motor imagery subjective abilities in young participants (20–30 years old), we gave them a translated version of the Movement Imagery Questionnaire–Revised Second version (MIQ-RS; Gregg, Hall, & Butler, 2010). In this test, each item entails performing a movement, visually or kinesthetically imagining that movement, and then rating the ease or difficulty of generating that image on a 7-point scale ranging from 1 (*very hard to see/feel*) to 7 (*very easy to see/feel*); the global score is calculated as a mean of the answers. According to the MIQ-RS, all young participants reported high motor imagery subjective abilities (visual scale Mean \pm $SD = 6.2 \pm 0.2$; kinesthetic scale Mean \pm $SD = 5.8 \pm 0.2$). To assess motor imagery skills in the elderly group (60–80 years old), we administered a translated version of the Kinesthetic and Visual Imagery Questionnaire (KVIQ-10; Malouin et al., 2007). Exactly as in the previous test, each item of the KVIQ-10 entails performing a movement, then visually and kinesthetically imagining it, and then rating the imagery performance on a 5-point scale ranging from 1 (*very hard to see/feel*) to 5 (*very easy to see/feel*); the global score is calculated as the total sum of the answers. According to the KVIQ-10, all elderly participants reported medium motor imagery subjective abilities (visual scale Mean \pm $SD = 15.7 \pm 0.9$; kinesthetic scale Mean \pm $SD = 14.9 \pm 0.8$).

No explicit standardized motor imagery test for children was found, so the 6-year-old and 10-year-old groups could not be tested.

Materials and Procedure

While blindfolded, each participant was asked to perform bimanual movements in different conditions that required continuous drawing of vertical lines and/or circles, without interruption, for 12 s per trial. Each participant sat in front of a table, upon which we put the tablet PC positioned to the right of the participant's sagittal midline. Subjects were always asked to draw vertical lines with the right hand, and only right-hand movements were registered on the tablet. When bimanual movements were requested, the left hand had to draw on a sheet of paper. For each trial, movement trajectories were automatically recorded by the tablet PC for the right hand, and an Ovalization Index (OI) was calculated as the standard deviation of the right-hand trajectory from an absolute vertical line. The definition of the OI required that the raw measured trajectories be preliminarily elaborated by removing confounding factors (slow lateral drift and inclination of the vertical drawing direction). The drawing performance was then segmented by identifying each cycle. The OI was finally computed as the average of the percentage ratio between the standard deviation of the horizontal drawing component and standard deviation of the vertical drawing component. The OI shows null values for drawings without ovalization and 100 values for circular trajectories (for a precise description of the OI computation, see Garbarini et al., 2012).

Conditions. Participants, blindfolded, were asked to perform bimanual congruent or noncongruent movements. In congruent movements, subjects were requested to draw lines with both hands, while in noncongruent movements the right hand drew lines while the left hand drew circles. Participants performed these tasks under two different modalities: real execution, where subjects were asked to actually perform the bimanual tasks with both hands, and motor imagery, where subjects were asked to actually perform right-hand movement and, simultaneously, to imagine performing movements with the left hand. Thus, the complete experimental design was composed of these four conditions (see Figure 1):

1. Real Congruent Lines-Lines (R-LL): Subjects were asked to simultaneously draw vertical lines with both hands.
2. Real Noncongruent Circles-Lines (R-CL): Subjects were asked to simultaneously draw vertical lines with the right hand and circles with the left hand.
3. Imagery Congruent Lines-Lines (I-LL): Subjects were asked to draw lines with the right hand while imagining that they were simultaneously drawing lines with the left hand.
4. Imagery Noncongruent Circles-Lines (I-CL): Subjects were asked to draw lines with the right hand while imagining that they were simultaneously drawing circles with the left hand.

