Activation and Inhibition of Bimanual Movements in School-Aged Children[1]

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Abstract—The development of motor activation and inhibition was compared in 6-to-12 year-olds. Children had to initiate or stop the externally paced movements of one hand, while maintaining that of the other hand. The time needed to perform the switching task (RT) and the spatio-temporal variables show different age-related evolutions depending on the coordination pattern (in- or anti-phase) and the type of transition (activation, selective inhibition, non selective inhibition) required. In the anti-phase mode, activation perturbs the younger subjects' responses while temporal and spatial stabilities transiently decrease around 9 years when activating in the in-phase mode. Aged-related changes differed between inhibition and activation in the anti-phase mode, suggesting either the involvement of distinct neural networks or the existence of a single network that is reorganized. In contrast, stopping or adding one hand in the in-phase mode shows similar aged-related improvement. We suggest that selectively stopping or activating one arm during symmetrical coordination rely on the two faces of a common processing in which activation could be the release of inhibition.

Key words: child development; switching; bimanual coordination; mirror movements

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Although considerable interest has focused on inhibition in child development in the last two decades, the possible common characteristics between activation and inhibition has seldom been addressed. Thus, the aim of the present study was to examine the relation between the development of activation and inhibition processes.

The development of inhibition processes could be a critical factor in normal cognitive development and aging [1—4]. Studies on inhibitory self-control (like Luria's finger tapping task, see [5]) showed aged-related improvement in preschool-aged children [6, 7]. Inhibition actually relates to different functions. Harnishfeger [8] emphasized a distinction between behavioral inhibition, that is, the "intentional control of overt behavior," mainly motor inhibition, and cognitive inhibition, that is, the intentional or unintentional control of mental contents or processes. Regarding motor processes, de Jong, Coles and Logan [9] further proposed a distinction between three types of motor inhibition: inhibition of any motor response whenever a stop signal occurs (stop-all, or non selective inhibition), inhibition of an ongoing response immediately followed by an alternative response (stop-change, or shifting), and inhibition of a single component of an ongoing motor response (selective-stop, or selective

inhibition). Oddly, except for de Jong et al. [9] and Coxon, Stinear and Byblow [10], the concept of selective inhibition has been used with a rather "perceptual" focus, i.e. the ability to correctly discriminate either a tone [11, 12] or a visual cue [13] to inhibit a response.

Research on inhibition usually rests on stop-signal tasks in which subjects are requested to react to a specific stimulus (activation trials), and have to withhold that response whenever a different stimulus (stop-signal) randomly occurs (inhibition trials). The temporal delay between the stimulus and the stop-signal varies across inhibition trials, so that the speed of inhibition (stop-signal reaction time, SSRT) can be measured in relation to the speed of activation as measured in activation trials. Performance is classically interpreted in reference to the horse-race model, as the inhibiting and activating processes are assumed to compete for the first finishing time [14].

Studies of inhibition in normally developing children remain scarce. Nevertheless, a few authors have used variants of the stop-signal paradigm [14, 15] to study inhibition, in a developmental or life-span perspective. Regarding non-selective inhibition, Williams, Ponesse, Schachar, Logan and Tannock [16] reported that the speed of both motor activation and inhibition increases between 6—8 years and 9—11 years of age. Similarly, Carver, Live-

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sey and Charles [17] found a significant improvement in inhibition across development when comparing children younger than 5.5 years, aged 5.5—7.5 years, 7.6—9.5 years, and adults. In contrast, Band, van der Molen, Overtoom and Verbaten [11], using several tasks inspired from the stop-signal paradigm in 5, 8 and 11 years old children, observed that the age-related evolution of motor activation and motor inhibition differed during childhood. While the speed of motor inhibition did not change, there was a significant developmental gain for activation, suggesting that the two types of processes rely on distinct mechanisms, as previously hypothesized by Logan and Cowan in adults [14]. Finally, van den Wildenberg and van der Molen [13] reported a faster evolution of non selective than selective inhibition between 7 and 10 years of age. Altogether, these studies suggest that motor activation, non selective inhibition and selective inhibition are distinct processes that develop at different rates during ontogeny: non selective inhibition is mature very early, whereas activation and selective inhibition progressively become efficient.

The different stop-signal tasks used in the above-mentioned studies may however not be quite appropriate when working with children. Specifically, a reliable measure of the speed of inhibition is indirect and requires an undesirable great number of trials since the temporal delay between the go and stop signals must be systematically varied.

In the present study, we aimed at assessing motor activation and inhibition in a more direct way, based on the functional properties of bimanual coordination. Indeed, bimanual coordinated actions require some exchange of activating and inhibiting messages between the cerebral structures controlling each hand [18, 19]. Except for symmetrical bimanual movements, which motor commands need only to contain activator messages, all other manual coordinations entail inhibitory signals to suppress the tendency to produce mirror movements. Hence, unimanual actions require addressing an inhibitory signal to one hand while non symmetrical bimanual actions require the selective inhibition of the mirror outflow as well as the activation of some specific commands. In "typical" child development, unintentional imitative movements of the contralateral hand are the clearest manifestations of inhibition immaturity [20—22], often attributed to an incomplete myelination of parts of the CNS [23—25].

Bimanual movements therefore appear particularly suited to assess the development of activation and selective as well as non-selective motor inhibition. Rhythmic bimanual movements have been extensively studied, both in adult and in children. They have been shown to come with two preferred modes of coordination: in-phase, in which homologous muscles of two limbs act synchronously, and anti-phase, in which homologous muscles act in a reciprocal way. These two modes of coordination appear to be stable under a variety of conditions, as demonstrated by a low variation rate in the phase delay between hands, most often with an advantage for the in-phase mode over the anti-phase mode ([26] for a review).

Recently, Sternad, Wei, Diedrichsen and Ivry [27] used a bimanual coordination task to study motor selective activation in adults.

