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Title

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Journal

Journal of Neurophysiology, 90(2)

ISSN

0022-3077

Authors

Takahashi, Craig D

Nemet, Dan

Rose-Gottron, Christie M

et al.

Publication Date

2003-08-01

DOI

10.1152/jn.01173.2002

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Peer reviewed

Neuromotor Noise Limits Motor Performance, But Not Motor Adaptation, in Children

Craig D. Takahashi,¹ Dan Nemet,² Christie M. Rose-Gottron,² Jennifer K. Larson,² Dan M. Cooper,² and David J. Reinkensmeyer¹

¹Department of Mechanical and Aerospace Engineering and Center for Biomedical Engineering, University of California, Irvine, 92697-3975; and ²Center for the Study of Health Effects of Exercise in Children and University of California, Children's Hospital, Irvine, California 92868-3201

Submitted 27 December 2002; accepted in final form 12 May 2003

Takahashi, Craig D., Dan Nemet, Christie M. Rose-Gottron, Jennifer K. Larson, Dan M. Cooper, and David J. Reinkensmeyer.

Neuromotor noise limits motor performance, but not motor adaptation, in children. *J Neurophysiol* 90: 703–711, 2003; 10.1152/jn.01173.2002. Children do not typically appear to move with the same skill and dexterity as adults, although they can still improve their motor performance in specific tasks with practice. One possible explanation is that their motor performance is limited by an inherently higher level of movement variability, but that their motor adaptive ability is robust to this variability. To test this hypothesis, we examined motor adaptation of 43 children (ages 6–17) and 12 adults as they reached while holding the tip of a lightweight robot. The robot applied either a predictable, velocity-dependent field (the “mean field”) or a similar field that incorporated stochastic variation (the “noise field”), thereby further enhancing the variability of the subjects' movements. We found that children exhibited greater initial trial-to-trial variability in their unperturbed movements but were still able to adapt comparably to adults in both the mean and noise fields. Furthermore, the youngest children (ages 6–8) were able to reduce their variability with practice to levels comparable to the remaining children groups although not as low as adults. These results indicate that children as young as age 6 possess adult-like neural systems for motor adaptation and internal model formation that allow them to adapt to novel dynamic environments as well as adults on average despite increased neuromotor or environmental noise. Performance after adaptation is still more variable than adults, however, indicating that movement inconsistency, not motor adaptation inability, ultimately limits motor performance by children and may thus account for their appearance of incoordination and more frequent motor accidents (e.g., spilling, tripping). The results of this study also suggest that movement variability in young children may arise from two sources—a relatively constant, intrinsic source related to fundamental physiological constraints of the developing motor system and a more rapidly modifiable source that is modulated depending on the current motor context.

INTRODUCTION

Children are generally less proficient at movement tasks compared with adults. For example, children show greater movement variability during a variety of motor tasks such as prehension (Kuhtz-Buschbeck et al. 1998), elbow flexion (Jansen-Osmann et al. 2002), and rapid goal-directed planar

arm movements (Yan et al. 2000). During bi-manual unloading tasks, children exhibit less refined timing and more often utilize muscle co-contraction strategies compared with adults (Schmitz et al. 2002).

Skillful movement requires the ability of the motor control system to adapt to a variety of external dynamic environments. Numerous studies have indicated that the adult human nervous system uses “internal models”—feedforward neural mappings between limb state and muscle force—to adapt to altered dynamic environments (e.g., Brashers-Krug et al. 1996; Scheidt et al. 2001; Shadmehr and Holcomb 1997; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 2000). Similarly, children as young as six were recently shown to implement internal models of motor-applied viscous force fields during 1 df elbow flexion movements (Jansen-Osmann et al. 2002). This finding suggests that children use feedforward, adaptive control strategies like adults and that these strategies are robust to the increased internal neuromotor noise that is present in the developing nervous system. It was also recently shown that adults are able to adapt and compensate for the approximate mean of a noisy robot-applied force field by using a dual strategy of internal model formation and impedance control (Takahashi et al. 2001), indicating that mature adaptive control systems are robust to environmental noise that more than doubles their movement variability. If the developing motor controller utilizes the same adaptive mechanisms as the adult controller, it would be expected that motor adaptation in children should also be robust to environmental noise as well as internal neuromotor noise, although performance may still ultimately be limited by neuromotor noise. The purpose of this study was to test this hypothesis by comparing the motor performance of children and adults before and after they adapted to variable force fields applied by a robot that more than doubled their movement variability.

METHODS

Forty-three children (ages 6–17) and 12 adults participated in the study, which was approved by the University of California Irvine Institutional Review Board. The age and gender distribution of the subjects is shown in Table 1. Subjects and their parents or legal

Address for reprint requests: D. J. Reinkensmeyer, Dept. of Mechanical and Aerospace Engineering, 4200 Engineering Gateway, University of California, Irvine 92697-3975 (E-mail: dreinken@uci.edu).

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TABLE 1. Key variables by subject age group

Variable	Ages			
	6–8	9–12	13–17	>17
Subject quantities	17 (10 M, 7 F)	13 (5 M, 8 F)	13 (7 M, 6 F)	12 (6 M, 6 F)
Noise field gain values	0.98 ± 0.47	0.98 ± 0.49	0.95 ± 0.45	0.97 ± 0.48
Subject strength, N	56.7 ± 17.2	107.0 ± 30.0	209.0 ± 66.6	257.3 ± 135.3
Peak speed, cm/s	56.9 ± 12.4	80.3 ± 16.8	93.2 ± 20.4	82.7 ± 15.5
Peak field force/subject strength, %	3.6 ± 1.2	2.8 ± 0.9	1.6 ± 0.4	1.5 ± 0.7
Direct effect magnitude, cm	2.94 ± 1.6	3.14 ± 0.7	2.67 ± 0.5	2.44 ± 0.4
Maximum lateral deviation, cm	3.93 ± 2.78	5.38 ± 1.5	3.67 ± 2.6	3.87 ± 1.3

Values are means ± SD. M, male; F, female.

guardians provided written informed consent. Subjects included in the study had no known neuromuscular impairments.

