Protracted development of visuo-proprioceptive integration
for uni-and bimanual motor coordination

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ABSTRACT

Sensory and motor processes undergo massive developmental changes over at least a decade in human development. Interdependencies between different sensorimotor control mechanisms as well as bodily abilities are difficult to assess when circumscribed experiments and small age ranges are employed. Here, we assessed coordinative abilities of 120 children aged 4-12 for the two hands or a hand with another sensory signal in multiple, highly comparable sensorimotor tasks. This multi-task approach allowed assessing the developmental trajectory and interplay of several aspects of motor control related to different coordinative requirements. Children were first able to symmetrically move the two hands, and only later to coordinate one hand with a proprioceptive or visual signal. The ability to strategically ignore sensory information was available last. The pattern of partial correlations among tasks suggests protracted, interdependent, chained development within individuals.

KEYWORDS

Proprioception; feedback; multisensory integration; sensorimotor processing; Lissajous

1. INTRODUCTION

Motor development protracts over almost two decades before humans possess full adult abilities. Mastering a new motor skill often changes the way children interact with and perceive their environment. This interplay sets the stage for learning further skills not only for motor function but also in sensory, cognitive and social domains (Adolph & Franchak, 2017; Adolph & Hoch, 2019; Hamilton et al., 2016). Unsurprisingly, then, sensory development, too, is characterized by extended timelines. For instance, children's multisensory processing differs markedly from that of adults until at least 8-10 years of age (for review, see, Burr & Gori, 2012; Gori, 2015). According to current theories of motor control, sensation and movement are linked by internal models. These are cognitive processes that predict the sensory consequences of ongoing, or planned, movement and adjust movement if required (Haar & Donchin, 2020; Shadmehr & Krakauer, 2008). However, knowledge about how this sensorimotor interplay and cognitive organization develops is fractured.

Given the extensive effort required for developmental research, many studies have focused on limited age ranges as well as on only one or few sensorimotor functions or tasks. This research strategy makes it difficult to characterize developmental trajectories and to determine how specific abilities build on others. Therefore, the protracted and interwoven nature of sensorimotor development calls for studies that investigate wide age ranges and multiple sensorimotor functions. In the present study, 120 children aged 4-12 years performed 6 sensorimotor tasks. All tasks used a common experimental framework of continuous, circular hand movement to contrast different requirements related to sensorimotor coordination. This approach allows characterizing developmental trajectories and dependencies of three aspects of sensorimotor control, which are illustrated in Fig. 1. We introduce the three aspects below.

Figure 1. Schematic of the three aspects of motor control investigated in this study.

The first aspect we considered (Fig. 1, blue shapes) is coordinating a hand movement with a sensory signal. One can view this type of task as the most basic implementation of a sensorimotor loop: Participants in our study aimed to continuously track a visual or passive-proprioceptive signal with their dominant hand. The visual signal was a visual cursor, the position of which participants had to match as closely as possible. For the passive-proprioceptive signal, we moved the participant's non-dominant hand and they had to track it continually with their dominant hand.

Adults effectively coordinate both goal-directed and continuous tracking movements based on visual as well as proprioceptive information (Buekers et al., 2000; Jones et al., 2010; Tanaka et al., 2009). Children learn to reach towards external targets and their own body during their first year of life (Chinn et al., 2019; Somogyi et al., 2018). Already at age 4-5, children adapt goal-directed hand movements to visual and kinesthetic perturbations, such as unexpected target displacement, visual rotations, or and hand-diverting forces (e.g. Contreras-Vidal et al., 2005; Ferrel-Chapus et al., 2002; Hay et al., 2005; Kagerer & Clark, 2014; Konczak et al., 2003). Nevertheless, performance improves until at least the age of 10 or 12 (e.g. Kagerer & Clark, 2014; P. H. Wilson & Hyde, 2013). Moreover, children aged 5-7 were able to track a visual target with their eyes and hand (Gauthier et al., 1988), with improvement evident until at least age 10-11, but possibly even until late adolescence (Van Roon et al., 2008; Zanone, 1990). However, development of such unimanual functions is often non-linear, with multiple

reports of large performance increases in a limited age interval, but also temporary performance decrements (e.g. Badan et al., 2000; Hay, 1978; Martel et al., 2020; Pellizzer & Hauert, 1996; Smyth et al., 2004). Despite a large body of work, previous studies have not yet compared visual and proprioceptive tracking within participants across the full developmental age range of about 4-12 years, in which massive, fundamental changes occur in sensorimotor development, and they have not related sensorimotor tracking in children to other sensorimotor functions.

The second aspect we consider (Fig. 1, red shapes) is the coordination of two body parts, operationalized as executing symmetrical movements with the two hands. Compared to unimanual movements, this task can rely on a third signal: the two hands can both be driven by a common motor command, which will "automatically" create symmetry. One could have two hypotheses regarding the impact of this additional signal: either it might be difficult to integrate with visual and proprioceptive information, so that bimanual coordination would develop later than unimanual coordination. Alternatively, the common motor signal for both limbs may provide an easy-to-use mechanism for coordination, making the bimanual task an easier task than unimanual coordination with an external or passive-proprioceptive signal.

Previous research clearly favors the latter. Young children often exhibit involuntary movement of the opposite hand along with an instructed, unimanual movement, and this phenomenon declines around 10 years of age; for instance, the left hand would pinch along with the right, although only a right-hand pinch was instructed (Cincotta & Ziemann, 2008; Lazarus & Todor, 1987). The occurrence of such movements has been associated with transfer between homologous motor areas via the corpus callosum. As this structure matures, involuntary bilateral movements decline (Cincotta & Ziemann, 2008; de Boer et al., 2012). In this framework, bilateral motor activation and simple, symmetrically coordinated movements should be performed more successfully, and at an earlier developmental stage than coordination with an external signal, for which the common motor signal does not exist.

Despite their preference for bimanual activity, young children usually show lower accuracy for bimanual symmetry than older children and adults (de Boer et al., 2012; Fagard et al., 1985; Jeeves et al., 1988; Lantero & Ringenbach, 2007), though this has not always been observed (Fagard, 1987). This developmental trajectory aligns with the protracted maturation of the corpus callosum. Yet, even if callosal maturation reduces automatic bilateral movement, adults preferentially synchronize bimanual movements symmetrically, especially when movement speed is high (e.g. Brandes, Rezvani, & Heed, 2017; Kelso, Scholz, &

Schöner, 1986; Spencer, Ivry, Cattaert, & Semjen, 2005; for review, see Gooijers & Swinnen, 2014). Moreover, older children and adults integrate visual information to aid (bimanual) motor coordination, whereas younger children appear not to do so. For instance, children aged 4 and 6 disregarded visual information during circle drawing, contrary to 8 year-olds and adults (Lantero & Ringenbach, 2007). Such results suggest critical developmental changes in sensorimotor integration during this age range. Therefore, the present study tested whether visual information about the two hands' current position, versus circling without any visual cues, improves children's bimanual, symmetric hand circling. The tasks we employ are directly comparable to the unimanual tracking tasks we devised.

The third aspect we consider (Fig. 1, ochre shapes) pertains to complex sensorimotor coordination that requires using visual information to overcome the symmetry constraints of the motor system that we just discussed. The findings we have reviewed so far were initially interpreted as indicating that bimanual coordination relies purely on synchronized motor commands (Cohen, 1971; Kelso, 1984; Riek & Woolley, 2005). However, other studies have demonstrated a pivotal role of perceptual signals (for review, see Shea et al., 2016), even culminating in the suggestion that symmetry in movement coordination relies entirely on perceptual rather than motor processing (Bingham, 2004). For instance, when the index fingers are wiggled with one hand turned up and the other down, movements are performed best when they are symmetrical in space, although such coordination requires concurrent activation of non-homologous muscles and, thus, cannot not rely on one single, common motor command (Brandes et al., 2017; Heed & Röder, 2014; Mechsner et al., 2001). Moreover, it is impossible for most adults to circle the two hands at different speeds (e.g., four turns with the left for every three turns with the right). Yet, this task becomes manageable when the different hand speeds are transformed into same-speed visual signals, akin to turning handles connected to cogwheels of different size (Mechsner et al., 2001); the required, asymmetrical movement pattern is achieved by symmetrically synchronizing the visual cues. Similarly, many studies used designs similar to the "Etch-A-Sketch" drawing toy (Fagard, 1987; Fagard et al., 1985; Jeeves et al., 1988; Preilowski, 1972, 1975; Swinnen, 2002; see https://en.wikipedia.org/wiki/Etch_A_Sketch), also termed "Lissajous" display (Chiou & Chang, 2016; Kovacs et al., 2009). Both the toy and the respective sensorimotor tasks require circular movement of two knobs or handles. Critically, one hand controls a cursor's horizontal, and the other hand its vertical position. By turning the knob/handle at different speeds, the cursor will move linearly along different slants. With this visual aid, adults and older children, but not young children, can maintain otherwise impossible,

