

# Development of Force Adaptation During Childhood

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**ABSTRACT.** Humans learn to make reaching movements in novel dynamic environments by acquiring an internal motor model of their limb dynamics. Here, the authors investigated how 4- to 11-year-old children ( $N = 39$ ) and adults ( $N = 7$ ) adapted to changes in arm dynamics, and they examined whether those data support the view that the human brain acquires inverse dynamics models (IDM) during development. While external damping forces were applied, the children learned to perform goal-directed forearm flexion movements. After changes in damping, all children showed kinematic aftereffects indicative of a neural controller that still attempted to compensate the no longer existing damping force. With increasing age, the number of trials toward complete adaptation decreased. When damping was present, forearm paths were most perturbed and most variable in the youngest children but were improved in the older children. The findings indicate that the neural representations of limb dynamics are less precise in children and less stable in time than those of adults. Such controller instability might be a primary cause of the high kinematic variability observed in many motor tasks during childhood. Finally, the young children were not able to update those models at the same rate as the older children, who, in turn, adapted more slowly than adults. In conclusion, the ability to adapt to unknown forces is a developmental achievement. The present results are consistent with the view that the acquisition and modification of internal models of the limb dynamics form the basis of that adaptive process.

*Key words:* development, human, inverse dynamics models, motor adaptation, motor control, motor learning, reaching

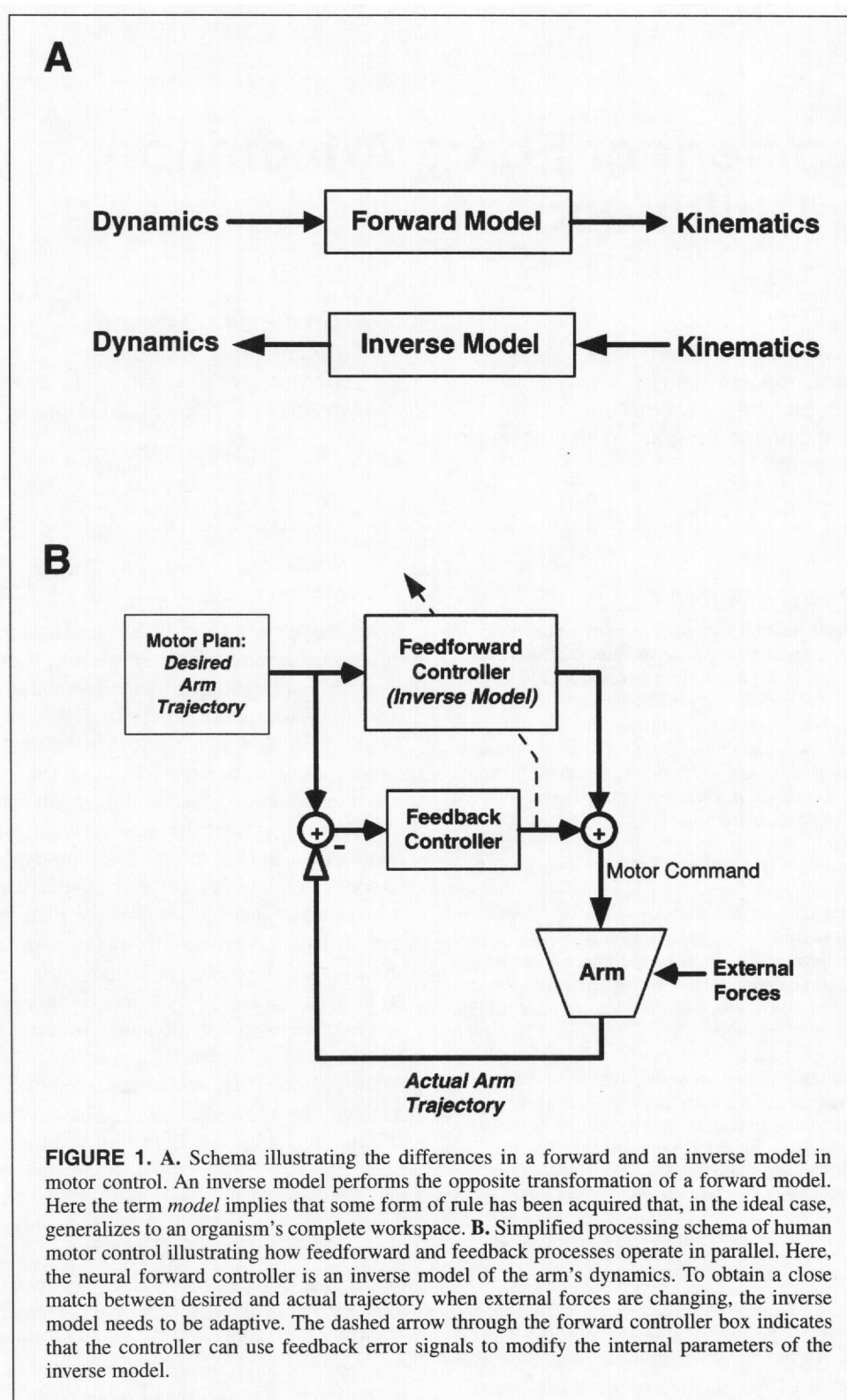
**A**dult humans learn to manipulate novel objects with relative ease. As the result of practice, those objects are moved along desired, preplanned trajectories. The trajectories remain surprisingly stereotypic for a wide range of movement speeds and amplitudes despite the complexity of the underlying limb dynamics (Atkeson, 1989). The results of recent research on goal-directed action in adult humans suggest that neural representations of the limb dynamics or kinematics, so-called internal motor models, form the basis of that control process. In general, two types of internal

