Development of action representation during adolescence

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Abstract

During adolescence the body undergoes many physical changes. These changes necessitate an updating of internal models of action. Here, we tested the hypothesis that internal models undergo refinement between adolescence and adulthood. We investigated the chronometry of executed and imagined hand actions, which relies on internal models, in 40 adolescents (24 males; mean age 13.1 years) and 33 adults (15 males; mean age 27.5 years). In two different motor imagery tasks, the time it took each participant to execute a hand movement was compared with the time it took them to imagine making that movement. For all participants, movement execution time significantly correlated with movement imagery time. However, there was a significant increase in the execution–imagery time correlation between adolescence and adulthood. Cognitive-motor efficiency per se did not change as indexed by both similar execution and imagery times on both tasks for the adolescents and adults. That it was only the correlation between imagined and executed actions that changed with age suggests that the developmental change was specific to generating accurate motor images and not a result of general cognitive improvement with age. The results support the notion that aspects of internal models are refined during adolescence. We suggest that this refinement may be facilitated by the development of parietal cortex during adolescence.

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1. Introduction

During adolescence, the body is subject to height, weight, organ and musculoskeletal development (Coleman & Hendry, 1989). Representations of the body and its kinematics might therefore be expected to change with age. This kind of “action representation” is a component of an internal forward model, which is a neural system that simulates the dynamic behaviour of the body in relation to the environment (Wolpert, Ghahramani, & Jordan, 1995). It has been proposed that these internal models make predictions about actions, limb kinematics and parameters of the external world and enable successful planning and execution of movement (Wolpert, 1997). Optimal motor control is thought to depend on an internal forward model making predictions of the consequences of the movement, based on an efference copy of the motor command (von Holst, 1954; Wolpert et al., 1995; Wolpert, 1997). Discrepancies between predicted states and desired states result in error signals that can be used to fine-tune actions and to provide the motor instructions required by the muscles to achieve the desired effect. Internal models are constantly updated based on the actions and experiences of the person in the world (Miall & Wolpert, 1996; Wolpert et al., 1995). As body kinematics change during adolescence, the representation and prediction of actions made by internal models require updating.

It has been posited that by studying conscious motor imagery, it is possible to access the unconscious process of action representation (Jeannerod, 1997). Motor imagery, which is thought to involve the activation of internal models of action, can be considered a first-person process of the participant feeling herself executing an action. A motor image is therefore a conscious equivalent to a prediction for that action (Jeannerod, 1994, 1997). Recently, Voss et al. have shown that internal model prediction occurs even in the absence of movement (Voss, Ingram, Haggard, & Wolpert, 2006). Impairment in internal models occurs in patients with parietal cortex lesions (Sirigu et al., 1996; Wolpert, Goodbody, & Husain, 1998) as well as in people...
with schizophrenia (Maruff, Wilson, & Currie, 2003). Together with neuroimaging studies (Gerardin et al., 2000; Lacourse, Orr, Cramer, & Cohen, 2005; Stephan et al., 1995), the results suggest that motor imagery is associated with activity in parietal cortex. This is supported by the proposal that internal models are stored in parietal cortex (Blakemore & Sirigu, 2003; Wolpert et al., 1998).

Psychophysical experiments have shown that there are parallels between the parameters affecting actual movements and imagined movements. In particular, the time course of imagined and executed actions is highly correlated in normal adults (e.g. Decety & Jeannerod, 1995; Sirigu et al., 1995, 1996). The temporal invariance between executed and imagined movements suggests that the same motor representation (internal model) governs an action whether it is executed or imagined, and time constraints operate in the same way in both modalities of action. A close association between execution and imagery time for a given action, therefore, is an indicator of the ability to represent that action. In patients with parietal lesions, however, this timing relationship is lost (Sirigu et al., 1996; Maruff et al., 2003; Wolpert et al., 1998).

