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RESEARCH ARTICLE

Developmental changes of the biomechanical effect in motor imagery

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Abstract Motor imagery has been investigated in childhood and early adolescence, but not across adolescence stages; moreover, available evidence did not clarify whether the involvement of motor information in mental rotation of body parts becomes stronger or weaker during development. In the present study, we employed the hand laterality task to assess motor imagery in ninety-seven typically developing adolescents divided into three age groups (i.e., 11–12, 14–15, and 17–18 years); mental rotation of objects and letters were also assessed. As a specific marker of the motor involvement in mental rotation of body parts, we assessed the so-called biomechanical effect, that is, the advantage for judging hand pictures showing physically comfortable positions with respect to hand pictures showing physically impossible or awkward positions. Results demonstrated that the biomechanical effect did not significantly affect early adolescents' performance, whereas it became significant in 14- to 15-year-old participants and even more stronger in 17- to 18-year-old participants; this pattern did not depend on an increase in processing speed to mentally rotate both corporeal and non-corporeal (objects and letters) stimuli. The present findings demonstrated that: (1) motor imagery undergoes a continuous and progressive refinement throughout adolescence, and (2) full exploitation of motor information to mentally transform corporeal stimuli can be attained in late adolescence only.

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Introduction

The development of motor imagery in children and early/middle adolescents has been investigated by means of different paradigms with contrasting results. Some studies measured correlation between the duration of actual movement execution and duration of imagined movements. This approach provided consistent evidence of an age-dependent increase in execution/imagery time coupling, thus supporting the idea that the ability to use motor strategies in action simulation gradually increases from childhood to early and middle adolescence (Caeyenberghs et al. 2009a, b; Choudhury et al. 2007a, b). These results fit with data obtained in some mental rotation experiments, showing that the contribution of motor processes to mental transformation of body parts becomes stronger during development (Caeyenberghs et al. 2009a). However, other mental rotation paradigms provided opposite results (Frick et al. 2009a; Funk et al. 2005; Krüger and Krist 2009). Funk et al. (2005) required 5- to 6-year-old children and young adults to mentally rotate hands while holding their own hands in different positions and found that hand posture affected children more than adults. Frick et al. (2009a) required 5-, 8-, and 11-year-old children and adults to execute a mental rotation task while performing a circular movement with their dominant hand. The authors found stronger motor effects in 5- and 8-year-old children than in 11-year-old children and adults. Krüger and Krist (2009) assessed performance of kindergarteners (aged 5–6 years), first graders (aged 7 years), and adults on mental rotation of body parts and found motor effects in all age groups, but analysis of response times suggested that the involvement of

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motor information was larger in children (7-year-olds) than in adults. Moreover, Krüger and Krist (2009) confirmed that 5-year-old children were slower and less accurate than a group of university students in mentally rotating hands. In a cross-sectional study assessing the development of motor imagery from childhood to early adolescence, Caeyenberghs et al. (2009a) showed that 7- to 8-year-old participants were slower and less accurate than 9–10 and 11- to 12-year-old children in mentally rotating hands and letters, whereas there were no differences between 9–10 and 11- to 12-year-old children.

From this brief review, it appears that developmental studies on mental rotation of body parts did not clarify whether the involvement of motor information in task performance becomes stronger or weaker during childhood, likely because of heterogeneity in experimental paradigms (and task difficulty) and in age groups undergoing motor imagery experiments.

In the present study, we aimed to investigate developmental changes in the contribution of motor information to mental rotation of body parts, by assessing motor imagery performance of healthy subjects from an age range not specifically studied hitherto (Gabbard 2009). In particular, we recruited adolescents of three age groups, that is, early (11- to 12-year-old), middle (14- to 15-year-old), and late (17- to 18-year-old) adolescence and adopted the classical hand laterality task that allows to analyze the influence of anatomical/biomechanical constraints on participants' performance.

