Development of state estimation explains improvements in sensorimotor performance across childhood

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King BR, Oliveira MA, Contreras-Vidal JL, Clark JE. Development of state estimation explains improvements in sensorimotor performance across childhood. J Neurophysiol 107: 3040–3049, 2012. First published February 29, 2012; doi:10.1152/jn.00932.2011.—Previous developmental research examining sensorimotor control of the arm in school-age children has demonstrated age-related improvements in movement kinematics. However, the mechanisms that underlie these age-related improvements are still unclear. This study hypothesized that changes in sensorimotor performance across childhood can be attributed, in part, to the development of state estimation, defined as estimates computed by the central nervous system, which specify both current and future hand positions and velocities (i.e., hand “state”). Two behavioral experiments were conducted, in which 6- to 12-year-old children and young adults executed goal-directed arm movements. Results from Experiment 1 revealed that young children (i.e., ~6–8 years) have less precise proprioceptive feedback for static (i.e., stationary) hand state estimation compared with older children (i.e., ~10–12 years), resulting in increased variability of target-directed reaching movements. Experiment 2 demonstrated that young children rely on delayed and unreliable state estimates during the execution of goal-directed hand movements (i.e., dynamic state estimation), resulting in both increased movement errors and directional variability. Collectively, these results suggest that improvements in sensorimotor behavior across childhood can be attributed, at least partially, to the development of both static and dynamic state estimation.

ADULTS EXECUTE GOAL-DIRECTED ARM MOVEMENTS WITH REMARKABLE SMOOTHNESS, CONSISTENCY, AND ACCURACY (e.g., Flash and Hogan 1985; Morasso 1981). However, changes in the developing sensorimotor system and in the physical characteristics of the body during childhood can impact the control and coordination of target-directed reaches. Indeed, previous developmental research examining sensorimotor control of the arm in school-age children has demonstrated age-related differences in movement smoothness and temporal and spatial variability, and movement speed (Bo et al. 2006; Contreras-Vidal 2006; Contreras-Vidal et al. 2005; Hay 1979; Jansen-Osmann et al. 2002; King et al. 2009; Pangelinan et al. 2011; Yan et al. 2000, 2003). Although characterizations of these age-related behavioral differences are pervasive, the mechanisms that underlie these improvements are still unclear. The current research investigated the hypothesis that improvements in state estimation, defined as estimates computed by the central nervous system (CNS), which specify both current and future hand positions and velocities (i.e., hand “state”), underlie the age-related behavioral differences in school-age children.

An accurate and precise estimate of hand state is critical for the successful execution of goal-directed arm movements (e.g., Vindras et al. 1998). Estimates of initial hand state and desired target position are thought to be transformed into an appropriate motor plan, which will drive the hand toward the target, a computation that is generally considered to be a function of a controller or inverse internal representation (Saber 2000; Shadmehr and Krakauer 2008; Shadmehr and Wise 2005). Importantly, the CNS can estimate the initial position of the hand, based on visual and/or proprioceptive feedback (Saber and Sabes 2003, 2005; van Beers et al. 1999). Whereas static visual acuity is relatively stable in school-age children (Nelson et al. 1984), age-related changes in proprioceptive functioning may result in impaired static state estimation in younger children when vision of the hand is absent (Contreras-Vidal 2006; King et al. 2010; von Hofsten and Rosblad 1988). Impaired static state estimation, in turn, may underlie the poor sensorimotor performance in younger children compared with older children or adults reported in the extant literature.

In addition to the localization of hand position prior to movement onset, state estimation during movement execution is critical for the detection of movement errors and the corresponding trajectory modifications. Relying on sensory afferents to provide state estimates during the execution of rapid, ballistic reaching movements can result in erroneous and inefficient movement trajectories, due to the delays in sensory processing. Thus predicting future states based on efference copies of motor commands can be used as an internal reference to circumvent processing delays, a finding that has been demonstrated in adults (Desmurget and Grafton 2000; Tseng et al. 2007; Wagner and Smith 2008; Wolpert and Flanagan 2001). This prediction can be combined with sensory feedback to provide an up-to-date, online state estimate (i.e., dynamic state estimation) (Izawa and Shadmehr 2008; Vaziri et al. 2006; Wolpert et al. 1995). The development of dynamic state estimation across childhood has not, to our knowledge, been investigated.

The aim of the current research was to investigate the hypothesis that the age-related improvements in goal-directed sensorimotor behavior, reported in the extant developmental literature, can be explained, at least partially, by improvements in static and dynamic state estimation. We conducted two experiments to examine the developmental trajectory of state estimation across 6- to 12-year-old typically developing children. Experiment 1 examined the effect of age-related im-
provenments in the accuracy and reliability of proprioceptive feedback for static state estimation on functional sensorimotor behavior, by having participants execute goal-directed arm movements toward peripheral targets when initial hand position was provided by proprioception only or simultaneous vision and proprioception. *Experiment 2* characterized the effect of age-related changes in dynamic state estimation, above and beyond the effects of static state estimation, on sensorimotor performance, by analyzing the participants’ movement trajectories when the desired target was unexpectedly displaced during the execution of a ballistic, goal-directed reach.