For each condition, six trials were registered, for a total of 24 trials, presented accordingly to the following counterbalanced se-

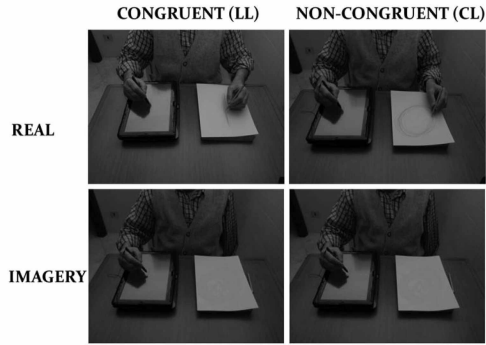


Figure 1. Experimental design. All participants actually performed congruent (lines-lines) movements (upper left corner), actually performed bimanual noncongruent (circles-lines) movements (upper right corner), imagined left-hand movements (lines) while performing actual movements (lines) with the right hand (lower left corner), and imagined left-hand movements (circles) while performing actual movements (lines) with the right hand (lower right corner).

quence: six Real (R-LL/R-CL randomized), six Imagery (I-LL/I-CL randomized), six Imagery (I-LL/I-CL randomized), and six Real (R-LL/R-CL randomized). Because it might be difficult to imagine a particular movement never tried before, the Imagery condition always followed the Real bimanual condition in all participants, leading to a counterbalanced design. We also assessed the general understanding of the Imagery task, explaining the task again and asking questions about its comprehension before the first Imagery block.

It is worth noting that participants' left arm, during the Imagery task, rested on their left side, aligned with their trunk, and participants did not hold the pen with their left hand. They were instructed to do this because we observed that it is possible, especially in young children, to let an involuntary movement start (i.e., performing circles) when imagining to perform movements (i.e., imaging circles), so we wanted to prevent this situation from happening.

To analyze our data, we performed a mixed analysis of variance (ANOVA), with a significance threshold of 0.05, and to further analyze significant interactions or main effects, we used a Duncan's multiple range post hoc test.

Results

We compared the four experimental groups, using the OI as the dependent variable and performing a $2 \times 2 \times 4$ mixed ANOVA with Task (Real and Imagery) and Condition (Congruent LL and Noncongruent CL) as two-level within-subject factors and Age group (6, 10, 20–30, 60–80) as a four-level between-subjects factor.

The ANOVA found main effects of Age group, $F(3, 76) = 11.5$; $p < .001$, $\eta_p^2 = .31$; Task, $F(1, 76) = 46.2$; $p < .001$, $\eta_p^2 = .38$; and Condition, $F(1, 76) = 89.1$; $p < .001$, $\eta_p^2 = .54$, and the significant interactions of Age Group \times Task, $F(3, 76) = 5.34$; $p = .002$, $\eta_p^2 = .17$; Task \times Condition, $F(1, 76) = 45.8$; $p < .001$, $\eta_p^2 = .38$; and Group \times Task \times Condition, $F(3, 76) = 6.3$; $p < .001$, $\eta_p^2 = .20$ (see Figures 2 and 3). The significant main effect of the Age group factor is explained by a reduction of the coupling effect, that

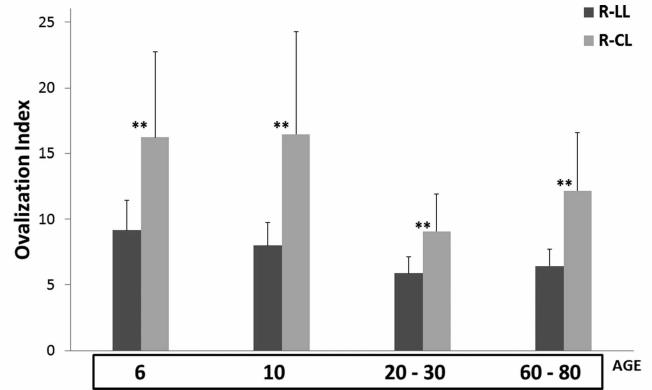


Figure 2. Real task results. The x-axis shows the four studied groups (6-, 10-, 20- to 30-, and 60- to 80-year-olds), and the y-axis the calculated Ovalization Index. Dark gray bars represent the Congruent condition, where subjects drew lines with both hands (R-LL). Light gray bars represent the Noncongruent condition, where subjects drew lines with the right hand and circles with the left hand (R-CL). ** $p < .01$. Error bars represent the standard error of the mean.

is, a reduction of the OI, between children (6- and 10-year-old groups) and adults (20- to 30-year-old and 60- to 80-year-old groups). The significant main effect of the Task factor was explained by a reduction of the OI from the Real situation, where subjects actually performed movements with both hands, to the Imagery situation, where subjects imagined left-hand movements and performed only right-hand movements. Finally, the significant main effect of the condition factor was explained by an increase of the OI from the Congruent (LL) condition to the Noncongruent (CL) condition.