In the hand laterality task, subjects are required to judge laterality of hand stimuli (i.e., to decide whether a hand stimulus is left or right); hands are presented in different spatial orientations, and psychophysical studies on adults demonstrated that subjects perform the task by mentally simulating movements of their own hands (Parsons 1987, 1994; Sekiyama 1982). In this task, the effect of biomechanical constraints determines faster response times when subjects have to judge hand pictures showing physically comfortable positions compared to pictures showing physically impossible or awkward positions (Cooper and Shepard 1975; Parsons 1987, 1994; Sekiyama 1982). More precisely, participants are consistently faster in judging a 90° oriented left hand (fingers pointing to the right) than a right hand at the same orientation; analogously, participants show an advantage when judging a 270° oriented right hand (fingers pointing to the left) with respect to the left hand at the same orientation (Conson et al. 2009; Cooper and Shepard 1975; de Lange et al. 2006; Parsons 1987, 1994; Sekiyama 1982; for evidence showing analogous effects of body constraints on different motor imagery tasks, see Bakker et al. 2008; Gabbard et al. 2007). The significant effect of biomechanical constraints, as revealed by a significant interaction between hand laterality (right or left hand stimulus) and spatial orientation (90° or 270° oriented hand), is thought to be a hallmark of the involvement of motor information in mental transformation of body parts (Parsons 1987, 1994; de Lange et al. 2006; Sekiyama 1982; van Nuenen et al. 2012); moreover, it has been reported that palms are more effective than backs in triggering motor information to mentally rotate hands (Krüger and Krist 2009; Parsons 1987, 1994). The biomechanical effect is not found in brain-damaged patients with severe lesions of the motor system (Conson et al. 2008, 2010). If the involvement of motor processes in hand rotation becomes stronger with development, then we should find a robust biomechanical effect in older and a weak effect in younger adolescents. The alternative hypothesis (i.e., motor contribution becomes weaker with development), instead, would receive support from the opposite pattern.

In order to verify whether developmental changes in motor imagery are specific to the transformation of body parts or involve other instances of mental rotation, we also assessed mental rotation of objects and letters (see also Krüger and Krist 2009). We could thus verify whether the exploitation of motor information in transformation of body parts is also accompanied by a general increase in processing speed or by an improvement of mental rotation efficiency. To clarify these issues, we verified whether participants performed all the mental rotation tasks by employing a rotation strategy, as shown by a linear increase in response times as a function of stimuli's spatial orientation (Shepard and Metzler 1971; Shepard and Cooper 1982). Moreover, we analyzed performance on stimuli in canonical orientation (0°-trials) that only require perceptual encoding and decision processes, and computed mental rotation speed for tilted stimuli (90°, 180°, and 270° trials) in each task (Frick et al. 2009a).

Methods

Participants

For the present study, we recruited students attending a Italian secondary school. Inclusion criteria were right-handedness, lack of present or past clinically evident neurological or psychiatric disorders, and normal general intelligence (Full Scale IQ: mean = 94.8, SD = 4.2), without significant differences (less than 15 points) between Verbal IQ and Performance IQ on the Wechsler Intelligence Scale for Children-Revised (WISC-R, Orsini 1993).

Our sample consisted of 97 normal participants (47 males and 50 females). As a function of age, the participants were divided into three groups: thirty-one early adolescents (11–12 years; mean age = 11.52; 15 males and 16 females), thirty-two middle adolescents (14–15 years; mean age = 14.5; 16 males and 16 females), and thirty-four late adolescents (17–18 years; mean age = 17.59; 16 males and 18 females). Individuals aged 13- and 16-year-old were not included to get the three groups well separated in terms of age. Full Scale IQ did not differ among age groups (independent samples *t* tests, all $t < 1$). All participants were unaware of purposes and predictions of the experiment at the time of testing. The study was conducted in accordance with the ethical standards of Declaration of Helsinki.

Experimental tasks

The participants included in the study underwent three mental rotation tasks employing: (1) hands, (2) objects, and (3) letters, presented in four possible orientations (0°, 90°, 180°, or 270° in clockwise direction); care was taken to keep dimensions of the stimuli roughly constant across the tasks (widest axis about 5.5 cm, visual angle about 6.5°; see Fig. 1). The three tasks were administered by means of a computerized procedure and were arranged to be as similar as possible in presentation and response modalities, although specific instructions differed (see below).

In the hand rotation task, stimuli were line drawings depicting left or right hands viewed from two perspectives (back or palm), and participants were required to decide whether each stimulus represented a left or a right hand. In the object (car) rotation task, stimuli consisted of the frontal view of two cars with a black patch on either the left or the right headlight; participants had to decide whether the black patch was placed on the car's right or the left headlight. In the letter rotation task, stimuli consisted of two capital letters (G and P) presented in canonical or mirror-reversed form, and participants were required to decide whether each stimulus was shown in normal or mirror-reversed form.

