Published in final edited form as:

Exp Brain Res. 2015 July ; 233(7): 2181–2194. doi:10.1007/s00221-015-4288-7.

Development of kinesthetic-motor and auditory-motor representations in school-aged children

Florian A. Kagerer¹ and Jane E. Clark²

Florian A. Kagerer: fkagerer@msu.edu

¹Department of Kinesiology, Michigan State University, 308 W Circle Drive, East Lansing, MI 48824, USA

²Department of Kinesiology, University of Maryland, College Park, MD 20742, USA

Abstract

In two experiments using a center-out task, we investigated kinesthetic-motor and auditory-motor integrations in 5- to 12-year-old children and young adults. In experiment 1, participants moved a pen on a digitizing tablet from a starting position to one of three targets (visuo-motor condition), and then to one of four targets without visual feedback of the movement. In both conditions, we found that with increasing age, the children moved faster and straighter, and became less variable in their feedforward control. Higher control demands for movements toward the contralateral side were reflected in longer movement times and decreased spatial accuracy across all age groups. When feedforward control relies predominantly on kinesthesia, 7- to 10-year-old children were more variable, indicating difficulties in switching between feedforward and feedback control efficiently during that age. An inverse age progression was found for directional endpoint error; larger errors increasing with age likely reflect stronger functional lateralization for the dominant hand. In experiment 2, the same visuo-motor condition was followed by an auditory-motor condition in which participants had to move to acoustic targets (either white band or one-third octave noise). Since in the latter directional cues come exclusively from transcallosally mediated interaural time differences, we hypothesized that auditory-motor representations would show age effects. The results did not show a clear age effect, suggesting that corpus callosum functionality is sufficient in children to allow them to form accurate auditory-motor maps already at a young age.

Keywords

Sensory integration; Proprioception; Visuo-motor; Auditory; Motor development; Children

Introduction

When we perform target-directed arm movements, our central nervous system (CNS) has to transform sensory information about limb and target position to motor commands, specifying the forces required to perform the movements. This transformation process has

been conceptualized through the notion of a forward model (Wolpert and Kawato 1998; Shadmehr and Krakauer 2008) computed by the CNS. The smoothness and accuracy of these movements depend to a large part on the integration of available sensory modalities (cross-modal level) into a common frame of reference (Jeannerod 1986) and on the integration between sensory and motor space (sensorimotor level).

Elemental perceptual capacities, such as vision, touch, and hearing, are typically established early in development, but the mapping between sensory and motor space, conceptualized as an internal model and the focus of this study, is inaccurate and ‘noisy’ and is over time refined through practice (Contreras-Vidal et al. 2005). This is reflected in the motor performance of young children, which is generally characterized by lower movement speed and smoothness and higher variability in drawing/aiming (Yan et al. 2000), grasping tasks (Olivier et al. 2007), or force production (Smits-Engelsman et al. 2008; Jansen-Osmann et al. 2002). This movement variability usually becomes smaller with increasing age and approaches adult performance around and after puberty, suggesting a fine-tuning of sensorimotor feedforward models over time. Under most circumstances, goal-directed upper limb movements likely depend most on vision and proprioception, but audition can come into play as well (Boyer et al. 2013). It has been known for some time that the availability of vision together with proprioception allows the system to code initial hand position more accurately than would be possible with one modality only (Elliott et al. 1991; Rossetti et al. 1994) and reduce variability during pointing movements (Desmurget et al. 1995). In circumstances where vision of the hand is available, and where there is a match between vision and proprioception, proprioception is downweighted (Proteau and Isabelle 2002), and vision dominates. In conditions where, for example, only the target is visible, but the moving hand is not, proprioception is upweighted. Using a spatial matching task in a group of children between 4 and 12 years of age, von Hofsten (Hofsten and Rösblad 1988) found that when the ‘target hand’ had to be localized with the ‘matching hand’ without vision of either hands, variability of the matching hand was highest (P–P condition), whereas when the target was visually available (V–P condition), it was substantially lower. The first scenario represents a unimodal condition, with sole reliance on proprioception, while the second one represents a bimodal condition where visual and proprioceptive frames of reference are congruent, but the absence of vision during the movement or target acquisition forces the system to upweight proprioception. Previous studies in adults have shown that variable errors, providing information about ‘noise’ in the proprioceptive system, indicate that localization in proprioceptively guided movements under both uni- and bimodal conditions is more accurate along movement ‘depth,’ whereas vision provides more accuracy along movement azimuth (van Beers et al. 1998).

Few studies have previously looked at children’s motor performance in simple tasks that depend primarily on sensory feedback other than visual; studies either focused on a small age range (King et al. 2009) or had limited kinematic description (Bard et al. 1990), or the task involved complexities like bilateral hand involvement or memory components (Hofsten and Rösblad 1988). Using a perturbation paradigm in a recent study in 5- to 12-year-old children, we showed that kinesthetically guided movements following a visuo-motor perturbation were less affected in the older children than in the younger ones, suggesting a visual-to-kinesthetic mapping that, with increasing age, becomes more robust against

interference from adaptive processes in other sensorimotor maps (Kagerer and Clark 2014a). That study informed us primarily about the response to a perturbation across modalities, but less about the quality of the 'raw' kinesthetic-motor integration. This was the purpose of the present study: to determine the development of sensorimotor representations in a sample of typically developing school-aged children between the ages of 5 and 12 years, under conditions of predominantly visual, kinesthetic, or auditory feedback, without an interfering perturbation. The first part of our study examined characteristics of visual-to-kinesthetic drawing movements in order to determine the contribution of kinesthesia to movement control during development and the development of kinesthetic-motor internal representations. It extends a previous study by Contreras-Vidal (Contreras-Vidal 2006) by adding an amplitude component and analyzing the influence of target direction. We hypothesized that movement proficiency would increase with age, reflected through reduced movement time and increased spatial accuracy, (Bard et al. 1990; Contreras-Vidal 2006), but that there would also be age-dependent effects of movement direction and movement amplitude, particularly affecting movements to the contralateral side more in younger children than in older ones (Bradshaw et al. 1988; Hofsten and Rösblad 1988).

The second part of our study extends the topic of sensorimotor integration by assessing auditory-motor integration. Instead of using a drawing task that put more weight on kinesthetic input, we used an auditory-to-motor drawing task, which aimed at determining the development of auditory-motor internal representations in typically developing children. Experiments on auditory-motor maps in the context of spatial localization of auditory targets have shown that adults can accurately point out auditory sources in space. A previous study in 5- to 10-year-old children using a visuo-motor adaptation paradigm with auditory pre- and post-adaptation test phases showed cross-modal effects in the children, independent of age group (King et al. 2009). It is important to note here that azimuthal (in the horizontal plane) sound localization depends to a large part on interaural time differences registered in corpus callosum (CC) fibers, as shown in animal experiments (Poirier et al. 1995). In humans, the important role of the CC is illustrated by findings that pointing toward auditory stimuli is less accurate in patients with callosal agenesis (Poirier et al. 1993). In the context of developmental research, the CC is of interest, because it is known to have a long maturational cycle, with white matter density changing until early adolescence (Muetzel et al. 2008). This together with its role in binaural auditory perception could make the CC an important factor modulating processes related to acquisition of auditory-motor representations. For this second experiment, we hypothesized that auditory stimuli of different frequency bands providing differing binaural cues (Abel et al. 2000) would affect the spatial accuracy of auditory-motor internal representations differentially in children and adults.