Studies using grip force modulation paradigms have shown that age four to age six is a critical time for the development of internal models (Blank, Heizer, & von Voss, 1999, 2000; Paré & Dugas, 1999). To our knowledge, there have been no studies to date on the development of internal models or action imagery beyond childhood and none has studied the development during adolescence. Perhaps because research on the development of the adolescent brain is relatively new, mechanisms of cognitive function during adolescence remain poorly understood. Recent MRI data has demonstrated that the parietal cortex, which is associated with internal models of action, undergoes a particularly protracted course of development compared with sensory regions of the brain such as the visual cortex (Giedd et al., 1999; Gogtay et al., 2004). In light of previous histological studies, these MRI data are thought to reflect synaptic pruning, the elimination of unused synapses, and a simultaneous process of myelination of developing fibre tracts occur during this period, stabilising in early adulthood (Huttenlocher, 1979; Yakovlev & Lecours, 1967).

Given the association of internal models with parietal cortex, it is logical to expect that parietal development might affect internal models. To investigate the hypothesis that internal models undergo a period of development during adolescence, we tested the ability of 40 young adolescents and a control group of 33 adults to use motor imagery. As an index of the development of the action representation system, we measured the correspondence between the time course of every participant’s executed (E) and imagined (I) actions in each age group, on two different motor imagery tasks. To compare this correspondence between age groups, we compared the execution–imagery (E–I) correlations of each individual in the two age groups. To determine whether developmental change was specific to the development of internal models and not a result of general cognitive-motor improvement, the change in E–I correlation with age was compared to the change in general cognitive-motor efficiency with age.

## 2. Method

### 2.1. Participants

Seventy-three participants were recruited and divided into two age categories. Forty adolescents (24 males; mean age 13.1 years, S.D. = 1.4) and 33 adults (15 males; mean age 27.5 years, S.D. = 7.9) took part in the study. Adolescent participants were from state comprehensive primary and secondary schools in the London area and adults were students and staff at University College London. Participants were all right handed and none had a history of psychiatric, neurological, developmental or learning disorder. Written informed consent was obtained from the participants and, for the adolescents, from their parents prior to the study, which was approved by the local research ethics committee.

### 2.2. Experimental procedure

During the piloting stage, the order of blocks was counterbalanced between participants, so that some started with the imagined condition and others with the executed condition. We found that starting with the imagined condition was challenging for subjects, who reported not knowing what to imagine. Therefore, it was decided that, during the actual study, participants would perform the tasks in blocks of executed actions followed by imagined actions. The order of task (triple 8 or fingers) administration was counterbalanced between participants. At the start of every block, for each task, participants were reminded to perform the actions as quickly and as accurately as possible.

#### 2.2.1. Triple 8 task

For each trial, participants were presented with a plain sheet of paper. Two parallel horizontal lines were drawn, with one towards the top of the sheet and the other pair towards the bottom. An example of the figure 8 was drawn between the top pair of lines such that its height spanned the width between the lines.

##### 2.2.1.1. Executed condition

Participants sat with their hand in a starting position with the tip of the pencil touching the centre of the X drawn between the bottom pair of lines (see Fig. 1A). When the experimenter said “go”, participants were instructed to draw a further three consecutive figure 8s as fast and as accurately as they could within the bottom pair of lines, without going outside the border of the lines. The width between the lines and therefore the sizes of the figure 8s varied. Three different sizes were used: 70, 35 and 18 mm high. There were three trials of each size of 8, on separate sheets of paper, for the executed condition and also for imagined condition. A stopwatch was used to record the duration of participants’ movement from the time the experimenter said ‘go’ to the time the participant said ‘stop’.

##### 2.2.1.2. Imagined condition

Participants were asked to imagine drawing the sequence of figures 8s as in the executed condition, but without using any movement of their hand. The experimenter confirmed that the participant had imagined the movement, then instructed them to say ‘stop’. The duration was recorded by the experimenter.