All stimuli were presented one at a time at the center of the monitor until response completion and were preceded by a fixation point (800 ms). A new trial started 1 s after participants' response to the previous trial. Each task consisted of 96 randomized trials: in the hand rotation, 6 trials were presented for each combination of hand view (back or palm), hand laterality (left or right), and orientation; in the object rotation, 6 trials were presented for each combination of car, position of the patch (left or right), and stimulus orientation; in the letter rotation, 6 trials were presented for each combination of letter (G or P), type of stimulus (canonical or mirror-reversed), and orientation.

Procedure

Participants were seated about 50 cm from a 15″ computer screen and gave their responses by pressing one of two centrally located keys with their index and middle fingers of the right hand; the stimulus–response association for each task was counterbalanced across participants. The left hand was placed palm-down next to the keyboard and both hands were covered with a black cloth. Participants were encouraged to respond as fast and correctly as possible; we recorded both reaction times (RTs, in ms) and accuracy. Stimulus presentation and data collection were controlled by a PC using Cedrus SuperLab version 4.

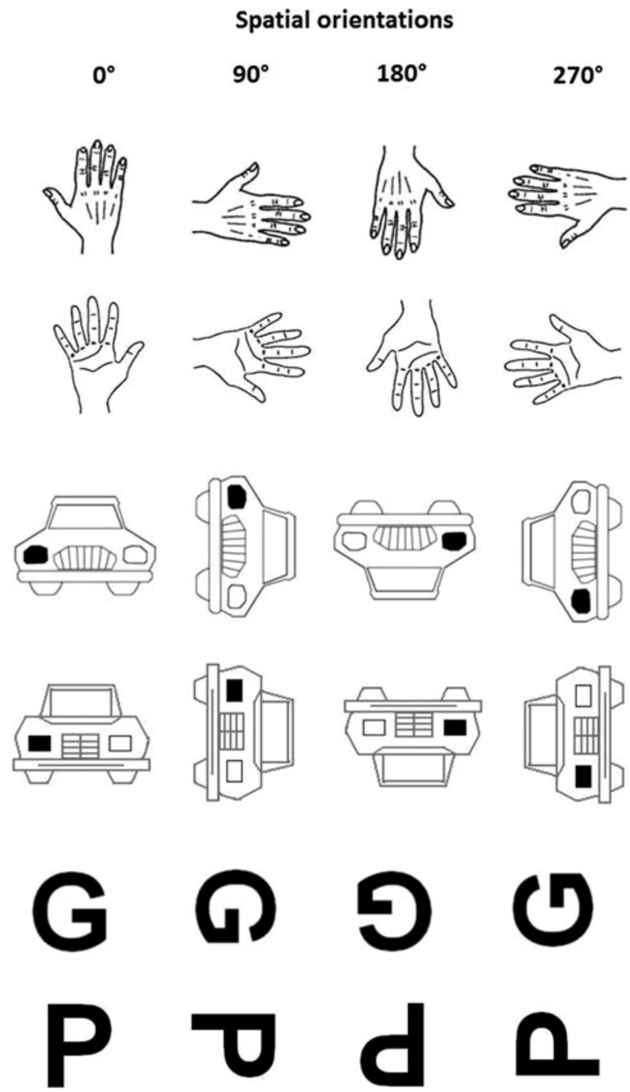

Fig. 1 Examples of stimuli used in the three mental rotation tasks: hand rotation (*first row* right hand in back posture; *second row* right hand in palm posture); object rotation (*third* and *fourth row* cars with a black patch on the right headlight); letter rotation (*fifth row* letter "G;" *sixth row* letter "P")

The order of the three tasks was counterbalanced across participants. Each task was divided into two blocks: a 3-min pause was allowed between the two blocks and after each task. A training period preceded the experiment. Before starting each task, at least eight practice trials were given; if a wrong response was provided, a feedback appeared on the monitor screen and the trial was repeated. Experimental session started only if the participants provided at least six consecutive correct responses. Testing was conducted individually, in a quite room within the school building, and lasted about 20 min.

Statistical analysis

The analysis of the hand laterality task specifically focused on the investigation of the biomechanical effect by means of a four-way mixed-design ANOVA with stimulus view (back or palm), stimulus laterality (left hand or right hand), and stimulus orientation (90° or 270°, the two spatial orientations that, in combination with hand laterality, can best reveal the effect of biomechanical constraints, as recalled above) as within-subject factors, and group (early adolescents, middle adolescents, or late adolescents) as a between-subject factor.