motor models can be distinguished. Inverse models are part of a neural controller that transforms planned kinematic trajectories into appropriate patterns of muscular innervation (Jordan, Flash, & Arnon, 1994; Kalveram, 1992; Wolpert, Ghahramani, & Jordan, 1995). In forward models, efferent motor commands that specify limb dynamics are transformed into a set of joint kinematics. Possible functions of a forward model are to predict the sensory consequences of efferent motor commands or to estimate limb dynamics (Wolpert & Kawato, 1998). In simple terms, an inverse model transforms the kinematic data of a movement plan into the necessary limb dynamics, whereas a forward model performs the opposite transformation; that is, it computes the joint kinematics on the basis of a set of dynamics (Figure 1A).

Evidence for inverse dynamic models (IDMs) has come from studies in which human adults were exposed to an unknown force field while they attempted to execute goal-directed arm movements (e.g., Shadmehr & Mussa-Ivaldi, 1994). The adults' arm trajectories showed two characteristic features that were highly indicative of an underlying neural model. First, after removal of the applied force field, the arm trajectories revealed an overshoot in the opposite direction. Such aftereffects would be typical of an inverse model that compensates the arm's dynamics plus the no longer existing external force field. Second, after learning a specific force field, participants were able to perform accurate movements to targets that they had never visited. That is, they showed the ability to generalize. Such behavior cannot be found in systems that store an association between dynamics and visited space in a look-up table.

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**FIGURE 1.** A. Schema illustrating the differences in a forward and an inverse model in motor control. An inverse model performs the opposite transformation of a forward model. Here the term *model* implies that some form of rule has been acquired that, in the ideal case, generalizes to an organism's complete workspace. B. Simplified processing schema of human motor control illustrating how feedforward and feedback processes operate in parallel. Here, the neural forward controller is an inverse model of the arm's dynamics. To obtain a close match between desired and actual trajectory when external forces are changing, the inverse model needs to be adaptive. The dashed arrow through the forward controller box indicates that the controller can use feedback error signals to modify the internal parameters of the inverse model.

In recent years, several studies have expanded our knowledge of IDMs. The main results of those studies have indicated the following: First, IDMs are adaptable. They are gradually built with practice (Shadmehr & Mussa-Ivaldi, 1994). Second, they are not global models of the whole workspace but rather are confined to neighboring regions of

the experienced workspace (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996). Third, learning of one model interferes with the learning of another IDM (Shadmehr & Brasher-Krug, 1997). And fourth, early stages of learning are driven by a delayed error-feedback signal (Thoroughman & Shadmehr, 1999). From a control point of view, the ability of inverse

dynamics models to adapt to changes in limb dynamics implies that kinematic motor plans do not have to be modified (Figure 1B). Without that adaptive ability, the motor control system would have to revise motor plans as soon as the overall dynamics changed. Thus, adaptation through inverse dynamics models is appealing, because it does not require the motor system to extensively relearn previous skills after it is exposed to changes in limb dynamics. The motor system can recover those skills by superimposing onto the original command an additional motor command that cancels the newly produced environmental forces (Conditt, Gandolfo, & Mussa-Ivaldi, 1997). Recent findings support the view that movement adaptation is primarily driven by the motor system's propensity for keeping the plan invariant despite changes in dynamic demands (Scheidt, Reinkensmeyer, Conditt, Rhymer, & Mussa-Ivaldi, 2000).