Since the Group \times Task \times Condition interaction encompassed all the other interactions, we further analyzed it using a Duncan's post hoc analysis: Relevant results are discussed below. In the Real

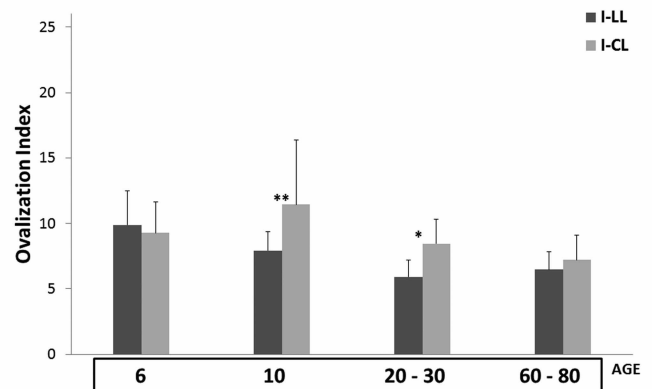


Figure 3. Imagery task results. The x-axis shows the four studied groups (6-, 10-, 20- to 30-, and 60- to 80-year-olds), and the y-axis the calculated Ovalization Index. Dark gray bars represent the Congruent condition, where subjects drew lines with the right hand and imagined lines with the left hand (I-LL). Light gray bars represent the Noncongruent condition, where subjects drew lines with the right hand and imagined circles with the left hand (I-CL). * $p < .05$. ** $p < .01$. Error bars represent the standard error of the mean.

task, Duncan's post hoc comparisons confirmed the presence of the bimanual coupling effect (i.e., significant increase of the OI value in Noncongruent R-CL versus Congruent R-LL condition) in all four groups (for each comparison, $p < .01$), showing the presence of this effect through all the different ages analyzed. In the Real Congruent condition R-LL, no difference was found between the four groups (for each comparison, $p > .08$), while in the Real Noncongruent condition R-CL we found a significant difference between child (6- and 10-year-old groups) and adults (20- to 30-year-old and 60- to 80-year-old) groups (for each comparison, $p < .004$), showing a decrease of coupling effect from children's groups to adults' groups. No difference was found in R-CL condition between 6- and 10-year-old children ($p = .1$) and between the 20- to 30-year-old and 60- to 80-year-old groups, although, in this case, the comparison approached significance ($p = .06$; see Figure 2).

In the Imagery task, Duncan post hoc comparisons confirmed the presence of the bimanual coupling effect (i.e., significant difference between Congruent I-LL and Noncongruent I-CL conditions) only in the 10-year-old ($p = .004$) and 20- to 30-year-old groups ($p = .04$). No significant differences between I-LL and I-CL were found in the 6-year-old group or in the 60- to 80-year-old group (for each comparison, $p > .5$; see Figure 3).

Comparing Real with Imagery tasks, we found no significant differences in all four groups between R-LL conditions and I-LL conditions (for each comparison, $p > .5$) suggesting that congruent bimanual movements have the same effect in real and imagined conditions through all the analyzed ages. In the 6, 10, and 60- to 80-year-old groups, significant differences were found between R-CL and I-CL (for each comparison, $p < .001$) with R-CL having a higher Ovalization Index than I-CL. Only in the 20- to 30-year-old group was no significant difference observed between R-CL and I-CL ($p = .6$), suggesting that noncongruent movements have the same effect in both Real and Imagery conditions only in the young-adults group.