Following previous studies (e.g., Kosslyn et al. 1998), to test whether the participants used a mental rotation strategy, we performed planned linear contrasts on participants' correct RTs for stimulus orientations from 0° to 180°. This analysis was conducted on each experimental task, separately for the three age groups. Then, to explore the effects of developmental changes and sex on mental manipulation of different stimuli, we conducted a three-way mixed-design analysis of variance (ANOVA) with task (mental rotation of hands, objects, or letters) as a within-subject factor, and group (early adolescents, middle adolescents, or late adolescents) and sex (males and females) as between-subject factors.

To verify whether changes in mental rotation skills across age ranges were related to an increase of general cognitive resource/processing speed, we analyzed RTs on 0° trials (Frick et al. 2009a) by means of a two-way mixed-design ANOVA with the task (mental rotation of hands, objects, or letters) as a within-subject factor and group (early adolescents, middle adolescents, or late adolescents) as a between-subject factor. Moreover, to investigate whether participants' mental rotation speed changed as a function of the age range, we computed the increase in response time in ms per 1° change in stimulus orientation (Frick et al. 2009a) and submitted it to a two-way mixed-design ANOVA with task (mental rotation of hands, objects, or letters) as a within-subject factor and group (early adolescents, middle adolescents, or late adolescents) as a between-subject factor. Post hoc comparisons were performed by t tests.

A preliminary analysis was conducted to assess whether participants' performance showed any marked speed-accuracy trade-off (e.g., Sanders 1998). To this aim, Pearson's correlations between the participants' RTs and accuracy were calculated for each mental rotation task.

Table 1 Mean accuracy rates (standard deviations) of the early adolescents, middle adolescents, and late adolescents on the three mental rotation tasks

	Hands	Objects	Letters
Early adolescents	.75 (.43)	.89 (.30)	.88 (.32)
Middle adolescents	.81 (.39)	.95 (.22)	.86 (.35)
Late adolescents	.85 (.35)	.94 (.23)	.90 (.28)

Results

Percentage of correct responses (accuracy) of the three groups on the three imagery tasks are shown in Table 1. The preliminary analysis demonstrated that RTs on correct responses were negatively correlated with accuracy on all the three imagery tasks (hands: $r = -.272$, $p = .009$; objects: $r = -.328$, $p = .001$; letters: $r = -.244$, $p = .016$). These findings make unlikely the presence of a speed-accuracy trade-off in any task, thus allowing us to perform further statistical analyses on RTs data only (Sanders 1998).

Effect of biomechanical constraints on hand rotation

The four-way mixed ANOVA assessing the biomechanical effect showed significant main effects of group, $F(2, 94) = 6.025$, $p = .003$, $\eta_p^2 = .114$, showing that early adolescents were slower (M = 2,991 ms, SD = 934) than both middle (M = 2,352 ms, SD = 817) and late adolescents (M = 2,450 ms, SD = 974), and of stimulus view, $F(2, 94) = 30.933$, $p = .0001$, $\eta_p^2 = .248$, with faster RTs to backs (M = 2,440 ms, SD = 760) than to palms (M = 2,779 ms, SD = 920). Moreover, results showed a significant interaction between hand laterality and stimulus orientation, $F(1, 94) = 43.920$, $p = .0001$, $\eta_p^2 = .318$, and significant second-order interactions among stimulus laterality, stimulus orientation and group, $F(2, 94) = 4.486$, $p = .014$, $\eta_p^2 = .087$, and among stimulus view, hand laterality and stimulus orientation, $F(1, 94) = 4.390$, $p = .039$, $\eta_p^2 = .045$. Other effects, including the third-order interaction among stimulus view, hand laterality, stimulus orientation, and group, were not statistically significant (all $p > .05$).