Until now, the evidence for inverse dynamic models has come mainly from psychophysical and electrophysiological studies of human adults (Kawato, 1999). Given the increasing support for the existence of adaptable neural models of limb dynamics and given that those IDMs supposedly form the basis for movement coordination and purposeful behavior, the following question arises: How and when in ontogenesis are those internal models formed? In a previous study, Jansen-Osmann, Richter, Konczak, and Kalveram (2002) showed that force adaptation in 6- to 10-year-old children transfers to untrained regions of their workspace—a sign that children indeed acquire some form of an inverse model of their limb dynamics.

It was our purpose in this study to investigate how force adaptation develops during childhood and to examine whether those data provide further evidence for the existence of inverse dynamic models in humans. We investigated how children learned to compensate novel external forces during the execution of simple goal-directed forearm movements and whether they adapted with the same precision and at the same rate as adults. Specifically, we exposed individuals to two different velocity-dependent forces (opposing and assisting damping) during movement execution in order to determine whether variations in damping induced different, age-dependent times toward adaptation.

## Method

### Participants

Seven adults and 39 healthy children between the ages of 4 and 11 years participated in the study. The sample of children consisted of four 4-year-olds and 5 children at each subsequent age (5 to 11 years). Children were recruited through advertisements in a local newspaper. Before testing, parents gave their informed written consent and answered a questionnaire about the motor development of their child. According to the parental reports, none of the tested children had experienced abnormal or delayed motor development during infancy or early childhood. Ninety percent of the participants were dominantly right-handed. The remaining children were left-handed or ambidextrous. We

determined hand dominance through parental report and through a subset of items from the Edinburgh Handedness Inventory (Oldfield, 1971).

After an initial kinematic analysis of the unperturbed movements, we found that variability in angular position and velocity was largest in children between the ages of 4 to 7 years, decreased drastically between 7 and 8 years of age, and showed only slight decreases afterward. On the basis of that finding, we decided to group the children into two age groups, 4–7 and 8–11 years of age, for further statistical analysis.

### Apparatus

Participants sat in an adjustable chair, facing a concave screen about 1.5 m ahead of them. Their right forearms were inserted into an orthosis that was attached to a lever of a robot manipulandum that allowed only flexion–extension movements of the forearm in the horizontal plane (Figure 2A, B). We adjusted the size of the orthosis to each participant's arm anthropometrics to ensure a secure and tight fit. The torque motor received its input from an ELTEC 84/68 K computer (Elektronik AG, Mainz, Germany). Participants viewed two illuminated arrows on the concave screen. The goal arrow indicated the required or target position; a hand arrow specified the actual angular position of the forearm. In our setup, 0° angular position corresponded to 90° elbow flexion (see Figure 2A).