#### 2.2.2. Fingers task

The fingers task was identical to that described by Sirigu et al. (1996). Two blocks of executed actions were followed by two blocks of imagined actions, with each block consisting of a sequence of five consecutive, continuous actions.

##### 2.2.2.1. Executed condition

Participants started with their hands placed firmly down on the surface of the table. When the experimenter said ‘go’, participants were required to touch the right thumb to the tip of the little finger and then to the tip of the index finger (see Fig. 1B). In each block, this action was repeated five times (one sequence was equivalent to the thumb touching both the little finger and the index finger; this whole motion was repeated five times as one repetitive continuous motion). Participants were instructed to say ‘stop’ to indicate that they had completed the sequence of actions. In half of the blocks, participants used their right hand and in half the blocks, their left hand. The experimenter used a stopwatch to time the duration of the action from the moment after she said ‘go’ to the moment the participant said ‘stop’.

##### 2.2.2.2. Imagined condition for both tasks

The imagined condition followed the executed action blocks. During this condition, participants were instructed to place their hands in the starting position for the action, but they were asked...
Fig. 1. Two motor imagery tasks were used to investigate the ability to represent actions. The tasks were administered in two blocks of executed (E) trials followed by two blocks of imagined (I) trials with the order of tasks counterbalanced between subjects. (A) Triple 8 task. Executed (E). Participants drew three consecutive figure 8s with a pencil, within the parallel pair of lines, as quickly and as accurately as they could. There were three size conditions of the figure 8: small, medium and large corresponding to varying widths of the parallel lines. They were timed between the time they were instructed to start and the time they said stop when they had finished. Imagined (I). Participants were timed to imagine making this action without moving their hand at all. (B) Fingers task. Executed (E). Participants moved their thumb between their little finger and index finger in a continuous sequence of five movements, as quickly and as accurately as possible. They were timed between the time they were instructed to start and the time they said stop when they had finished. This was repeated with both the right and left hands. Imagined (I). Participants were timed to imagine making this action without moving their hand at all.

to keep as still as possible during the imagined trials. When the experimenter said ‘go’, participants were required to imagine doing the action exactly as in the executed condition, but without moving. As in the Action condition, participants were told to say ‘stop’ out loud to indicate they had finished the mental movements.

2.2.3. Instructions

Each participant was given a demonstration by the experimenter at the beginning of the task. To ensure that participants had fully understood the instructions, they were given a practise condition consisting of three example trials, which were not included in the main experiment.

In the imagined condition, the experimenter always stressed that participants should ‘really feel themselves making the movement.’ In other words, they were to avoid objectifying themselves by imagining a visual image of their hand moving. Rather, they were supposed to feel as if they were actually moving their hand in a first-person perspective of the motor image. If the participant lost count of the number of movements, lost concentration during a trial, or expressed any problems, then that trial was subsequently excluded from the analysis.

2.3. Florida Praxis Imagery Questionnaire (FPIQ)

The imagery questionnaire was adapted from the children’s version (Wilson, Maruff, Ives, & Currie, 2001) of the Florida Praxis Imagery Questionnaire (Ochipa et al., 1997). The questionnaire consisted of seven questions in each of four subscales, each designed to test different aspects of praxis imagery: kinaesthetic, body position, action and object. Correct answers indicated that the participant was able to correctly image the action required to arrive at the answer. The questionnaire was used to check for outliers on a group by group basis, to ensure that all data analysed was from participants able to carry out praxis imagery. This questionnaire is designed to tap both visual and motor representations in separate subscales.

2.4. Statistical analysis

2.4.1. Individual reaction time data for imagined and executed actions

For each participant, the mean movement duration for all the trials (nine for the triple 8 task, eight for each condition of the fingers task) under the executed and imagined conditions was calculated. To investigate how well these data correlated across participants, each participant’s mean executed RT (E) was plotted against his or her mean imagined RT (I), for each task. Individual correlations provide information about motor imagery ability, which would be masked by comparing group means. A Pearson’s product moment correlation was calculated between the mean E RT and mean I RT.