Materials and methods

Participants

Sixty-seven children between 5 and 12 years of age participated in experiment 1, and 51 children between 5 and 12 years old in experiment 2 (see Table 1); 42 of those children participated in both experiments. The difference in participation in the two experiments was

a result of general availability of the children during the period of data collection. Parents or guardians of the children provided informed consent prior to participation, and the children gave assent. All participants were right-handed, as determined by their preferred hand used to complete everyday activities, and had normal or corrected vision. Previous to experiment participation, all children were screened with the Movement Assessment Battery for Children (MABC, 2nd edition) (Henderson and Sugden 1992); a score at or above the 20th percentile was necessary for inclusion. The sample of participants in experiment 1 had an average MABC score of 60.7 (± 22.8) and that of participants in experiment 2 had an average of 58.63 (± 24.65).

Additionally, 11 right-handed adults (mean age 22.25 ± 1.6 years) completed both experiments, after having provided informed consent prior to participation. The Institutional Review Board at the University of Maryland, College Park, approved the experimental procedures.

Apparatus and procedure

In both experiments, participants were seated in front of a table supporting a wooden stand that was elevated approximately 15 cm above the digitizing tablet (Wacom InTuos™). A 15" computer LCD screen was placed flat on top of the wooden stand. The experimental setup was oriented such that the cursor position displayed on the computer screen was directly above the actual pen position on the digitizing tablet. The wooden stand prevented vision of the hand during task performance. OASIS software 8.29 (Kikosoft, Nijmegen) was used for stimulus presentation and data acquisition. Data were recorded at a sampling rate of 200 Hz. Participants used a digitizing pen to move from a starting position toward either visual targets presented on the LCD (experiment 1) or auditory targets coming from the rear edge of the monitor (experiment 2). Visual feedback of start position, target locations, and movement paths was provided on the computer monitor. In experiment 2, participants performed a similar center-out task as in experiment 1, but here they were blindfolded during certain experimental phases and asked to move the pen toward a sound coming from one of two loudspeakers positioned at 45° or 135° with respect to the start position.

The LCD screen displayed a red dot (diameter 0.5 cm) in the center ('home position'). Participants positioned the pen such that the cursor appeared inside this home position. Once stationary in the home position for a period of 1000 ms, a blue dot (diameter 0.5 cm) appeared at 25°, 90°, or 155° relative to and 9 cm away from the home position. Participants were asked to move from the home position to the target position 'as fast and as straight as possible'; throughout the movement, the home and target positions were displayed on the LCD screen. During the first phase of the experiment (visual baseline: 24 trials, 8 per target), online visual feedback of the pen position was provided on the monitor. In the second phase of the experiment, the kinesthetic condition, visual feedback of the pen was removed. Participants were instructed to move fast and straight to an endpoint, which they thought would match the visual target on the display, and then stop. After remaining motionless for 500 ms, the target disappeared, and participants returned to the home position for the next trial. In order to help participants homing in, the pen trace re-appeared when the pen was within 2 cm of the home position; by showing participants the starting position of

the hand, we avoided proprioceptive drift (Wann and Ibrahim 1992). During the kinesthetic phase, one of four targets was presented on the LCD screen, at 45° or 135°, and at a distance of either 7 or 11 cm from the home position; 32 trials (8 per target) were administered during this condition; see Fig. 1 for the experimental setup.

The baseline phase of experiment 2 was identical to that of experiment 1. However, during the second phase, participants were blindfolded and acoustic stimuli were presented in one of two speakers positioned at 45° and 135° relative to the visually presented home position. The centers of two speakers were 22 cm away from the home position (see Fig. 1). Acoustic stimuli were presented either as broadband white noise or as one-third octave noise centered at 0.5 kHz. Prior to each trial, the experimenter guided the right hand of each participant to the home position. Once motionless in the home circle for 500 ms, participants were presented with an intermittent sound from one of the two speakers and were instructed to move the pen fast and straight toward the perceived sound source. Thirty-two trials (8 per target) were administered. The stimulus sequence in both experiments was pseudo-randomized, but was the same for all participants. The time series of *x/y*-position data of the pen were stored on a PC for off-line analysis. The two experiments lasted approximately 20 min each. If participants performed both experiments within the same day, a short rest period was given between the experiments.

Data analysis

The time series of each trial were subjected to a dual pass eighth-order Butterworth filter with a cutoff frequency of 10 Hz. Movement onset was determined using an algorithm by Teasdale et al. (1993), which locates the sample *S1* at which the time series exceed 10 % of its maximum velocity (*Vmax*), works back from there to determine the first sample *S0* which is $[(Vmax/10) - (Vmax/100)]$, then finds the standard deviation (SD) of the series between *S1* and *S0*, and again works back from *S0* to the first sample (*S0* - SD), which marks the onset. From the time series for each trial, the following variables were computed: movement time (MT, in sec), defined as the time between movement onset and offset; root-mean-squared error (RMSE, in cm), defined as the perpendicular distance between the actual movement path and a straight line between home position and target, normalized with respect to movement extent; and constant endpoint error, defined as the signed distance between movement endpoint and the respective target location, calculated as errors parallel (EPpar) and orthogonal to the movement direction (EPorth). Endpoint error was of interest only in the kinesthetic condition of experiment 1 (during the visual baseline condition, targets had to be hit, so these variables were not relevant during that condition).

Further, initial directional error (IDE, in degrees) was calculated as the angular difference between an ideal vector between the home position and a target and the direction of the actual movement vector at 90 ms after movement onset. This interval was chosen in order to assess directional error prior to any visual-feedback-driven corrective movements. A positive IDE indicated a counterclockwise deviation, whereas a negative IDE indicated a clockwise deviation from the ideal target vector. Additionally, we assessed the standard deviation of IDE (IDESD) as a measure of variability of individual directional accuracy across the trials of an experimental phase.

For statistical analysis, trials 1–24 were averaged by target to represent baseline performance, and trials 25–56 were averaged by target to represent performance during the kinesthetic (experiment 1) or the auditory condition (experiment 2). For the baselines in both experiments, separate mixed-model repeated-measure ANOVAs were computed for MT, RMSE, IDE, and IDESD, with age group (5–6, 7–8, 9–10, 11–12 years, adults) as between-subject and target (3) as within-subjects factors. For the kinesthetic phase in experiment 1, target had 2×2 levels (two amplitudes, two directions). For the auditory phase in experiment 2, sound (white noise, one-third octave noise) was the within-subjects factor. In this condition, IDE and IDESD were the only variables of interest, since movement endpoint was not controlled.

Statistically significant main effects and/or interactions were followed up by Dunn–Sidak-adjusted pairwise comparisons for within-subjects factors, and Scheffé tests for age group comparisons.