### Procedure

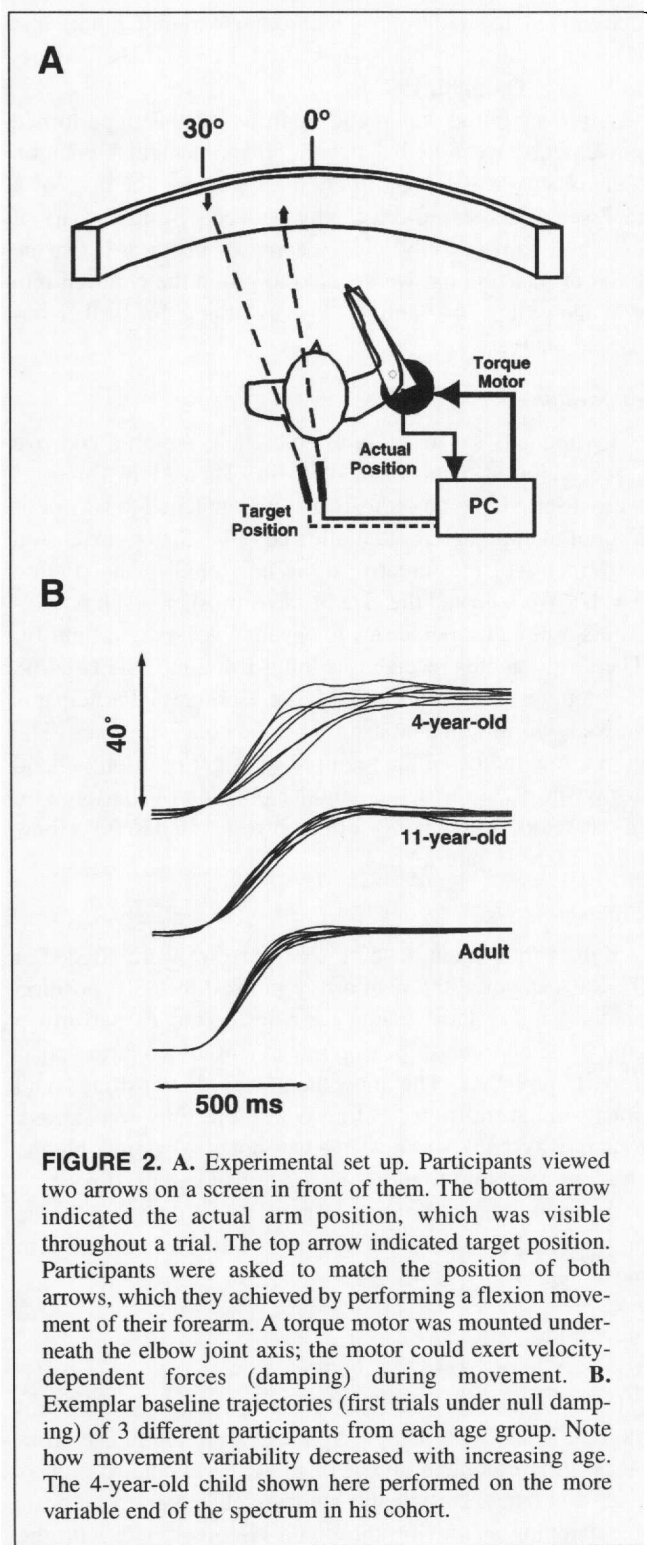
Before movement onset, the two arrows were aligned at 0°. Subsequently, the goal arrow jumped to a 30° position on the screen. Participants were instructed to perform a goal-directed forearm flexion movement to that target-position (Figure 2A). The movement was demonstrated and practiced several times before data collection was started. Reacting as quickly as possible was not emphasized, but the children were told to move accurately and at a fast pace.

A torque motor (Figure 2A) generated a damping torque proportional to the angular velocity of the participant's arm movement:

$$F_d = -\mathbf{B}\omega, \quad (1)$$

where  $\mathbf{B}$  is the damping coefficient and  $\omega$  is the angular velocity of the forearm. Positive damping opposed the arm motion. Trials with damping present were administered in blocks (the complete layout of the experimental design is discussed later). Participants subjectively experienced positive damping as moving through a viscous liquid, with the movements "getting harder" the faster they attempted to flex the arm. Negative damping assisted forearm flexion and was experienced as "if someone pushed the arm" in the direction of the intended movement.

We deliberately chose a velocity-dependent force and not a constant force as the external perturbation. Knowing that children's arm anthropometrics and inertia change with age, we felt that the application of a constant bias force was not



warranted. By selecting sufficiently small values of  $B$ , we ensured that the application of a movement velocity-dependent force would not subject the children to an external force that they could not possibly compensate. Using a force that was coupled to each child's own movement velocity implies that children could self-select the degree of the imposed perturbation. Throughout testing, the experi-

menter checked that the children did not deliberately make extra-slow arm movements but performed movements above their preferred, yet not excessive, speeds. Post hoc analysis revealed that the younger children had, on average, moved somewhat faster than their older peers, although given the large variability in the data, they were not significantly different from each other (young group, mean  $V_{max} = 136.5$  deg/s,  $SD = 28.6$  deg/s; older group, mean  $V_{max} = 113.6$  deg/s,  $SD = 16.1$  deg/s).