According to Fagard [28], these two modes of bimanual coordination evolve during childhood with a progressive dissociation of the role of each hand: 5 and 7 year-old children produce more rapid and precise in-phase than anti-phase movements, while the difference between the two modes of coordination decreases between 7 and 9 years of age. In the same vein, Barral, Debû and Rival [29] studied motor activation and inhibition in 5, 8, and 11 years-old by means of three reaction time (RT) visuo-manual aiming tasks: unimanual, mirror-symmetrical or parallel bimanual. They found that, in the youngest children, bimanual mirror movements were initiated faster than unimanual or bimanual parallel (both involving selective inhibition to prevent mirror movements) movements. RTs were still longer for parallel bimanual movements than for mirror and unimanual ones at 8 years of age, while they no longer differed across condition thereafter. Thus, these results suggested a different age-related evolution of the activation and inhibitory mechanisms with higher RTs being interpreted as the result of a greater need for information processing in goal-directed movements.

In order to address the issue of the functional relationships between motor activation, non selective inhibition and selective inhibition, we compared their developmental trajectories in school-aged children. We hypothesized that dissimilarities in these trajectories would provide some insight about functional independence of the underlying processes.

MATERIAL AND METHODS

We used a stop-signal protocol adjusted for bimanual coordination, simple enough to be used with children. Basically, participants were requested to engage or stop one hand in coordination with the ongoing, regular and periodic to-and-fro movements of the other hand. Such an experimental set-up enabled us to measure the "effort," or cost, of switching between two patterns of movements by assessing the time needed to stop or activate one hand (RT) as well as the perturbations of the spatial and temporal characteristics of the movement of the other hand.

Participants. Eighty-five children, recruited in a local school, participated in the study (8 were left-handed). None of them suffered from any known movement or behavioral disorders. Children were divided into 4 age groups following a cluster analysis (K-means clustering, $F(3, 81) = 452.43$; $p < 0.05$). The first group was composed of 12 girls and 16 boys (mean age: 6 years 8 months, $SD = 4.7$ months; range: 5;11 to 7;4), the second group of 11 girls and 10 boys (mean age: 8 years 2 months, $SD = 4.9$ months; range: 7;6 to 8;7), the third group of 9 girls and 10 boys (mean age: 9 years 2 months, $SD = 4$ months; range: 8;8 to 9;11), and the last group of 10 girls and 7 boys (mean age: 10 years 10 months, $SD = 3.9$ months; range:

10;4 to 11;6). The study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki, 18 July, 1964) and the general procedure was approved by the local ethics committees.

Experimental Design. Upper limbs movements were recorded using two adapted joysticks connected to a computer. The handles of the joysticks were replaced by cylindrical stems of aluminum (length = 29 cm and diameter = 1.8 cm), allowing larger movements when held at their extremities. The maximum range of movement was of +/−20 degrees around the central position of the joystick. The springs that maintain the joysticks' handles into a vertical position were removed. The two joysticks were positioned on the two sides of a chair and their distance was adjusted to the child's height (Fig. 1). Children were sat to comfortably hold the extremities of the stems, arms and forearms being respectively vertical and horizontal.

The required movements were performed in the medio-lateral direction with respect to the body. The displacements of the joystick in the *x* and *y* axes were monitored and recorded at a frequency of 250 Hz using the *Presentation* 9.13. software. Auditory stimuli served as metronome and as imperative signal. The metronome was a low-pitched tone whereas the distinct imperative auditory signal was high-pitched.

Procedure. Before each experimental session, the manual preference of the child was evaluated using a questionnaire of laterality including five items (inspired from Bryden [30]). The child was then invited to sit on the chair, her/his back to the experimenters to minimize attentional biases. Throughout the recording session, she/he was required to fix a point in front of her (him) to limit head movements. The child was then instructed to perform lateral abduction and adduction arm movements. The movements involved internal and external rotations of the shoulders combined with flexion and extension of the elbows, so as to be as rectilinear as possible. The child was requested to follow the rhythm of the metronome (2.48 Hz), synchronizing the movement reversal points with the auditory signals.

The task consisted in engaging or stopping the non-dominant hand in response to the imperative signal. Under the control, unimanual conditions, the non-dominant hand was to start or stop moving with the metronome while the dominant hand motionlessly held the joystick. Thus, for the control activation trials, the child sat motionless, holding the two joysticks, until the imperative signal, and then started moving the non-dominant hand in rhythm (Fig. 2a). For the control inhibition trials, the child started performing the rhythmical movements with the non-dominant hand and stopped moving upon hearing the imperative signal (Fig. 2b). Similarly, under the bimanual conditions, two types of transition were possible: activation and inhibition. In the first case, a trial started with a unimanual movement of the dominant hand, and continued with a bimanual movement, either in anti-phase (Fig. 2c) or in-phase (Fig. 2e), after the imperative signal was delivered. Conversely, for inhibition trials, the subject started with a bimanual movement and
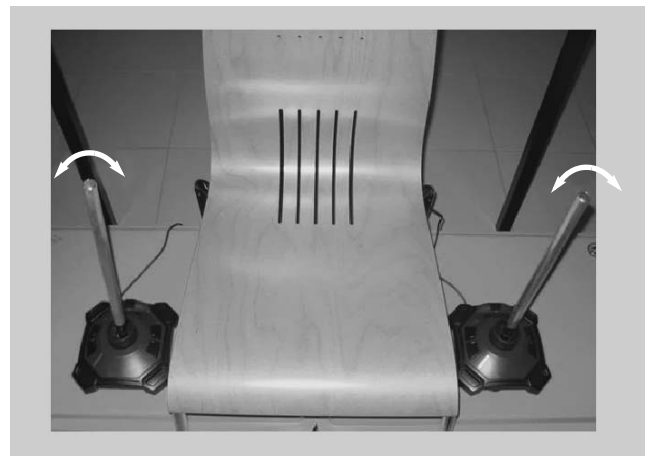

Fig. 1. Experimental design. The two joysticks are positioned on each side of the chair. The child sat back to the experimenter. Larger alternated movements were allowed with cylindrical stems of aluminum replacing the handles of the joysticks.

switched to a unimanual movement, stopping her/his non-dominant hand upon hearing the imperative signal (anti-phase: Fig. 2d; in-phase: Fig. 2f). Under all bimanual conditions, the child was requested not to interrupt the ongoing movement of the dominant hand when engaging or disengaging the non-dominant hand. For each trial, the imperative signal was randomly delivered so as to occur at different time points of the trial and of the cycle of the metronome.