asymmetric bilateral hand movements. Children performed Lissajous and other, similar tasks successfully at around 8-10 years of age – that is, significantly later than the tasks we introduced earlier (Fagard, 1987; Fagard et al., 1985; Jeeves et al., 1988; Leinen et al., 2016). Like unimanual coordination, bimanual asymmetry requires coordination with a signal that does not directly reflect limb position. However, in contrast to unimanual coordination, participants must downweigh proprioceptive information, because only transformed visual information contains the correct information about how the two hands should be positioned relative to each other at any given moment. Moreover, it is critical to overcome the motor system's default tendency for symmetry. In our study, participants had to turn two handles, either with or without symmetrical visual aid, in a 2:3 relation – that is, two full circles of one hand while the other does three. Again, the tasks were designed such that performance can be compared with the remaining tasks employed in our study.

In sum, the present study addressed the development of three aspects of motor control: unimanual coordination with an external visual or passive-proprioceptive guiding signal; visual and proprioceptive coordination of active, symmetrical, bimanual control; and the ability to overcome the motor system's symmetry preference through focusing on visual information. If movement coordination is entirely perceptually driven, as has been suggested at least for the type of tasks we used here (Bingham, 2004), then bimanual coordination is but a subcategory of a more general ability to coordinate motorically by means of perception. Under this assumption, one might expect that uni- and bimanual coordination show similar developmental trajectories. In contrast, if – as suggested by research on callosal transfer – motor synchronization plays a critical role in bimanual coordination, then one might expect different developmental trajectories for bimanual and unimanual tasks, with bimanual emerging earlier than unimanual coordination. Nonetheless, visual feedback may be integrated with motor signals to improve symmetric motor coordination, at least by older children. Given that previous research suggests such visual-motor integration to emerge rather late, visually guided, asymmetrical coordination should also emerge late. Critically, addressing these aspects in a within-subject design, albeit cross-sectionally, allows assessing whether functions that emerge later rely on development of those functions that emerge earlier by correlating performance across tasks. Last not least, we tested a group of adults and compared children's to adults' performance to establish at which age children's performance might be considered mature.

2. METHODS

2.1. Participants and ethical approval

We enrolled children at public science popularization events, school visits to our lab, and via flyers, until we had recruited at least 12 children of each age from 4-12 years that met our inclusion criteria. Of 138 tested children, 120 were included in the final sample (52 girls, 68 boys). All included participants had normal or corrected-to-normal vision and were free of any known neurological, visual, and tactile impairments and disorders. They were born in regular term ($> 37^{th}$ gestational week), scored between 70 and 130 on a short IQ test, and passed screening for attentional disorders, learning disabilities and delayed psychomotor acquisition (see supplementary information for details). We determined hand dominance with the quick oral version of the Edinburgh scale, asking participants their hand preference for writing, drawing, and using a scissor or spoon (Oldfield, 1971). Younger children handled scissors and briefly wrote something, so we could assess their hand dominance directly, which we additionally confirmed with parents. Four 4-year-olds were unable to follow the task instructions or did not want to complete the study.

We also enrolled a group of 12 adults (6 female, mean age: 27.2 years; s.d.: 2.2 years). We replaced one adult who exhibited unusual difficulty in handling the experimental setup and exhibited accuracy outside 2 s.d. of the adult sample in some experimental tasks.

The study was approved by the local ethics committee of Bielefeld University. Adult participants and children's parents gave written informed consent prior to the experiment. Children gave oral consent after they had received all information prior to the study. Children received a small gift of about 10 € value for their participation. Participants of the adult group received course credit.

2.2. Experimental setup, tasks, and procedure

2.2.1. Technical setup

All tasks were implemented in the KINARM End-Point-Lab (Fig. 2A, BKIN Technologies Ltd, Kingston, Ontario, Canada), a robot that serves as a hand manipulandum for hand

movements in a 2D horizontal plane in front of the user. Participants grab one or two handles, the position of which is continually recorded at a sampling rate of 1000 Hz. Mobility of the handles can be constrained by the robot, allowing us to restrict movement to the circular trajectories required for our tasks. A monitor projects from above onto a mirror placed above the hands, so that visual information displayed on the mirror appears to be located below the mirror, in the same plane as the hands. We provide videos of the screen display for all tasks in the Supplementary Information. Depending on their body height, participants were seated on a height-adjustable chair, or stood on an adjustable platform, so that their elbows were angled at 90°. Most children aged 7 and older were tall enough to be seated. With this arrangement, all participants could reach sufficiently far into the workspace to comfortably move the handles and their arms could move without obstruction. An opaque apron attached to the participant's neck prevented vision of the arms, and the display mirror was opaque, so that participants could not see their hands. This setup allowed us to fully control visual feedback about hand position via cursors on the screen.

Fig. 2. Illustration of the general setup. A, The Kinarm Endpoint Lab device. The display is mounted above the hand-held handles, and visual stimuli appear as if they are located at the level of the hands. An apron (not shown) was attached so that the participant could not see their hands. B, illustration of the task display. Circles indicated where each hand could be moved. The hands could move freely between trials. Once the participant moved to the blue starting positions, movement was restricted along the circles and participants fixated the central, white square. A short motivational sentence was displayed after every two trials.

2.2.2. Task display

Fig. 2B illustrates the task display. In all tasks, the display showed two same-colored circles of 10 cm diameter. They were 20 cm apart, visually separated by a fence-styled line down the middle of the display. A fixation square was placed in the middle of the fence, at the height of the circles' midpoints. Some of the 6 tasks required movement of one, and other tasks movement of both hands; whenever the right hand had to be moved, it could only move along the trajectory underneath the right circle outline, and equivalently for the left hand and circle. The starting point for hand movement in a given trial was always the innermost circle position, which were marked with blue, 1 cm diameter dots on the circles. We created child-friendly designs and story lines to support children's motivation to complete the study. Each child chose one of several stimulus themes that each featured four 2 cm diameter characters to represent hand position (see Fig. 2B & Video in the Supplementary Material with the visual display for each task).

2.2.3. Tasks

We report on 6 tasks in which participants had to move one or both hands in circles. Together, they address the three aspects of motor control we laid out in the introduction. The task setup mimicked turning handles attached to wheels by allowing participants to move two handles along fixed circular trajectories. We assessed how well they coordinated the position of one or both hands, i.e. relative movement phase along the circle. We present the tasks in the order used for the logic of the paper; note, that children performed the tasks in a different order, which we report below (see Procedure). Tasks 1 and 2 tested unimanual coordination; tasks 3 and 4 assessed bimanual, symmetric coordination; and tasks 5 and 6 addressed sensory selectivity in bimanual motor coordination.

*Task 1 – Match the Cursor: Unimanual Visual Coordination (Uni-Vis)***:** Participants had to coordinate their unimanual movement with an externally controlled visual signal. They saw a visual cursor on the screen above their hands moving along the circular trajectory that represented the movement area of their non-dominant hand. The cursor was computer-controlled, and participants rested the non-dominant hand rested on their lap. Participants had to symmetrically match the cursor position with their dominant hand, the position of which, too, was visualized as a cursor. There were six trials of 20 s duration each.

Task 2: Match the Other Hand: Unimanual Proprioceptive Coordination (Uni-Prop): The Kinarm robot passively moved the participant's non-dominant hand. Participants had to symmetrically match the passive movement of their non-dominant hand with their dominant hand. They were instructed to relax the passively guided arm and let the robot lead them without actively supporting the movement. No visual feedback of either hand's position was available. There were six trials of 20 s duration each.

Task 3 – Bimanual 1:1 Coordination Without Vision (Bi-NoVis): Participants had to move the two unseen hands symmetrically in six trials of 10 s duration each. The task appeared visually identical to Uni-Prop.

Task 4 – Bimanual 1:1 Coordination With Vision (Bi-Vis): Participants had to move the two hands symmetrically while receiving feedback about hand position in form of cursors on the screen above their hands. They performed six trials of 10 s duration each. The task appeared visually identical to Uni-Vis.