To become familiar with the apparatus, each participant performed several practice trials. We then recorded 10 trials without any additional damping (null force) to establish their baseline kinematic performance. Following the baseline trials, six experimental blocks were administered. Each block contained a series of 10 trials in which participants performed forearm movements under one of three different damping conditions ( $B = -1, 0,$  and  $3$  cNm/deg, where cNm [centiNewtonmeter] = force necessary to move a mass of 10 grams over a distance of 1 m). At the end of the experiment, another 10 trials under zero damping were recorded. The sequence of blocks was the same for all participants, ensuring that participants experienced five distinct types of transitions between blocks. During three transitions, damping increased ( $-1$  to  $3$  cNm/deg,  $-1$  to  $0$  cNm/deg, and  $0$  to  $3$  cNm/deg), whereas it decreased in the two remaining conditions ( $0$  to  $-1$  cNm/deg and  $3$  to  $0$  cNm/deg). Inter-trial intervals were pseudorandom and ranged between 4 and 10 s. The order of presentation of the damping conditions is shown in Table 1.

#### Measurements

A potentiometer and tachometer measured angular position and velocity at the motor shaft for each trial. The data were sampled at 520 Hz and were digitized with a 12-bit analog-to-digital converter (Burr-Brown MPV 904). We stored the digital data on hard disk and then filtered the data offline with a second-order Butterworth filter at a cutoff frequency at 10 Hz by using MATLAB Version 6.1 software (Mathworks, Natick, MA). The length of each trajectory was standardized to 900 samples ( $\sim 1.7$  s). To accomplish comparability between the trajectories, we aligned the curves to movement onset. Movement onset was defined as the point in time when angular position exceeded  $2^\circ$  with respect to the starting position. All data preceding the movement onset by more than 100 samples were discarded.

**Baseline trajectory.** For each participant, we averaged the trajectories of the first 10 trials. During these initial trials, no external damping was applied ( $B = 0$  cNm/deg). We termed the resulting mean curve the *baseline trajectory*.

**Baseline movement variability.** In a first step, we determined the end of the first movement unit by finding the second zero-crossing in the angular acceleration time series data after movement onset (a movement unit was defined as one acceleration and deceleration phase). To obtain measures of natural movement variability, we then computed each participant's mean ( $M_{POS}$ ) and standard deviation

**TABLE 1**  
**Order of Presentation and Magnitude of Damping Force in Blocked Trials**

	No damping (baseline)	Positive damping	No damping	Negative damping	Positive damping	No damping	Negative damping	No damping
Force	0	3	0	-1	3	0	-1	0

*Note.* Each block contained 10 trials. The magnitude of the damping force is indicated in the second row. Units are centiNewtonmeters times seconds per degree (cNms/deg). The order of presentation was the same for all participants.

( $SD_{POS}$ ) of angular position at the end of the first movement unit for all baseline trials. We calculated spatial variability at that particular temporal event because at that point in time the transport phase of reach has ended. It is thus the latest point in the trajectory at which we could reasonably assume that the observed kinematics were largely the result of feedforward control and were not extensively influenced by the processing of afferent feedback.

*Spatial error.* To quantify the degree of spatial deviation during any damping condition with respect to a participant's baseline trajectory, we computed the cumulative absolute difference between the actual angular path and the baseline trajectory. We refer herein to that variable as the *trajectory difference score* (TD score). Mathematically, the TD score is the sum of the absolute differences of each pair of time-angle data during a specific trial.

*Length of adaptation.* To quantify when a participant had adapted to a particular damping condition, we employed two measures. With the first measure, we assessed how long it took to adapt to a new force field. To arrive at that measure, we computed the mean group TD scores of each trial for each group (yielding seven means for each of the three age groups). Then, the group mean TD scores during the baseline were subtracted from the trial mean TD scores and divided by the maximum TD score of the respective block, as follows:

$$D = [\text{mean}(\text{TD}_{\text{trial}}) - \text{mean}(\text{TD}_{\text{baseline}})] / \text{max}(\text{TD}_{\text{block}}). \quad (2)$$

Thus, the values of  $D$  ranged between 1 and 0 within each block. Third, using a least square method, we fitted an exponential function as follows:

$$D = \exp(-z * \text{trial number}). \quad (3)$$

The exponent  $z$  is a measure of steepness; that is, the larger the value of  $z$ , the steeper the curve. Consequently,  $1/z$  is a measure of adaptation, with the unit trials (a larger number for  $1/z$  means it took more trials to adapt to baseline performance). For the sake of clarity, we refer herein to  $1/z$  as the estimated *adaptation time*.