Finally, even though counterbalancing within participants is adequate for a complete repeated-measure design like ours (Shaughnessy, Zechmeister, & Zechmeister, 2006), since conditions followed a specific order we checked possible learning effects between them. Thus, we confronted the difference between C-L and L-L (i.e., the coupling effect) in the first block of trials versus the same coupling effect in the last block of trials, performing a Student pairwise t test. The analysis showed that three out of the four groups presented a significant reduction of the coupling effect (i.e., a motor learning component) between the first and the last trials of the experiment: the 6-year-old group, $t(19) = 3.5$, $p = .002$; the 20- to 30-year-old group, $t(19) = 3.4$, $p = .003$; and the 60- to 80-year-old group, $t(19) = 3.27$, $p = .004$. Only the 10-year-old group did not show a learning effect between the first and the last trials. Since two groups that showed a learning effect did not show any effect in the motor imagery task (the 6- and 60- to 80-year-old groups), and one group that did not show a learning effect had a significant effect in the motor imagery task (the 10-year-old group), we can conclude that learning components did not influence motor imagery. This learning effect was, however, corrected by the counterbalanced design (i.e., the first, less precise, trials were balanced by the last, more precise, trials).

Discussion

In the current study we compared four different age groups (6-, 10-, 20- to 30-, and 60- to 80-year-olds) using a bimanual spatial task to better understand the development of bimanual coordination. We used the same task to also study the evolution of motor imagery, specifically the effect of motor imagery on bimanual movements, through the same four age groups. Our results showed that bimanual coupling effects are present in all the groups considered but were significantly higher in children and elderly adults and that the impact of motor imagery on bimanual movements had a significant effect only in 10-year-old and 20- to 30-year-old participants.

In particular, in the Real task, where participants actually performed movements with both hands, our results confirmed the presence of bimanual coupling in all four age groups considered, suggesting that interference between different motor programs is a consistent effect through all of one's life. Furthermore, our data indicated that the strength of this coupling effect changes across different ages: It was found to be significantly higher in children (6 and 10 years old) than in adults (20–30 and 60–80 years old), and it tends to be stronger in elderly than in young adults. The first finding is consistent with the previous research concerning frontoparietal network and its importance in motor control development. Indeed, it has been shown, in children between 8 and 16 years old, that frontal lobe epilepsy compared with temporal and global epilepsy, leads to more coordination deficits, in particular for younger children between 8 and 12 years old (Lassonde, Sauerwein, Jambaqué, Smith, & Helmstaedter, 2000). Furthermore, frontoparietal areas mature and fully develop between 6 and 10 years of age (Gogtay et al., 2004). Our results, showing a decrease in coupling effect from children to young adults, can be explained by these neuro-anatomical findings. We also found that a bimanual coupling effect is still present in the elderly group (60–80 years of age), and its effect tends to be higher than the young adults' effect. This slight tendency could be linked to frontal-parietal deterioration shown in the elderly population (Temprado et al., 2003) and could be related to a difficulty in suppressing the preferred (i.e., congruent) bimanual coordination modes observed in this population (Swinnen et al., 1998). However, in our study, it seems that this deterioration did not lead to a significant variation in the coupling effect. This last result can be explained by a recent study in which it has been shown that, during complex bimanual movements, older adults (61–79 years old) tend to overactivate the same frontoparietal areas active in younger adults (21–31 years old), presumably as a compensation mechanism (Goble et al., 2010).

In the Imagery task, we asked participants to perform movements with their right hand and to simultaneously imagine movements with their left hand, without actually executing them. This task let us investigate the influence of motor imagery on this spatial bimanual task. Our results showed that, when the motor imagery ability is more developed and stable, as in young adults and older children, the imagined movement imposes constraints on the real movement that are similar to those encountered during the actual execution of the bimanual task. According to the literature, which has suggested striking similarities between real and imagined movements from both a