The experimental session included six pseudo-randomized conditions, 3 for activation (unimanual, in-phase activation, anti-phase activation), and 3 for inhibition (unimanual, in-phase inhibition, anti-phase inhibition). The two first conditions were always unimanual and served as control trials, while the four others were counterbalanced between subjects. For each condition, each child performed five 12 s trials, for a total of 30 trials.

Data analysis. All analyses were carried out using *Matlab.* Displacements along the *y* axis were negligible and therefore only displacements along the *x* axis were analyzed. Because movement were not perfectly aligned with a frontal plane, we had to rebase the bi-dimensional data, shifting the *x*−*y* coordinates into a new frame of spatial references having for *x* axis the principal *x* axis of the performed movement. The data for the *x* axis were filtered using a Butterworth filter of order 2, with a cut-off frequency of 5 Hz.

For each trial, the onset and the stop of the non-dominant hand were visually identified. Activation onset was defined as the first displacement data point following the go signal; for inhibition, the stop was defined as the first inflexion in the displacement plot (arrow on Fig. 1b) following the stop signal. The delay between the imperative signal and the response of the child (i.e. the *reaction time* [ms]) was then measured. Because RTs were measured from different cinematic events for the onset and the stop
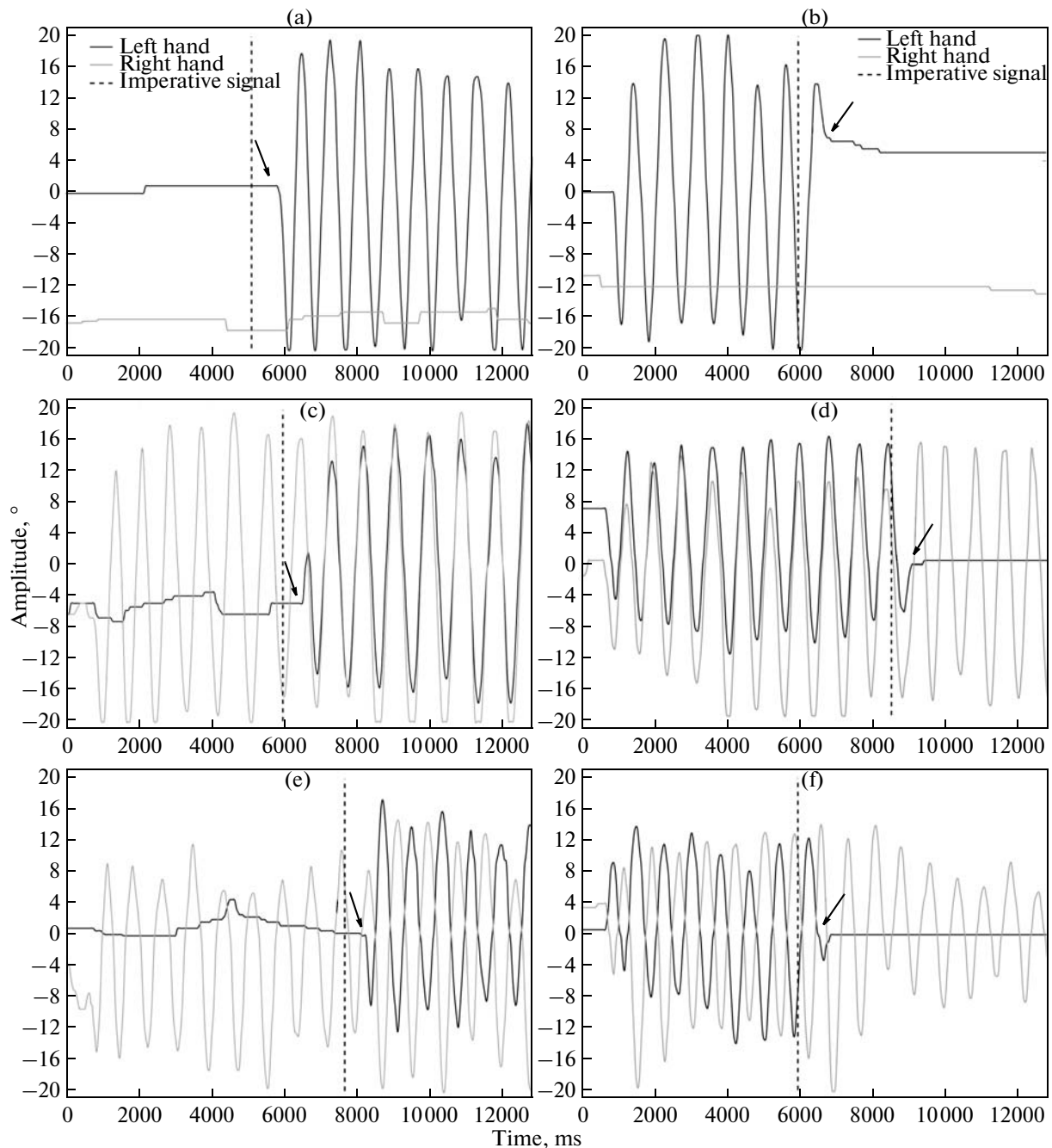
Fig. 2. Data from a right-handed child: time series of the lateral displacements of the two hands (grey; dominant right hand; black: non dominant left hand) for the two types of transition (activation: right column and inhibition: left column) under unimanual and both bimanual (in-phase and anti-phase) conditions. In the activation trials, the left hand is activated to produce unimanual (a), bimanual anti-phase (c) or bimanual in-phase (e) movements. For inhibition trials the children stopped the left hand from unimanual (b), bimanual anti-phase (d) and bimanual in-phase (f) movements. The vertical dashed line symbolizes the imperative signal for the transition. The amplitude of the movement is expressed in degree, with 0 corresponding to the vertical position of the joystick. The black arrows point up the time events used to mark RTs in activation or inhibition conditions.

of the hand, the results were separately analyzed for activation and inhibition.