Results

Experiment 1: visuo-motor condition

During baseline, the younger children moved generally slower and with lower movement linearity than the older children. Movement paths of one representative 5-year-old child, one 12-year-old child, and one adult are shown in Fig. 2. Repeated-measures ANOVA on MT showed significant main effects for age group [$F(4, 73) = 10.78, p < 0.001$] and target [$F(2, 146) = 17.74, p < 0.001$]; there was no statistically significant interaction. Post hoc analysis showed that across targets, the 5- to 6-year-olds moved significantly slower than the 11- to 12-year-old children or the adults (both $p < 0.001$); the difference to the 9- to 10-year-old children was marginally significant ($p = 0.06$). The 7- to 8- and 9- to 10-year-old children were also significantly slower than the adults ($p < 0.001$ and $p < 0.05$, respectively), whereas the 11- to 12-year-olds did not differ from the adults. Between-target comparisons showed that for all age groups, MT to the 25° target significantly shorter than to the 155° and the 90° target (all $p < 0.001$); see Table 2 and Fig. 2a for the MT findings.

RMSE differed significantly between age groups [$F(4, 73) = 5.11, p < 0.001$] and target [$F(2, 146) = 43.72, p < 0.001$]; there was no significant interaction. The 5- to 6-year-olds had significantly higher RMSE than the 9- to 10-year-old children ($p < 0.05$). The 7- to 8-year-old children also performed slower than the 9- to 10-year-olds ($p = 0.01$). Post hoc between-target comparisons revealed that for all age groups, RMSE was significantly higher when participants moved to the 155° compared with the 25° target, or the 90° target ($p < 0.001$ and $p = 0.01$, respectively); see Table 2 and Fig. 2b for RMSE.

IDE showed a significant main effect for target [$F(2, 146) = 25.70, p < 0.001$], originating in movements to the 155° target showing negative IDE, but positive IDE for movements to the 25° and 90° target. The differences between the 155° and the 25° , or the 90° target were significant ($p < 0.001$ and $p < 0.001$, respectively). Negative IDE for 155° target indicates movements with an initial direction smaller than 155° , while positive IDE values to the other two targets indicate initial movement directions slightly larger than the target angle;

see Table 2 and Fig. 2c for IDE. It is important to note that overall the deviations from the 'ideal' target angle were very small.

At the same time, variability of IDE showed that overall directional accuracy at movement onset varied systematically as a function of age: Variability was highest in youngest age group, but with increasing age, the directional tuning became more focused with respect to the target angle, resulting in lower variability. IDESD differed significantly between age groups [$F(4, 73) = 9.37, p < 0.001$]; post hoc group comparisons showed that the 5- to 6-years-olds were significantly more variable than the 11- to 12-years-olds and the adults. A significant main effect for direction [$F(2, 146) = 6.33, p < 0.001$] indicated that variability was overall higher for the ipsilateral target, compared with the other two targets. Post hoc comparisons showed that across all age groups IDESD for the 25° target was highest, compared with the 155° and the 90° target (all $p < 0.001$); see Table 2 and Fig. 2d for the IDESD findings. As can be seen in Fig. 2d, the higher IDESD for the ipsilateral target appears to be slightly more pronounced in the 5- to 6-, 7- to 8-, and 9- to 10-year-old children than in the older children and the adults.

Kinesthetic condition

The second phase of the experiment was characterized by the absence of visual feedback, requiring participants to rely predominantly on kinesthetic information in order to move to the targets as accurately as possible. Representative movement path exemplars are shown for one 5-year-old child, one 12-year-old child, and one adult in Fig. 3. In this condition, MT differed significantly between age groups [$F(4, 73) = 5.09, p < 0.001$], movement direction [$F(1, 73) = 9.53, p < 0.001$], and amplitude [$F(1, 73) = 115.70, p < 0.001$]; none of the interactions were statistically significant. Post hoc comparisons showed that the 5- to 6-, 7- to 8-, and 9- to 10-year-old children moved significantly slower than the adults. The direction effect indicated that movements toward the 135° target took longer than to those to the 45° target (across groups and movement amplitude: 1.52 ± 0.58 s vs. 1.45 ± 0.60 s; $t = 3.16, p < 0.001$). The amplitude effect originated of course in the fact that targets 3 and 4 were farther out than targets 1 and 2, therefore taking longer (close targets: 1.36 ± 0.57 s; far targets: 1.61 ± 0.61 s; $t = -11.42, p < 0.001$); see Table 3 and Fig. 3a.

Similarly, RMSE in the kinesthetic condition showed significant main effects for age group [$F(4, 73) = 9.97, p < 0.001$], direction [$F(1, 73) = 4.83, p < 0.05$], and amplitude [$F(1, 73) = 94.33, p < 0.001$]. Post hoc comparisons showed that RMSE was significantly higher for the 5- to 6- and 7- to 8-year-olds than for the 9- to 10-year-old children and the adults, and marginally higher than for the 11- to 12-year-old children. Again, across age groups, movements toward the 135° target resulted in higher RMSE than movements toward the 45° target (0.22 ± 0.09 mm; $t = 2.13, p < 0.05$). Across groups and direction, the longer movement amplitude resulted in higher RMSE (close targets: 0.20 ± 0.08 mm, far targets: 0.26 ± 0.10 mm; $t = 9.83, p < 0.001$); see Table 3 and Fig. 3b.

The same analysis on IDE did not reveal any significant differences. Variability of IDE, however, showed main effects for group [$F(4, 73) = 4.70, p < 0.001$] and direction [$F(1, 73) = 5.25, p = 0.02$], reflecting overall higher variability for movements toward the 45° target, as well as a significant Group x Direction interaction [$F(4, 73) = 5.28, p < 0.001$]. Post hoc

tests showed that the 5- to 6-year-olds had significantly higher IDESD than the other children and the adults when moving to the 135° target (all $p < 0.05$) and also showed, together with the 7- to 8-year-olds, higher IDESD for the 45° target, compared with the 11- to 12-year-old children and the adults; see Table 3 and Fig. 3c, d.

We also analyzed constant endpoint error both parallel and orthogonal to the movement (EPpar, EPorth), indicating under- or overshoot (or ‘movement depth’) of the target, and lateral displacement of the movement endpoint relative to target location, respectively. For EPpar, there was a significant main effect for amplitude [$F(1, 73) = 32.66, p < 0.001$]. As illustrated in Fig. 4a, this was due to a general overshooting of the close targets, and undershooting for the far targets, except in the 9- to 10-year-old children and the adults; see also Table 3 for the group means. Across age groups and movement direction, the close targets were overshoot on average by 0.56 ± 1.25 cm, whereas the far targets were only slightly undershot (-0.18 ± 1.81 cm).

Analysis of the endpoint error orthogonal to the movement showed significant main effects for direction [$F(1, 73) = 104.16, p < 0.001$] and amplitude [$F(1, 73) = 15.43, p < 0.001$], and a Group x Direction interaction [$F(4, 73) = 4.30, p < 0.001$]; this interaction was driven by EPorth values of the adults moving to the 135° target being significantly larger compared with the 9- to 10- and the 5- to 6-year-old children (both $p < 0.05$). No group differences were found for movements to the 45° target. The positive values for the 135° target indicate that movements ended up to the left of the target, and the negative values for the 45° target indicate that movements ended up to the right of the target. For the adults, the results showed that the error was greater when moving to the contralateral, as compared to the ipsilateral target (see Table 3; Fig. 4b).