**MATERIALS AND METHODS**

**Participants**

Right-handed children (6–12 years) and adults (18–22 years) were recruited for these studies. Detailed participant characteristics for each experiment are included in Table 1.1 To ensure typical and healthy development, the parents of the child participants completed a neuropsychological health questionnaire to preclude any neurological deficits or developmental delay. Additionally, the children were screened with the Movement Assessment Battery for Children, Second Edition (MABC-2; Henderson and Sugden 2007). Participants were included in the study if they scored at or above the 25th percentile. Scores above the 15th percentile suggest no indication of motor coordination difficulties (Henderson and Sugden 2007). Handedness of the children was determined based on MABC-2 criterion, which included placing a writing implement on a table in front of a participant’s midline; the hand used to draw a picture was recorded as the preferred hand. Adult participants also completed a neurological health questionnaire to ensure no known neurological or motor impairments. Handedness of the adults was determined by the Edinburgh Handedness Inventory (cumulative score >40) (Oldfield 1971). All experimental procedures were approved by the Institutional Review Board at the University of Maryland, College Park. Adult participants and parents or legal guardians of child participants provided informed consent prior to participation. Additionally, informed assent was obtained from the children upon completion of the experiment, the children received a small toy prize. Both the children and adults received a modest monetary compensation.

*Ten of the child participants and eight of the adults completed Experiment 2 immediately before completing Experiment 1. The 10 child participants were approximately evenly spread out among the different ages (i.e., one 6 year old, 7 year old, 8 year old, and 11 year old and two 9 year olds, 10 year olds, and 12 year olds). Participation in both tasks in the same testing session had no influence on the results for the following reasons. First, participants in both experiments completed familiarization trials and ample practice trials to ensure that all individuals were comfortable with the experimental apparatus prior to participation. Second, Experiment 2 did not contain any perturbation (i.e., visual feedback rotation), which would negatively impact performance on Experiment 1.*

**Table 1. Experiments 1 and 2 participant characteristics**

<table>
<thead>
<tr>
<th>Group</th>
<th>Gender</th>
<th>Mean Age ± SD (yr)</th>
<th>Age Range (yr)</th>
<th>MABC Percentile Range</th>
<th>Edinburgh: Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
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<tr>
<td>Children</td>
<td>19 F; 22 M</td>
<td>9.35 ± 1.84</td>
<td>6.1–12.7</td>
<td>25–95</td>
<td>N/A</td>
</tr>
<tr>
<td>Adults</td>
<td>4 F; 4 M</td>
<td>20.1 ± 0.84</td>
<td>19.2–22.0</td>
<td>N/A</td>
<td>71.0 ± 19.1</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
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<td></td>
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<tr>
<td>Children</td>
<td>18 F; 22 M</td>
<td>9.40 ± 2.00</td>
<td>5.9–12.7</td>
<td>25–95</td>
<td>N/A</td>
</tr>
<tr>
<td>Adults</td>
<td>7 F; 6 M</td>
<td>20.1 ± 0.89</td>
<td>18.7–22.0</td>
<td>N/A</td>
<td>74.4 ± 18.6</td>
</tr>
</tbody>
</table>

MABC, Movement Assessment Battery for Children; F, female; M, male.

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**Apparatus**

Participants were seated in a height-adjustable chair in front of a robotic manipulandum (InMotion2, Interactive Motion Technology, Cambridge, MA), which moved freely in two dimensions. Participants were instructed to use their dominant (right) hand to move the manipulandum, as required by the tasks (see Procedures). A vertically oriented computer monitor presented the task stimuli and when appropriate, visual feedback of the participants’ performance. For *Experiment 1*, an occluding board was positioned above the manipulandum to prevent the participants from viewing the position of their hand or the manipulandum during task performance. For *Experiment 2*, the lights in the testing room were turned off, and participants were fitted with customized goggles to restrict vision of the participants’ limbs. For both experiments, participants were instructed that the goal of the tasks was to move the manipulandum from a start position to a desired target as fast and as accurately as possible. The time series of the *x*/*y* coordinates of the manipulandum position was sampled at 200 Hz.