Tasks 3 and 4 were quite easy to perform, and we chose a short trial duration to avoid children getting bored and demotivated.

Task 5 – 2:3 Coordination With Veridical Hand Position Feedback (2:3-NoTransform): Participants had to concurrently perform three circles with their dominant, and two with their non-dominant hand. Hand position was indicated by visual cursors, as in Uni-Vis and Bi-Vis. Accordingly, if the task was performed correctly, the two cursors did not move symmetrically. This kind of task is very difficult even for adults and constituted the baseline 2:3 coordination task. Participants performed six trials of 20 s duration each.

Task 6 – 2:3 Coordination With Transformed Feedback (2:3-Transform): Participants had to perform 2:3 coordination as in 2:3-NoTransform. However, cursor position did not reflect the hands' veridical location, but was transformed to appear symmetrical: For the dominant hand, the cursor completed one full circle on the display while participants performed 3 circles with their hand. For the non-dominant hand, the cursor completed one circle while the hand circled twice. Accordingly, participants could correctly perform the task by maintaining symmetrical visual feedback on the display. We explained this task feature in detail to participants. They performed 3 x 6 trials of 20 s duration each.

We conducted more trials in Task 6, 2:3 Transform, because we expected that participants would learn the required asymmetrical coordination with some practice, based on previous

reports (Chiou & Chang, 2016; Kovacs et al., 2009, 2010; Kovacs & Shea, 2011). We tested potential learning in a seventh task, Retention, in which 2:3 transformed visual feedback was provided only at the beginning of each trial and then removed. With such a procedure, a previous study reported coordination learning in adults (Kovacs & Shea, 2011). However, in our study here, neither children nor adults were able to perform this seventh task correctly. This finding indicates that none of our participants learned the 2:3 coordination independent of visual feedback. We omit a detailed report of this seventh task for the sake of brevity (but see supplementary information).

Trial structure. For all tasks, each trial began with the participant moving their hand(s) to the starting position(s) (Fig. 2B, blue dots). A beep of 150ms duration instructed to begin circling in the inward direction (i.e. left hand clockwise and right hand counter-clockwise) until a beep of 300ms duration signaled the trial's end. Participants were to look at the fixation square throughout the trial. The experimenter monitored fixation visually and additionally reminded the participant about fixation every two trials. We repeated trials if the participant did not fixate as instructed. For all tasks, participants performed three practice trials during which we gave oral feedback on whether task performance complied with the instructions. If necessary, we added up to two additional practice trials. During experimental trials, we gave no feedback about performance. However, if the participant moved in the wrong direction (e.g. counter-clockwise for the left hand), we explained the mistake and repeated the trial. This happened seldom, though more with younger than older children, and was not specific to one task.

After every two trials, we displayed short sentences for 5 s to frame the experiment as a story and support children's motivation. We read the sentences aloud for children who could not yet read. Sentences playfully framed the tasks and commended them for their continuous effort. Examples of the framing story and sentences are available in the supplementary information.

Procedure. Participants first played a short game to acquaint themselves with the Kinarm. Then, they performed the experimental tasks. Participants always started with the bimanual coordination tasks, Bi-NoVis and Bi-Vis (Task 3 and 4 in this report). We used this order because we wanted to avoid that performance without vision would benefit from experience of the visual task if it were done first. Then, Uni-Vis, Uni-Prop (Task 1 and 2), and 2:3-NoTransform (Task 5) were conducted in randomized order by participants drawing pieces of paper in an envelope. The session ended with 2:3 tasks: 2:3-Transform (Task 6) had to be conducted after 2:3-NoTransform because it potentially involved learning. In turn, Retention

(omitted from this report, as explained above) tested learning of 2:3-Transform and, thus, had to be assessed last.

All tasks were 3-5 min long, except for 2:3-Transform, which lasted 12 min. Participants rested between tasks; in the 12 min 2:3 Transform task, they took an additional break in the middle.

Some participants did not perform all tasks. Table 1 lists the number of individuals per year of age and task. We lost some data due to equipment failure; this was especially prevalent for the passive-proprioceptive task, Uni-Prop (Task 2), which we could not run for several months; thus, the low number of participants is *not* due to younger children being unable to perform the task, but to the restraint of having to acquire our data within the time range defined by project funding. We decided to include the imperfect data because the remaining N is still about 50, and data are complete for some age groups, allowing fully qualified analysis. In contrast, the low number of younger participants in the 2:3 tasks (Tasks 5 and 6) are due to task difficulty, not technical problems. Most 4- and 5-year-olds failed in the 2:3 tasks, and some found these tasks very discouraging, leading to low motivation to complete them. Sometime into data acquisition, therefore, we stopped acquiring the 2:3 tasks for children younger than 6 years.

Table 1. Participant numbers for all tasks. Low participant numbers in Task 2 were due to temporary equipment failure that selectively affected this task. Low participant numbers in Tasks 5-6 were due to task difficulty for the younger children.

Age Group Number of included participants	4 yo n = 14	5 yo n = 12	6 yo n = 12	7 yo n = 12	8 yo n = 12	9 yo n = 16	10 yo n = 18	11 yo n = 12	12 yo n = 12	Adults n = 12
Task 1 – Match the Cursor: Unimanual Visual Coordination – Uni-Vis	14	12	12	12	11	16	18	12	12	12
Task 2 – Match the Other Hand: Unimanual Proprioceptive Coordination – Uni-Prop	1	2	3	5	4	7	6	12	12	12
Task 3 – Bimanual 1:1 Coordination Without Vision – Bi-NoVis	14	12	12	12	12	16	18	12	12	12
Task 4 – Bimanual 1:1 Coordination With Vision – Bi-Vis	14	12	12	12	12	16	18	12	12	12
Task 5 – 2:3 Coordination With Veridical Hand Position Feedback – 2:3-NoTransform	6	3	11	12	11	16	18	12	12	12
Task 6 – 2:3 Coordination With Transformed Feedback – 2:3-Transform	5	3	11	12	12	16	18	12	12	12

2.3. Data processing

We analyzed data in Matlab (version: R2015aSP1). Each hand's position time series was filtered using a low pass Butterworth filter with a cut-off frequency of 10 Hz.

We base our report on the unsigned phase difference between the two positions that are coordinated: the two hands in bimanual tasks; the visual cursor or the passively guided hand and the active hand in unimanual tasks, and the two transformed locations in the 2:3 tasks. By discounting the sign, we ignore which position leads the other – for instance, whether the dominant hand is ahead of the non-dominant hand or vice versa. Some previous studies have, instead, reported the percentage of performance within a certain interval, for instance +/-30° phase angle as the "percentage of adequate coordination" (Mechsner et al., 2001, 2007) or "time on task" (e.g. Bingham et al., 2018). Qualitatively, this measure renders similar results as the phase difference (Brandes et al., 2017), but we report it in the Supplementary Information to aid comparison with earlier work.

We coded individual positions as the angle between the starting position and the location along movement direction. Thus, when the hands were at the lowest position, their phase angle was 90°, at the outermost position it was 180° etc. In the bimanual tasks, we computed the phase angle difference of the two hands. In the unimanual tasks, we computed the phase angle difference between the actively moved hand and the position of the leading signal, that is, the visual cursor (Uni-Vis) or the passively moved hand (Uni-Prop). In the 2:3 tasks, we divided the faster hand's phase angle by 3, the slower hand's phase angle by 2, and subtracted the two to assess the phase difference relative to the instructed, non-symmetrical movement.

2.4. Data analysis and statistics

We statistically analyzed data in R (R Core Team, 2018; R: 3.5.1; R Studio: 1.1.456). We implemented multilevel Bayesian modeling with the R package *brms* (Bürkner, 2017).

We addressed our research questions by separately analyzing the symmetrical tasks 1-4 and the 2:3 tasks 5-6, respectively. Analysis of the symmetrical tasks allows gauging the ability to coordinate a hand with visual and proprioceptive information, as well as exploiting motor information of one hand to guide the other. Thus, this analysis addresses the first two aspects discussed in the introduction (Fig. 1, blue and red shapes). In contrast, the comparison of tasks 5 and 6 specifically addresses the ability of visual synchrony information to coordinate non-

symmetrical bimanual movement, thus addressing the third aspect laid out in the introduction (Fig. 1, ochre shapes).