Analysis of the motor transitions involved the definition of two time windows for the data of the dominant hand: a pre-transition window corresponding to the 7 half-cycles of movement preceding the imperative sig-nal, and a transition window, also 7 half-cycles long, start-ing from the half-cycle including the imperative signal. Comparison of the two windows yielded relevant infor-mation regarding the temporal and/or spatial perturba-tions of the dominant hand's movement resulting from the activation or inhibition of the non dominant hand.
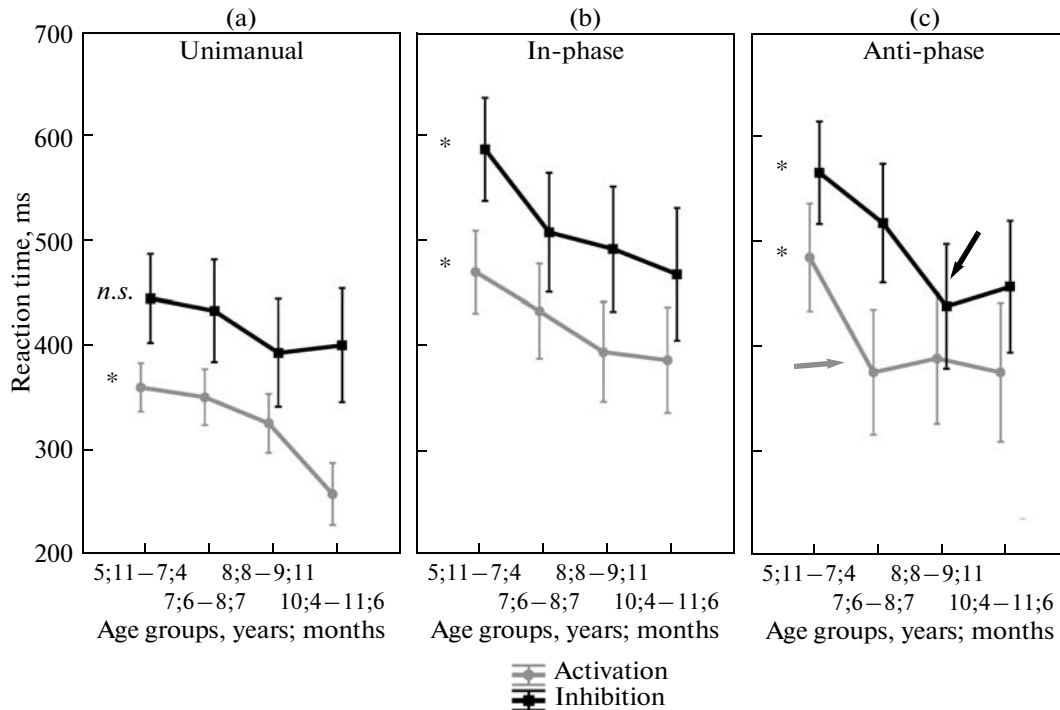
Fig. 3. Age-related evolution (the four groups of age are on the x axis) of RTs for the non dominant hand under the three conditions (unimanual, bimanual in-phase and bimanual anti-phase, in panels a, b and c, respectively) and according the two types of transition (Activation: grey; Inhibition: black). In the right panel (c), black and grey arrows indicate the plateaus for each transition. Vertical bars represent standard errors. * = significant Age Group effect; *n.s.* = non significant Age Group effect.

For each trial, five variables were computed for the dominant hand: (a) The *period error* that is the difference between the period of the metronome (404 ms) and the mean period of the movement during the pre-transition window; this variable assesses the precision of the movement relative to the required tempo, (b) the *perturbation* variable, that is the difference between the mean periods of the transition and pre-transition windows; positive values indicate a slowing down and negative values express acceleration, (c) the *amplitude* variable, that is the angle covered by the stem of the joystick, (d) the *variability of the period* and (e) the *variability of the amplitude* within each window, assessed by the coefficients of variation (standard deviation divided by mean). Because of the number of trials ($N = 5$ per condition), we used the median values of these variables, together with RTs, as the dependant variables for the statistical analyses. Non-parametric tests were used when assumptions for ANOVA were violated. An alpha level of 0.05 was used for all statistical tests, and the proportional reduction in error (*PRE*) is reported for all significant results obtained for the parametric tests.