2.4.2. Comparison of E–I correlations between groups

Fisher’s Z was used to test whether the size of the correlations between executed and imagined movement duration significantly differed between the age groups and between genders on each task. According to this test, if the Z value was above 1.96, the correlations were significantly different at the $p < .05$ level, and if the Z value was 2.58 or over, the correlations were significantly different at the $p < .01$ level.

2.4.3. The effect of action size (triple 8 task)

To investigate the effect of size of the figure 8, a between subjects $3 \times 2 \times 2$ (size $\times$ age $\times$ gender) ANOVA was used.

2.4.4. The effect of laterality (fingers task)

Group means of RT were analysed using a between subjects $2 \times 2 \times 2$ (hand $\times$ age $\times$ gender) ANOVA to explore laterality for the fingers task. The
Table 1
Florida Praxis Imagery Questionnaire (FPIQ)

<table>
<thead>
<tr>
<th>Subscale</th>
<th>Adolescents</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
<td>Range</td>
</tr>
<tr>
<td>Kinaesthetic</td>
<td>5</td>
<td>2–7</td>
</tr>
<tr>
<td>Position</td>
<td>6</td>
<td>3–7</td>
</tr>
<tr>
<td>Action</td>
<td>6</td>
<td>4–7</td>
</tr>
<tr>
<td>Object</td>
<td>7</td>
<td>4–7</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>26</td>
</tr>
</tbody>
</table>

There were no differences between age groups in imagery questionnaire scores, indicating that both adolescents and adults were able to image actions correctly. The questionnaire was used to identify outliers—participants whose scores fell 3 S.D. below the mean score for each group.

The effect of laterality for this task was also analysed by comparing E–I correlations for the left and right hand within each age group.

3. Results

3.1. FPIQ

All participants scored highly on the FPIQ, and there were no differences between groups in the mean total scores or in any of the subscales (mean score (adolescents) = 24; mean score (adults) = 26 out of a total of 28; see Table 1). A participant’s imagery and action data were excluded from the analysis if his or her mean FPIQ score fell three or more standard deviations below the mean score for each group. Participants described a simulation that was sensorimotor, rather than visual.

3.2. Action imagery task

Participants who showed a discrepancy between imagined and executed action times that were three standard deviations above or below the mean in either of the two tasks were also considered outliers. There were two outliers for the fingers task (two adults) and two outliers for the triple 8 task (one adult and one adolescent).

3.2.1. Execution–imagery (E–I) correlations

3.2.1.1. Triple 8 task. The correlation between the timing of actual (E) and imagined (I) actions was significant for both age groups ($R^2$ (adolescents) = 0.58; $R^2$ (adults) = 0.87; $p < .01$ for both). However, the correlation between E and I for individuals in the adult group was significantly higher than that of individuals in the adolescent group ($Z' = 2.61; p < 0.01$). There was no effect of gender on either the executed or imagined conditions ($Z'$ (adolescents) = 1.10; $Z'$ (adults) = 0.17). Thus, performance on both tasks indicated that the ability to form accurate action representations—as indexed by the strength of the correlation between executed and imagined actions—significantly improves between early adolescence and adulthood (see Fig. 2A).

3.2.1.2. Fingers task. In the second task, the correlation between E and I was also significant for both age groups ($R^2$ (adolescents) = 0.82; $R^2$ (adults) = 0.96; $p < .01$ for both). Again, the correlation between E and I for individuals in the adult group was significantly higher than that of individuals...
in the adolescent group ($Z = 3.20; p < 0.01$). There was no effect of gender ($Z$ (adults) = 0.492; $Z$' (adolescents) = 1.24).

In line with the results from the first task, performance on the fingers task indicated that the ability to form accurate action representations significantly improves between early adolescence and adulthood (see Fig. 2B).