Protocol

The seated subject held the end effector of a 3 df lightweight robot arm (PHANTOM 3.0, SensAble Technologies) with the dominant hand (Fig. 1A). Each subject started with the reaching hand resting on the lap. A computer-controlled light-emitting diode (LED) prompted the subject to raise the hand to a physical “start” target—the tip of a small compliant plastic pointer—positioned two hand widths out from the center of the sternum. After attaining the start target, the computer sounded a tone, prompting the subject to reach out to a similar “finish” target, positioned just inside the boundary of the reaching workspace and aligned with the start target in the anterior direction (i.e., in front of the subject). After the subject attained the finish target, the computer sounded another tone, prompting the subject to return the hand to the lap, where the subject was allowed to rest for 1 s. After each movement the computer provided visual feedback on the reach speed (just right = desired reach time ±5%; too fast; or too slow). The desired reach time was determined from a test conducted at the beginning of the experiment in which the subject performed the same reaching exercise, only reaching as fast as possible to the finish target

(20 trials or reaches). To scale the experimental conditions to each subject’s “maximum” movement speed, the desired reach time was set to be 118% of the mean of the reach times of the fastest three trials in this test.

Subjects were exposed to five sequential dynamic environments, called “stages” (Fig. 1B). In the first stage (null field 1), the robot did not actively apply forces to the subject for 20 trials. Two distinct viscous curl force fields, a mean field and a noise field, were applied in separate trial blocks (stages 2 and 4) according to the equation

$$F = k \cdot b \times v \quad (1)$$

where k is a scalar gain, $b = [0 \ 3.65 \ 0]^T$ Ns/m is a three-element vector that points straight up vertically per reference frame (Fig. 1A) for right-handed subjects, v is a three-element vector representing the velocity of subject’s hand in space, and F (the force applied by the robot) is a three-element vector formed from the cross-product of b and v (and multiplied by k). The resulting force, applied only during the outward reach, was leftward (orthogonal to the plane spanned by b and v) for right-handed subjects, and rightward for left-handed subjects.

In the mean field (50 trials), the force was applied according to Eq. 1, where the gain was constant ($k = 1$) for each reach. The force in the

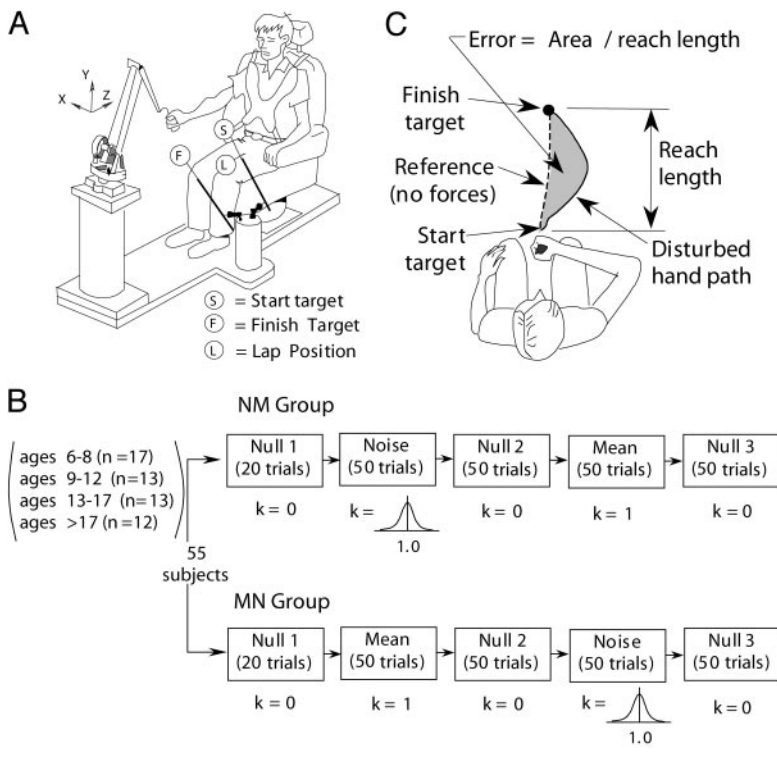


FIG. 1. Experimental design. A: subjects reached while attached to a lightweight robot arm. B: subjects were exposed to 5 sequential dynamic environments. Noise-then-mean (NM) subjects were exposed to the noise field in stage 2 and the mean field in stage 4, and vice versa for the mean-then-noise (MN) subjects. C: summary of experimental measures.

noise field (50 trials) was also applied according to Eq. 1, but the force gain varied across different trials randomly and unpredictably according to a normal distribution with a mean of 1.0 and a SD of 0.5. The gain values were truncated to ± 1.0 about the mean. In addition, the gain of the first trial of the noise field was always set at 1.0 to facilitate comparisons with the reaching error in the first trial of the mean field. The effect of the noise field was to apply a different magnitude of force for each reach, but the average magnitude over many reaches differed by no more than 5% across all subject groups (Table 1).

The order of presentation of the noise and mean fields was randomized across subjects. Noise-then-mean (NM) subjects ($n = 27$) were exposed to the noise field in stage 2 and then to the mean field in stage 4. The order was reversed for mean-then-noise (MN) subjects ($n = 28$). The subject quantities were balanced between the NM and MN subject groups to control for possible ordering effects (e.g., exposure to the noise field first might alter performance in the mean field or vice versa). Statistical comparison (paired 2-sided *t*-test) of the MN and NM subject performances found no significant ordering effects for a variety of key measures including variability in the force fields, final error in the field, modeled gain, direct effect magnitude, and aftereffect magnitude.