**Experiment 1**

**Procedures.** The aim of the first experiment was to examine the effect of age-related improvements in the accuracy and reliability of proprioceptive feedback for static state estimation on functional sensorimotor behavior. Participants were asked to make 15 cm arm movements from one of five starting locations to a single target (0.625 cm diameter) located away from the body and start positions. The target circle was positioned 70°, 80°, 90°, 100°, or 110° with respect to the five different start circles. Prior to each trial, the experimenter held the arm of the robot and moved the manipulandum to the appropriate starting position (i.e., passive arm movements). Note that the starting positions were not depicted on the computer monitor viewed by the participant; rather, they represented *x/y* coordinates, which serve as the initial manipulandum position prior to movement onset. Additionally, no visual feedback of the manipulandum’s position was provided during the passive movements. The experimental protocol included two conditions: vision (V) and no vision (NV). During the V condition, once the manipulandum was moved to the appropriate starting position by the experimenter, and the participant remained motionless for a duration, which varied randomly between 200 and 400 ms, a yellow circle (0.375 cm diameter) appeared, depicting the real-time position of the manipulandum (i.e., visual feedback of current hand position). Simultaneously, a red circle appeared, indicating the desired target position. Once the participant remained motionless for an additional time period (randomly varied between 1,000 and 1,150 ms), the target circle turned green, providing a “GO” signal for movement onset. This delay period allowed the participants sufficient time to localize the target and starting positions and plan the appropriate movement. If the manipulandum was moved outside of a 1.875-cm diameter surrounding the center of the start position, prior to the appearance of the GO signal, then the trial reset, and the experimenter returned the manipulandum to the desired start position. The participants were instructed to move to the target as fast
and as accurately as possible at any time after the GO signal (green circle) appeared. Once the manipulandum was moved out of the start position, the yellow circle, depicting current hand position, disappeared; thus there was no online visual feedback of the participants’ movement trajectory to the target circle. Participants were instructed to stop when they felt that they reached the target. Once motionless for 500 ms, the yellow circle, depicting the manipulandum’s position, reappeared, providing end-point (EP) visual feedback of the manipulandum. This marked the termination of the trial, and the experimenter moved the manipulandum to the appropriate starting position for the next trial. To ensure that performance reflected ballistic arm movement as opposed to a target localization task, participants were next trial. To ensure that performance reflected ballistic arm movement (i.e., static state estimation), the dependent variables were instructed to complete each movement in less than 1,200 ms (excluding the 500-ms “hold” period at the conclusion of the movement). If movement duration exceeded this value, instructions prompting participants to speed up were provided on the computer monitor. If the movement were completed in less than 1,200 ms, the following strategies were used to maximize motivation and attention: 1) one of four potential “rewarding” sounds were played on an external laptop computer; 2) a picture depicting two children “high-living” appeared on the monitor; and 3) 100 performance points were awarded. Participants were instructed that the goal of the experiment was to obtain as many performance points as possible. Critically, in the V condition, participants could use visual (provided via the computer monitor) and proprioceptive feedback to estimate the static position of their hand prior to movement onset. The NV condition was similar to the V condition; however, there was no visual feedback of the manipulandum position prior to movement onset in the NV condition. Participants had to rely on the available proprioceptive feedback to estimate the static position of the arm.

Prior to the experimental protocol, participants completed 10 reaching movements (two/start position) with real-time visual feedback of the manipulandum position. These practice trials allowed the participants to become familiar with the experimental apparatus. The participants then completed one practice cycle of the V condition (10 trials; two/start position; pseudorandomly selected) and one practice cycle of the NV condition (10 trials; two/start position; pseudorandomly selected). After the completion of the practice phases, participants alternated between cycles of the V and NV conditions (three cycles each). The alternating blocked design controlled for potential order effects. Although a random sequence of the two conditions is ideal, our previous studies have indicated that this design is difficult for the youngest children to complete, and therefore, we used a blocked design. The experimental protocol consisted of 90 trials in total, including the 30 practice trials, and took ~20–35 min to complete.

Data analysis. Customized MATLAB (MathWorks, Natick, MA) scripts were used to mark movement onset and offset via an interactive algorithm. The time series of two-dimensional (x/y) spatial coordinates were dual-pass filtered with an eighth-order Butterworth filter (cutoff frequency = 10 Hz). Movement onset was the first sample in which the manipulandum reached 10% of its peak velocity (PV). Movement offset was the first sample in which the manipulandum was below 2.0 cm/s and remained below this threshold for 150 ms. Onset and offset for each trial were visually inspected and if necessary, manually re-marked.

As the primary difference between the two conditions was the availability of visual feedback of hand position prior to a goal-directed arm movement trajectory to the target circle, the dependent variables of interest were those that reflected movement planning. Data were statistically parameterized with the following linear regression

\[ Y = (b_0 + y_1 x) + ((b_1 + y_2 x) \cdot \text{(age)}) + e \]  

(1)

where \( Y \) = dependent measure (i.e., DE or Var DE); \( b_0, b_1, \) and \( y_1, y_2 \) = estimated fixed effects for the V condition; \( y_0, y_1 \) = adjustments to the \( b \) parameters for the NV condition; \( C = 1 \) if NV condition; 0 = otherwise; and \( e \) = residuals.

The parameter \( b_1 \) provides an assessment of the age-related changes (i.e., the slope) of the dependent variables (DE and Var DE) for the V condition, whereas \( y_1 \) assesses the difference in the age-related changes between the two conditions. With this parameterization, the sum of \( b_1 \) and \( y_1 \) is equal to the age-related changes for the NV condition. The parameterization in Eq. 1 is best suited to address the hypothesis that removing visual feedback of initial hand position differently impacts performance in the younger children compared with the older children (i.e., whether \( y_1 \) is significantly different from zero). A linear model compared with quadratic or single-exponential models was chosen, because it is parsimonious, offers clear and interpretable results, and provided the best fit of the data. The adult participants were not included in the regression analyses described above, because the assumption that the same age-related trend across 5–12-year-old children would continue throughout adolescence is not justified in the extant literature. Rather, their data were compared with the performance of the 11–12-year-olds using a 2 (group) \( \times \) 2 (experimental condition) ANOVA to determine whether the oldest children tested in the current study performed comparably with adults.