RESULTS

Reaction Time. As there were no effect nor interactions involving the Sex factor, the data were pooled and analyzed using a 4 (Age Group) × 3 (Condition) ANOVA design for activation and inhibition separately. RTs data are depicted on Fig. 3. Concerning the Activation condi-

tion, statistical analyses showed main effects for both factors: RTs decreased with age, $F(3, 81) = 5.79$, $p < 0.05$, $PRE = 0.176$, and differed across conditions, $F(2, 162) = 33.89$, $PRE = 0.294$. Mean RTs values were: unimanual, $M = 329$ ms ($SD = 71$); bimanual in-phase, $M = 428$ ms ($SD = 109$); and bimanual anti-phase, $M = 415$ ms ($SD = 145$). Post hoc analyses revealed that RTs were significantly shorter for unimanual than for bimanual activations (in-phase and anti-phase, all $p < 0.05$) which did not differ from each other ($p = 0.30$). We further analyzed the evolution of the RTs with age under the three experimental conditions separately. Under the unimanual condition, RTs decreased with age, $F(3, 81) = 10.83$, $p < 0.05$, $PRE = 0.286$. Post-hoc analyses did not reveal significant differences between the 3 youngest groups of age, who all differed from the oldest one (all $p < 0.05$). Under the in-phase bimanual condition, RTs also decreased with age, $F(3, 81) = 3.10$, $p < 0.05$, $PRE = 0.103$. Post hoc analyses revealed that the youngest group of age significantly differed from the two oldest (all $p < 0.05$). Under the anti-phase bimanual condition, RTs were also affected by age, $F(3, 81) = 3.72$, $p < 0.05$, $PRE = 0.121$. Post hoc analyses showed that the RTs of the youngest children were significantly longer than those of the three older age groups (all $p < 0.05$), which did not differ from each other (all $p > 0.05$).

In the Inhibition condition, the results also showed main effects for the Condition, $F(2, 162) = 19.45$, $p < 0.05$, $PRE = 0.193$, and Age Group, $F(3, 81) = 5.28$, $p <$
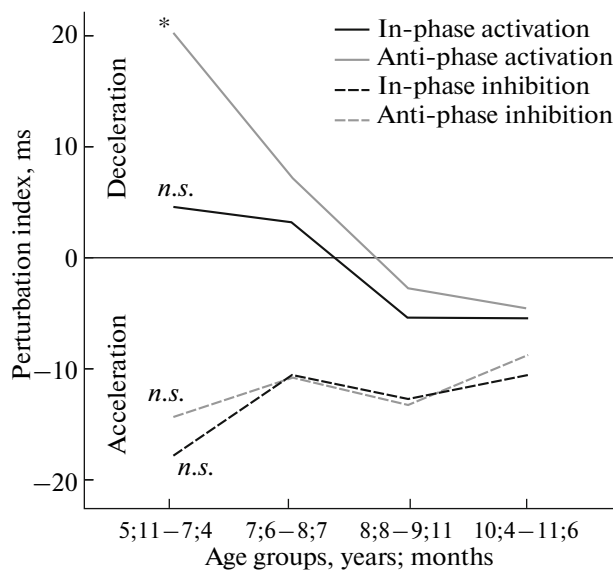
Fig. 4. Evolution of the Perturbation variable (in ms) according to the four age groups (on the x axis). This variable measures the difference between the transition and pre-transition mean periods of movement for the dominant hand (active throughout the whole trial). Positive values indicate a slowing down of the movement and negative values express acceleration at the transition. Dashed lines represent data for inhibition and solid lines data for activation under the two bimanual conditions (In-phase: black; Anti-phase: grey). * = significant Age Group effect; *n.s.* = non significant Age Group effect.

0.05, $PRE = 0.163$ factors. Mean RT values were: unimanual condition, $M = 422$ ms ($SD = 114$), bimanual in-phase condition, $M = 524$ ms ($SD = 138$), and bimanual anti-phase condition, $M = 505$ ms ($SD = 139$). Post hoc analyses revealed that RTs under the unimanual condition were significantly shorter than RTs under the two bimanual conditions (in-phase and anti-phase, $p < 0.05$) which did not differ from each other ($p = 0.24$). Analyses of the influence of Age Group under each of the three conditions revealed different patterns. Under the unimanual condition, the effect of Age Group was not significant, $F(3, 81) = 1.08$, $p = 0.36$. Under the bimanual in-phase condition, RTs decreased with age, $F(3, 81) = 3.71$, $p < 0.05$, $PRE = 0.193$. Post-hoc analyses revealed that the difference was only significant between the two youngest age groups. Under the bimanual anti-phase condition, the effect of Age group was significant, $F(3, 81) = 4.53$, $p < 0.05$, $PRE = 0.120$. Post hoc analyses did not reveal any significant difference between either the two youngest, or the two oldest, groups of age, while RTs significantly differed between the two younger and the two older groups of age (all $p < 0.05$) (Fig. 3).

Period error and perturbation. Under the activation condition, the mean value for all the children of the period error before the transition was -1.7 ms ($SD = 22.8$) and did not change with age (all $ps > 0.05$). At all ages, children performed the unimanual movement preceding a transition at a similar tempo. Regarding the inhibition condition, the period errors were 2.8 ms ($SD = 24.1$) under the

in-phase and 10.4 ms ($SD = 29.6$) under the anti-phase conditions, and did not change with age. Children performed the bimanual movements at similar frequencies at all ages during the window preceding the transition.

Kruskal-Wallis analyses on perturbation data revealed an effect of the Age factor in the anti-phase condition restricted to the activation task, χ^2 (3, $N = 85$) = 9.56, $p < 0.05$ (Fig. 4, grey solid line). Pair-wise comparisons using Mann-Whitney tests revealed that the youngest group significantly differed from the third ($Z = -2.212$, $p < 0.05$) and from the oldest group ($Z = -2.272$, $p < 0.05$). In the youngest, the data show a drastic slowing down of the active hand while engaging the second hand in the anti-phase pattern. The effect of age was not observed when activating in the in-phase condition (Fig. 4, black solid line).

Regarding the inhibition task, analyses of Perturbation did not reveal any significant Age Group effect, whatever the pattern of bimanual coordination prior to the transition. In each group of age, children accelerated at the transition from bimanual to unimanual movements (Fig. 4, dashed lines)

Variability of period. Whatever the age group, Wilcoxon tests revealed that the temporal variability significantly increased at the transition as compared to the pre-transition in both activation and inhibition conditions (all $ps < 0.05$).