### 3.2.2. Relationship between action time and age

The second set of regression analyses (see Fig. 3A and B) revealed no significant correlation between age and movement execution time ($E$) for the triple 8 task ($R^2 = 2.9 \times 10^{-4}; p = 0.89$) nor for the fingers task ($R^2 = 0.041; p = 0.1$). This indicates that both age groups performed the motor execution tasks equally well (in terms of timing).

Similarly, there was no significant correlation between age and imagery time ($I$) for the triple 8 task ($R^2 = 0.044; p = 0.082$) or the fingers task ($R^2 = 0.042; p = 0.1$). These control regression analyses show that there was no difference between age groups in terms of carrying out a motor execution task, and other general factors such as understanding task instructions, making a hand action, and reaction time. There were no differences between genders in either the $E$ or $I$ condition.

### 3.2.3. Size of action (Triple 8 task)

There was a main effect of size of action (handwriting size) ($F(2,64) = 84.3; p < .0001$), indicating that on average across both the $I$ and $E$ trials participants performed the actions increasingly slowly as the size of the figure 8 increased (mean RT for small 8 = 4.32 s, S.E. = 0.16; medium 8 = 5.16 s, S.E. = 0.21; large 8 = 6.26 s, S.E. = 0.27). There was a significant interaction between size of action and age ($F(2,130) = 6.83; p < .01$) but post hoc $t$-tests comparing RT of each size between groups were not significant.

### 3.2.4. Laterality (fingers task)

The ANOVA revealed no effect of the hand used for the fingers action on RT ($F(1,64) = 0.34; p = 0.55$). There was no interaction between hand and age group ($F(1,64) = 0.53; p = 0.47$) or between hand and gender ($F(1,64) = 0.15; p = 0.70$). Furthermore, a comparison between $E$–$I$ correlations for each hand showed no difference in strength of the $E$–$I$ association between hands for adolescents or ($R^2$ (left hand) = 0.79; $R^2$ (right hand) = 0.82; $Z = 0.44$, n.s.) or for adults ($R^2$ (left hand) = 0.94; $R^2$ (right hand) = 0.92; $Z = 0.54$, n.s.).

### 4. Discussion

The results of the current study demonstrate a tight correlation between action execution ($E$) and imagery ($I$) times in both adolescents and adults for two different imagery tasks: the fingers task and the triple 8 task. However, for both tasks, there was a significant increase in the degree of correspondence between $E$ and $I$ between adolescence and adulthood. To our knowledge, this is the first study to demonstrate that although adolescents are able to form motor images, this ability improves between adolescence and adulthood. Drawing on previous results from functional imaging and lesion studies, we suggest that this is due to refinement of action representation during adolescence.

#### 4.1. $E$–$I$ correlation in each age group

The FPIQ scores indicate that both age groups were equally able to form motor images. To ensure that that imagined actions were “felt actions”, or first-person simulated actions, participants were instructed to imagine themselves as the agent of the action in the imagery conditions. Moreover, when retrospectively asked about their strategy, participants reported using a motor strategy as instructed.
Furthermore, the high correlations between E and I in both groups corroborate results from previous psychophysical experiments (Decety & Jeannerod, 1995; Decety & Michel, 1989; Sirigu et al., 1995, 1996), supporting the notion that there are parallels between the parameters affecting executed and imagined movements. This indicates that the imagery conditions for both tasks were tapping action representations in both adults and adolescents. The relationship between movement time and task difficulty for executed actions is expressed by Fitts’ Law, a model of human psychomotor behaviour (Fitts, 1954). The same phenomenon has been found to extend to imagined actions (Decety & Jeannerod, 1995; Sirigu et al., 1995, 1996). This reflects the finding that subjects make the same speed-accuracy trade-offs for both executed and imagined actions, for example, by slowing down in order to reach accurately to increasingly small targets, or by taking longer to walk to increasingly distant targets (Decety & Jeannerod, 1995; Maruff, Wilson, Trebiolcock, & Currie, 1999a; Sirigu et al., 1995, 1996; Stevens, 2005). Unlike previous findings (Maruff et al., 1999b), results of the fingers task indicate that performance is not influenced by laterality for either of the age groups.