For the second measure, we set the following criterion: Participants were said to have adapted to a new force field when angular position at the end of the first movement unit ranged within 1  $SD$  of the mean position during the baseline trials ( $M_{POS} \pm SD_{POS}$ ) in at least two consecutive trials.

Hence, the number of trials required to reach that criterion was a measure of adaptation. We refer herein to that variable as *trials to adaptation* in order to distinguish it from estimated adaptation time. Both measurements indicated the length of adaptation. The distinction between the measures refers to the distinction between an estimated (local) time constant and the effective learning time. Trials to adaptation indicated how many trials it took the participant before his or her arm position at the end of the first movement unit fell within so-called normal limits. Adaptation time, which was computed on the basis of the cumulative difference score, described the spatial deviation of a complete trajectory from the baseline trajectory. Because the measure trials to adaptation was determined at the end of the first movement unit, feedforward processes largely influenced its value, whereas adaptation time reflected the complete trajectory, which was likely influenced by feedforward and feedback processes.

## Results

### Basic Movement Variability

Because it is known that general movement variability does decrease during childhood and possibly confounds the kinematic effects during the force field conditions, we first computed the baseline movement variability of our sample of children (null force). The analysis of the angular kinematics confirmed that movement variability in the baseline condition decreased with increasing age.  $SD_{POS}$  at the end of the first movement unit was  $3.1^\circ$  for the younger children, whereas for the older children,  $SD_{POS}$  was computed as  $2.2^\circ$ ,  $F(1, 37) = 13.9$ ,  $p < .001$ .  $SD_{POS}$  for the adults was  $1.5^\circ$ . Jansen-Osmann et al. (2002) had previously reported that the path variability of 10- to 11-year-old children was still different from that of adults. The average length of the movement units was 276 ms ( $SD = 20$  ms) for the young and 324 ms ( $SD = 30$  ms) for the older group of children. Given that eye-hand visual reaction times are approximately in the same range during middle to late childhood ( $\approx 250$ – $350$  ms; Montes-Mico, Bueno, Candel, & Pons, 2000; Pellizzer & Hauert, 1996), that finding implies that visual feedback could not have played a major role in shaping the movement trajectories up to that point. That assessment was further supported by the finding that at the end of the first movement

unit, children had, on average, covered 76%–100% of the required angular path toward the target (22.8°–30° of a 30° flexion movement).

### Adaptation to Changes in Damping

Participants experienced two basic types of transitions. Damping either increased or decreased between two neighboring blocks of trials. Incrementing damping produced a characteristic hypometric trajectory (Figure 3A, B). In comparison with baseline performance, movement time was systematically prolonged, and the slope of the position trajectory was not as steep. Lowering damping induced a hypermetric trajectory (Figure 3C, D). With respect to the baseline trajectory (null force), goal position was attained faster, but the flexion movement was not appropriately decelerated, resulting in a target overshoot and in subsequent correction movements.