Moreover, in the activation task, the effect of Age Group was significant under the four conditions showing an aged-related decrease of variability (Kruskal-Wallis test, before the transition/in-phase: χ^2 (3, $N = 85$) = 17.28, $p < 0.05$, before the transition/antiphase: χ^2 (3, $N = 85$) = 18.92, $p < 0.05$, after the transition/in-phase: χ^2 (3, $N = 85$) = 14.90, $p < 0.05$, after the transition/anti-phase: χ^2 (3, $N = 85$) = 8.19, $p < 0.05$). For activation in the in-phase bimanual pattern, Mann-Whitney pair-wise comparisons revealed a significant decrease in variability between the two youngest groups ($Z = -2.375$, $p < 0.05$) and between the two oldest groups ($Z = -2.514$, $p < 0.05$). The increase in variability seen between the 7;6–8;7 and the 8;8–9;11 groups fell short of significance ($Z = -1.175$, $p = 0.80$) (black solid line on Fig. 5, left panel).

The effect of Age Group on the variability of the movement was also significant in the inhibition task (before the transition/in-phase: χ^2 (3, $N = 85$) = 17.06, $p < 0.05$, before the transition/anti-phase: χ^2 (3, $N = 85$) = 23.04, $p < 0.05$, after the transition/in-phase: χ^2 (3, $N = 85$) = 19.20, $p < 0.05$, after the transition/anti-phase: χ^2 (3, $N = 85$) = 16.77, $p < 0.05$). Whatever the bimanual pattern (in-phase or anti-phase), the temporal variability of movements decreased monotonously with age (Fig. 5, right panel).

Amplitude of movement. As there were no effect nor interactions involving the Sex factor, the data regarding amplitude of movement were pooled and analyzed using a 4 (Age group) × 2 (Transition: activation, inhibition) × 2 (Condition: bimanual in-phase, bimanual anti-phase) × 2 (Window: pre-transition, transition) ANOVA with
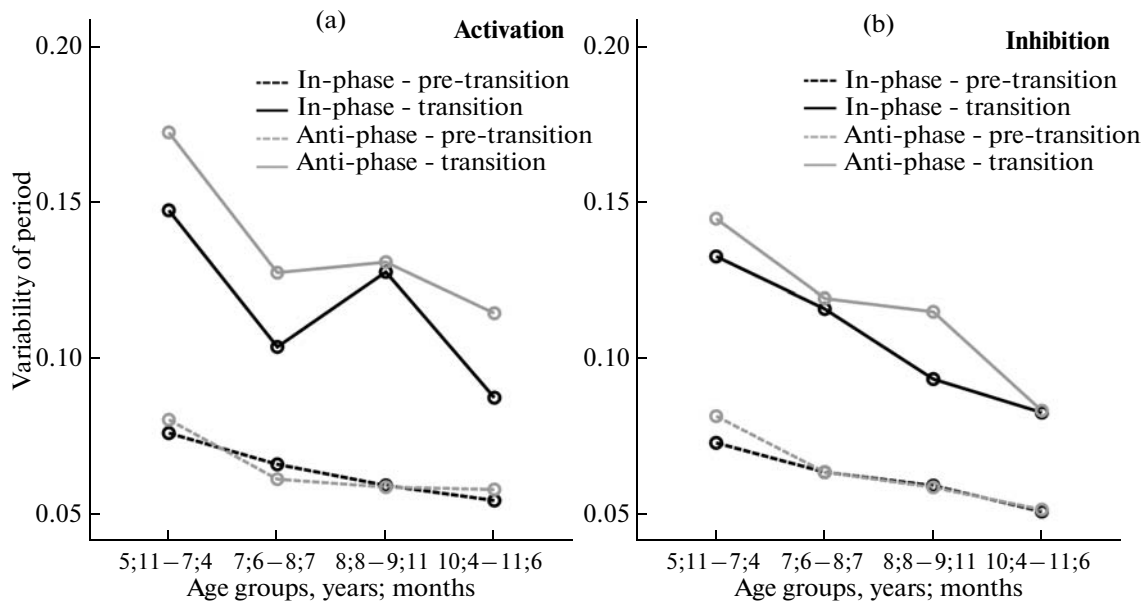
Fig. 5. Evolution with age of Variability of period (measured by the coefficient of variation of the period) for the dominant hand before (Pre-transition, dashed lines) and during (Transition, solid lines) the transition stage for the two bimanual conditions (black: in-phase; grey: anti-phase). The left panel (a) shows data for activation and the right panel (b) data for inhibition.

repeated measures on the last three factors. The analysis revealed a main effect for Window, $F(1, 81) = 41.79$, $p < 0.05$, $PRE = 0.340$, an interaction between Transition and Window, $F(1, 81) = 13.87$, $p < 0.05$, $PRE = 0.146$, as well as an interaction between Transition, Condition and Window, $F(1, 81) = 8.04$, $p < 0.05$, $PRE = 0.090$. An overall increase in movement amplitude was observed after the transition. In addition, analyses of the origin of the double interaction revealed a significant Window × Transition interaction for the anti-phase pattern, $F(1, 81) = 22.52$, $p < 0.05$, $PRE = 0.454$, but not for the in-phase one. Activating in the antiphase pattern triggered a significant increase in movement amplitude (transition minus pre-transition = 2.6 degrees), $F(1, 81) = 22.52$, $p < 0.05$, $PRE = 0.454$, that was not observed for inhibiting (transition minus pre-transition = 0.2 degree). In the in-phase transition, the effect of transition did not differ significantly for activation and inhibition (activation: transition minus pre-transition = 1.4 degree; inhibition: transition minus pre-transition 0.7 degree).