Moreover, we applied three different statistical approaches. First, we predicted the unsigned phase angle with *Task* and *Age in Months* as independent variables, treating *Age* as a continuous predictor. *Age* was mean-centered, allowing to interpret potential interactions with reference to the sample's mean age. We included only the children's data in this model, as higher performance of adults, combined with the large gap between their and the children's age in months, might have led to artificial correlations of age with coordination performance.

Second, we compared unsigned phase angle across *Tasks* and *Age in Years*, this time treating Age as a categorical variable. Here, adults were included as one group, so that we could compare post-hoc at which age children performed comparably to adults. Moreover, comparisons were also possible between the children's age groups, allowing to detect trend reversals and performance plateaus which would be missed by a continuous, linear predictor.

Third, we tested whether performance in some of our six tasks was related. Given that one expects performance in any task to improve with age, all tasks will be trivially related via age. Therefore, we computed correlations between tasks while partialling out age to isolate any potential age-independent task relationships.

We implemented the first and second analyses as Bayesian mixed models. Mixed models cope well with different numbers of observations across conditions, small samples, and groups of different sample size (Boisgontier & Cheval, 2016). Because participants performed continuously for an extended duration, they performed several circles. We derived the dependent variable, the averaged *unsigned phase angle difference* in degrees, for each full circle of the dominant hand. With trial durations of 10 and 20 s, respectively, for the different tasks, this strategy rendered multiple observations per trial and, thus, captured performance variability within trials, rather than averaging together entire 10 or 20 s chunks into a single measurement value. At the same time, using one value per circle (and not more) kept model fitting computationally tractable.

Model 1 used as predictors the within-subject, categorical variable *Task* (Task 1-4: Uni-Vis, Uni-Prop, Bi-NoVis and Bi-Vis,), the between-subject, continuous variable *Age* (in months), and the interaction between *Task* and *Age*. The model was defined as: Phase_Difference ~ Task × Age + (1|subject) + (1|trial), thus allowing random effects per subject and trial.

Model 2 used the predictor *Age* grouped by year as a categorical variable. The model was defined as: Phase_Difference ~ Task × Age_Group + (1|subject) + (1|trial).

Model 3 was defined just like Model 1, except that Task comprised the 2:3 tasks (Task 5-6: 2:3-NoTransform, 2:3-Transform).

Similarly, *Model 4* was defined just like Model 2, except that Task comprised the 2:3 tasks (Task 5-6: 2:3-NoTransform, 2:3-Transform).

Bayesian mixed models have the additional advantage of allowing to assess null effects. The Highest Density Interval (HDI) represents the 95% interval of a parameter estimate's posterior (i.e., estimated based on the experimental data) distribution. When the HDI clusters around 0, operationalized as the complete HDI falling within +/-0.1 standard deviations of the dependent variable (termed the Region of Practical Equivalence, ROPE, of effect sizes; Kruschke, 2011, 2018), one concludes that the parameter does not have an effect. On the flip side, if the HDI does not fall within the ROPE, it is considered credible that the parameter has an effect. In some cases, only part of the HDI might fall within the ROPE. This inconclusive result prohibits concluding both a difference between conditions and equivalence. When we applied ROPE analysis to compare children's to adults' performance, we interpreted this latter case as indicating that children's performance did not yet resemble adult performance, given that the two groups' performance could not be considered equivalent.

For each main effect and interaction, we report the estimate of the mean (β) and its $HDI_{95\%}$. We used the R package *sjstats* (Lüdecke, 2018) to compute the ROPE for each model and infer the presence of statistical effects (ROPE limits for each model: Model 1: [-4.1; 4.1]; Model 2: [-3.9; 3.9]; Model 3: [-5.4; 5.4]; Model 4: [-5.4; 5.4]; numbers refer to the dependent variable: phase difference in degrees). To get meaningful values for models with a continuous predictor *Age*, we standardized the posterior distribution of this covariate (and respective interactions) by multiplying the covariate and respective interaction estimates (and their respective HDIs) by the standard deviation of subjects' age. The SD of subjects' age differed between Tasks 1-4 (Models 1 and 2: 30.3) and Tasks 5-6 (Models 3 and 4: 25.3) because fewer children completed tasks 5-6 than 1-4 (see Methods).

Model fitting used a Gaussian likelihood and the *brms* package's default weakly-informative, improper, flat priors for population-level ("fixed") effects. The estimation of parameters' posterior distribution was obtained by Hamiltonian Monte-Carlo sampling with 4 chains,

1,000 sample warmup, and 11,000 iterations, and checked visually for convergence (high ESS and Rhat ≈ 1).

We implemented our third analysis, the assessment of whether there were age-independent developmental dependencies across tasks, as Bayesian partial correlations. We correlated the unsigned phase angle between pairs of tasks, but removed the effect of age as implemented in the R package *BayesMed* (Wetzels & Wagenmakers, 2012) using a default Jeffrey's-Zellner-Siow prior set-up. The obtained Bayes Factor (BF) expresses the odds of the H1, a true correlation, compared to the H0 of a zero correlation. A BF between 3 and 10 indicates moderate evidence for the H1, while values >10 above are considered strong evidence (Wetzels et al., 2011).

3. RESULTS

3.1. Uni- and bimanual, symmetric coordination (Tasks 1-4)

3.1.1. Model 1: Age as continuous predictor

We assessed the variability of children's coordination performance in a model that predicted the unsigned phase difference between the two coordinated signals – a visual or proprioceptive signal and a hand (unimanual tasks), or the two hands (bimanual tasks). Figure 3 illustrates performance in the four tasks included in the model.

Fig. 3.

Unsigned phase difference between the two hands in unimanual Tasks 1 and 2 (blue and black) and bimanual Tasks 3 and 4 (dark and light red) for children (left panel) and adults (right panel). The dashed lines represent the 30° threshold under which we considered subjects to perform well (see supplement for analyses using this threshold to define the dependent variable). Colored circles represent the mean for each age group; bars show the s.d. Fewer than half of the 4-8 year-old participants performed Task 2 (Uni-Prop; black), the means are thus likely to be non-representative (means in Uni-Prop are not shown for 4- to 5-year-old children, because n $\leq$ 2).

In the two unimanual tasks, participants had to synchronize the movement of their dominant hand with a circling dot (Uni-Vis) or with their passively moved, non-dominant hand (Uni-Prop). β estimates reflect improvement with age: Negative slope values indicate that improving performance, as the phase difference between hand and sensory stimulus decreased by the number of degrees specified by β_{Age} with each standardized age unit (30.3 months in Model 1, see Methods). Slope coefficients for the two unimanual tasks were indeed negative and different from 0 (Uni-Vis: β_{Age} = -21.8, $HDI_{95\%}$ = [-23.8; -19.7], Fig. 3: blue; Uni-Prop: β_{Age} = -19.5, $HDI_{95\%}$ = [-21.8; -17.1], Fig. 3: black; see Table 2), thus indicating that children performed them better with increasing age. There was no credible difference for the contrast between the two tasks, indicating that the Intercept coefficient was similar for Uni-Prop than Uni-Vis (difference of Uni-Prop and Uni-Vis, β = -4.0, $HDI_{95\%}$ = [-5.5; -2.6]; see Table 2). Moreover, there was no credible *Task $\times$ Age* interaction contrast either (β = 2.9, $HDI_{95\%}$ = 0.8; 3.8]; see Table 2), indicating that the slope did not differ between unimanual tasks. Thus, the two unimanual tasks did not differ in any of their estimated parameters.

In the two bimanual tasks, participants had to symmetrically rotate their hands, with (Bi-Vis) or without (Bi-NoVis) additional visual feedback of their hand position. Both slope coefficients were negative and different from 0 (Bi-NoVis: β_{Age} = -8.8, $HDI_{95\%}$ = [-10.9; -6.7]; Bi-Vis: β_{Age} = -7.7, $HDI_{95\%}$ = [-9.9; -5.7]; see Table 2). In equivalence to the unimanual tasks, negative slope values indicate that the phase difference between the two hands decreased by the number of degrees specified by β_{Age} with each standardized age unit of 30.3 months (Fig. 3; light and dark red dots). There was neither a credible difference between the intercepts of the two bimanual tasks, nor a *Task $\times$ Age* interaction, indicating that the parameters of the two bimanual tasks were not credibly different (see Table 2 for a summary of all model estimates). Thus, performance and its improvement with age were similar in the two bimanual tasks.