Experiment 2

Procedures. The second experiment sought to characterize the effect of age-related changes in dynamic state estimation, above and beyond the effects of static state estimation, on sensorimotor performance. Participants were asked to make discrete reaching movements from a single start circle (0.75 cm diameter) to one of five target positions (0.75 cm diameter) located 15 cm away from the body and start circle. The target circles were positioned 20°, 55°, 90°, 125°, and 160° with respect to the start circle. Prior to each trial, the participant positioned the robotic manipulandum in the start position, the locations of which were depicted on the computer monitor. The cursor diameter depicting the manipulandum’s position was 0.25 cm. Once the manipulandum was motionless in the start position for a duration, which varied randomly between 200 and 400 ms, a red target circle appeared. Participants were instructed not to initiate movement until both the target and start circles turned green, which occurred after the manipulandum remained motionless for an additional time period, varying randomly between 200 and 350 ms. (This hold period for Experiment 2 is less than that in Experiment 1, because participants did not need additional time to localize initial hand location, as they actively moved their hand to the starting position prior to each trial.) The color of start and target circles turned green as a GO signal for movement onset, and participants were instructed to move as soon as possible. If the manipulandum moved outside of the start position prior to the GO signal, the trial reset, and the participant returned the manipulandum to the start position. Once the participant exited the start position and moved toward the target circle, the visual feedback depicting current hand (e.g., manipulandum) position disappeared, effectively removing any online visual feedback of the participants’ movement trajectories. Participants were instructed to stop and hold still when they felt they reached the target circle. Once motionless for 500 ms, the yellow circle depicting the manipulandum’s position re-appeared, providing EP visual feedback of the participants’ movements. This marked the termination of the trial, and the participants returned to the start position for the next trial. Participants were instructed to complete each movement in between 300 and 1,200 ms (excluding the 500-ms hold period at the conclusion of the trial). If the movement was not completed in time, the same prompt as used in

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Experiment 1 appeared, informing participants to speed up. To maximize motivation and attention, the same rewarding stimuli as used in Experiment 1 were provided if the movement was completed within this time window.

The experiment contained two conditions: single- and double-step. The single-step condition was exactly as described in the preceding paragraph. A target appeared, and the participants executed a rapid arm movement toward the target following a GO signal. For the double-step condition (25% of the total number of trials; randomly inserted), the target circle “jumped” to one of the adjacent target locations at the time of movement onset. Participants were instructed to modify their movement trajectory as fast as possible to reach the displaced target.

Prior to the experimental protocol, participants completed 30 practice single-step trials; the first 15 provided real-time visual feedback of the manipulandum position during the reaching movement. These practice trials allowed the participants to become familiar with the experimental apparatus. Data from the practice trials were excluded from analysis. Participants subsequently completed 80 experimental trials; 20 randomly selected trials were the double-step condition. Participants were told a priori that the targets may switch positions and that they should attempt to hit the new target as fast as possible. The experimental protocol consisted of 110 trials in total, including the 30 practice trials, and took ~20–35 min to complete.

*Data analysis.* Initial data processing, including marking movement onset and offset, was identical to Experiment 1. Additionally, the time at which the participants generated a corrective movement to the displaced targets (double-step trials only) was marked as the local minima of the tangential velocity profile after PV of the movement toward the initial target (i.e., the first zero crossing of the acceleration profile after PV). This marking effectively separated the initial and corrective movements and was visually inspected and manually remarked if necessary.

The dependent variables for the single-step condition (and for the initial movements of the double-step trials) were DE, intraindividual Var DE, and reaction time (RT). DE and Var DE were computed as described for Experiment 1. RT was the duration between the GO stimulus and movement onset. Means for DE and Var DE and medians for RT were computed for each individual. RT medians, as opposed to means, were computed to minimize the influence of large, single-trial values, which can potentially be attributed to lapses in attention. Child data from the single-step condition and the movements to the initial targets in the double-step trials were statistically parameterized with the following age-based linear regression

$$Y = \beta_0 + (\beta_1 \cdot \text{age}) + \epsilon$$  

(2)

where \(Y\) = dependent measure; \(\beta_0, \beta_1\) = estimated fixed effects for the single-step condition; and \(\epsilon\) = residuals.

A statistical test of the \(\beta_1\) parameter assesses the magnitude of the age-related changes in DE, Var DE, and RT for the single-step condition and initial movements of the double-step trials. Similar to Experiment 1, a linear model was chosen, because it is parsimonious, offers clear and interpretable results, and provided the best fit of the data.

For the movements to the displaced targets in the double-step condition, the dependent variables were DE of the secondary movement (DE\(_{\text{DS}}\)), intraindividual variability of DE\(_{\text{DS}}\) (Var DE\(_{\text{DS}}\)), and time to correction (TTC; see Fig. 1 for a schematic of these measures). The time at which the participant initiated a corrective movement toward the displaced target was marked and herein referred to as COR. As described above, this point was defined as the local minima of the tangential velocity profile after PV of the movement toward the initial target. The variable TTC is the duration between the time at which the target is displaced and COR. DE\(_{\text{DS}}\) is computed as the difference (measured in degrees) between the participant’s corrective movement vector, defined as the vector between spatial coordinates at COR and PV of the secondary movement, and an ideal vector that
Var DE$_{\text{eqs}}$ are analyzed with a similar series of linear regressions; however, the first-level analyses consisted of DE and Var DE, respectively, as the independent variables. This approach allowed us to differentiate age-related changes in dynamic state estimation, as probed by the corrective movements to the displaced targets, from differences in both static state estimation and controller, as any differences in these underlying processes are also present in the analysis of the single-step trials (i.e., DE and Var DE). Similar to Experiment 1, adult participants were not included in the regression analyses. Their data were statistically compared with the performance of the 11- to 12-year-old children using two-sample $t$-tests to determine whether age-related improvements continue beyond the oldest children tested in the current study.