psychophysical and a neuroimaging point of view (Ehrsson et al., 2003; Jeannerod, 1994), our findings suggest that motor imagery triggers the same motor intention/programming cascade of events as does motor execution. Furthermore, our experimental paradigm allowed us to quantify the participants' motor imagery ability and to compare different age groups with respect to it. In the Imagery task we found a significant bimanual coupling only in the group of 10-year-old children and in the young adults' group (20–30 years old). The lack of effect in the group of little children (6 years old) can be ascribed to the fact that during this age motor imagery ability is not yet developed enough to cause a coupling effect. According to the literature (Bideaud & Courbois, 1998; Molina, Tijus, & Jouen, 2008), it has been suggested that there is a sort of age cutoff for motor imagery development around 7 years of age: Children younger than this have difficulty imagining themselves acting unless the simulated activity is sustained by their actual activity. In other words, once children stop acting, they also lose the ability to think about themselves acting. On the contrary, after 7 years of age, children seem to be able to evoke motor imagery independently of any real motor activity. Our data confirmed the absence of a detectable influence on bimanual coordination, at least for the test we employed, before 7 years of age and the emergence of it after this age. Indeed, we did not find any coupling effect in the imagery condition in 6-year-old children; whereas older children (10 years old) showed a significant coupling effect, implying a development of the motor imagery skill. This imagery coupling effect was still present in the 20- to 30-year-old group, but while in the 10-year-old group we found a higher coupling effect in the Real condition versus the Imagery condition, the young-adults group showed no differences between real and imagined bimanual movements, suggesting a more complete and stable development of motor imagery during early adulthood. In a previous study, we did not observe a significant bimanual coupling effect for the Imagery condition in an elderly group, tested as age-matched healthy controls for the brain-damaged patients (Garbarini et al., 2012). Similarly, in this study we did not find a significant coupling effect for the Imagery condition in the elderly group between 60 and 80 years old. These findings, suggesting that motor imagery ability may decline with age, are consistent with a study of Mulder and colleagues (2007), who showed that elderly participants, over 64 years old, were worse in motor imagery ability than younger participants, particularly in relation to motor imagery from an internal (first-person) perspective, as in our bimanual test.

These final results show that actual and imagined bimanual movements only partially follow the same development. In our view, the amount of coupling/interference effect observed is an inverse measure of the motor control during actually performed movements (i.e., the higher the effect, the lower the simultaneous control over both hands), but it could also be considered a direct measure of the imagery skill of the subjects (i.e., the higher the effect, the higher the skill to use an imagined movement to elicit an effect on an actually performed movement). From a cerebral point of view, frontoparietal areas involved in motor control are already developed enough to elicit, by actually performed movements, a coupling effect of the same size between 6 and 10 years old. Instead, a coupling

effect in motor imagery appears only around 10 years old, suggesting that the development of other critical structures could be involved in this latter cognitive process. In young adults, between 20 and 30 years old, the frontoparietal network is stable enough to maintain the lower coupling effect observed through all groups that actually performed movements and is also developed enough to elicit the same effect during the Imagery task. Furthermore, even if frontal and parietal regions start to deteriorate in the elderly population, a coupling effect in these subjects is only slightly worse (higher) than the effect in younger subjects, probably because of an overactivation of the same areas linked to a major effort during motor control (Goble et al., 2010). In Imagery conditions, instead, the coupling effect tends to disappear in older adults, suggesting in this case that the overactivation of these areas may not be enough to maintain an intact motor imagery skill. Yet, an imagery coupling effect depletion in elderly subjects could still be explained with the deterioration of other cortical structures within this population.

As a limitation of the study, it has to be taken into account that other indirect measures of motor imagery (i.e., MIQ-RS and KVIQ-10) failed to correlate with our bimanual task results, thus making it hard to collect a second subjective measure of the motor imagery skill. Specifically, the ceiling effect found in adults and the difficulty found in applying a subjective test to young children could have both affected the validity of our results. Furthermore, we are aware that four age groups do not fully represent all the developmental stages from childhood to old age, and more differentiation between groups could help us in better interpreting our results and generalizing them from the experimental sample to the real population. Future developmental studies on coupling effect using methods, like functional magnetic resonance imaging, and more differentiation between age groups, especially in the critical younger and older groups, could furthermore enlighten the cerebral relationship between real and imagined bimanual movements through development.

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