Post hoc comparisons (paired t tests) on the interaction between stimulus laterality and stimulus orientation showed that participants were significantly faster in judging left than right 90° oriented hands (left, M = 2,303 ms, SD = 795; right, M = 2,826 ms, SD = 1,169; $p = .0001$), whereas the opposite was true at 270° orientation (left, M = 2,913 ms, SD = 1,146; right, M = 2,320 ms, SD = 759; $p = .0001$). This finding strongly reflects the effect of biomechanical constraints on mental rotation of hand stimuli (Parsons 1987, 1994; Sekiyama 1982). However, such a biomechanical effect was significant in middle and late adolescents but

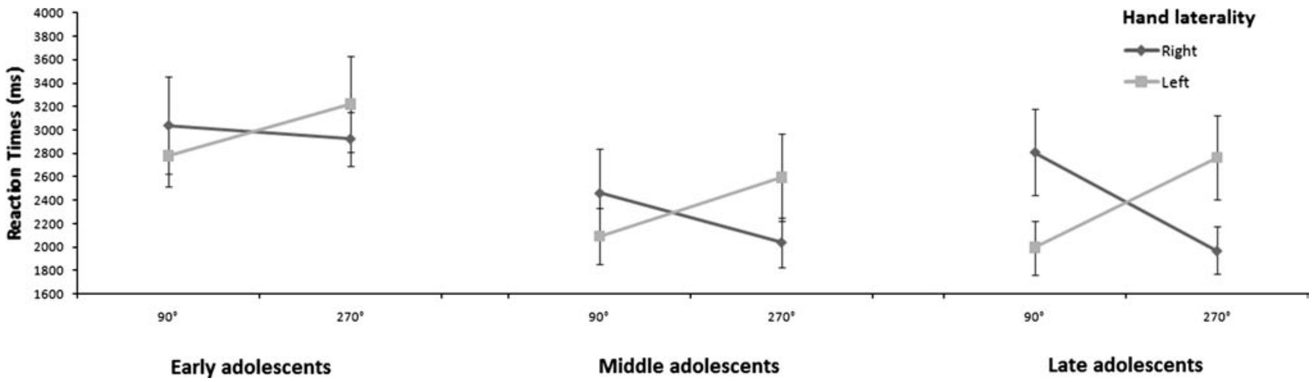

Fig. 2 Mean RTs on the hand rotation task for the three age groups by degree of stimulus orientation and hand laterality (i.e., biomechanical effect); *bars* represent 95 % CIs

not in early adolescents, as revealed by post hoc comparisons (paired *t* tests) on the interaction among stimulus laterality, stimulus orientation, and group (early adolescents: 90° left vs. right, $p = .189$, 270° left vs. right, $p = .149$; middle adolescents: 90° left vs. right, $p = .004$, 270° left vs. right, $p = .0001$; late adolescents: 90° left vs. right, $p = .0001$, 270° left vs. right, $p = .0001$; see Fig. 2).[1]

Post hoc comparisons (paired *t* tests) on the interaction among stimulus view, hand laterality, and stimulus orientation demonstrated that although the biomechanical effect was significant when participants judged both backs and palms, it was stronger on palms (90° oriented hands: left, M = 2,508 ms, SD = 1,072; right, M = 3,100 ms, SD = 1,454; $p = .0001$; 270° orientation: left, M = 3,113 ms, SD = 1,301; right, M = 2,370 ms, SD = 980; $p = .0001$) than on back views (90° oriented hands: left, M = 2,093 ms, SD = 1,085; right, M = 2,502 ms, SD = 799; $p = .0001$; 270° orientation: left, M = 2,701 ms, SD = 1,267; right, M = 2,273 ms, SD = 905; $p = .002$). It is worth recalling here that the third-order interaction among stimulus view, hand laterality, stimulus orientation, and group was not statistically significant, thus showing that the strength of the biomechanical effect in the three age groups was not influenced by stimulus view.

Effect of stimulus orientation and task on mental rotation

Results of planned linear contrasts showed that in all the three groups and on each of the three tasks, there was a significant linear trend in RTs for the increasing stimulus orientation from 0° to 180° (early adolescents: hand rotation, $F(1, 30) = 129.824$, $p = .0001$, $\eta_p^2 = .812$, object rotation, $F(1, 30) = 47.527$, $p = .0001$, $\eta_p^2 = .613$; letter rotation, $F(1, 30) = 20.069$, $p = .0001$, $\eta_p^2 = .401$; middle adolescents: hand rotation, $F(1, 31) = 34.115$, $p = .0001$, $\eta_p^2 = .524$; object rotation, $F(1, 31) = 60.116$, $p = .0001$, $\eta_p^2 = .660$, letter rotation, $F(1, 31) = 44.942$, $p = .0001$, $\eta_p^2 = .592$; late adolescents: hand rotation, $F(1, 33) = 97.352$, $p = .0001$, $\eta_p^2 = .747$, object rotation, $F(1, 33) = 93.656$, $p = .0001$, $\eta_p^2 = .739$, letter rotation, $F(1, 33) = 39.482$, $p = .0001$, $\eta_p^2 = .545$). Figure 3 shows RTs of the three age groups on hand, object, and letter rotation plotted against the four stimulus orientations (0°, 90°, 180°, and 270°).