To assess the role of kinesthetic feedback in the test phase of this task further, we performed a correlation analysis between RMSE and IDE scores, separately for each target direction, and averaged across movement amplitude. One may expect these two variables to be highly correlated if vision constituted the primary source of feedback: If a child started in the wrong direction, she/he would continue in this direction since there was no feedback to trigger a corrective movement. Alternatively, a lack of correlation between IDE and RMSE would indicate that kinesthetic feedback is playing a critical role during the movement by modifying the movement path during later stages of the movement. Results showed that statistically significant correlations were present in the 5- to 6-year-olds for the 135° target ($r = 0.38, n = 13, p < 0.05$), in the 7- to 8-year-olds for the 45° target ($r = 0.35, n = 19, p < 0.05$), and in the 9- to 10-year-olds for both targets (135°: $r = 0.51, n = 20, p < 0.01$; 45°: $r = 0.45, n = 20, p < 0.01$), but not for the oldest children or the adults.

Experiment 2: visuo-motor condition

This condition was identical to that in experiment 1, and consequently, the focus was again on MT, RMSE, IDE, and IDESD. Again, MT differed significantly between age groups [$F(4, 58) = 7.06, p < 0.001$] and target [$F(2, 116) = 16.11, p < 0.001$]; no interaction was present. Post hoc comparisons showed that across targets, the 5- to 6-year-old children moved significantly slower than the adults ($p < 0.001$), as did the 7- to 8-year-olds ($p = 0.01$) and the 9- to 10-year-olds ($p = 0.03$). Between-targets comparisons showed that for all age

groups, MT for the 25° target was shortest, compared with the 155° and the 90° target ($p = 0.02$, and $p < 0.001$, respectively). The values for MT, RMSE, IDE, and IDESD in experiment 2 are shown in Table 4 and allow the reader to compare them to those from experiment 1, shown in Table 2.

RMSE showed significant main effects for age group [$F(4, 58) = 5.66, p < 0.001$] and target [$F(2, 116) = 17.29, p < 0.001$], but no interaction. The age group effect originated in the 9- to 10- and the 11- to 12-year-old children having significantly lower RMSE than the younger children and the adults ($p = 0.01$ and $p < 0.001$, respectively). Post hoc between target comparisons showed that across all age groups, RMSE was significantly higher when participants moved to the 155° target compared with the 25° target or the 90° target (both $p < 0.001$); see Table 4.

IDE differed significantly only between targets [$F(2, 116) = 44.11, p < 0.001$]. Post hoc comparisons identified the negative IDE to the 155° target compared with the positive IDE values for the 25° and the 90° targets as source for this effect. The difference between the 25° and the 155° targets was significant, as was the difference between the 155° and the 90° targets (both $p < 0.001$). These results mirror the ones from experiment 1, confirming that the participant pool of experiment 2 performed very similar to that involved in experiment 1.

For variability of IDE, there were significant main effects for age group [$F(4, 58) = 8.13, p < 0.001$] and target [$F(2, 116) = 3.87, p = 0.02$]; there was no interaction. Post hoc analysis showed that the 5- to 6-, 7- to 8-, and 9- to 10-year-old children were significantly less variable than the adults ($p < 0.001$ for the two younger groups, $p < 0.05$ for the 9- to 10-year-olds). Between-target comparisons showed that across all age groups, IDESD was significantly higher when participants moved to the 155° target compared with the 90° target ($p = 0.02$); see Table 4.

Auditory-motor condition

In this condition, the instructions focused on directing the movements toward the acoustic stimuli, without constraining movement amplitude. The only variable of interest, therefore, was IDE. A repeated-measures ANOVA showed a significant main effects for direction [$F(1, 58) = 27.68, p < 0.001$] and noise [$F(1, 58) = 4.21, p < 0.05$]. Additionally, there were significant direction $\times$ age group [$F(4, 58) = 2.88, p < 0.05$] and noise $\times$ age group interactions [$F(4, 48) = 2.85, p < 0.05$]. The source for the former interaction was the 7- to 8- and the 9- to 10-year-old children who showed a clear dichotomy of positive IDE values for the 135° target and negative IDE values for the 45° target; in these two groups, the IDE differences were significant (7–8 years: mean diff. = 30.94°, $t = 3.33, p = 0.01$; 9–10 years: mean diff. = 26.88, $t = 5.11, p < 0.001$). This finding means that participants of these groups started their movements too shallow with respect to the target angles. This replicates findings from a previous study investigating cross-modal adaptation in 9- to 11-year-old children (King et al. 2011).

As can be seen from Fig. 5, the noise $\times$ age group interaction is due to lower IDE in the adults in the ‘white noise’ compared with the ‘one-third octave noise’ condition (mean diff.: 7.70°, $t = 2.83, p = 0.02$), indicating a more accurate direction planning for the white noise

condition. Averaged across targets, the children from all age groups performed with higher IDE during both noise conditions. For variability of IDE, no statistically significant differences between groups or conditions were found.

Discussion

The purpose of this study was to determine developmental characteristics of target-directed hand movements under conditions of feedback other than the visual modality in children between 5 and 12 years of age. To our knowledge, no detailed studies across this age range exist about the characteristics of cross-modal (kinesthetic-motor or auditory-motor) representations in children. With respect to visuo-motor representations, previous studies have suggested that those are not particularly well defined in children. In two experiments, we examined the accuracy of kinesthetically or auditorily guided pointing movements toward ipsilateral or contralateral targets. Our visuo-motor baseline findings for both experiments confirm earlier findings about an age-dependent progression in motor proficiency in children, reflected by faster movement times and smaller spatial error with increasing age. In both baselines, children in the youngest age group performed slower than those in the oldest age group or the adults. Movement linearity showed a non-monotonous developmental course, again with the youngest children having the highest RMSE, the 9- to 10-year-old group the lowest, and again a slight increase in the 11- to 12-year-olds and the adults. The decreased movement linearity of the older children and the adults, however, is unlikely to originate in different muscle torque contributions to the net torques deployed; it has previously been shown that net torques in arm movements are very similar across a broad range of movement speeds in horizontal movements (Dounskaia et al. 2002).

Our baseline findings support previous results about an age-performance progression from similar studies (Contreras-Vidal 2006) and extend them with respect to effects of target direction and target amplitude. Generally, movements to the ipsilateral side (i.e., toward the right) were faster and spatially less variable. Coming close to or crossing the midline toward the contralateral target generally took longer and also increased spatial variability. This midline effect has been documented previously in the developmental literature: Early in infancy, movements that cross the body midline occur very infrequently, but increase during the first 28 months, reflecting the higher complexity of such movements compared with when the limb ipsilateral to the desired target is used. This has been linked to the developing hemispheric lateralization (Provine and Westerman 1979), which additionally appears to be modulated by environmental constraints on the reaching behavior of infants (van Hof et al. 2002). In adults, a directional bias in pointing performance has been shown for either hand when moving to contralateral versus ipsilateral targets (Boulinguez et al. 2001). This is likely due to functional differences between the cortical hemispheres with respect to visuo-motor processing (Di Stefano et al. 1980) and movement planning (Ishihara et al. 2002) and might underlie the slower performance of the right hand in midline-crossing movements. Another possibility for the directional bias is that it is at least in part due to biomechanical constraints. This was acknowledged in the study by Boulinguez et al. (2001), in which movements to contralateral targets require more complex shoulder movements than to ipsilateral ones. At the same time, movement amplitude in their study was 30 cm, whereas it was only 9 cm in our experiment, which likely minimized the biomechanical contribution to

the directional bias, although contribution of interaction torques from the shoulder cannot be ruled out in our study. Our results showed higher IDE for the contralateral target, reflecting less accurate movement planning; this was true across all age groups, which would indicate that the hypothesized functional hemispheric differences with respect to feedforward control are established in children of the age range used in this study and do not change dramatically with age in this age range, as long as vision of the movement is available. What appears to change with age, however, is the variability of planning (reflected through IDESD), indicating a noisier visuo-motor forward representation in the younger children than the older ones; this was independent of movement direction.