Variability of movement amplitude. After controlling for the influence of Sex, a 4 (Age group) × 2 (Transition: activation, inhibition) × 2 (Condition: bimanual in-phase, bimanual anti-phase) × 2 (Window: pre-transition, transition) ANOVA with repeated measures on the three last factors was carried out on the variability of movement amplitude. The analysis revealed main effects of Age Group, $F(3, 81) = 7.09$, $p < 0.05$, $PRE = 0.208$, and Window, $F(1, 81) = 219.06$, $p < 0.05$, $PRE = 0.730$. The interaction between the Age Group and Window factors also reached significance, $F(3, 81) = 6.53$, $p < 0.05$, $PRE = 0.194$, revealing an age-related decrease in amplitude variability for both the pre-transition and transition win-

dows (respectively, $F(3, 81) = 3.09$, $p < 0.05$, $PRE = 0.102$ and $F(3, 81) = 8.23$, $p < 0.05$, $PRE = 0.233$). Overall, although spatial variability decreased significantly with age for both windows, the slope of age-related changes is steeper for the transition than for the pre-transition.

DISCUSSION

The main objective of the present study was to examine the developmental changes in the motor activation and inhibition processes using a bimanual paradigm. We particularly focused on the cost of the motor changes measuring the time needed to activate or inhibit an arm's movement while the other arm continues to perform rhythmically alternating movements. Interferences with the ongoing movement were also analyzed through the changes provoked by the transition in the tempo and its variability, as well as in the movement amplitude and its variability. We will first discuss the results for the control, non selective task during which children were asked to perform unimanual motor change (inhibition or activation).

Non selective motor changes. In the unimanual task, the significant age-related decrease in RT observed for activation, and not for inhibition, is in agreement with previous findings showing that the processes involved in the activation of a motor response improve as children grow up, whereas it is not the case for inhibition. Indeed, Band et al. [11] reported that inhibition times did not change across ages in a stop-all task, but found a developmental gain in the processing of activation. In Williams et al. [16], although the go- and stop-signal RTs both significantly decreased between 6—8 years and 9—12 years of

age, a close examination of the reported data shows that the rates of improvement were dissimilar. Indeed, the younger children were approximately 50 ms slower than the elders when stopping, whereas they were 170 ms slower when activating. Indeed, Williams et al. [16], concluded, regarding non selective inhibition, that it "is one of the earliest emerging control processes [...]" and that it "[...] would make sense from an evolutionary perspective, given the significance of inhibitory control for survival" (p. 212). Thus, taken together, ours and published results support the hypothesis that the processes governing inhibition of a speeded motor response are, at least in part, independent from those governing its activation [12, 15, 16].

Selective versus non selective changes. In contrast to the unimanual condition, RTs significantly decreased with age for the bimanual inhibition task (i.e. when stopping one hand during a bimanual rhythmical task). This provides support for previous findings showing that non selective and selective motor inhibitions follow distinct developmental routes: Unimanual stop or stop-all tasks relate to non selective motor inhibition, whereas stopping one of the components of an ongoing bimanual task refers to selective motor inhibition. Thus, it appears that non selective motor inhibition processing is mature very early in child development, whereas selective motor inhibition processes mature more slowly.

Increased RTs in the selective as compared to non selective inhibition tasks likely reflect the cost of processing required to stop one of the components during a bimanual movement. Similar differences between selective-stop versus stop-all tasks have also been observed by others in adults [9, 10] and children [13]. In an unpublished study cited by Logan [15], participants were able to selectively inhibit their responses in two- or four-choice reaction tasks, but it took them longer than for non selective inhibition. In addition, the delays in inhibiting were longer for the four-choice than for the two-choice tasks. Logan interpreted this pattern of results as suggesting two inhibition modes: a global mode for non selective inhibition and a local mode for selective inhibition. The global mode can be faster because all responses can be stopped indiscriminately (all-or-none), but the local mode is slower because it requires discriminating between responses. Such an idea of a two-level control, originally proposed by Bullock and Grossberg [31], relates to the distinction between so-called central and peripheral motor processes involved in the control of limb movements. In this model, central processes are concerned with the programming of movement (instantiation of amplitude and direction for example), whereas the peripheral processes are responsible for sending out the Go signal to the motor neurons pools, interactively with the central command. In line with that view, de Jong et al. [32] proposed that peripheral inhibition is faster than central inhibition and that non-selective inhibition is implemented through the fast peripheral inhibition mechanisms [9, 33]. Indeed, electrophysiological data showed that the amplitude of the Lateralized Readiness Potentials

(LRPs) in a non-selective inhibition task is the same, whether or not there is an overt movement [34]. LRPs are thought to reflect central preparatory processes and are classically believed to indicate whether and when a motor response is selected.

Van den Wildenberg and van der Molen [13] claimed that additional cognitive computational resources could explain the extra time, or cost, required for selective inhibition. In the current study, the average cost of selective vs. non selective inhibition was 133 ms for the first age group (5;11—7;4 years), 80 ms for the second (7;6—8;7), 73 ms for the third (8;8—9;11) and 63 ms for the elders (10;4—11;6). We can thus speculate that the developmental gain in the cognitive resources involved in selective motor inhibition processes is the greatest at younger ages, i.e. between 6 and 8 years of age. The central inhibition hypothesis appears best suited to explain such an improvement.

In addition, our results showed that selectively engaging one hand while the other hand is already active increases RTs as well as spatial and temporal variability whatever the type of pattern (in-phase or anti-phase) as compared to the condition that required activating the same arm alone. However, the developmental gain in the differential cost of activating in unimanual vs. bimanual conditions followed a different pattern from that observed for inhibition: the average additional cost under bimanual conditions was 118 ms for the first age group (5;11—7;4), 54 ms for the second (7;6—8;7), 66 ms for the third (8;8—9;11) and 124 ms for the oldest (10;4—11;6). As for inhibition, we suggest that the developmental gain observed between the first two groups can be explained by the increased cognitive resources available for the transition. The difference in unimanual and bimanual activation costs in the oldest group is a consequence of the abrupt decrease of RTs for the unimanual arm activation, while the developmental evolution of bimanual activation resembles that observed for inhibition.