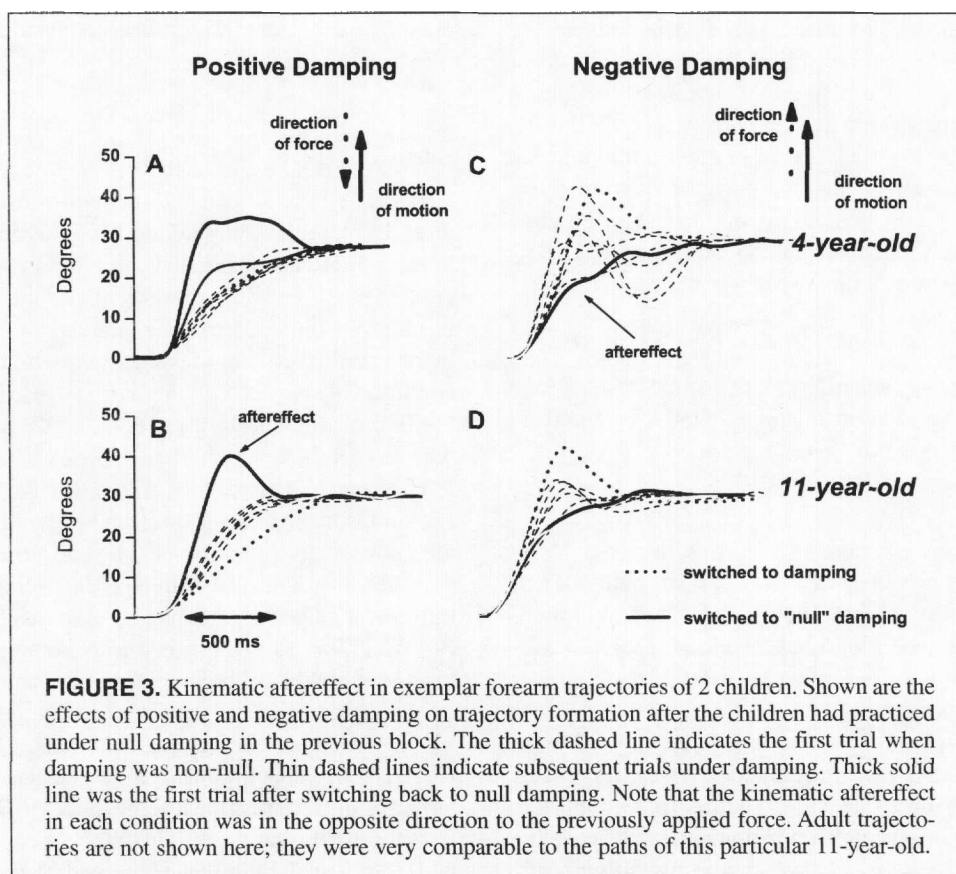
#### Effect of Damping on the Forearm Path Decreased With Increasing Age

We found that the deviation from the baseline trajectory during the seven experimental blocks was significantly different between groups. A 3 (age) × 3 (damping factor) repeated measures analysis of variance (ANOVA) on TD score yielded a significant main effect for damping,  $F(2, 86) = 3.39, p < .038$ , and for age,  $F(2, 43) = 71.02, p < .0001$  (Figure 4A). Subsequent Bonferroni post hoc quantitative

comparisons revealed that the youngest children were more affected by force field changes than were the older children, who, in turn, were more influenced in their joint trajectories than the adults. Furthermore, positive and negative damping induced significant spatial deviations with respect to the no-force-field condition,  $F(1, 43) = 5.05, p < .03$ , and  $F(1, 43) = 7.45, p < .009$ , respectively. The difference between positive and negative damping was not significant, although our own observations and participants' reports suggested that negative damping was harder to compensate. An examination of the group means of TD score for each trial verified that the extent of spatial deviation was different between groups throughout all experimental trials, not just during the transitions between force fields (Figure 4B).