Kinesthetic-motor condition

Performance in the kinesthetic condition showed similar characteristics: Movements became faster with increasing age, and the directional bias was present for both MT and RMSE, in form of longer MTs and higher RMSE values for movements to the contralateral targets. It is interesting to note that RMSE tended to be overall lower than in the visual condition, particularly so in the adults. This is due to the fact that visual feedback processes related to online control of the movements, particularly during the 'homing-in' phase, are absent in this condition and reduce the overall 'cost' of movement control, resulting in higher linearity. This reduction was more substantial in the older children and adults, indicating that they were less reliant on visual feedback and could 'trust' their kinesthetic feedback more, than young children (Yan et al. 2000).

Whereas RMSE speaks more to feedback control, IDE reflects the feedforward, or planning, component of a movement. When visual feedback of the movement was not available, variability in the youngest children was substantially higher than in the older children and the adults, irrespective of target direction. An interesting pattern was found in the 7- to 8- and 9- to 10-year-olds, whose directional planning was more variable for movements to the ipsilateral, as compared to the contralateral target; this counters the findings in the visual condition, where we found a directional bias favoring the ipsilateral side, steadily improving with age. At the same time, non-monotonous performance progression during development has been documented previously in aiming tasks: When visual information of the moving limb was not available, children around 7–8 years of age showed less spatial accuracy than 5-year-old or 11-year-old children (Hay 1979; Hay et al. 1994). Findings from these studies suggested that the youngest children used predominantly feedforward control, which brought arm movements reasonably close to the target. On the other hand, 7- to 8-year-old children seemed to use an 'intermediate' strategy, consisting of a mix of feedforward and feedback control that was not well integrated and, as a result, degraded the performance. In older children, this integration of both processes operated more efficiently and enabled them to become more accurate again. This increasing efficiency in applying a particular control mode might also contribute to kinesthetic-motor representations that are more 'robust' against perturbations, as we have shown in a previous study (Kagerer and Clark 2014b). In this context, the high IDESD scores for movements to the ipsilateral target could be seen as performance degradation, compared to the lower variability for movements to the contralateral target in the 7- to 8- and 9- to 10-year-olds. It seems plausible that the slightly slower movements to the contralateral targets resulted in different, more feedback-based

control processes in this age bracket, whereas the faster movements to the ipsilateral targets tended to have a larger feedforward component—but not efficient enough to ensure consistent performance when reliance on kinesthetic information was necessarily high. In a way, this is reflected in the lateral component of the endpoint error (EP_{orth}): Among the younger children, the 7- and 8-year-old children had the highest error values (if not statistically different from the other children), to either of the two targets. These findings add to a more detailed picture of the development of kinesthetic-motor internal representations, connecting different (and likely inconsistently applied) control modes, during this transitional period to movements that are more difficult (contralateral), versus those that are easier to control (ipsilateral).

What stands out in the lateral endpoint results, however, are those for the adults and the older children: Results for both groups, particularly for movements to contralateral targets, counter the developmental trend that, overall, accuracy increases with age. It is interesting to look at these results in the light of the control-specialization hypothesis put forward by Sainburg (2002) (Mutha et al. 2013). Instead of approaching handedness from a perspective where the dominant hand is ‘strong’ for all aspects of movement and the non-dominant hand is just overall less proficient, they postulate that dominant arm control relies on prediction of dynamics, whereas the non-dominant arm specializes on positional stability, e.g., at the movement endpoint. In a recent study (Mutha et al. 2013), they found that during rapid reaching movements to lateral or medial targets, the dominant (right) hand’s performance was characterized by larger endpoint variability than that of the non-dominant left hand. A recent computational model related to this hypothesis proposes a so-called serial hybrid control scheme, in which initial feedforward control is followed by impedance control toward the end of the movement (Yadav and Sainburg 2011). The model states further that one crucial control difference between dominant and non-dominant arm is the time during movement at which control switches from predictive to impedance mode; in adults, the dominant arm whose ‘strong suit’ is predictive control switches to impedance control later than the non-dominant arm. Looking only at the dominant arm (since only that was used in our study), we can speculate about the possibility of this control mode-switching in development. In this context, we would hypothesize that with increasing age the shift from predictive to impedance control mode occurs later; in young children, the dominant arm system would switch earlier from predictive to impedance mode, thus emphasizing the control of steady-state limb posture. As a result, one would not expect differences in the initial feedforward control between the young children, the older children, and the adults—which is in accordance with our IDE results. Further, the emphasis of the system on early impedance control would facilitate relatively high endpoint accuracy, which decreases with a shift to later impedance control with increasing age. This would be reflected in the increasing variable error with increasing age. The possibility of an ‘intermittent stage’ (Hay et al. 1994) remains, during which there is a developmental transition (and inconsistency) in the ability to switch from one control mode to another. At the same time, we acknowledge the limitations of this interpretation, since we only tested the dominant hand and cannot complement our interpretation with data from the non-dominant hand.

Another important aspect of our study is the findings with respect to movement amplitude—participants had to move to either close (7 cm) or far (11 cm) targets. The rationale for this

was part of the overall goal to determine whether internal kinesthetic-motor maps change as a function of age. In adults, kinesthesia has been shown to be more sensitive along movement ‘depth,’ with respect to the shoulder of the moving limb, as opposed to direction (van Beers et al. 1998). We found amplitude effects for MT, RMSE, and EPar—but in none of these instances, there were interactions involving group, indicating that there was no differential effect of age on movement extent under conditions of predominantly kinesthetic feedback. Movement linearity (measured through RMSE) and endpoint accuracy values (measured through EPorth) were lower for the near targets, which supports previous findings showing that hand positions at shorter distances from the shoulder were localized more accurately than positions that were farther away (van Beers et al. 1998). The fact that all age groups were affected similarly suggests that kinesthetic-motor integration is already largely functional at 5–6 years of age in this type of task. The results of the correlation between feedforward control (expressed through IDE) and feedback control (RMSE) indicate that movement control at that age very likely weights feedforward and feedback processes differently (upweighting feedback control) than it does in older children and adults who seem to shift earlier in the movement to feedforward processing. A potential shortcoming of our approach with respect to movement depth was that the amplitude differences were rather small and that the kinesthetic error signal might not have been large enough to trigger age-dependent feedback processes.

Auditory-motor condition

The results of our auditory-motor experiment showed that all age groups performed relatively accurate, with directional errors of less than 10° on average. It has been argued previously that even when we reach to auditory targets, those targets are represented in eye-centered coordinates and that orienting head movements help to update this reference frame (Pouget et al. 2002). However, participants in our experiment were blindfolded and therefore did not have any visual stimuli available, and their head was positioned in a chin- and forehead rest and was not moving.