RESULTS

Experiment 1

No age-related differences in mean DE. Mean DE for the V and NV conditions were analyzed with Eq. 1. Neither the $\beta_1$ parameter nor the sum of the $\beta_1$ and $\gamma_1$ parameters was significant ($P > 0.05$), indicating that there were no age-related differences in mean DE within either of the conditions. (Note that the sum of $\beta_1$ and $\gamma_1$ is the age-based slope for the NV condition.) The $\lambda_1$ parameter, representative of the difference in the age-based slopes between the two conditions, was also not significant. These results suggest that the movement trajectories of the young children (e.g., 6–7 years) were as accurate, on average, as the trajectories of the old children (e.g., 11–12 years) for both the V and NV conditions. Similarly, results of the 2 (condition) $\times$ 2 (group) ANOVA revealed no significant differences between the 11- to 12-year-old children and the adult participants ($P > 0.05$).

Removal of visual feedback of initial hand position disproportionately affects the variability of reaching trajectories in young children. Individual variability of DE is depicted for the V and NV conditions in Fig. 2. Both the $\beta_1$ and the ($\beta_1 + \gamma_1$) parameters were statistically significant ($\beta_1 = -0.37, \text{SE} = 0.15, P = 0.02; \beta_1 + \gamma_1 = -0.80, \text{SE} = 0.19, P = 0.001$). This indicates that Var DE significantly decreased as a function of age in both experimental conditions. Moreover, the $\gamma_1$ parameter was also significant ($\gamma_1 = -0.43, \text{SE} = 0.19, P = 0.033$), demonstrating that the age-based slope for the NV condition was greater (in magnitude) than the age-based slope for the V condition (Fig. 2C). This finding indicates that removal of visual feedback of initial hand position disproportionately affected the variability of reaching movements in the younger children compared with the older children, suggesting that the less-precise proprioceptive feedback for static state estimation in the younger children results in decreased sensorimotor performance.

To determine whether the oldest children in our study performed comparably with adults, we conducted a 2 (condition) $\times$ 2 (group: 11–12 year olds/adults) ANOVA. The condition main effect was significant [$F_{(1, 15)} = 39.7, P < 0.001$]; however, the group main effect and the condition by group interaction were not. Although directional variability was larger in the NV condition for both groups, the lack of a significant group effect or interaction demonstrates that the directional variability of 11–12 year olds was similar to that of the adults.

Experiment 2

Average movement trajectories during single- and double-step trials for a group of young children ($n = 6$; mean age = 6.3 years), old children ($n = 6$; mean = 12.2 years), and adults ($n = 6$; mean = 20.5 years) are depicted in Fig. 3. The six adults were randomly selected from the full sample, whereas the young and older child groups consist of the six youngest and oldest child participants, respectively. During single-step trials, movement paths of the three groups were relatively straight. Although the young children appear to have increased movement variability, the mean performance of the three groups was relatively similar in the single-step condition.
Conversely, there appears to be substantial age-related improvements in performance in the double-step condition. The younger children were more variable and consistently “overshot” the displaced target position. The movements by the adults and to a lesser extent, the older children, were more accurate and consistent. Detailed statistical analyses of performance are included in the subsequent sections.

**Younger children moved at similar PVs as older children.** Since the purpose of this experiment was to examine age-related improvements in dynamic state estimation (i.e., during movement execution), it is critical to verify that there were no age-related differences in movement velocity across the child participants. Slower movement speeds may depend more on static- as opposed to dynamic state estimation. Age-related differences in the children were analyzed with Eq. 2. Importantly, there were no age-related differences in PV for the single-step and the initial movements of the double-step trials ($P > 0.05$). There were also no age-related differences in PV for the corrective movements in the double-step condition ($P > 0.05$). Last, results from two-sample t-tests revealed that the adult participants moved at similar speeds as the 11- to 12-year-old children for both the single-step trials and the corrective movements of the double-step trials ($P > 0.05$).

**Dynamic state estimation in younger children compared with older children and adults is delayed and unreliable.** There were no age-related differences in DE ($P > 0.05$) for the single-step and the initial movements of the double-step trials (Fig. 4A), indicating that on average, the trajectories of the 6–7 year olds were as accurate as the older children. This finding is consistent with the results from Experiment 1. Interestingly, there were significant age-related decreases in $D_{\text{EDS}}$ ($\beta_1 = -2.59, P = 0.038$); the older children were able to accurately modify their movement trajectory toward the displaced targets, whereas the younger children demonstrated large, positive errors (Fig. 4B). Positive $D_{\text{EDS}}$ values are indicative of an overshot of the displaced target positions (see movement trajectories of the young children in Fig. 3). This systematic overshot can be interpreted as relying on delayed sensory feedback to estimate hand state during movement execution. Specifically, the direction of the secondary movements in the younger children would be directed exactly, on average, toward the displaced target position, assuming the estimate of hand state prior to the corrective movement was actually an estimate at some time point in the past. The estimates of hand state at the time of correction appear to be based on prior positions rather than the actual current state in the younger children. Conversely, the direction of the secondary movements in the older children and adults was directed, on average, precisely toward the displaced target position (i.e., $D_{\text{EDS}} \sim 0$), suggesting that the hand state estimate prior to the corrective movement was accurate, despite the fact that the hand was moving toward the initial target position. In summary, the pattern of movement errors demonstrated by the children suggests that younger children relied on delayed sensory feedback for dynamic state estimation, whereas the older children and adults used an up-to-date estimate, presumably the result of state prediction. To ensure that the age-related differences in $D_{\text{EDS}}$ can be attributed to improvements in dynamic state estimation and not other underlying processes, such as static state estimation or the controller, we conducted the two-level linear regression analysis described above. The first level of analysis regressed DE on $D_{\text{EDS}}$, and the second level subsequently regressed age on the residuals of this first-level analysis. With this approach, errors, which are common across the two conditions—errors that can be attributed to the controller or static state estimation, for example—are effectively partitioned out. This leaves the movement-related errors, which are the result of underlying processes specific to the double-step condition (i.e., dynamic state estimation). The children exhibited a significant age-related decrease in $D_{\text{EDS}}$ residuals ($\beta_1 = -2.61, P = 0.029$), demonstrating that the improvements in $D_{\text{EDS}}$ can be attributed to improvements in dynamic state estimation. There were no significant differences between the 11- to 12-year-old children and the adults in DE or $D_{\text{EDS}}$ ($P > 0.05$), demonstrating that these older children were as accurate as the adults for both single- and double-step movements.