The third and fifth stages were null fields (50 trials each), for which the robot did not actively apply forces to the subject, allowing measurement of the aftereffect and providing a "washout" of the previous force field. Subjects were given 1-min rests after trials 45 and 145 to avoid fatigue. Note that because the applied force field was velocity dependent and because the desired reach time was scaled to each subject's maximum movement speed, the forces applied by the robot were also scaled to each subject's maximum movement speed. Thus smaller children, who moved more slowly, experienced smaller applied forces.

An estimate of strength for each subject was obtained by measuring the maximum isometric force generated in the vertical direction by each arm. The subject lifted the arm upward with as much force as possible with the forearm strapped to a six-axis force-torque transducer (Assurance Technologies, Theta Model) that was positioned so that the hand was ~ 10 cm out from the torso at the midline and 10 cm above the lap. The maximum voluntary strength was taken to be the maximum of two attempts (Table 1). Strength was evaluated in the vertical, rather than horizontal, direction because the hardware setup was simpler. Shoulder strength in the vertical and horizontal directions differs by $\sim 20\%$ in adult populations (Hughes et al. 1999). Strength was correlated with maximum movement speed ($R^2 = 0.54$, $P < 0.001$).

Data analysis

A computer sampled the three-dimensional position of the robot tip (and thus the subject's hand position) at 1,000 Hz as inferred from rotational sensors at the robot joints. Because the force field pushed the hand to the left or right, disturbances to the reaching trajectory were mainly in the horizontal plane. Statistical analysis indicated that trajectories were not significantly disturbed in the vertical direction on initial exposure to or removal of the field. Thus reaching errors were quantified as the area between the trial path and a reference path projected onto the horizontal plane (*X-Z* plane, Fig. 1A), divided by the distance between the start and finish targets (Fig. 1C). The resulting geometric measure of error is the spatial average lateral deviation away from the reference path and thus does not depend on reach length. For right-handed subjects, reach paths that were to the right of the reference path were given positive values, whereas those to the left were given negative values. The reference path was selected to be the average path of the trials in the last half of null field 1 (trials 11–20). The average was computed by aligning the path data to an initial velocity threshold (75 mm/s) and computing the mean across the corresponding sampling points. For these trials, the subjects had presumably acclimated to using the robot but still had no perturbing

force field applied to them. The averaged hand paths across subject groups during the different exposure stages (Fig. 2) were computed in the same fashion over the applicable range of trials and subjects.

Several kinematic measures of reaching were used to quantify the subject response to the force fields. The "direct effect" of a field was quantified as the reaching error in the first trial of that force field (trials 21 and 121). The "performance improvement" was quantified as the percent difference in the reaching error between the first reach in the field and the mean of the last 20 reaches in the field. The "aftereffect" was quantified as the reaching error in the first trial after a force field was removed (trials 71 and 171), normalized by the direct effect size of the same field to correct for inter-subject variation in arm impedance. A subject with greater arm impedance would be expected to exhibit a smaller direct effect as well as aftereffect (Takahashi et al. 2001). Normalizing by direct effect would therefore correct for inter-subject differences in arm endpoint impedance. Statistical analyses described throughout this paper were repeated using nonnormalized aftereffects and similar results were obtained. For all analyses, data points exceeding 1.5 SD away from the group mean were defined as outliers and were removed in a single iteration prior to statistical testing. The data analysis for the left-handed subjects was mirror-symmetric about the sagittal plane so that application of the field always produced a negative reaching error.

As subjects adapted to the force fields and de-adapted after removal of the force fields, they exhibited a gradual reduction in error with practice. The rate of adaptation and de-adaptation was determined by fitting a single exponential curve with a constant offset to the trial series error using a least squares fit by the Gauss-Jordan method

$$E(t) = ae^{-(t/\tau)} + b \quad (2)$$

where E is error, t is trial, and τ is the time constant of the fit exponential. Because the trial series errors of individual subjects were highly variable and typically not amenable to curve fitting, the curves were fit to the averaged trial series data within each age group, obtained by ensemble averaging the trial series data across subjects in the respective age group. The rate of adaptation was quantified as the "time constant" (τ) of the fit exponential.

Subjects adapted to the noise field with repetitive reaching practice.

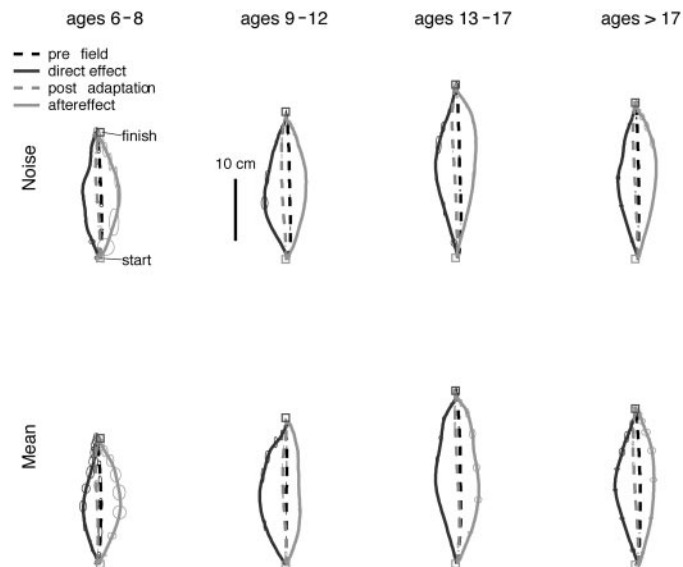


FIG. 2. Average hand paths before (prefield; i.e., trials 11–20), during (direct effect, trials 21 and 121; and postadaptation, last 20 trials in force fields), and after (aftereffect, trials 71 and 171) exposure to the noise (*top*) and mean (*bottom*) fields. The paths are ensemble averages across subjects within each age group (ages 6–8, ages 9–12, ages 13–17, and ages >17; each represented in 1 column). Ellipses show SD across subjects. Paths are shown from top view (see Fig. 1C for perspective).