Interestingly, we did not find a developmental trend for the one-third octave noise, which is more difficult to localize, because it provides primarily interaural temporal difference cues (Wightman and Kistler 1992) which are transcallosally mediated. This suggests that the degree of CC functionality across this age range is obviously sufficient to provide the basis for a comparable development of auditory-motor internal representations and supports earlier findings showing that children between 5 and 10 years of age have developed spatial-to-motor transformations across modalities (King et al. 2009). In the light of the one-third octave noise being the more challenging condition that would challenge CC functionality more, it is easy to see that we would not expect to see big differences between the age groups in the white noise condition. White noise is normally easy to localize, because both binaural and spectral cues are available (Abel et al. 2000). Our results indicate that this did not make a difference for the children (with the possible exception of the 9- to 10-year-olds). The negative IDE found in the adults for the white noise condition indicates movements with a slight clockwise directional bias toward the sound sources, but more important than the directional bias is the fact that absolute IDE was smaller. This might suggest that the adults were able to extract spectral cues from the signal better than most of the children.

With increasing age, it becomes harder for the auditory system to extract spectral cues from an acoustic signal (Abel et al. 2000), but given the young age of our adult group, this might be a possibility for their lower IDE in this condition. A limitation for interpreting our findings here is certainly that we did not assess CC functionality through psychophysical measures, such as auditory- or visual-evoked potentials, which would have been beyond the scope of this study.

Conclusion

The results of two experiments show that under conditions of visually guided target-directed movements, there is an age progression with respect to movement speed and movement linearity, as well as variability of feedforward control. The higher control demands for movements toward the contralateral side were reflected in similar ways for all age groups in higher movement times and decreased spatial accuracy. This was also true when vision was not available. This indicates that kinesthetic-motor internal representations are functional in young children already, but improve with age. One pattern that deviated from the typical pattern of movements to ipsilateral targets generally being spatially more accurate in this condition was the more variable feed-forward component to ipsilateral targets in 7- to 10-years-old children. This result supports, and extends, previous findings suggesting that the control system in children of this age range goes through a transition that affects the ability to switch from feedforward to feedback control efficiently. Our results suggest that movement direction (contralateral vs. ipsilateral) engages different control modes during this time. Another important finding for the kinesthetic-motor condition was the higher directional endpoint errors in the adults, compared with those of children. This might reflect a higher degree of functional lateralization not yet present in the children: The dominant hand in adults has previously been shown to be more proficient in trajectory control, but less proficient in endpoint accuracy control (Sainburg 2002). The fact that we did not find any group effects for movement amplitude in the kinesthetic-motor condition shows further that the children's ability to integrate movement depth information is functional at young age already, confirming previous findings that children can utilize kinesthesia with reasonable accuracy from early on (Tahej et al. 2012). Additionally, the results show that the development of kinesthetic-motor internal representations progresses with age, but undergoes a period of 'uncertainty' in terms of control modes, with inefficient switching between 'noisy' feedforward control and feedback control.

In the auditory-motor condition, the results did not support our hypothesis of differential auditory-motor integration depending on age: All age groups performed with very similar directional accuracy, suggesting that corpus callosum functionality which is important when it comes to interaural time integration is functional at young age. Only in the white noise condition, which provides spectral cues in addition to temporal cues, do adults appear to have a slight advantage. Overall, our results confirm that auditory-motor internal representations appear to be functional in target-directed movement tasks already at the age of 5–6 years, with only little changes as the children get older.

Acknowledgments

This research was supported by National Institute of Child Health and Human Development Grants R03-HD-050372 to FAK, and R01-HD-42527 to JEC.

References

- Abel SM, Giguère C, Consoli A, Papsin BC. The effect of aging on horizontal plane sound localization. *J Acoust Soc Am*. 2000; 108:743–752. [PubMed: 10955641]
- Bard C, Hay L, Fleury M. Timing and accuracy of visually directed movements in children: control of direction and amplitude components. *J Exp Child Psychol*. 1990; 50:102–118. [PubMed: 2398328]
- Boulinguez P, Nougier V, Velay JL. Manual asymmetries in reaching movement control. I: study of right-handers. *Cortex*. 2001; 37:101–122. [PubMed: 11292156]
- Boyer EO, Babayan BM, Bevilacqua F, Noisternig M, Warusfel O, Roby-Brami A, Hanneton S, Viaud-Delmon I. From ear to hand: the role of the auditory-motor loop in pointing to an auditory source. *Front Comput Neurosci*. 2013; 7:26.10.3389/fncom.2013.00026 [PubMed: 23626532]
- Bradshaw JL, Spataro JA, Harris M, Nettleton NC, Bradshaw J. Crossing the midline by four to eight year old children. *Neuropsychologia*. 1988; 26:221–235. [PubMed: 3399040]
- Contreras-Vidal JL. Development of forward models for hand localization and movement control in 6- to 10-year-old children. *Hum Mov Sci*. 2006; 25:634–645.10.1016/j.humov.2006.07.006 [PubMed: 17011659]
- Contreras-Vidal JL, Bo J, Boudreau JP, Clark JE. Development of visuomotor representations for hand movement in young children. *Exp Brain Res*. 2005; 162:155–164.10.1007/s00221-004-2123-7 [PubMed: 15586275]
- Desmurget M, Rossetti Y, Prablanc C, Stelmach GE, Jeannerod M. Representation of hand position prior to movement and motor variability. *Can J Physiol Pharmacol*. 1995; 73:262–272. [PubMed: 7621365]
- Di Stefano M, Morelli M, Marzi CA, Berlucchi G. Hemispheric control of unilateral and bilateral movements of proximal and distal parts of the arm as inferred from simple reaction time to lateralized light stimuli in man. *Exp Brain Res*. 1980; 38:197–204. [PubMed: 7358103]
- Dounskaia NV, Ketcham CJ, Stelmach GE. Influence of biomechanical constraints on horizontal arm movements. *Mot Control*. 2002; 6:366–387.
- Elliott D, Carson RG, Goodman D, Chua R. Discrete vs. continuous visual control of manual aiming. *Hum Mov Sci*. 1991; 10:393–418.
- Hay L. Spatial-temporal analysis of movements in children. *J Mot Behav*. 1979; 11:189–200.10.1080/00222895.1979.10735187 [PubMed: 23962287]
- Hay L, Fleury M, Bard C, Teasdale N. Resolving power of the perceptual- and sensorimotor systems in 6- to 10-year-old children. *J Mot Behav*. 1994; 26:36–42.10.1080/00222895.1994.9941659 [PubMed: 15757832]
- Henderson, S.; Sugden, D. The movement assessment battery for children. Psychological Cooperation; London: 1992.
- Ishihara M, Imanaka K, Mori S. Lateralized effects of target location on reaction times when preparing for manual aiming at a visual target. *Hum Mov Sci*. 2002; 21:563–582. [PubMed: 12620712]
- Jansen-Osmann P, Richter S, Konczak J, Kalveram K-T. Force adaptation transfers to untrained workspace regions in children: evidence for developing inverse dynamic motor models. *Exp Brain Res*. 2002; 143:212–220.10.1007/s00221-001-0982-8 [PubMed: 11880897]
- Jeannerod M. Mechanisms of visuomotor coordination: a study in normal and brain-damaged subjects. *Neuropsychologia*. 1986; 24:41–78. [PubMed: 3517680]
- Kagerer FA, Clark JE. Development of interactions between sensorimotor representations in school-aged children. *Hum Mov Sci*. 2014a; 34:164–177.10.1016/j.humov.2014.02.001 [PubMed: 24636697]
- Kagerer FA, Clark JE. Development of interactions between sensorimotor representations in school-aged children. *Hum Mov Sci*. 2014b10.1016/j.humov.2014.02.001