Overall, the extra time needed to perform a motor transition (activation and inhibition) is associated with an increase in spatial and temporal variability at the period of transition, which depends neither on the type of transition (inhibition or activation) nor on the bimanual pattern (in-phase or anti-phase). Our results showed that the reduction of the variability of movement amplitude as children grow up was more important during the transition than during the mere production of a rhythmical movement (pre-transition). This suggests additional resources involved in selective changes that develop distinctly from those involved in the production of motor coordination per se.

Influence of bimanual patterns on selective changes. Our results show that the evolution of the motor changes is affected by the bimanual coordination: RTs decreased regularly with age in the in-phase pattern (Fig. 3, central panel) whatever the motor change, whereas there was some step-like decrease in the anti-phase pattern (Fig. 3, right panel). Moreover, in the latter, a plateau was reached earlier for activation (7;6—8;7 years) than for inhibition

(8;8—9;11 years). The central mechanisms for both selective inhibition and activation are thus affected by the bimanual constraints of the task. Studies in adults suggest that anti-phase patterns may involve additional inhibitory processes for suppressing the more intrinsic tendency towards mirror movements. Indeed, Serrien, Cassidy and Brown [35] showed an increase in inter-hemispheric EEG coherence during anti-phase as compared to in-phase bimanual movements, possibly related to the greater need for information processing. Moreover, a large network of cortical areas is thought to be involved in the control of complex bimanual movements.

The influence of the specific constraints of the task on motor transition is further supported by the measures of perturbation. Indeed, the Perturbation variable (slowing down or accelerating the dominant hand tempo following the motor change) showed an age-related effect for the anti-phase pattern only. The addition of one arm induced a drastic deceleration of the other arm in the youngest participants. This effect decreased with age to switch to a slight acceleration in the two older groups. The absence of age effect when activating in in-phase is in accordance with the developmental literature, as in-phase (or mirror-like) bimanual movements are present very early in the motor repertoire of the child, whereas anti-phase bimanual movements are progressively acquired [28]. In all age groups, the selective stop of one arm induced an acceleration of the tempo of the other arm, suggesting a transient low-level effect of transfer of "energy" from a two components motor behavior to a single component one. In other words, when children selectively inhibit one arm they can not refrain from increasing the speed of the remaining arm, whatever the bimanual pattern.

The different age-related trends observed in the present experiment between in-phase and anti-phase patterns confirm that the neural components involved in the production of anti-phase movements might differ from those involved in the in-phase ones, and that the two networks mature asynchronously. More specifically, the smooth decrease in RTs for both activation and inhibition transitions under the in-phase condition could be interpreted in two ways: (1) activation and inhibition depend on a common process, or (2) they depend on distinct processes that mature synchronously over the ages tested here. In contrast, the discrepancy between the plateaus for inhibition and activation in the antiphase pattern could reflect the involvement of heterogeneous, asynchronously developing mechanisms including various cortical and subcortical structures.

In sum, activation and inhibition mechanisms involved in selective motor transitions do not show similar developmental changes, depending on the complexity of the bimanual coordination.

As can be seen on Fig. 5a, after a marked improvement between the first (5; 11—7;4) and the second (7;6—8;7) age groups, the temporal stability deteriorated in the in-phase pattern in the third group (8;8—9;11). In other words, when children aged about 9 years switched from unimanual to bimanual movements, they showed a temporary difficulty to enter an in-phase mode of coordination. Such an effect, contrasting with the monotonous increase in temporal stability during the pre-transition window, is unexpected as the in-phase coordinative mode is thought to be the easiest to produce. This age-related instability is reminiscent of developmental inverted U-shaped trend documented in several studies of visual-motor processes in the considered age range [36—40]. Mounoud et al. [39] interpreted such a regression on the basis of clinical exchanges with the children. From 6—7 years of age, children become rather suddenly aware of the properties of their action. Before this age, action appears to be executed on a more spontaneous or automatic manner which prevents a conscious access to these properties. More precisely, these authors showed that, in the case where a unimanual motor response must be synchronized with an external, periodic visual stimulus, a destabilization in performance is observed at the age of 6—7 years. Before this age, the behaviour is stable but the child is unaware of the fact that he/she actually fails to correctly adjust his/her response to the specific constraints of the task. The modification in the level of consciousness of action would cause a temporary decrease of performance. In our experiment, the decrease in performance occurred at about 9 years of age. This time-lag could be explained by the specific constraints of the tasks (synchronisation of complex bimanual coordination).

Pre-transition period: the production of a regular rhythm. Although it was not the primary goal of the present study, our data shed light on the developmental time course of performance of continuous, externally paced, rhythmic movements of the dominant arm between the ages of 6 and 12 years. At all ages, children were able to produce an errorless average tempo before the transition, no matter whether performing unimanual or bimanual movements. This result corroborates those of Mounoud et al. [39] showing that successful visual-manual tracking of a simple periodic signal is acquired from the age of six. In addition, the present data also show that the temporal stability of the movement increases with age both for unimanual and bimanual patterns. Regarding the spatial dimension, although the amplitude of the movement was not strictly constrained in our experimental set-up, the children performed the task with similar average amplitudes across ages.

CONCLUSIONS

In conclusion, the present study provides an original protocol to compare the performance of activation and inhibition during childhood. Using a transition paradigm, we showed that activation and inhibition globally improve with age, although improvement follows distinct developmental trends depending on the complexity of the motor task. Specifically, in the unimanual and bimanual anti-phase tasks, aged-related changes differed between inhibition and activation, suggesting either the involvement of distinct neural networks or the existence of a single net-

work that is reorganized differently. In contrast, stopping or adding one hand during a mirror-like bimanual movement (in-phase) shows similar aged-related improvement. We suggest that selectively stopping or activating one arm during symmetrical coordination rely on the two faces of a common processing in which activation could be the release of inhibition.

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