One measure of adaptive ability in the noise field was the modeled gain. The modeled gains were quantified by linearly regressing reaching error and field gain (k) over the last 20 data points in the noise field. The modeled gain was quantified as the “zero crossing” of the regression line—that is, the field gain at which subjects minimized their reaching error (Scheidt et al. 2001; Takahashi et al. 2001).

The application of slightly different field strengths on each trial in the noise field allowed an estimate of limb impedance to be made (Takahashi et al. 2001). Specifically, impedance was quantified as the slope of the regression line of the spatial average lateral force magnitude and the spatial average lateral deviation from baseline (i.e., the reaching error) over the last 20 trials in the noise field. This slope indicated the relationship between the average displacement of the hand and the average displacing force and is equivalent to the stiffness of the limb if the limb behaves like a linear spring in the perturbation direction. We also calculated limb impedance by regressing time averaged force against time averaged lateral deviation and peak force against peak deviation. The calculated impedance values were similar for each technique.

For analysis purposes, children were grouped into three age categories: ages 6–8, ages 9–12, and ages 13–17 (Table 1). Adults were grouped as ages >17. Because the onset of puberty can vary between subjects, we also performed the data analysis with slightly redefined age groups (ages 6–8, ages 9–11, ages 12–17, and ages >17) and obtained similar results.

RESULTS

Both children and adults adapted to the mean and noise fields

The hand paths before, during, and after application of the noise and mean force fields were similar across groups (Fig. 2). The pattern of reaching errors, quantified as the spatial average of the lateral deviation, was also similar across age groups (Fig. 3). All age groups exhibited an increased reaching error (i.e., a

“direct effect”) when the forces were initially applied (trials 21 and 121), reduced their trajectory error with practice in the field, and exhibited a mirror-image trajectory error (i.e., an aftereffect) when the forces were unexpectedly removed (trials 71 and 171).

Statistical analysis of performance confirmed the use of internal models and motor adaptation with repetitive reaching practice in all age groups (Fig. 4). The initial, unexpected application of the first force field significantly perturbed all age groups away from baseline ($P < 0.001$, t -test, both the noise and mean fields, 1st direct effect). The direct effect magnitudes did not depend on the age grouping although there was a nearly significant trend for the direct effect to be smaller for adults (Fig. 4A, ANOVA linear contrast, $P = 0.09$). With repeated reaching practice, all age groups showed significant performance improvement (paired 1-sided t -test across subjects; $P < 0.001$, both fields) that did not depend on age grouping (Fig. 4B, ANOVA linear contrast; $P = 0.25$ noise field; $P = 0.26$ mean field). In addition, a linear regression of time constants of the ensemble averaged trial series error across age groups revealed that adaptive rates in the force fields (i.e., the rate of error reduction) also did not depend on age grouping (Fig. 4C; $R^2 = 0.44$, $P = 0.33$ noise field; $R^2 = 0.28$, $P = 0.47$ mean field). The performance improvements ultimately resulted in final error values (the average over the last 20 trials of each field) that did not depend on age grouping (Fig. 4D, ANOVA linear contrast, $P = 0.22$ noise field, $P = 0.30$ mean field). Finally, all age groups showed significant aftereffects away from baseline (t -test; $P \leq 0.001$, both fields) on removal of the force fields. However, the aftereffect magnitude did not depend on age grouping (Fig. 4E, ANOVA linear contrast, $P = 0.33$ noise field, $P = 0.63$ mean field).

Both children and adults formed a model of the approximate

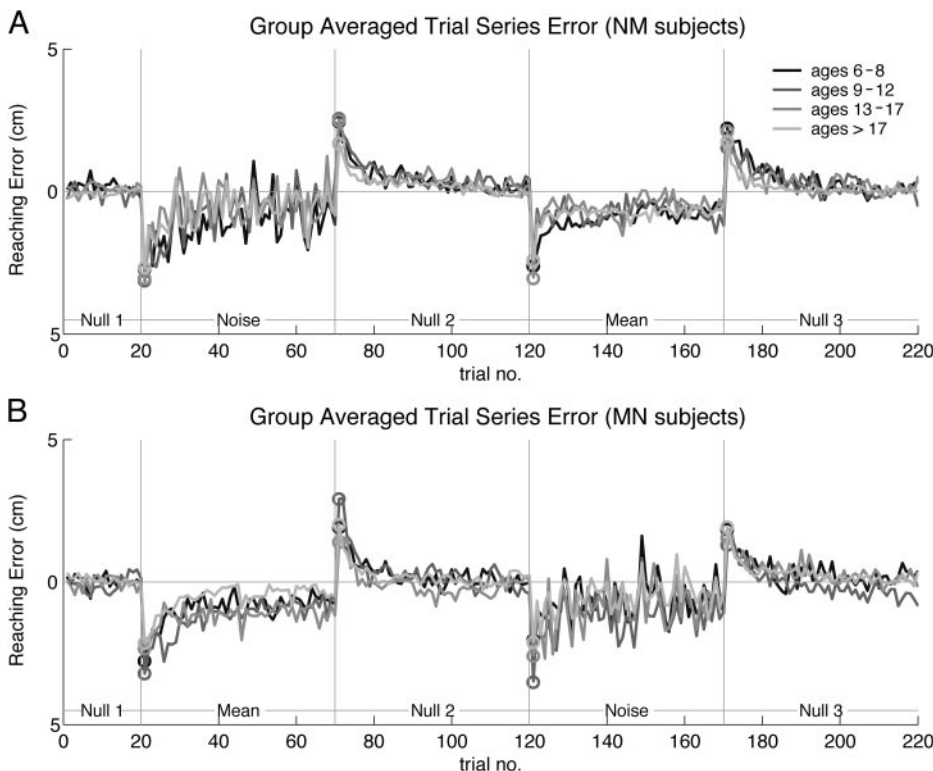


FIG. 3. Trial series reaching error. Each line is an ensemble average of data from each age group (ages 6–8, ages 9–12, ages 13–17, and ages >17). All age groups displayed large initial errors (direct effects) on unexpected exposure to the applied force fields on trials 21 and 121, followed by a re-acquisition of approximate pre-exposure performance. Unexpected removal of the field at trials 71 and 171 resulted in after-effects, which also decayed over time. A: NM subjects. B: MN subjects.