- King BR, Kagerer FA, Contreras-Vidal JL, Clark JE. Evidence for multisensory spatial-to-motor transformations in aiming movements of children. *J Neurophysiol.* 2009; 101:315–322.10.1152/jn.90781.2008 [PubMed: 18987123]
- King BR, Kagerer FA, Harring JR, Contreras-Vidal JL, Clark JE. Multisensory adaptation of spatial-to-motor transformations in children with developmental coordination disorder. *Exp Brain Res.* 2011; 212:257–265.10.1007/s00221-011-2722-z [PubMed: 21584627]
- Muetzel RL, Collins PF, Mueller BA, Schissel AM, Lim KO, Luciana M. The development of corpus callosum microstructure and associations with bimanual task performance in healthy adolescents. *NeuroImage.* 2008; 39:1918–1925.10.1016/j.neuroimage.2007.10.018 [PubMed: 18060810]
- Mutha PK, Haaland KY, Sainburg RL. Rethinking motor lateralization: specialized but complementary mechanisms for motor control of each arm. *PLoS ONE.* 2013; 8:e58582.10.1371/journal.pone.0058582 [PubMed: 23472210]
- Olivier I, Hay L, Bard C, Fleury M. Age-related differences in the reaching and grasping coordination in children: unimanual and bimanual tasks. *Exp Brain Res.* 2007; 179:17–27.10.1007/s00221-006-0762-6 [PubMed: 17091289]
- Poirier P, Miljourns S, Lassonde M, Lepore F. Sound localization in acallosal human listeners. *Brain.* 1993; 116(Pt 1):53–69. [PubMed: 8453465]
- Poirier P, Lepore F, Provençal C, Ptito M, Guillemot JP. Binaural noise stimulation of auditory callosal fibers of the cat: responses to interaural time delays. *Exp Brain Res.* 1995; 104:30–40. [PubMed: 7621939]
- Pouget A, Ducom JC, Torri J, Bavelier D. Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition.* 2002; 83:B1–B11. [PubMed: 11814488]
- Proteau L, Isabelle G. On the role of visual afferent information for the control of aiming movements toward targets of different sizes. *J Mot Behav.* 2002; 34:367–384.10.1080/00222890209601954 [PubMed: 12446251]
- Provine RR, Westerman JA. Crossing the midline: limits of early eye-hand behavior. *Child Dev.* 1979; 50:437–441. [PubMed: 487884]
- Rossetti Y, Tadary B, Prablanc C. Optimal contributions of head and eye positions to spatial accuracy in man tested by visually directed pointing. *Exp Brain Res.* 1994; 97:487–496. [PubMed: 8187860]
- Sainburg RL. Evidence for a dynamic-dominance hypothesis of handedness. *Exp Brain Res.* 2002; 142:241–258.10.1007/s00221-001-0913-8 [PubMed: 11807578]
- Shadmehr R, Krakauer JW. A computational neuroanatomy for motor control. *Exp Brain Res.* 2008; 185:359–381.10.1007/s00221-008-1280-5 [PubMed: 18251019]
- Smits-Engelsman BCM, Westenberg Y, Duysens J. Children with developmental coordination disorder are equally able to generate force but show more variability than typically developing children. *Hum Mov Sci.* 2008; 27:296–309.10.1016/j.humov.2008.02.005 [PubMed: 18358552]
- Tahej P-K, Ferrel-Chapus C, Olivier I, Ginhac D, Rolland J-P. Multiple representations and mechanisms for visuomotor adaptation in young children. *Hum Mov Sci.* 2012; 31:1425–1435.10.1016/j.humov.2012.02.016 [PubMed: 22704964]
- Teasdale N, Bard C, Fleury M, Young DE, Proteau L. Determining movement onsets from temporal series. *J Mot Behav.* 1993; 25:97–106.10.1080/00222895.1993.9941644 [PubMed: 15064201]
- van Beers RJ, Sittig AC, Denier van der Gon JJ. The precision of proprioceptive position sense. *Exp Brain Res.* 1998; 122:367–377. [PubMed: 9827856]
- van Hof R, van der Kamp J, Savelsbergh GJR. The relation of unimanual and bimanual reaching to crossing the midline. *Child Dev.* 2002; 73:1353–1362. [PubMed: 12361305]
- von Hofsten C, Rösblad B. The integration of sensory information in the development of precise manual pointing. *Neuropsychologia.* 1988; 26:805–821. [PubMed: 3194047]
- Wann JP, Ibrahim SF. Does limb proprioception drift? *Exp Brain Res.* 1992; 91:162–166. [PubMed: 1301369]
- Wightman FL, Kistler DJ. The dominant role of low-frequency interaural time differences in sound localization. *J Acoust Soc Am.* 1992; 91:1648–1661. [PubMed: 1564201]
- Wolpert DM, Kawato M. Multiple paired forward and inverse models for motor control. *Neural Netw.* 1998; 11:1317–1329. [PubMed: 12662752]

- Yadav V, Sainburg RL. Motor lateralization is characterized by a serial hybrid control scheme. *Neuroscience*. 2011; 196:153–167.10.1016/j.neuroscience.2011.08.039 [PubMed: 21889579]
- Yan JH, Thomas JR, Stelmach GE, Thomas KT. Developmental features of rapid aiming arm movements across the lifespan. *J Mot Behav*. 2000; 32:121–140.10.1080/00222890009601365 [PubMed: 11005944]

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

Fig. 1.

Stimulus display, showing the positions of the home position (H) for both experiments, and the three targets v_1 , v_2 , and v_3 , one of which was displayed at a trial during the visuo-motor condition of each experiment. Targets k_{1-4} indicate the targets presented during the kinesthetic-motor condition (experiment 1), with participants being instructed to move toward these targets without visual feedback of the pen trace. The speaker positions during the auditory phase of experiment 2 are indicated by a_1 and a_2 ; participants had to move toward these targets while the auditory stimuli were presented. The angles of these two targets relative to the home position were the same as for the targets displayed during the test phase of experiment 1. The *oval* on the lower edge of the tablet denotes the position of the chinrest

Fig. 2.

On *top*, exemplar movement paths of one 5-year-old child, one 12-year-old child, and one adult for the visual condition are shown. The *bar graphs* show MT, RMSE, IDE, and IDESD for the five age groups during the visual baseline in experiment 1; *error bars* denote standard error. The *lines* and *asterisks* indicate significant group differences ($p < 0.02$)

Fig. 3. On *top*, exemplar movement paths of one 5-year-old child, one 12-year-old child, and one adult for the kinesthetic condition are shown; the *top row* illustrates movements to the ‘close’ targets, the *bottom row* those to the ‘far’ targets. The bar graphs show MT, RMSE, IDE, and IDESD for the five age groups during the kinesthetic phase in experiment 1; *error bars* denote standard error. The *lines* and *asterisks* indicate significant group differences ($p < 0.02$)

Fig. 4.