The two unimanual tasks exhibited large effects of *Task* and *Task × Age* interactions when contrasted with the bimanual tasks (see Table 2 for all model estimates). Unimanual intercepts were higher, indicating that the performance was worse at younger ages (higher error), and the negative slopes were steeper indicating larger improvement with age, in the unimanual than in the bimanual tasks.

Table 2. Beta Estimates reflecting the comparison between Tasks 1 to 4 in Model 1. For Age, negative β Estimates indicate that performance was better with higher age (smaller error for each standardized unit of Age of 30.3 months, see Methods). For Task, positive β Estimates indicate that Intercept was higher in the first task of each line, meaning that for this specific task, there was a higher error at younger ages. The interaction Task × Age reflects differences in steepness of improvements with Age. The Lower and Upper Confidence Interval (CI) values constitute the 95% High Density Interval (HDI), which represent the interval in which 95% of the values will be found. Credible differences are indicated in bold (HDI outside of the Region Of Practical Equivalence in which there is no effect [-4.1; 4.1]). ESS stands for the Effective Sample Size as calculated during Bayesian model fitting.

Effect	Contrasts	β Estimate	Lower CI	Upper CI	ESS
Age	**Uni-Vis**	**-21.8**	**-23.8**	**-19.7**	**2799**
	Uni-Prop	**-19.5**	**-21.8**	**-17.1**	**3617**
	Bi-NoVis	**-8.8**	**-10.9**	**-6.7**	**2883**
	Bi-Vis	**-7.7**	**-9.9**	**-5.7**	**2830**
Task	Uni-Prop – Uni-Vis	-4.0	-5.5	-2.6	45019
	Bi-Vis – Bi-NoVis	-0.9	-2.0	0.3	30090
	Uni-Vis – Bi-NoVis	**30.0**	**29.0**	**31.1**	**31264**
	Uni-Vis – Bi-Vis	**30.9**	**29.8**	**31.9**	**94400**
	Uni-Prop – Bi-NoVis	**26.0**	**24.5**	**27.6**	**29358**
	Uni-Prop – Bi-Vis	**26.9**	**25.3**	**28.4**	**48025**
Interaction Task × Age	Uni-Prop – Uni-Vis	2.3	0.8	3.8	44379
	Bi-Vis – Bi-NoVis	1.2	-0.00	2.4	29807
	Uni-Vis – Bi-NoVis	**-12.7**	**-13.9**	**-11.8**	**29714**
	Uni-Vis – Bi-Vis	**-14.0**	**-15.1**	**-13.0**	**95520**
	Uni-Prop – Bi-NoVis	**-10.6**	**-12.1**	**-9.1**	**26986**
	Uni-Prop – Bi-Vis	**-11.7**	**-13.3**	**-10.2**	**46982**

3.1.2. Model 2: Age grouped by year

In the second model, we grouped children into yearly cohorts and contrasted performance between tasks for each cohort as well as for the adult group. Results of this analysis are illustrated in see Fig. 4. Table 3 presents estimates for the four tasks.

Coordination was better for bimanual than for unimanual tasks across all experimental groups, including adults. This difference was more pronounced for younger than for older children. In the unimanual tasks, 7-year-old (Uni-Prop – Uni-Vis: β_{Task} = -17.0, $HDI_{95\%}$ = [-21.1; -13.1]; see Table 3) and 8-year-old children (Uni-Prop – Uni-Vis: β_{Task} = -14.8, $HDI_{95\%}$ = [-19.3; -10.5]; see Table 3) were better in Uni-Prop as compared to Uni-Vis (compare black and blue dots in Figure 3), while there was no difference between the tasks for older participants. Yet, given the low number of children aged 4-7 that participated in Uni-Prop (due to technical failure, see Methods), we do not think the differences between the two tasks are interpretable.

Performance between the two bimanual tasks did not credibly differ at any age, including adults. There was a single exception for the cohort of age 5 (Bi-Vis – Bi-NoVis: β_{Task} = -11.1, $HDI_{95\%}$ = [-15.1; -7.2]; see Table 3), for which coordination was worse when no visual feedback was available (compare light and dark red large dots in Figure 3).

Table 3. Beta Estimates of the within comparison between Tasks 1 to 4 for each age group in Model 2. Comparison with Task 2 (Uni-Prop) was not processed for children aged 4-5 years as only few children per group performed the task (≤ 2). Positive β Estimates indicate that performance was worse in the first task of each line. The Lower and Upper Confidence Interval (CI) values constitute the 95% High Density Interval (HDI), which represent the interval in which 95% of the values will be found. Credible differences are indicated in bold (HDI outside of the Region Of Practical Equivalence in which there is no effect [-3.9; 3.9]). ESS stands for the Effective Sample Size as calculated during Bayesian model fitting.

Group	Contrasts	β Estimate	Lower CI	Upper CI	ESS
Adults	Task 2 – 1: Uni-Prop – Uni-Vis	0.8	-2.0	3.7	27516
	Task 4 – 3: Bi-Vis – Bi-NoVis	-1.8	-5.1	1.4	10206
	Task 1 – 3: Uni-Vis – Bi-NoVis	**10.1**	**7.0**	**13.2**	**9937**
	Task 1 – 4: Uni-Vis – Bi-Vis	**11.9**	**8.9**	**15.0**	**22603**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**10.9**	**7.8**	**14.0**	**9937**
	Task 2 – 4: Uni-Prop – Bi-Vis	**12.7**	**9.6**	**15.7**	**24608**
12yo	Task 2 – 1: Uni-Prop – Uni-Vis	-1.8	-4.7	1.0	50814
	Task 4 – 3: Bi-Vis – Bi-NoVis	-0.6	-4.1	2.8	42184
	Task 1 – 3: Uni-Vis – Bi-NoVis	**15.6**	**12.5**	**18.9**	**42836**
	Task 1 – 4: Uni-Vis – Bi-Vis	**16.3**	**13.0**	**19.4**	**55388**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**13.8**	**10.6**	**17.0**	**42133**
	Task 2 – 4: Uni-Prop – Bi-Vis	**14.5**	**11.4**	**17.7**	**53941**
11yo	Task 2 – 1: Uni-Prop – Uni-Vis	-0.4	-3.2	2.5	52734
	Task 4 – 3: Bi-Vis – Bi-NoVis	0.3	-3.0	3.5	47841
	Task 1 – 3: Uni-Vis – Bi-NoVis	**16.6**	**13.5**	**19.7**	**44550**
	Task 1 – 4: Uni-Vis – Bi-Vis	**16.3**	**13.2**	**19.4**	**54139**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**16.2**	**13.1**	**19.3**	**44548**
	Task 2 – 4: Uni-Prop – Bi-Vis	**15.9**	**12.8**	**18.9**	**52734**
10yo	Task 2 – 1: Uni-Prop – Uni-Vis	-0.7	-4.2	2.8	49678