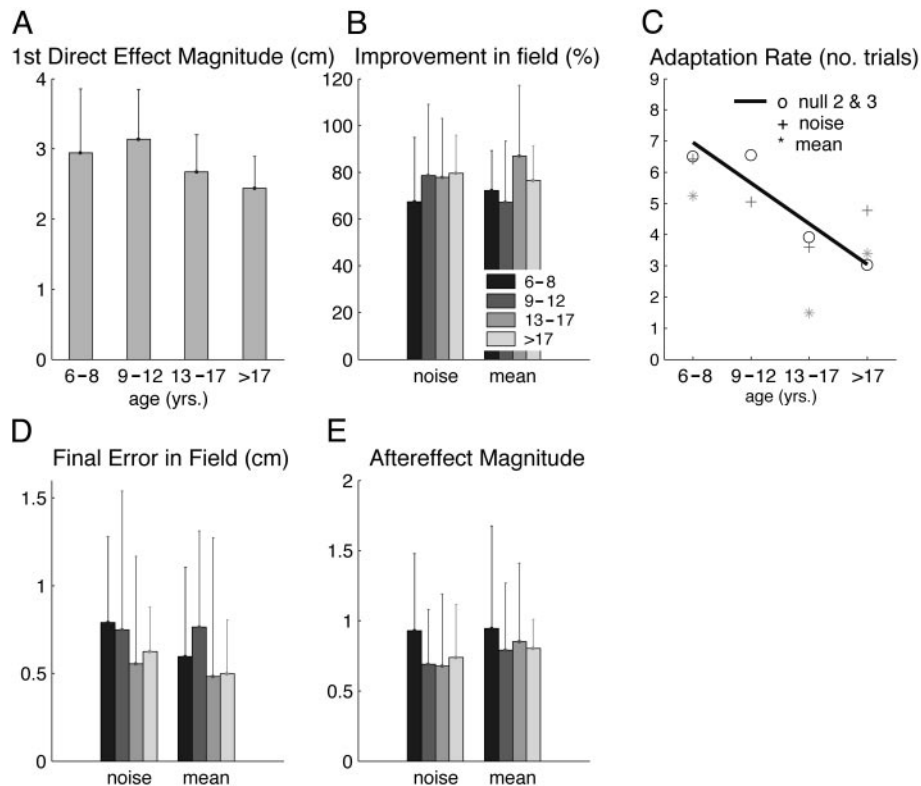


FIG. 4. Comparison of motor adaptation patterns. First direct effect magnitude (A) and performance improvement (B) in fields did not depend on age grouping. C: linear regression of adaptation rates in the force fields were not significant, but de-adaptation rates for combined data from fields 2 and 3 were significant ($R^2 = 0.90$, $P = 0.05$, —). D: error at end of field did not depend on age grouping. E: aftereffect magnitude also did not depend on age grouping. Error bars show SD across subjects.

mean of the noise field, with the mean modeled gain between 0.71 and 0.84 (Fig. 5A, t -test compared with 0, $P < 0.001$, for each age group). The modeled gain (i.e., the 0-crossing of the linear regression of error vs. field gain at the end of the noise field) did not depend on age grouping although there was a nearly significant trend for the modeled gain to be smaller for adults (ANOVA linear contrast, $P = 0.06$). Power (at the 0.05 level of significance for a type I error) was >0.80 for values of modeled gain <0.70 and >0.92 (all children groups).

Adults exhibited higher levels of estimated limb impedance (quantified as the slope of the linear regression of the average spatial force strength against reaching error) compared with children both at the beginning (i.e., the 1st trial) and end (i.e., over the last 20 trials) of the noise field (Fig. 5B; ANOVA linear contrast, $P < 0.001$). Only the ages 9–12 group showed significant increases in limb impedance at the end of the noise field compared with that at the beginning of the field (paired 1-sided t -test, $P = 0.001$). Impedance increases for the ages 13–17 group approached significance ($P = 0.08$). Aftereffect

size was not significantly smaller after noise field exposure compared with following mean field exposure (paired 1-sided t -test; $P = 0.34$, ages 6–8; $P = 0.14$, ages 9–12; $P = 0.33$, ages 13–17; $P = 0.13$, ages >17).

Children moved more slowly and exhibited greater movement variability than adults, although the youngest children reduced their variability with practice

Despite the ability of the children to adapt to the mean and noise fields like adults, several key differences in the children's motor performance were apparent. Children moved more slowly than adults as evidenced by a significant increase of reach time with decreasing age grouping (Fig. 6A, ANOVA linear contrast, $P < 0.001$). There was also a trend for children to de-adapt more slowly in the null fields than adults. A linear regression of the time constants of the ensemble averaged trial series error ("de-adaptation rates") across all age groups