Directional variability was examined by computing the SD of each individual’s DE and $D_{\text{EDS}}$ scores (Fig. 5). Consistent with previous research, there were significant age-related differences in Var DE for the single-step and initial movement of the double-step trials ($\beta_1 = -0.35, P = 0.036$). Significant age-related decreases in Var $D_{\text{EDS}}$ ($\beta_1 = -1.45, P < 0.01$) were also revealed, indicating that the secondary movements to the displaced targets were less consistent in the younger children compared with the older children. This increased variability can be interpreted as a less-reliable dynamic state estimate prior to the corrective movement. To verify that the age-related decreases in Var $D_{\text{EDS}}$ can be attributed to dynamic state estimation, as opposed to other underlying processes, we again conducted the two-level linear regression; the first level partitioned out Var DE from Var $D_{\text{EDS}}$, and the second level regressed the residuals from the first level, with age as the independent factor. The age-related decrease in the Var $D_{\text{EDS}}$ residuals was significant ($\beta_1 = -1.18, P = 0.015$), providing evidence for greater variability in dynamic state estimation in the younger children (i.e., 6–7 years). The 11- to 12-year-old children were significantly more variable than the adults in their movements to the initial targets, as indicated by larger Var DE ($t = 2.17, P = 0.042$). However, there were no significant differences between the older children and the adults in Var $D_{\text{EDS}}$ ($P > 0.05$), suggesting that these older

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Fig. 4. **Experiment 2**: DE. Mean DE (A), $D_{\text{EDS}}$ (DS DE; B), and $D_{\text{EDS}}$ Resids (C; residuals based on linear regression with DE as a predictor) are depicted as a function of age. Dotted lines represent 95% prediction intervals. Mean values for the adults are shown in the bar graphs to the right.
children were as consistent as the adults in the corrective movements to the displaced targets.

**Age-related differences in the TTC to the target perturbation are accounted for by differences in RT.** Age-related differences in median RT for the single-step trials and the initial movements of the double-step trials are depicted in Fig. 6A. The slope of this age-based regression was significant ($\beta = -15.50, P < 0.001$), indicating that RT decreased as a function of age in the child participants. Age-related decreases in median TTC (Fig. 6B) for the double-step trials were also significant ($\beta = -17.8, P < 0.01$). This suggests that older children (i.e., 11–12 years) compared with younger children (i.e., 6–7 years) responded faster to the displaced target position. To determine whether these age-related differences in TTC can be attributed to delays in dynamic state estimation, as opposed to age-related processing delays, which are independent of dynamic state estimation, we conducted the two-level linear regression. The slope of the age-based regression on residuals based on linear regression with RT as a predictor (Fig. 6C) was not significant ($\beta = -6.03, P = 0.24$), suggesting that the age-related differences in TTC can be explained by age-related processing delays. To determine differences between the oldest group of children (11–12 years) and the adult participants, we conducted two-sample t-tests on both median RT and TTC. Median RT of the adults was substantially faster than that of the 11- to 12-year-old children ($t = 2.72, P = 0.013$), indicating that age-related reductions in RT persist through adolescence. Median TTC was not statistically different among the adults and 11- to 12-year-old children ($P > 0.05$), demonstrating that the older children responded to the target perturbation as fast as the adults.

**Summary.** The results from Experiment 2 demonstrated significant age-related differences across 6- to 12-year-old children in both directional error (DE$_{DS}$) and variability (Var DE$_{DS}$) in a double-step reaching task. Since both of these measures depend on the accurate localization of the hand during movement execution, these results suggest that dynamic state estimation is a rate limiter in the development of sensorimotor control of the arm. Importantly, these differences were above and beyond the influence of static state estimation and the controller, as any differences in these underlying processes were also present in the single-step trials and the initial movements of the double-step trials. Moreover, the older children performed almost identically to the adults, suggesting that dynamic state estimation is adult like by 11–12 years.