	Task 4 – 3: Bi-Vis – Bi-NoVis	0.4	-2.3	3.1	45014
	Task 1 – 3: Uni-Vis – Bi-NoVis	**18.4**	**15.9**	**20.9**	**46753**
	Task 1 – 4: Uni-Vis – Bi-Vis	**18.0**	**15.5**	**20.5**	**51275**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**17.7**	**14.0**	**21.3**	**45732**
	Task 2 – 4: Uni-Prop – Bi-Vis	**17.3**	**13.6**	**20.9**	**49678**
	Task 2 – 1: Uni-Prop – Uni-Vis	-0.2	-3.5	3.2	51457
	Task 4 – 3: Bi-Vis – Bi-NoVis	0.7	-2.3	3.6	45100
9yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**25.7**	**23.0**	**28.5**	**44843**
	Task 1 – 4: Uni-Vis – Bi-Vis	**25.1**	**22.5**	**27.9**	**51449**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**25.5**	**21.8**	**29.1**	**44764**
	Task 2 – 4: Uni-Prop – Bi-Vis	**24.8**	**21.2**	**28.2**	**53298**
	Task 2 – 1: Uni-Prop – Uni-Vis	**-14.8**	**-19.3**	**-10.5**	**50880**
	Task 4 – 3: Bi-Vis – Bi-NoVis	1.3	-2.1	4.6	44391
8yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**36.8**	**33.6**	**40.1**	**44130**
	Task 1 – 4: Uni-Vis – Bi-Vis	**35.5**	**32.3**	**38.6**	**52690**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**22.0**	**17.4**	**26.6**	**43045**
	Task 2 – 4: Uni-Prop – Bi-Vis	**20.6**	**16.1**	**25.2**	**50880**
	Task 2 – 1: Uni-Prop – Uni-Vis	**-17.0**	**-21.1**	**-13.1**	**53270**
	Task 4 – 3: Bi-Vis – Bi-NoVis	-2.6	-6.1	0.7	43507
7yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**37.9**	**34.7**	**41.1**	**44120**
	Task 1 – 4: Uni-Vis – Bi-Vis	**40.5**	**37.4**	**43.6**	**54290**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**20.9**	**16.6**	**25.0**	**43510**
	Task 2 – 4: Uni-Prop – Bi-Vis	**23.4**	**19.4**	**27.7**	**55335**
	Task 2 – 1: Uni-Prop – Uni-Vis	-1.8	-6.7	3.0	48897
	Task 4 – 3: Bi-Vis – Bi-NoVis	-2.4	-5.7	1.2	44214
6yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**41.8**	**38.6**	**45.0**	**45359**
	Task 1 – 4: Uni-Vis – Bi-Vis	**44.2**	**40.9**	**47.3**	**54585**
	Task 2 – 3: Uni-Prop – Bi-NoVis	**39.9**	**34.9**	**44.9**	**43111**
	Task 2 – 4: Uni-Prop – Bi-Vis	**42.3**	**37.3**	**47.4**	**49675**
	Task 4 – 3: Bi-Vis – Bi-NoVis	**-11.1**	**-15.1**	**-7.2**	**40397**
5yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**41.7**	**38.3**	**45.1**	**43051**
	Task 1 – 4: Uni-Vis – Bi-Vis	**52.8**	**49.3**	**56.2**	**52421**
	Task 4 – 3: Bi-Vis – Bi-NoVis	1.6	-1.9	5.1	43354
4yo	**Task 1 – 3: Uni-Vis – Bi-NoVis**	**56.9**	**53.7**	**60.1**	**43111**
	Task 1 – 4: Uni-Vis – Bi-Vis	**55.4**	**52.3**	**58.3**	**53084**

With this second model, we also assessed at what age children performed comparable to adults (see Table S1 in the supplementary information). For the unimanual tasks, children up to age 10 performed credibly worse than adults. In contrast, there was no credible performance difference Uni-VisUni-Propfor 11 and 12-year-old children compared to adults (see Figure 4, the blue and black lines cross the red dashed lines only for the 11 and 12-year-old children). However, there was also not sufficient evidence for practical equivalence between 11 and 12 year-olds and adults, with part of the posterior parameter distribution

outside the ROPE. The current data, thus, do not allow us to conclude that development is complete by age 12.

Children performed better in the bimanual than in the unimanual tasks. For Bi-NoVis, children up to age 8 showed credibly higher phase error than adults (see Figure 4; light and dark red lines cross the vertical dashed lines only for the younger groups). In contrast, for 9 to 12-year-old children, performance neither differed credibly from adults, nor could it be considered practically equivalent. For Bi-Vis, performance of children up to age 9 differed credibly from adults, whereas 10-12 year-olds neither differed from adults, nor did they perform equivalently.

Fig. 4.

Illustration of age group effects in Tasks 1-4 in Model 2, with Task and Age group as independent variable. The area between whiskers represents the highest density interval (HDI$_{95\%}$), that is the area with 95% of the values, and the dot represents the mean β estimate. Following this model, with the adult group as the

reference, the differences between adults and the other groups are credible if they do not include the Region Of Practical Equivalence (ROPE: [-3.9; 3.9]; indicated by the vertical dashed lines).

3.2. Sensory dominance in bimanual motor coordination (Tasks 5+6)

3.2.1. Model 3: Age as continuous predictor

As the third aspect of motor control, we investigated the ability of children to perform asymmetric coordination.

Fig. 5.

Unsigned phase difference between the two hands in the 2:3 coordination tasks for children (left panel) and adults (right panel). The lowest dashed lines represent the 30° threshold under which we considered subjects to perform well. The higher dashed line (83°) represents the phase angle when participants (incorrectly) perform 1:1 coordination. Coloured circles are the mean for each age group; error bars denote s.d. Fewer than half of the 4-5-year-old participants performed Task 5 (yellow), the means are thus likely to be non-representative.

Figure 5 shows that performance in 2:3-Transform improved with age (green dots), as reflected by a negative, non-zero slope coefficient (β_{Age} = -14.0, HDI$_{95\%}$ = [-16.4; -11.5]). The negative slope value indicates that the phase difference between hands decreased by the

respective amount of degrees with each standardized age unit of 25.3 months; this unit differed from the previous analyses because most young participants did not perform the 2:3 tasks so that the included participants differed between Models 1/2 and 3/4. In contrast, performance in the 2:3-NoTransform did not credibly vary with age (Fig. 5, yellow dots; β_{Age} = -4.8, $HDI_{95\%}$ = [-7.1; -2.3]). There was a credible difference between tasks for both *Task* and *Task × Age* interaction contrasts, indicating that the intercept and rate of improvement was smaller for 2:3-NoTransform than 2:3-Transform (β_{Task} = -13.6, $HDI_{95\%}$ = [-14.9; -12.3]; $\beta_{Interaction}$ = -9.4, $HDI_{95\%}$ = [-10.6; -8.1]). During a 2:3 coordination, the correct phase difference between the two hands changes from moment to moment. If a participant incorrectly performed symmetrical (i.e., 1:1) coordination, a pattern that often emerges automatically, then the resulting average error will be about 83°. In Fig. 5, we plot this error as a reference line, together with participants' performance. Note, that performance in 2:3-NoTransform (Fig. 5, yellow color) mostly scatters around this 83° line across all ages, including adults. Thus, participants across all age groups were unsuccessful when visual feedback simply indicated the limbs' current position along their respective circles. In contrast, performance improved in the older groups (Fig. 5, green color), starting around age 10, when visual feedback was transformed such that visual symmetry signaled correct motor performance.

3.2.2. Model 4: Age grouped by year

In model 4, we contrasted performance between 2:3-NoTransform and 2:3-Transform within each age group. Beta estimates for these comparisons are shown in Table 4. In brief, performance between the two tasks credibly differed in all age groups older than 9, suggesting a consistent use of transformed visual feedback to perform the coordination from this age on. Notably, a credible difference was also present at 7, but not at 8 years. This data pattern may perhaps suggest a temporary performance decrement around age 8, though the numerical differences between ages 7, 8, and 9 are small and, thus, we would not emphasize this result. Children younger than 7 were unable to use transformed feedback (Table 4).

Table 4. Beta Estimates of the within comparison between Tasks 5 and 6 for each age group. Negative β Estimates indicate that performance was better in Task 6 (2:3-Transform) than Task 5 (2:3-NoTransform). The Lower and Upper Confidence Interval (CI) values constitute the 95% High Density Interval (HDI), which represent the interval in which 95% of the values will be found. Credible differences are indicated in bold (HDI outside of the Region Of Practical Equivalence in which there is no effect [-5.4; 5.4]). ESS stands for the Effective Sample Size as calculated during Bayesian model fitting.

Group	β Estimate	Lower CI	Upper CI	ESS
Adults	**-44.5**	**-48.4**	**-40.8**	**9404**
12 yo	**-29.8**	**-33.8**	**-25.8**	**49812**
11 yo	**-27.1**	**-30.6**	**-23.6**	**55497**
10 yo	**-18.3**	**-21.2**	**-15.3**	**57593**
9 yo	**-8.6**	**-11.5**	**-5.7**	**59358**
8 yo	-8.4	-12.2	-4.6	51499
7 yo	**-10.6**	**-14.6**	**-6.8**	**50458**
6 yo	1.5	-2.4	5.3	50358
5 yo	-0.8	-8.7	7.4	38758
4 yo	1.7	-4.7	8.3	41345

Comparison of each age group's performance in 2:3-NoTransform with that of adults did not reveal a credible difference for any age cohort, in line with the above result that 2:3-NoTransform did not improve with age (see Fig. 6 how the yellow lines always cross the vertical dashed lines; statistics reported in Table S2 of the supplementary information). In the 2:3-Transform, the adult group performed better than all age cohorts except the 12-year-olds (see Fig. 6; only the green line of the 12-year-old group crosses the vertical dashed line; $\beta =$ 9.3, $HDI_{95\%} = [-0.75; 19.3]$, but 12-year-olds' performance neither differed credibly from, nor was practically equivalent to, adult performance.