Constant error parallel (EPpar) and orthogonal to the movement direction (EPorth). Since there was no direction effect for EPpar, the results are shown across movement direction; *error bars* denote standard error. The *lines* and *asterisks* indicate significant group differences ($p < 0.05$) for the 135° target

Fig. 5. IDE (averaged across target) for each age group for the auditory-motor condition. *Empty circles* denote white noise and *filled circles* one-third octave noise condition; *error bars* indicate standard error

Table 1
Age range, means (in years), standard deviation, sample size, and gender distribution for each age group in the two experiments

Age group (years)	Experiment 1			Experiment 2		
	<i>n</i>	Gender distribution	Age range (years), mean (SD)	<i>n</i>	Gender distribution	Age range (years), mean, SD
5–6	13	9 f, 5 m	5.08–6.67, 6.04 (0.53)	13	8 f, 6 m	5.08–6.99, 6.04 (0.69)
7–8	19	11 f, 8 m	7.00–8.58, 7.74 (0.53)	13	7 f, 7 m	7.08–8.50, 7.69 (0.50)
9–10	20	6 f, 13 m	9.08–10.67, 9.84 (0.51)	15	5 f, 10 m	9.08–10.67, 9.90 (0.53)
11–12	15	6 f, 9 m	11.0–12.83, 11.8 (0.57)	11	5 f, 6 m	11.0–12.83, 11.8 (0.56)
Adults	11	7 f, 4 m	18.92–24.60, 22.25 (1.60)	11	7 f, 4 m	18.92–24.60, 22.25 (1.60)

Table 2

Means (standard deviations) for the variables of interest in the visuo-motor condition of experiment 1

Between groups					
Group [yrs]	MT [s]	RMSE [cm]	IDE [deg]	IDESD [deg]	
5–6	1.69 (0.50)	0.33 (0.09)	4.37 (6.59)	15.79 (4.08)	
7–8	1.47 (0.37)	0.32 (0.08)	6.56 (4.97)	13.72 (2.30)	
9–10	1.31 (0.31)	(*)	* 4.66 (4.39)	13.90 (2.22)	
11–12	1.14 (0.29)	*	4.70 (4.44)	11.06 (2.07)	*
Adults	0.82 (0.27)	* 0.29 (0.05)	3.14 (5.02)	10.93 (4.06)	*
Between targets					
25°	1.22 (0.42)	0.26 (0.10)	8.46 (10.39)	14.77 (5.36)	
155°	1.34 (0.47)	*	* -1.00 (7.88)	* 12.33 (5.08)	*
90°	1.38 (0.49)	* 0.23 (0.08)	* 7.14 (8.45)	* 12.56 (4.03)	*

Shaded cells indicate that this group's means were significantly different from those below (within the same column and section) marked with asterisks ($p < 0.05$); asterisks in parentheses indicate a trend ($p = 0.06$)

Table 3
Means (standard deviations) of the variables of interest in the kinesthetic-motor condition of experiment 1

Between groups		MT [s]	RMSE [cm]	IDE [deg]	IDESD [deg]		EPX [cm]		EPY [cm]	
Group [yrs]					135°	45°	135°	45°	135°	45°
5–6	1.85 (0.65)		0.28 (0.06)	5.16 (7.57)	18.75 (5.51)	17.62 (5.14)	–0.24 (1.03)	0.06 (1.03)	–0.47 (0.89)	–0.06 (1.01)
7–8	1.66 (0.51)		0.29 (0.09)	6.21 (5.44)	12.87 (3.59)	* 17.48 (4.08)	–0.62 (1.93)	0.62 (1.65)	–0.67 (1.57)	–0.30 (1.65)
9–10	1.47 (0.55)		0.19 (0.06)	* 3.57 (5.37)	12.04 (3.63)	* 16.81 (4.54)	–0.37 (0.97)	0.52 (1.08)	–0.62 (0.88)	–0.39 (1.15)
11–12	1.35 (0.17)	(*)	0.21 (0.07)	* 4.47 (5.90)	13.28 (4.01)	* 13.51 (4.58)	* –1.18 (1.34)	1.06 (1.41)	–1.01 (0.77)	0.04 (1.03)
Adults	0.81 (0.50)	* *	0.17 (0.05)	* 3.37 (4.36)	14.07 (4.97)	* 12.61 (2.55)	* –1.98 (1.06)	* 0.98 (1.18)	–0.72 (1.74)	–0.12 (1.09)
Between targets										
45° near	1.33 (0.59)		0.19 (0.08)	3.54 (11.48)	near					
45° far	1.57 (0.63)		0.25 (0.11)	3.40 (11.28)	13.72 (6.31)	15.88 (5.85)	–0.79 (1.30)	0.78 (1.14)	–0.18 (1.13)	0.19 (1.04)
135° near	1.38 (0.57)		0.21 (0.09)	5.12 (8.23)	far					
135° far	1.65 (0.61)		0.27 (0.11)	6.53 (8.65)	13.95 (6.51)	15.76 (6.35)	–0.79 (1.70)	0.49 (1.71)	–1.22 (1.41)	–0.58 (1.57)

In the 'Between groups' section of the table, shaded cells indicate that this group's means were significantly different from those below (within the same column) marked with asterisks ($p < 0.02$); asterisks in parentheses indicate a trend ($d = 0.07$). In the 'Between targets' section, means (SD) are listed separately for each direction and amplitude

Table 4

Means (standard deviations) for MT, RMSE, IDE, and IDSD the visuo-motor baseline, and the auditory-motor condition in experiment 2

Visuo-motor condition			Auditory-motor condition			
Between groups						
Group [yrs]	MT[s]		RMSE [cm]	IDE [deg]	IDSD [deg]	IDE [deg]
5-6	1.40 (0.29)		0.38 (0.13)	6.02 (5.50)	15.15 (2.85)	6.74 (7.61)
7-8	1.26 (0.29)		0.30 (0.11)	4.76 (5.57)	14.70 (3.70)	3.49 (5.31)
9-10	1.20 (0.39)		0.24 (0.05)	5.31 (5.25)	12.97 (2.85)	4.0 (4.32)
11-12	1.05 (0.17)	(*)	0.21 (0.05)	3.96 (3.38)	11.51 (3.03)	6.54 (7.27)
Adults	0.81 (0.19)	* *	0.29 (0.09)	3.84 (4.42)	8.97 (2.56)	1.84 (5.94)
Between targets						
25°	1.08 (0.32)		0.26 (0.13)	9.35 (8.96)	14.12 (6.22)	135° wn 14.60 (14.26)
155°	1.16 (0.37)	*	0.34 (0.16)	* -1.74 (7.09)	* 12.46 (4.22)	135° obn 12.37 (12.62)
90°	1.23 (0.39)	* *	0.24 (0.10)	* 6.82 (7.10)	* 11.89 (4.65)	45° wn -7.42 (17.55)
						45° obn -1.66 (17.89)

Shaded cells indicate that this group's means were significantly different from those below (within the same column and section) marked with asterisks ($p < 0.05$); asterisks in parentheses indicate a trend ($p = 0.08$). In the auditory-motor condition, 'wn' denotes white noise, and 'obn' one-third octave band noise