We did not find an isochronous effect for handwriting size in the triple 8 task. Previous studies have shown that participants have a tendency to keep execution time constant independent of movement size of handwriting by changing the velocity according to the changing amplitude (Decety & Michel, 1989; Viviani & McCollum, 1983). Given that naive participants normally believe that writing with larger amplitudes should take more time, this isochrony principle has previously been taken to confirm the use of participants’ use of motor imagery rather than folk knowledge. However, the triple 8 task was designed to constrain the movement by the lines within which the three repeated figure 8s were restricted. In addition, accuracy and speed were emphasised in the instructions. In contrast, in studies where the isochrony principle held true, writing movements were “free” (Viviani & McCollum, 1983), for example, one’s own handwriting for a sentence (Decety & Michel, 1989). Free movements such as writing text enable the use of one’s own unique style of movement and the velocities particular to individual handwriting. In the current study, however, the participant’s velocity is more controlled with respect to the target lines. Our figure of 8 task thus involves accuracy and is therefore perhaps still subject to speed-accuracy constraints that affect timing according to movement trajectory. Informal questioning indicated that participants were naive about motor imagery phenomena.

4.2. Development of E–I correlation during adolescence

The high correlation between E and I in both groups, together with the significant increase in correlation between adolescence and adulthood, suggests that while the action representation system is established by adolescence, it continues to develop to some degree (see Fig. 2A and B). The developmental change was specific to motor imagery and was not a consequence of general cognitive-motor improvement. The second set of regression analyses (see Fig. 3A and B) revealed no significant correlation between movement execution time (E) and age for the triple 8 task or for the fingers task. This indicates that both age groups performed the motor execution tasks equally well (in terms of timing). Similarly, there was no significant correlation between age and imagery time (I) for the triple 8 task or the fingers task. This suggests that the developmental effect (an increase in the correlation between E and I with age) is specific to the ability to form accurate motor images based on internal models of action, rather than the ability to imagine movement per se. These control regression analyses show that there was no difference between age groups in terms of carrying out a motor execution task, and other general factors such as understanding task instructions, making a hand action, and reaction time.

4.3. Internal models in the brain

It has long been suggested that the mental processes that contribute to the covert simulation of an action are also involved in the actual performance of that action (Binet, 1885; Stricker, 1885). William James, for example, argued in his ideomotor theory of action that “every mental representation of a movement awakens to some degree the actual movement which is its object” (James, 1890). Motor imagery studies using walking, writing, drawing and simple hand action tasks in normal adults (Decety & Jeannerod, 1995; Decety & Michel, 1989; Sirigu et al., 1995, 1996) indicate that the same motor representation governs an action whether it is executed or imagined, and time constraints operate in the same way in both modalities of action.

It is thought that motor imagery might be analogous to efference copy (Decety, Jeannerod, & Prablanc, 1989; Jeannerod, 1997). Efference copy is generated by the brain in parallel with every motor command, and is believed to be crucial to action planning (Wolpert et al., 1995). Internal models make predictions of the consequences of actions on the basis of efference copy (Wolpert et al., 1995). Lesion studies (Sirigu et al., 1996; Wolpert et al., 1998) as well as neuroimaging studies (Gerardin et al., 2000; Stephan et al., 1995) suggest that the parietal cortex is involved in storing and updating internal models of actions, including monitoring efference copy received from motor outputs. Data from motor imagery studies of parietal lesion patients indicate that their imagined actions do not follow Fitts’ law, and as such, they are unable to form accurate internal representations of actions (Sirigu et al., 1996; Wolpert et al., 1998). Similarly, children with developmental coordination disorder (DCD) have been shown to demonstrate weaknesses in their action representation system (Maruff et al., 1999a). It has been proposed that a weak correlation between executed and imagined actions is due to an “impaired ability to process efferent copy signals” and that the problem may have its origin in the neural circuitry underlying internal models (cf. Maruff et al., 1999a, p. 1323).