As regards performance of boys and girls from the three age groups on the experimental tasks, results of the three-way mixed ANOVA showed significant main effects of task, $F(2, 182) = 159.347$, $p = .0001$, $\eta_p^2 = .637$, and group, $F(2, 91) = 13.187$, $p = .0001$, $\eta_p^2 = .225$; the main effect of sex, and all first-order and second-order interactions were not statistically significant (all $p > .05$). Post hoc comparisons (paired *t* tests) on the main effect of task showed that the participants' responses were slower on hands (M = 2,614 ms, SD = 914) with respect to both letters (M = 1,580 ms, SD = 549; $p = .0001$) and objects (M = 1,571, SD = 869; $p = .0001$), whereas they did not differ between letters and objects ($p = .812$). Post hoc comparisons (paired *t* tests)

[1] To verify whether the lack of a significant biomechanical effect in early adolescents could be accounted for by increased variance in their performance blurring the effect, we tested for the homogeneity of variances between the different age groups. To this aim, we first calculated difference in RTs for mental rotation of 90° oriented right (awkward position) and left hand (comfortable orientation), and the difference in RTs for 270° oriented left (awkward position) and right hand (comfortable orientation; e.g., Conson et al. 2010). Then, these delta values underwent Levene's test of homogeneity of variances between groups. Levene's test showed significantly larger variance in middle versus early adolescents on the 270° delta value ($F = 5.896$, $p = .018$), whereas all remaining comparisons were not significant (early vs. middle adolescence: 90°, $F = 1.407$, $p = .240$; early vs. late adolescence: 90°, $F = .305$, $p = .583$; 270°, $F = .342$, $p = .561$; middle vs. late adolescence: 90°, $F = 3.871$, $p = .053$; 270°, $F = 2.792$, $p = .100$). These data ruled out the possibility that the lack of a significant biomechanical effect in early adolescents could be ascribed to increased variability of their performance with respect to the other two age groups.

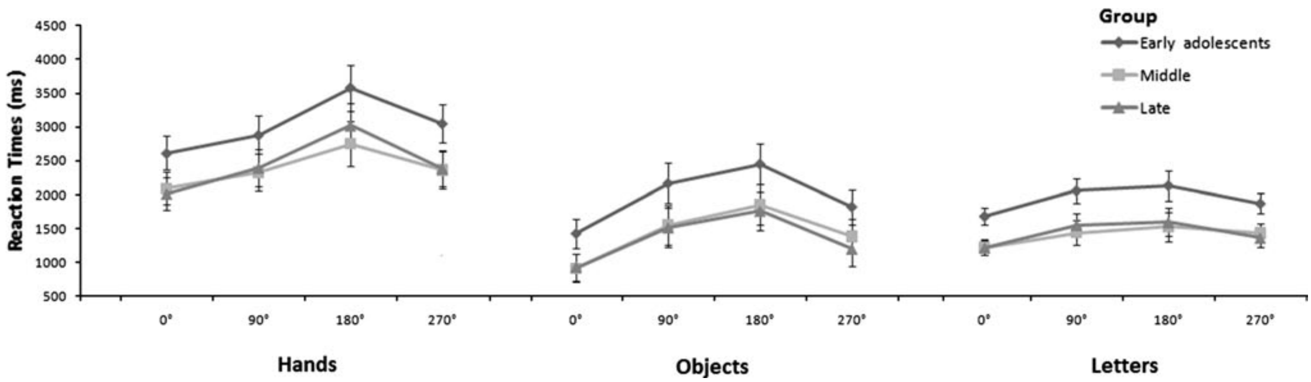

Fig. 3 Mean RTs of mental rotations of hands, objects, and letters plotted against the four stimulus orientations separately in the three age groups; *bars* represent 95 % CIs

on the main effect of group showed that early adolescents were significantly slower (M = 2,308 ms, SD = 862) than both middle (M = 1,737 ms, SD = 672; p = .0001) and late adolescents (M = 1,744 ms, SD = 647; p = .0001), whereas middle and late adolescents did not differ between each other (p = .948).