**DISCUSSION**

The current research examined the effects of static and dynamic hand state estimation on sensorimotor performance in 6- to 12-year-old children. Our results revealed two key findings: 1) young children (i.e., ~6–8 years) have less precise proprioceptive feedback for static state estimation compared with older children (i.e., ~10–12 years), resulting in increased movement trajectory variability; and 2) young children compared with older children rely on delayed and unreliable state estimates during the execution of ballistic, goal-directed arm movements, resulting in increased movement errors and directional variability. Collectively, these results suggest that age-related improvements in static and dynamic state estimation may, in part, account for age-related improvements in sensorimotor performance.

**Poor proprioceptive functioning for localization of initial hand position in the younger children increases directional variability of reaching movements.** Results from Experiment 1 revealed that the age-related improvements in directional variability in the NV condition were significantly different from the age-related improvements in the V condition (i.e., significant $\gamma_1$ parameter in Eq. 1). The critical difference between the two conditions was that the NV condition required participants to use proprioceptive feedback to localize the initial static hand position, whereas participants could use vision and proprioception in the V condition. Thus the difference in the age-related improvements between the two conditions can be explained by improved proprioceptive functioning for static hand localization in the older children. This interpretation is consistent with

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2 To verify that the results presented in the main text were not due to analyzing median values, we also computed mean RT and TTC values. Analyses of the means were consistent with those of the medians.
previous research (Contreras-Vidal 2006; King et al. 2010; Pickett and Konczak 2009; Visser and Geuze 2000). Linear improvements in proprioceptive acuity have been reported across 5- to 12-year-old children (e.g., Visser and Geuze 2000). These improvements in proprioceptive functioning influence multisensory-motor integration (King et al. 2010) and static state estimation for hand localization, as demonstrated in the current study. Importantly, the differences in the age-related improvements between the two conditions in the current research cannot be explained by age-related improvements in other processes involved in goal-directed reaching movements, such as the controller. The function of the controller is to transform desired movement trajectories into the appropriate motor commands. However, in Experiment 1, any influence of the controller remained constant across the two experimental conditions.

Significant age-related decreases in directional variability in the V condition, when both visual and proprioceptive estimates of hand position were available, were also revealed in Experiment 1. Assuming static visual acuity is developed prior to the ages investigated in this study (Ellenberger et al. 1999; Leat et al. 2009; Nelson et al. 1984), decreases in movement variability in the V condition cannot be attributed to improvements in visual functioning for static state estimation. Interestingly, research by Sober and Sabes (2003) suggests that when both the visual and proprioceptive systems provide estimates of hand position, vision contributes more to the state estimate when computing the spatial difference vector between current and desired positions, whereas proprioception contributes more to the state estimate when the difference vector is transformed into the appropriate joint-based motor commands. In the context of the current study, age-related improvements in proprioceptive functioning for hand localization may also explain the age-related decreases in directional variability, even when visual information of hand position was provided, a result demonstrated in the current study and in previous research (Contreras-Vidal et al. 2005; King et al. 2009; Pangelinan et al. 2011).

Online movement corrections in younger children are dependent on delayed and unreliable state estimates. The primary finding from Experiment 2 was that older children (~10–12 years) and adults compared with the younger children (~6–8 years) were more accurate and less variable in their corrective movements to displaced targets. The pattern of errors demonstrated by the younger children suggests that their corrective movements were based on delayed and unreliable state estimates. These age-related improvements in performance can be attributed to improvements in dynamic state estimation, which are above and beyond the effects of static state estimation and the controller. The influence of static state estimation and the controller was consistent across reaches to both the initial and the displaced targets. By using two-level linear regressions, we differentiated age-related improvements between the two conditions in the current study. Importantly, the differences in the age-related improvements between the two conditions in the current research cannot be explained by age-related improvements in other processes involved in goal-directed reaching movements, such as the controller. The function of the controller is to transform desired movement trajectories into the appropriate motor commands. However, in Experiment 1, any influence of the controller remained constant across the two experimental conditions.

The age-related improvements in dynamic state estimation demonstrated in the current research may potentially be attributed to developmental changes in the underlying neural substrates. Optimal dynamic state estimation is thought to be the result of combining state predictions with delayed sensory feedback (Gritsenko et al. 2009; Izawa and Shadmehr 2008; Wolpert et al. 1995), a process that is dependent on the posterior parietal cortex and cerebellum (Bastian 2006; Miall et al. 2007; Miall and King 2008; Shadmehr and Krakauer 2008). Previous research has demonstrated structural changes in both the parietal cortex and cerebellum across the age range examined in the current study (Giedd et al. 1999; Tiemeier et al. 2010). Future studies should attempt to reveal the relationship among these structural changes, changes in the function of the brain regions, and age-related improvements in state estimation and sensorimotor performance.

Age-related decreases in the time to initiate corrective movements. Results from Experiment 2 demonstrated that the dependent variable TTC, defined as the duration between target displacement and the initiation of the corresponding corrective movement, significantly decreased as a function of age across childhood. However, this finding can be explained by age-related improvements in RT and is not specific to online trajectory modifications. Specifically, after RT was partialled out, the age-related decreases in the time it takes to initiate a corrective movement during movement execution were not significant. The assessment of RT, in the context of the current study, provided an estimate of the time it took to detect the GO signal and send the preselected motor commands to the appropriate muscles (i.e., a simple RT paradigm). Conversely, the assessment of TTC provided an estimate of the time it took to detect the target jump; select or compute the appropriate motor commands, which will move the hand to the new target position; and send these commands to the periphery. The critical distinction is that the movements to the initial target were cued, and the participants had a hold period lasting over 1,000 ms to plan the movement. Conversely, in the double-step condition, participants did not know if or where the target was going to jump and had to compute the appropriate motor commands once they detected the target jump. The results of the two-level linear regression suggest that the time it took to complete this additional processing step (e.g., computation of the appropriate commands) did not significantly change as a function of age.