4.4. Development of the brain and internal models during adolescence

In light of several neurophysiological and lesion studies of motor imagery (Gerardin et al., 2000; Lacourse et al., 2005; Sirigu et al., 1995, 1996; Stephan et al., 1995), one possible interpretation of the current results is that the development in motor
imagery found may be linked to the maturational processes in the parietal cortex. During the last decade, neuroimaging studies have shown that cortical development is much more protracted than previously believed. Structural MRI studies have demonstrated grey and white matter development in the parietal cortex throughout adolescence, which may reflect synaptic pruning and myelination during this period (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003; Toga, Thompson, & Sowell, 2006). Given that myelin speeds up neural signalling and that synaptic pruning is essential for the fine tuning of functional networks of brain tissue, the occurrence of these processes in the brain during adolescence should lead to increased neural efficiency (Huttenlocher, 1979; Sowell et al., 1999). Within this context, there are two possible explanations for the increasing ability to form motor images with age, observed in the current study. Firstly, the maturational processes in parietal circuitry may give rise to an increased ability to process efference copy signals with age, during adolescence. Thus, increased myelination and synaptic pruning in parietal cortex could account for the improvement in motor imagery. A second explanation could be that during adolescent growth, internal models are refined such that motor predictions take account of new hand size and dynamics. This may be a consequence of development of the neural networks supporting internal models. Brain imaging studies are required to investigate this possibility.

In addition to the parietal cortex, histological and MRI data have provided evidence for considerable development in prefrontal cortex during adolescence (Giedd et al., 1999; Gogtay et al., 2004; Huttenlocher, 1979; Sowell et al., 2003; Toga et al., 2006). It is possible that the increase in correspondence between imagined and executed timings of actions results from an improvement in working memory that is linked to the maturation of the prefrontal cortex. Indeed the refinement of internal models reflected by the current data may result from the development and plasticity of frontal and parietal circuitry and reciprocal connections with the cerebellum, a brain region additionally linked to internal models (Blakemore & Sirigu, 2003). Future studies are necessary to determine the differential involvement of cortical circuits in motor imagery for adolescents compared with adults.

Studies of the development of grip force modulation suggest that internal models are established between the ages of four and six (Blank et al., 1999, 2000; Paré & Dugas, 1999). However, none has investigated the development of internal models during the transition from childhood into adulthood. Our results fit with a previous study that compared children (aged between 7 and 11 years) and adults on a force adaptation paradigm. This showed that internal representations of arm dynamics were less precise in children and less stable in time than those of adults (Konczak, Jabseb-Osmann, & Kalveram, 2003).

4.5. Conclusion

Our data suggest that development continues beyond childhood, possibly in response to physical changes in the body during the transition into adulthood, and facilitated by cortical development in the brain. Given that body shape is subject to considerable development during puberty and adolescence, neural representations of limb dynamics and therefore predictions for actions might be less accurate in adolescents than in adults. If limb kinematics change, due to changed body size, the representation and prediction of actions made by internal models need to be updated on the basis of experience with the new body shape. The refinement of internal models may be supported by the maturation of parietal cortex during adolescence. The notion that the action representation system is still developing during adolescence has consequences for the understanding of typical development of control of thought and action, and may have applications for understanding motor impairment in developmental disorders such as DCD and autism. Furthermore, recent empirical and theoretical work has underscored the relevance of action representation for self-consciousness and the understanding of other minds (Jackson & Decety, 2004; Rizzolatti & Craighero, 2004). The finding that action representation develops during adolescence may have implications for the understanding of social cognitive development during adolescence, and the neural substrates that link motor and social cognition.

References