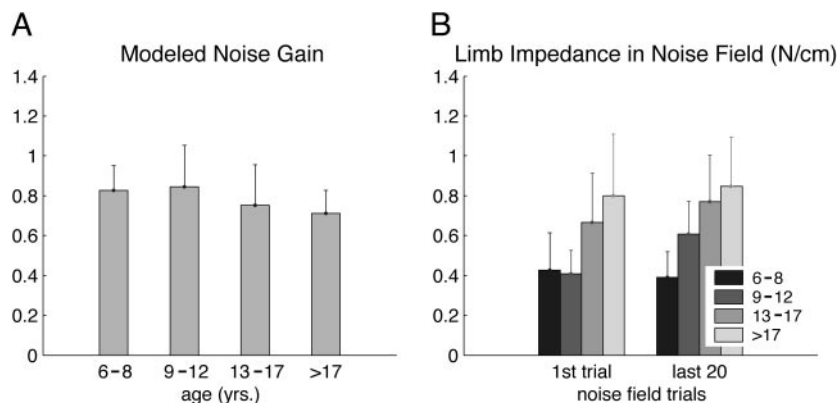


FIG. 5. Measures of adaptation to the noise field. A: modeled noise field gain did not depend on age grouping. B: limb impedance levels depended on age grouping both at the beginning and end of the field (ANOVA linear contrast, $P < 0.001$). Impedance levels did not generally show a significant increase except for the ages 9–12 group (paired 1-sided t -test, $P = 0.001$). The impedance increases for the ages 13–17 group approached significance ($P = 0.08$). Error bars show SD across subjects.

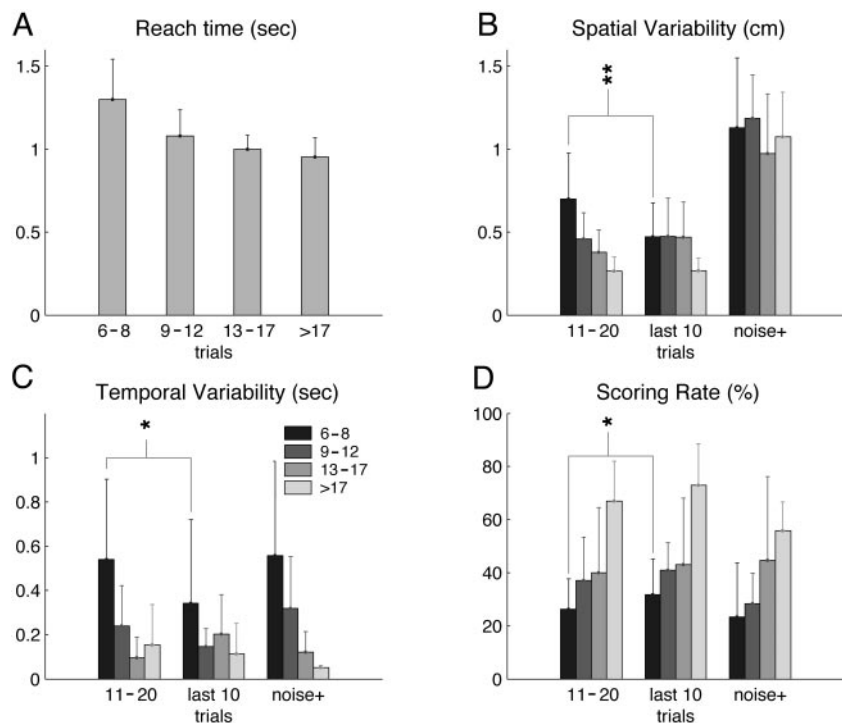


FIG. 6. Motor performance measures. *A*: reach time depended on age grouping (ANOVA linear contrast, $P < 0.001$). *B*: spatial variability depended on age grouping early in the experiment (mean over trials 11–20, ANOVA linear contrast over children groups, $P < 0.001$) but became independent of age grouping ($P = 0.99$) by the end of the experiment (i.e., last 10 trials). Children ages 6–8 significantly reduced their spatial variability (paired 1-sided t -test; ** $P < 0.01$) by the end of the experiment, but adults still maintained significantly lower levels compared with all other children groups (ANOVA planned comparison, $P = 0.002$). Spatial variability was significantly increased by the end of the noise field (“noise+” indicates last 10 trials of noise field) for all age groups (paired 1-sided t -test, $P < 0.001$ all age groups) to levels that did not depend on age grouping (ANOVA linear contrast, $P = 0.39$). *C*: temporal variability also depended on age grouping over trials 11–20 (ANOVA linear contrast over children groups, $P < 0.001$) but became independent of age grouping by the last 10 trials of experiment ($P = 0.38$). Children ages 6–8 significantly reduced their temporal variability (paired 1-sided t -test, * $P \leq 0.05$) by the end of the experiment. *D*: children ages 6–8 improved their timing score rate (percent “just right,” t -test, * $P \leq 0.05$) by the end of the experiment. Error bars show SD across subjects.

showed a significant linear trend (Fig. 4C, $R^2 = 0.90$, $P = 0.05$, null fields 2 and 3 combined).

Children also showed more initial trial-to-trial spatial and temporal variability (SD of reaching error and reach time, respectively, across trials) in their arm movements in the null field. There was a significant linear trend in spatial (Fig. 6B, ANOVA linear contrast across children groups and across all age groups, $P < 0.001$) and temporal (Fig. 6C, $P < 0.001$) movement variability with age grouping near the beginning of the experiment (i.e., the last half of null field 1, trials 11–20). The youngest children (ages 6–8) had significantly higher initial movement variability compared with the ages 9–12 group ($P < 0.001$ spatial, $P = 0.02$ temporal, Bonferroni-adjusted), the ages 13–17 group ($P < 0.001$ spatial, $P < 0.001$ temporal), and to adults ($P < 0.001$ spatial; $P = 0.001$ temporal). Consistent with this increased variability, children scored the desired movement time (total number of “just rights”) less often than adults (Fig. 6D, ANOVA linear contrast, $P < 0.001$).