Results of the two-way mixed-design ANOVA on 0° trials showed significant effects of task, $F(2, 188) = 138.228$, $p = .0001$, $\eta_p^2 = .595$, and group, $F(2, 94) = 18.632$, $p = .0001$, $\eta_p^2 = .284$; task by group interaction was not statistically significant ($p > .05$). Post hoc comparisons (paired t tests) on the main effect of task showed that the participants were slower on hands (M = 2,240 ms, SD = 796) with respect to both letters (M = 1,369 ms, SD = 478; p = .0001) and objects (M = 1,087, SD = 756; p = .0001); moreover, they were significantly slower on letters than objects (p = .0001). Post hoc comparisons (paired t tests) on the main effect of group showed that early adolescents were significantly slower (M = 1,906 ms, SD = 673) than both middle (M = 1,407 ms, SD = 543; p = .0001) and late adolescents (M = 1,383 ms, SD = 448; p = .0001), whereas middle and late adolescents did not differ between each other (p = .788).

Results of two-way mixed-design ANOVA performed on the increase in response time in ms per 1° change in stimulus orientation showed a significant main effect of task, $F(2, 188) = 5.608$, $p = .004$, $\eta_p^2 = .056$, whereas the main effect of group and the task by group interaction were not statistically significant (all $p > .05$). It is worth noting here that the lack of a significant main effect of group was due to the absence of a relevant increase in rotation speed with increasing age (RTs increase in ms per 1° change in stimulus orientation: early adolescents: M = 1.249 ms, SD = 1.14; middle adolescents: M = 1.176 ms, SD = .85; late adolescents: M = .977 ms, SD = .59). Post hoc comparisons (paired t tests) on the main effect of task showed that the participants' speed was significantly slower on hands (M = 1.329 ms, SD = 1.86) and objects (M = 1.392 ms, SD = 1.89) with respect to letters (M = .668 ms, SD = 1.23; both $p < .006$), whereas it did not differ between hands and objects (p = .813).

Discussion

In the present study, we used the hand laterality task to assess whether the contribution of the motor system to mental rotation of hands changes across adolescence stages. Results showed a significant interaction between laterality and orientation of hand stimuli, consistent with the biomechanical effect, in middle adolescents and in late adolescents.

The lack of a significant biomechanical effect in early adolescents could suggest that they do not implement motor strategies to mentally simulate hand movements, but performed the hand laterality task by adopting alternative strategies, for example, visuospatial transformation (Kosslyn et al. 2001). We do not argue that normally developing early adolescents cannot perform motor imagery, but rather we suggest that they do not fully rely on motor information to mentally transform body parts. More precisely, we hypothesize that a full deployment of motor information in motor imagery could be achieved in early adolescents under specific experimental manipulations favouring the activation of the motor system. This hypothesis would be consistent with data showing that active movements executed during the imagery task can influence imagery performance in children (Frick et al. 2009b), toddlers (Rieser et al. 1994), and infants (Acredolo et al. 1984; Benson and Uzgiris 1985). For instance, Frick et al. (2009a) demonstrated strong motor effects in children who were required to make active circular movements with their dominant hand during a mental rotation task. A similar "motor-enhancement" might also explain Funk et al.'s data (2009) showing that children's performance on the hand laterality judgements is enhanced when participants' posture (palm-up or palm-down) is compatible with stimuli's posture (palm or back views of hand stimuli), thus showing deployment of sensorimotor information in motor imagery. Our findings, instead, did not fit data by Krüger and Krist (2009) in children. In a first experiment, the authors did not observe any biomechanical effect in a modified version of the hand laterality task (i.e., a visual matching task on back views). In a second experiment, Krüger and Krist "tried to provoke a motor effect and to compare it across different age groups" (p. 244, 2009) by using only palm views that are known to be more effective than backs in eliciting the biomechanical effect (Parsons 1987, 1994); results showed that the biomechanical effect was present in all the age groups, and it was stronger in children than in adults. In the present study, we did not observe a significant biomechanical effect in early adolescence in either hand perspectives, that is, back and palm views. A specific methodological aspect could account for discrepancy between Krüger and Krist's (2009) and the present data. The authors employed a matching task requiring participants to decide which of two hand images presented in the lower left and right of the computer screen matched the hand image displayed in the middle of the screen. Here, instead, we used the classical hand laterality task requiring subjects to make a left/right decisions on a single hand image. It is possible to speculate that the matching task could be highly effective in triggering deployment of motor information during mental transformation of hand stimuli (see Frassinetti et al. 2011 and Urgesi et al. 2007, for evidence on recognition of body parts), but this interpretation should be directly tested in future studies.