Fig. 6.

Illustration of age effects in Tasks 5 (2:3-NoTransform) and 6 (2:3-Transform). The area between whiskers represents the highest density interval (HDI95%), that is the area with 95% of the values, and the dot represents the mean β estimate. Following this model, with the adult group as the reference, the differences between adults and the other groups are credible if they do not include the Region Of Practical Equivalence (ROPE: [-5.4; 5.4]; indicated by the vertical dashed lines). Adults performance was not credibly different from any of the groups in the 2:3-NoTransform as all the $HDI_{95\%}$ cross the red dashed line. Adults performance was not credibly different from 12-year-old children in 2:3-Transform but was better as compared to all the other groups of children.

3.3. Relationship between tasks beyond improvement with age

3.3.1. Relationship between bimanual and unimanual tasks

To assess whether performance in the bimanual and unimanual tasks is related beyond a global age improvement, we computed their correlation with age partialed out (see Table 5). The two unimanual tasks exhibited high correlation ($\rho = 0.6$; $HDI_{95\%}= [0.3; 0.85]$; BF = 264),

though the confidence interval was wide due to the low N available for Uni-Prop. In contrast, correlations between uni- and bimanual tasks were smaller, ranging from .28 to .42, with only the higher correlations exhibiting BFs that suggest reliable relationships. Counterintuitively, higher correlations were obtained for Bi-NoVis with Uni-Vis and for Bi-Vis with Uni-Prop. For the two visual uni- and bimanual tasks (Bi-Vis and Uni-Vis) and the two proprioceptive tasks (Bi-NoVis and Uni-Prop), correlations were estimated to be lower. We reiterate that results of analyses that include Uni-Prop should be regarded with caution due to the low N at younger ages. The lower correlations for this task may be related to this methodological limitation rather than a true difference.

Table 5. Two-sided correlations between Tasks 1 to 6, with Age partialed out. Credible correlations are in bold, as indicated by a Bayesian Factor ≥ 3. BF represents the relative evidence of one hypothesis (the presence of a correlation) over another (no correlation). BF between 3 and 10 indicates moderate evidence for a correlation, while everything above indicates strong to extreme evidence (BF>100), and everything below is can be considered as anecdotal, suggesting an absence of correlation. Lower and Upper Confidence Interval values constitute the 95% HDI.

Tasks	Coefficient	Lower CI	Upper CI	BF	Sample (N)
Uni-Vis / Uni-Prop	**0.58**	**0.30**	**0.85**	**264**	**51**
Bi-NoVis / Bi-Vis	**0.70**	**0.57**	**0.84**	**2.60e15**	**120**
Bi-NoVis / Uni-Vis	**0.42**	**0.18**	**0.67**	**16.5**	**119**
Bi-NoVis / Uni-Prop	0.29	-0.06	0.64	0.44	51
Bi-Vis / Uni-Vis	0.28	0.02	0.54	0.60	119
Bi-Vis / Uni-Prop	**0.40**	**0.10**	**0.69**	**3.4**	**51**
2:3-NoTransform / 2:3-Transform	**0.40**	**0.17**	**0.64**	**23.2**	**100**
Uni-Vis / 2:3-Transform	**0.30**	**0.08**	**0.52**	**3.0**	**100**
Uni-Prop / 2:3-Transform	0.33	0.04	0.62	1.49	50
Bi-NoVis / 2:3-Transform	0.08	-0.09	0.26	0.17	101
Bi-Vis / 2:3-Transform	0.10	0.07	0.27	0.22	101

Note, for Uni-Prop, participants had to let their non-dominant hand be passively guided. It is theoretically possible that children did not conform to this instruction. If children had, instead, actively moved their non-dominant hand, then they would effectively have performed a Bi-NoVis task. Both the much worse performance of the unimanual tasks, and the lower correlations between unimanual and bimanual tasks than those between the bimanual tasks, indicate that children did not perform bimanual coordination and, thus, did not actively synchronize their hands, during Uni-Prop.

3.3.2. Relationship between bimanual tasks

In the bimanual tasks, the partial correlation was 0.70 (HDI$_{95\%}$ = [0.57; 0.84]; n =120; two-sided test; BF = 2.60e15; Table 5). This high correlation implies that a child that was good in one task was also good in the other, and, thus, suggests that the two tasks are driven by common underlying mechanisms.

3.3.3. Relationship between asymmetric coordination tasks

Finally, we asked how performance in the 2:3 tasks was related amongst each other and with the 4 symmetrical tasks within participants (see Table 5). Partial correlation between the two 2:3 tasks, partialing out age, revealed a credible correlation of 0.40 (HDI$_{95\%}$ = [0.17; 0.64]; two-sided test; n = 100, BF = 23.2). Thus, a child who performed well with veridical feedback performed well also with transformed feedback, and a child who performed badly in the veridical feedback task gained less from transformed feedback. Correlations with the symmetrical tasks were overall low. They were lowest with the bimanual tasks, and higher, though moderate in size, for the unimanual tasks.

4. DISCUSSION

Our study investigated three aspects of motor control in children aged 4-12 through 6 uni- and bimanual circling tasks acquired in a cross-sectional, within-subject design. We report four main findings. First, unimanual tracking tasks assessed coordination of the dominant hand with a sensory, visual or passive-proprioceptive, signal. Young participants performed poorly and, despite continued improvement with age, performance was not equivalent to that of adults even in our oldest age groups, even if it was, at the same time, not credibly different. Second, symmetrical bimanual tasks assessed the ability to coordinate the two hands symmetrically both with and without visual hand position cues. Children performed these tasks with much less error than the unimanual tasks already at age 4. Accordingly, improvement across age was less marked, though, again, performance was not equivalent to that of adults even for the oldest age groups of our study. Moreover, bimanual coordination was independent of the visual display of hand position at all ages. Third, asymmetric motor tasks assessed the development of being able to overcome the motor symmetry bias through symmetric visual guidance. This ability was absent until age 9, and only at age 12 was

asymmetric performance no longer credibly different from that of adults – and even at this age, performance was not completely adult-like, suggesting that further development would be observable throughout puberty. Fourth, evidence for cascade-like dependencies of the different functional aspects across development was weak. Whereas performance correlated highly within each set of tasks (unimanual, bimanual symmetric, 2:3 asymmetric), correlations were in the range of small to medium or entirely absent across these three functional domains. We will discuss these four points in turn.

Unimanual tracking exhibits protracted and extensive development

Performance was comparable for visual and passive-proprioceptive tracking, and performance in the two tasks was highly correlated. These findings suggest a common developmental process for the use of sensory input for coordination. However, due to technical failure of our apparatus, the number of young participant in the proprioceptive task was low, which may have concealed differences especially in the affected, lower age groups.

The large variability and low accuracy of younger children in unimanual tracking strike as surprising, given that children exhibit motor adaptation to visual and proprioceptive perturbation in the context of online motor control already at age 4 (e.g. Contreras-Vidal et al., 2005; Konczak et al., 2003). A critical difference is that sensory information in adaptation tasks refers to the moving limb itself while the movement target remains fixed, whereas in the tasks used here, both the tracked signal and the tracking hand continuously change position. Furthermore, in experiments in which goal-directed movements are performed repeatedly, each new movement can be adapted according to the registered error of the previous movement(s). In contrast, continuous coordination requires continually integrating the external cue to derive the required correction of the ongoing movement. Our results suggest that these abilities develop later than those responsible for online corrections of discrete movements. Under this perspective, it is interesting to note that the developmental timeline of our tasks appears similar to that of target interception – another task that requires moving the body in response to a moving stimulus. Children around 12 can intercept moving objects similarly effectively as adults, even if some aspects of performance keep developing well into adolescence (Daum et al., 2007; Rothenberg-Cunningham & Newell, 2013).