Age-related improvements in sensorimotor performance. Although several explanations of the age-related improvements in performance have been posited in the developmental literature, two of the most pervasive are: 1) improvements in sensorimotor performance are the result of changes in the underlying control mechanisms (i.e., feedforward vs. feedback) used by children (Bard et al. 1990; Hay 1978, 1979; Hay et al. 1991); and 2) improvements in sensorimotor performance are the result of the fine-tuning of acquired, internal representations, which specify the relationships between (sensory) input and (motor) output (Bo et al. 2006; Contreras-Vidal et al. 2005; Jansen-Osmann et al. 2002). We propose that our interpretation of the results in the research described here, namely that state estimation underlies the development of sensorimotor control, expands on previous conceptualizations and offers a more comprehensive and unifying explanation of the age-related improvements reported in the extant literature. Specifically,
age-related improvements in proprioceptive functioning result in more precise estimates of static hand position. Moreover, the ability to predict future hand states improves as a function of age. These improvements in static and dynamic state estimation, in turn, contribute to age-related improvements in functional sensorimotor behavior. Collectively, it is suggested that the development of proprioceptive functioning and the ability to predict future hand states based on descending motor commands are rate limiters in the development of sensorimotor control of the arm.

Research by Hay and colleagues (Bard et al. 1990; Hay 1978, 1979; Hay et al. 1991) suggested that the improvements in sensorimotor behavior across school-age children can be explained by changes in the contributions of feedforward and feedback control. Specifically, the execution of reaching movements by 7- to 8-year-old children was considered to be feedback dependent. Conversely, the performance of younger children (i.e., 5–6 years) was thought to be feedforward dependent, and the performance of older children (i.e., ~10–12 years) was thought to be a combination of the two strategies. We suggest that the results of our research provide a comprehensive and mechanistic explanation for Hay and colleagues’ results (Bard et al. 1990; Hay 1978, 1979; Hay et al. 1991). For example, the 7- to 8-year-old children, who Hay and others would identify as feedback dependent (Bard et al. 1990; Hay 1978, 1979; Hay et al. 1991), are classified as such, because these children are incorporating the more-reliable and accurate proprioceptive feedback compared with the 5–6 year olds into the planning and execution of goal-directed arm movements. The improved functioning of proprioceptive feedback at ~7–8 years of age results in an increased use of feedback-dependent control. Conversely, the 10- to 12-year-old children can accurately and reliably predict future states of the system, rather than relying solely on delayed sensory feedback. The ability to predict future states of the arm suggests the presence of a forward model, as the delays in sensory processing are effectively circumvented. Whereas Hay and colleagues (Bard et al. 1990; Hay 1978, 1979; Hay et al. 1991) characterized age-related changes in the underlying control strategies, our results suggest that these changes can be explained by the development of state estimation, specifically, proprioceptive functioning and state prediction.

It has also been posited that the progressive fine-tuning of acquired inverse internal representations across childhood contributes to the age-related improvements in sensorimotor performance (Bo et al. 2006; Contreras-Vidal et al. 2005; Jansen-Osmann et al. 2002; King et al. 2009). (Inverse internal representations can be considered a specific type of controller or control policy.) These inverse internal representations approximate the motor commands necessary to achieve a task, given the current state of the system and the desired future states (Shadmehr and Wise 2005; Wolpert and Kawato 1998). This explanation is consistent with the findings in the current research. A comparison of sensory feedback and predicted sensory consequences generated by the forward model is thought to serve as an error signal that drives motor learning (Davidson and Wolpert 2005). Sensory prediction errors have been shown to be critical for updating inverse internal representations to adapt to externally imposed manipulations (Tseng et al. 2007). Although the results of this study cannot be attributed solely to the inverse internal representation or controller, it is possible that the development of the predictive forward model may actually drive the age-related improvements in the fine-tuning of the inverse internal representations reported in previous research.

**Age-related, not age-determined, improvements.** It should be emphasized that the improvements in state estimation and sensorimotor performance, demonstrated in the current study, are age related, not age determined. We simply used age as a proxy to represent developmental processes. Despite the significant findings, an examination of our results reveals substantial interindividual variability, which is not accounted for by age (i.e., many 7- to 8-year-old children performed better than 9–10 year olds). The improvements reported in this research are likely to be a function of the task-specific experiences specific to each individual and are not the result of maturational processes, which simply unfold as a function of age. Future research should examine what specific experiences are considered sufficient to drive age-related changes in state estimation and sensorimotor behavior.

**Conclusion**

The experiments in the current research demonstrated age-related improvements in sensorimotor performance in two goal-directed reaching tasks. Based on the experimental designs and the statistical analyses used, these improvements in performance are attributed to improvements in static and dynamic state estimation. We suggest that age-related improvements in state estimation are responsible, at least partially, for the age-related improvements in sensorimotor control of reaching, frequently reported in the extant literature. Future research should investigate the development of the neural structures underlying static and dynamic state estimation and the influence of these developmental processes on sensorimotor behavior.

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**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**AUTHOR CONTRIBUTIONS**


**REFERENCES**