Despite their more highly variable start, the youngest children (ages 6–8) were able to significantly reduce their trial-to-trial spatial (Fig. 6B, paired 1-sided t -test for ages 6–8, $P = 0.006$) and temporal (Fig. 6C, paired 1-sided t -test for ages 6–8, $P = 0.05$) variability by the end of the experiment (i.e., over the last 10 trials of null field 3). This reduction resulted in spatial variability levels that were not significantly different from the remaining children groups, although the adult group maintained significantly lower spatial variability compared with the children groups (ANOVA with a planned comparison, $P = 0.002$ spatial; $P = 0.14$ temporal). Furthermore, by the end of the experiment, there was no longer a significant linear trend in spatial (ANOVA linear contrast across all children groups, $P = 0.99$) and temporal (ANOVA linear contrast across all children groups, $P = 0.38$) variability with age grouping. Consistent with this decrease in variability, the

youngest children scored the desired movement time more frequently by the end of the experiment (Fig. 6D, paired one-sided t -test, $P = 0.03$).

DISCUSSION

Children showed similar patterns of adaptive behavior compared with adults in both the mean and noise fields. They exhibited direct effects when unexpectedly perturbed by the robot forces, reduced their trajectory error at comparable rates with practice in the force fields, and exhibited comparable aftereffects on unexpected removal of the forces. The children also formed a model of the approximate mean of the noise field that was comparable to that of the adults. They achieved this adaptive performance even though they moved with greater trial-to-trial variability both before and after motor adaptation. This greater motor variability apparently caused them to achieve the desired movement time less frequently than adults. These findings suggest that children as young as age 6 possess adult-like neural systems for forming internal models and that these neuro-adaptive systems are robust to variability associated with internal physiological constraints as well as additional variability imposed by the external dynamic environment. Performance after motor adaptation by children, however, ultimately remains limited by increased movement variability.

One caveat in interpreting these results is that the children were operating proportionally closer to their maximum strength during the force field perturbation because the magnitude of the field was scaled to movement speed rather than arm strength, and adults were only 1.5 times faster but 4.5 stronger than the youngest children (Table 1). However, it seems unlikely that this difference would affect adaptation ability since the peak forces applied to the youngest children were still $<4\%$ of their maximum shoulder strength (Table 1).

In addition, the given field strengths resulted in an initial kinematic perturbation to movement that was comparable between groups as measured by the area reaching error and the maximum lateral deviation of the direct effect (Fig. 2, Table 1). If kinematic error is the signal that drives adaptation (Goodbody and Wolpert 1998; Scheidt 1998; Scheidt et al. 2000), then the driving signal for adaptation was about the same magnitude across ages.

Another caveat is that the younger children may have exhibited greater relative movement variability in the force field due to the relatively greater force demand. Variability increases with applied force in isometric force generation in adults (Jones et al. 2002). However, this effect would be expected to be small since, as noted in the preceding text, the external forces applied to the youngest subjects were <4% of their maximum strength. Moreover, the children still exhibited greater variability even in the absence of the field, consistent with previous reports (Jansen-Osmann et al. 2002; Kuhtz-Buschbeck et al. 1998; Yan et al. 2000).

Adaptive control by children: formation of internal models and impedance control

The results of the present study are consistent with recent findings indicating that children ages 6–10 can form internal models during a bimanual load-lifting task (Schmitz et al. 2002) and during single degree-of-freedom elbow movements (Jansen-Osmann et al. 2002). During bi-manual unloading tasks, the adult neuromotor system forms anticipatory models of the effects of unloading while attempting to maintain forearm posture (Massion and Dufosse 1988; Massion et al. 1999) and exhibits aftereffects when the external forces are unexpectedly removed (Lum et al. 1992). Schmitz et al. (2002) found that children can also form such internal models, but they exhibit less refined timing and more often utilize muscle co-contraction strategies compared with adults. Studying viscous loading of single degree-of-freedom elbow movements, Jansen-Osmann et al. (2002) found age-related differences in aftereffect magnitude and longer de-adaptation rates in young children and concluded that children formed models, albeit less precisely—perhaps due to less precise tuning of dynamics parameters. In the present study, younger children had longer de-adaptation rates, consistent with results by Jansen-Osmann et al. (2002), but the aftereffect magnitude was comparable across all age groups. The apparent adult-like performance of the children's adaptive control systems in the present study may be due to differences in the type of movement practiced (i.e., free reaching in three space versus constrained, 1 df elbow flexion movements), or the type of perturbation applied (viscous curl field in gravity vs. viscous load in a gravity-eliminated environment or vs. self-imposed postural perturbation).

A simple computational process that is robust to noise may underlie both adult and child motor learning. Adults are able to learn to compensate for the approximate mean of substantially variable force fields (Scheidt et al. 2001; Takahashi et al. 2001). A linear adaptive parametric model, using information from only a limited number of previous practice trials, can account for the ability to achieve a sort of moving average (Scheidt et al. 2001). Preliminary analysis of the data from the present experiment indicates a similar computational process

can adequately model the performance of children (Takahashi et al. 2002).

Limb impedance, estimated from the differential trajectory errors produced by the noise field, increased with age. This age-dependent increase is likely accounted for by the relatively smaller forces experienced by the younger children compared with adults because muscle stiffness increases with muscle force (Hunter and Kearney 1982; Mirbagheri et al. 2000; Weiss et al. 1988; Zhang et al. 1998).

Limb impedance did not increase consistently across age groups in response to the environmental variability of the noise field. Consistent with this finding, aftereffects were not significantly smaller after exposure to the noise field compared with after exposure to the mean field (Fig. 4E). This is in contrast to previous studies that suggest that the nervous system manages variable or destabilizing dynamic environments not just by internal model formation but also by impedance control (Burdet et al. 2001; Milner 2002; Milner and Cloutier 1993; Takahashi et al. 2001; Wang et al. 2001). One possible explanation for the lack of a clear impedance control effect in the present study is related to the specific design of the reaching task. For instance, in a previous study conducted in this laboratory (Takahashi et al. 2001), adult subjects reached alternately to two targets from a resting position on a cantilever beam that extended across the lap and exhibited increased impedance and diminished aftereffects after exposure to a noise field. In the current study, subjects were required to locate a starting position before reaching out. The increased muscle activation necessary to raise the arm against gravity and stabilize the hand to accurately attain a relatively small point in space may have increased the limb impedance to levels high enough at the start of movement to mask or render unnecessary further impedance increases during the movement.