Symmetric bimanual coordination is motor-driven and available early, but still exhibits protracted development

Children performed symmetric bimanual coordination with much higher accuracy than unimanual coordination already at age 4. Thus, availability of a motor command strongly improved coordination. This result is well in line with previous research that has demonstrated the general ability of children even at a young age to perform symmetrically, even if performance improves across childhood, likely in dependence of maturation of the corpus callosum (Cincotta & Ziemann, 2008; de Boer et al., 2012; Jeeves et al., 1988). The present results on uni- and symmetric bimanual coordination viewed together suggest that the common motor command available in bimanual coordination is available early, well in line with the occurrence of uninstructed, mirror-symmetric movements in children (Cincotta & Ziemann, 2008; de Boer et al., 2012; Lazarus & Todor, 1987). In fact, availability of visual information on hand position did not improve circling performance at any age in our study, suggesting that symmetric bimanual coordination may be entirely motor-driven, at least for tasks like ours, in which positional information alone, but not spatial accuracy regarding the trajectory, is relevant. This is in line with previous work reporting that, in such tasks, visual feedback is not necessary or even detrimental (Fagard & Pezé, 1992). In contrast, integration was evident when children had to draw circles by hand within two boundaries, that is, a task that not only required positional symmetry, but also spatial accuracy in placing the pen (Lantero & Ringenbach, 2007) in contrast to simply pushing a handle forward, as in our apparatus. An influence of vision has also been demonstrated in other paradigms that involved self-guided, rather than spatially restricted, bimanual movements (Brandes et al., 2017; Mechsner et al., 2001). Thus, visual cues may be integrated only under specific, spatially challenging requirements.

Accordingly, symmetric bimanual coordination is quite evidently a different motor capability than unimanual coordination: given that the development of unimanual coordination lags several years behind that of bimanual coordination, it is unlikely that bimanual coordination is merely a special case of general coordinative abilities, as might be inferred from the suggestion that phase symmetry in motor coordination tasks such as the one we employed here is perceptually-driven (Bingham, 2004). It is all the more notable that, nonetheless, uni- and bimanual coordination were correlated in the range of 0.3 across all task pairs. Our correlation analysis controlled for age, so that the relationship between tasks does not simply reflect common improvement due to age. Thus, unimanual coordination with signals that are not self-produced appears to partly build on functionality that is implicit in symmetric bimanual coordination, although it cannot exploit a motor signal for coordination. What could be the common mechanism? Given that visual-motor integration did not appear relevant for

our bimanual task, the link may be cognitive rather than sensory. Both types of tasks rely on continuous monitoring and relating two ongoing, constantly moving entities. In current models of motor control, monitoring is a feature of state estimation, that is, deriving the state of body and world based on issued motor commands, their expected sensory consequences, and the incoming sensory evidence. We suggest that it is refinement of such motor control functionality that is at the heart of the common development of our different tasks. In fact, development of state estimation functionality in the age interval investigated here has been previously suggested based on the finding that 6-8 year-old children estimated their hand position less precisely than older children and young adults (King et al., 2012).

Asymmetric bimanual coordination is related to unimanual tracking

Children were first able to perform asymmetrical movement above chance level based on visual guidance in the 2:3 coordination task starting at age 9, and performance was better the older the child. These results are in line with previous studies that tested asymmetric coordination but employed Lissajous-type paradigms (Fagard, 1987; Fagard et al., 1985; Jeeves et al., 1988; Leinen et al., 2016). Asymmetric control of the hands requires uncoupling the two hemispheres' motor commands, an ability which becomes increasingly efficient around age 10 when the corpus callosum matures, and other automatic, bilateral phenomena such as mirror movements subside (Fagard et al., 2001; Preilowski, 1972). Importantly, however, in our study performance in the 2:3 task was credibly correlated with the unimanual tasks. Thus, the ability to integrate visual feedback, as is required to track an external or passive-proprioceptive signal, is also important to use symmetric visual guidance to coordinate several limbs independently. In other words, visual guidance of motor control does not just rely on suppression of default hemispheric coupling, but also on the ability to couple with the sensory signal – and this ability, too, aproached adult performance only around the age of 10 in our study. It is, moreover, of note that age 10 is also the time when children first exhibit adult-like optimal multisensory integration (Burr & Gori, 2012; Gori, 2015). Thus, multiple structural-anatomical, cognitive, and sensorimotor prerequisites appear to mature around the age of 10, together allowing the emergence of the perceptual guidance of movement (Bingham, 2004). It is of interest that none of the participants succeeded in retaining the newly acquired coordination. This result implies that participants did not develop an internal model for the task's motor structure, so that they were unable to correctly relate the consequences of their movement to the 2:3 phase requirements. Instead, they kept relying on visual feedback to correct their position online, which may explain the correlations with

the unimanual tasks. We also find it worth pointing out that 2:3 coordination was unrelated to "regular", symmetric bimanual coordination. One might have expected a negative correlation, with high performance in symmetric coordination presumably indicating particularly strong cross-hemispheric coupling or, alternatively, an inability to inhibit cross-hemisphere communication, respectively. However, such a relationship does not appear to exist.

Evidence for non-linear developmental trajectories

We have so far emphasized the largely linear improvement across age in the different tasks devised in our study. In the 2:3 task, our analysis suggested that children may perform less successfully at age 8 than at ages 7 and 9. Notably, this interpretation rests on small numerical differences in our data and may, thus, not replicate. If taken at face value, this result suggests a non-linear effect in development, with a potential, temporary performance dip around age 8. Several previous studies have reported that children's sensorimotor performance is temporarily impaired around the age of 8 (Badan et al., 2000; Hay, 1978; Martel et al., 2020; Pellizzer & Hauert, 1996; Smyth et al., 2004). Commonly, this temporary decline is interpreted to be due to a developmental change that involves employment of adult-like motor control strategies; this re-organization is thought to lead to transient disorganization of motor processing, with neither old nor new processes working with full efficiency.

Yet, even if our data support this notion of a transient performance decrement due to massive developmental restructuring, it is also salient that individual data points vary considerably. As is evident in our Figures 3 and 5, which display single participant performance, many data points would not allow grouping a child into a specific age group with confidence. Rather, some very young children exhibit good performance, just as some much older children still exhibit rather poor performance. Whether this variability is simply indicative of interindividual differences in overall motor control, or rather of extended time interval, in which development proceeds – with some children developing much faster than others – cannot be inferred from our cross-sectional data.

Limitations

We note several shortcomings of our study. First, technical failure led to the undesirable loss of almost half of our data points for unimanual, passive-proprioceptive tracking.

Second, cross-sectional assessment limits interpretation of the data. For instance, we cannot conclude whether all children undergo similar development but simply start at different time

points, or whether development can be compressed or extended in some individuals. Similarly, the group-wide linear developmental trends do not imply similar, linear development in individuals. Instead, it is well possible that each individual exhibits step-like changes which cannot be uncovered when measuring every participant at only a single time point. Clearly, longitudinal assessment would, therefore, provide additional merit but requires exceptional financial and time-related effort. As is evident from our correlational analysis, the high number of participants of our study, together with the large number of experimental tasks, nevertheless allow valid conclusions about developmental questions.

Third, although we aimed at testing a wider-than-usual range of functions and tasks, we chose to focus on a single paradigm that involves the upper limbs. We deem the direct comparability of the 6 devised tasks a major strength of our study. Yet, this comparability comes at the price of unknowable generalizability to other paradigms and body parts.

Finally, we have tried to estimate at which age the different tasks are probably mature by comparing children's to adults' performance. Such comparisons have caveats. For one, though differences between groups are not credible for some comparisons, the overall parameter probability distributions still look markedly different, and so one should not infer equivalence, especially given the sample size per age group. For practical equivalence, posterior distributions must be narrower to fit within the ROPE, which will require larger samples of same-age subgroups. Furthermore, it is commonly assumed that performance will remain adult-like once it has reached adult level at some age; yet, transient impairment of some motor control functions has been reported during adolescence (Viel et al., 2009). Thus, characterization of performance in our six tasks at ages beyond those of our study awaits dedicated exploration.

Summary and conclusions

To conclude, performance of children aged 4-12 across 6 experimental tasks based on a common, underlying movement coordination paradigm suggests interdependent, serial development of different motor control functions. Mastery of symmetrical bimanual coordination may rely predominately on motor-related, interhemispheric transfer and develops first. Yet, even this seemingly basic ability improves until at least age 9, likely dependent on callosal maturation. Unimanual synchronization with externally produced signals develops later, and proceeds until at least age 11. Importantly, this ability depends in part on symmetric bimanual coordination, as suggested by correlations between bimanual and

unimanual performance. This dependence may be mediated by their common reliance on state estimation for motor control. Finally, guiding asymmetric movement by focusing on visual symmetry develops last and appears to be based on multiple determinants, namely callosal maturation, multisensory integration, and flexibilization of the coupling between sensory and motor information.

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DECLARATION OF CONFLICTING INTERESTS:

There are no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data, code and material used in this study are available on the website of the Open Science Framework (OSF) at the following link: https://osf.io/x9u27/.

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