The lack of a significant activation of motor strategies to mentally rotate hand stimuli in early adolescents might be related to the specific maturation patterns of brain structures involved in action prediction processes. Models of motor control posit that frontal cortex and cerebellum, together with the posterior parietal cortex, are involved in a functional circuit subtending movement prediction and action simulation (Blakemore and Sirigu 2003; Deconinck et al. 2009; Desmurget and Sirigu 2009; Jeannerod 2001; Wolpert et al. 1995). The hand laterality task requires participants to mentally match their own hand with the visual stimulus and, in terms of action prediction, to activate internal models predicting consequences of mentally simulated actions. The present results might be compatible with the idea that an incomplete maturation of the fronto-parietal circuit can account for ineffective use of motor imagery in early adolescents (Choudhury et al. 2007a, b) and that action prediction processes become effective by middle adolescence and fully operative in late adolescence when the critical brain structures reach their maturational peak (Gogtay et al. 2004; Westlye et al. 2010).

Independently from deployment of motor strategies, participants of all the three age groups showed increasing RTs from 0° to 180° orientations in the hand laterality task, and in object and letter rotation as well. In their seminal study on mental rotation, Shepard and Metzler (1971) found that the time needed for solving the task increased linearly as a function of angular disparity between the stimuli. Such a finding has been replicated in virtually all mental rotation experiments and is considered as a proof that participants are actually rotating stimuli in their mind rather than adopting a different cognitive strategy (Kosslyn et al. 1998; Parsons 1987; Shepard and Cooper 1982). In a classical developmental study, Marmor (1975) presented children with drawings of panda bears in different spatial orientations; children were required to judge whether the two bears in a pair were the same or different. Four- and 5-year-old children were able to use mental rotation, as revealed by the linear increase in their response times as a function of angular disparity (Marmor 1975, 1977). Subsequent studies showed that 4-year-old participants were able to rotate familiar stimuli, such as animal images (Estes 1998), whereas 5- (Kosslyn et al. 1990) and 6-year-old children (Estes 1998) could rotate more complex stimuli, although they were slower and less accurate than adults. Therefore, we can maintain that in our study, all groups complied with test instructions and mentally rotated stimuli to solve the tasks independent from the kind of the stimulus material. Early adolescents were always significantly slower than both middle and late adolescents, whereas middle and late adolescents did not differ between each other. Such significant reduction of RTs from early to middle adolescence was evident for stimuli in canonical orientation (0°-trials) that do not require any mental transformation in order to provide correct response. Therefore, it would appear that early adolescents were significantly slower than both middle and late adolescents because they took longer time to encode visual stimuli, to make a decision and to provide the response (Frick et al. 2009a). Instead, an index of mental rotation speed, that is, the increase in response time in ms per 1° change in stimulus orientation (Frick et al. 2009a), did not differ across the three age groups. Taken together, these data revealed that faster mental rotation performance of middle and late adolescents with respect to early adolescents was likely due to an increase in general processing resources not specifically related to mental rotation processes. We could speculate that developmental changes in visuospatial and working memory skills that are in progress in these age ranges (for a review, see Paus 2005) could account for such a general age-related increase in processing speed.

In conclusion, we demonstrated here that the involvement of motor information in mental rotation of body parts becomes progressively stronger across adolescence. A significant interaction between laterality and orientation of hand stimuli (the biomechanical effect) was absent in early adolescents, emerged in middle adolescents and became stronger in late adolescents. Thus, our data are consistent with the idea that motor imagery undergoes a continuing refinement throughout adolescence (see Gabbard 2009 for a recent review) getting full effectiveness in late adolescence only. Such a developmental pattern of motor imagery is not related to changes in processing speed that, instead, increased from early to middle adolescence but did not improve further in late adolescence. Combined behavioral and neuroimaging studies are needed to directly investigate the neural correlates of developmental trajectories of motor imagery across adolescence.

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