Sources and mutability of movement variability in children

The increased spatial and temporal variability in the movements of young children are consistent with the results of numerous studies on arm movement in children (e.g., Jansen-Osmann et al. 2002; Kuhtz-Buschbeck et al. 1998; Yan et al. 2000). There are two general ways that this increased movement variability might arise. First, it may reflect a fundamental physiological constraint in the capability of the developing nervous system. For instance, movement variability has been considered to be a manifestation of inherent noise in the neuromotor system (Fitts 1954; Schmidt et al. 1979), which may fundamentally constrain motor planning (Harris and Wolpert 1998). Such inherent noise may arise for example, from variability in single-neuron firing patterns, which may in turn be attributable to noise in membrane biophysical properties (Azouz and Gray 1999; Shadlen and Newsome 1998). Motor neuron recruitment mechanisms may also affect motor output variability (Jones et al. 2002).

The developmental constraints on such noise mechanisms are unclear. Structural maturation of motor tracts, including myelination and axon diameter changes, is an ongoing process through adolescence (Fietzek et al. 2000; Muller and Homberg 1992; Paus et al. 1999). Immaturity in neural transmission might increase motor variability by affecting the integrity of neural signals. Alternately, we recently performed simulations of a population-coding model of movement control that incor-

porates neural firing rate variability and summation of responses from broadly tuned neurons (Reinkensmeyer et al. 2003). These simulations indicate that trial-to-trial movement variability increases as the population size decreases because the magnitude of the population vector decreases more quickly than its SD for decreasing cell populations, provided physiological levels of firing rate noise (Lee et al. 1998) are present. Thus in a population-coding framework that incorporates firing-rate noise, a less-experienced nervous system with fewer directionally tuned cells would be expected to exhibit greater variability. A third possibility is that movement variability is greater because children have more difficulty attending to their movements. For instance, (Yan and Thomas 2002) demonstrated that children with attention deficit hyperactivity disorder exhibit more variable and slower movements compared with control subjects. However, the youngest children *decreased* their variability later in the experiment when presumably they would have more difficulty attending to the repetitive task. The work of Todorov and Jordan (2002) suggests that variability may increase if children have not learned how to optimally distribute variability in redundant dimensions. Identifying actual physiological constraint mechanisms in the developing nervous system is an important future direction.

Second, increased movement variability may reflect a systems-level process implemented by the developing nervous system for functional benefit (cf. Manoel Ede and Connolly 1995). For example, because the motor control system of a child must perform in the context of continuously changing system parameters (body mass, dimension, neural properties, etc.), it may have to constantly perform system-identification procedures to optimize its performance. System-identification techniques often involve obtaining a rich experience through a thorough investigation of the configuration space. Thus movement variability in children may be an intentional feature of such a functional optimization process. If so, the pediatric neuromotor controller may opt to reduce intentional noise when presented repeatedly with the same task, trading off system-identification processes for better performance.

The results of the present study are consistent with the combined presence of these two mechanisms. Young children (ages 6–8) quickly reduced their spatial and temporal variability with practice. This rapid reduction of variability with practice is consistent with a systems-level mode switching rather than alteration in a fundamental physiological constraint, which would not be expected to change appreciably over the short time period measured here. The physiological constraint mechanism would more likely express itself as age-related baseline variability that changes slowly through a developmental process. Consistent with this idea was the inability of children in the present study to reduce their variability to adult levels, even with practice.

Reduction of movement variability with practice has been observed before in adults during rapid aiming movements (Abrams and Pratt 1993; Darling and Cooke 1987; Gottlieb et al. 1988) and in rhesus monkeys during planar reaching (Georgopoulos et al. 1981). The adult subjects in the present study did not exhibit a reduction of movement variability during the adaptation portion of the experiment, possibly because the time frame considered was insufficiently long to observe this effect. The relatively greater reduction in movement variability in the youngest children in this study is consistent with the results of

Thomas et al. (2000), who observed a relatively greater increase in the duration of the primary submovement and corresponding decrease in jerk for children practicing a rapid aiming movement.

Implications and directions for future research

This study suggests or reinforces several key ideas for the understanding of motor control in the developing nervous system. First, regardless of the mechanisms, this study confirms that children's movement is inherently more variable than adults even after motor adaptation. Thus increased movement variability likely plays a key role in children's appearance of incoordination and more frequent motor accidents even at well-learned dynamic tasks (e.g., spilling, tripping). Increased movement variability likely also constrained the younger children to plan slower movements to consistently attain the target with a fixed accuracy requirement (Harris and Wolpert 1998). Second, the study confirms that the computational processes that support internal model formation are implemented by the nervous system early in development and thus likely support not only motor learning of new tasks at a young age but the continual control adjustments needed to compensate for the morphological growth associated with development. From this perspective, the effects of increasing limb size can be viewed as ongoing changes in the force field induced by limb mechanics; children as young as age 6 can compute the internal models needed to predictively compensate for this force field. Third, young children's ability to reduce movement variability more rapidly than other age groups provides a possible mechanism for the casual observation that they appear to improve more rapidly than other age groups in specific motor tasks. In particular, we hypothesize that they may appear to improve more rapidly not because they form internal models more accurately or quickly than adults, but because they more quickly reduce their movement variability after starting from a higher level of variability. Finally, the paradigm and measures developed in this study might ultimately prove useful in the clinical setting as a minimally invasive, relatively simple tool to aid in the diagnosis and treatment of children who have difficulty mastering motor tasks, for example, due to neurological disorders, or as a predictor of activity-related, orthopedic injuries that may be linked to increased motor variability.

DISCLOSURES

This work was funded by a University of California Irvine Multi-investigator Faculty Research Grant from the Council on Research, Computing and Library Resources grant and National Center for Research Resources Grant M01RR-00827.

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