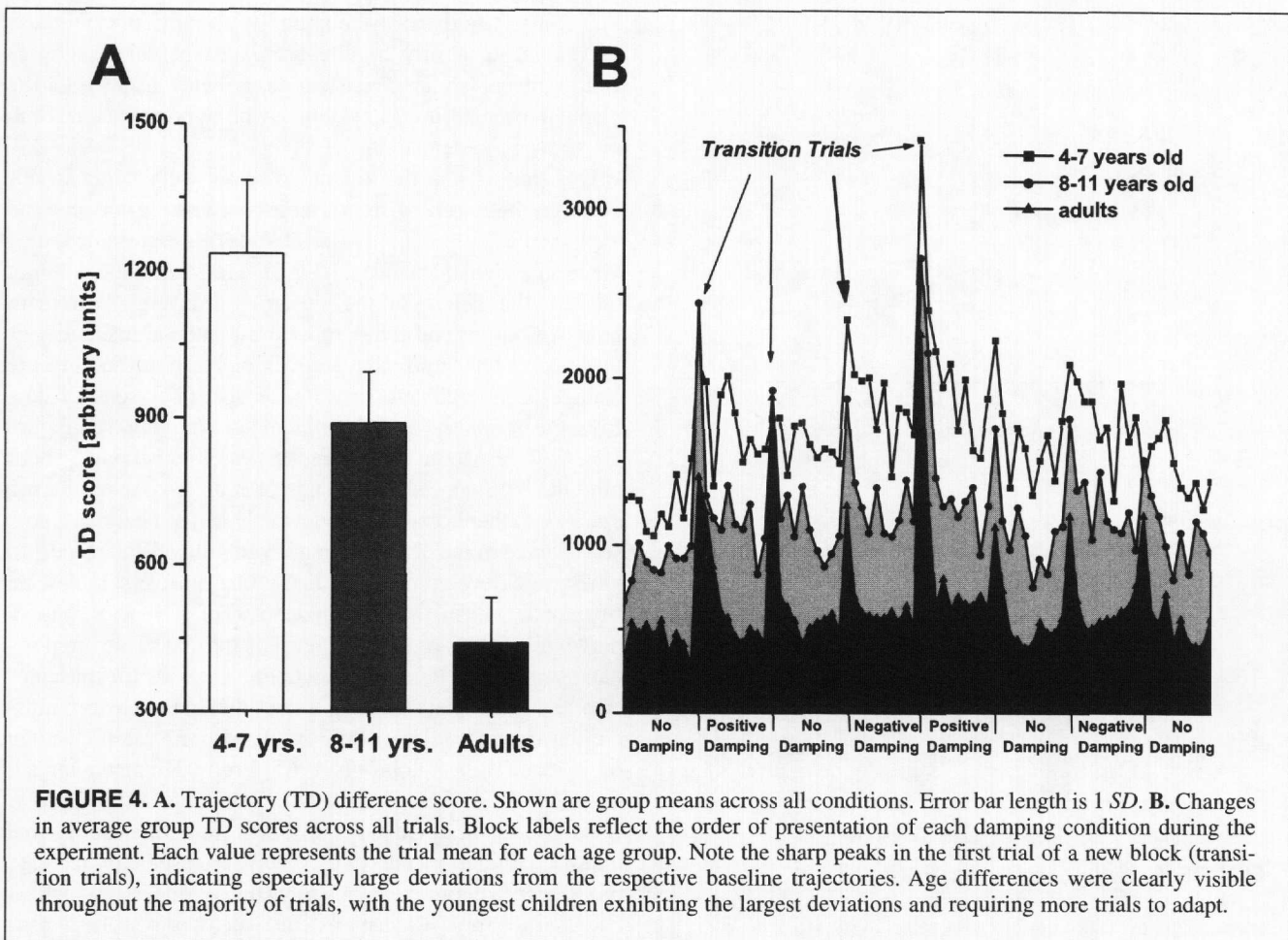
#### Time to Adaptation Decreased With Increasing Age

The graph of the individual participant means for adaptation time over chronological age illustrates that the older children and adults adapted faster than the younger children (Figure 5A). That finding was supported by a 3 (age) × 3 (damping factor) repeated measures ANOVA on adaptation time, which yielded a significant main effect for age,  $F(2, 12) = 11.46, p < .0016$ . The younger children (4–7 years) needed an average of 7.3 trials before adapting to a new damping force condition, whereas the mean adaptation times were 2.3 trials for the older children (8–11 years) and 1.2 trials for the adults. Within each group, the adaptation



**FIGURE 3.** Kinematic aftereffect in exemplar forearm trajectories of 2 children. Shown are the effects of positive and negative damping on trajectory formation after the children had practiced under null damping in the previous block. The thick dashed line indicates the first trial when damping was non-null. Thin dashed lines indicate subsequent trials under damping. Thick solid line was the first trial after switching back to null damping. Note that the kinematic aftereffect in each condition was in the opposite direction to the previously applied force. Adult trajectories are not shown here; they were very comparable to the paths of this particular 11-year-old.





**FIGURE 4.** A. Trajectory (TD) difference score. Shown are group means across all conditions. Error bar length is 1 *SD*. B. Changes in average group TD scores across all trials. Block labels reflect the order of presentation of each damping condition during the experiment. Each value represents the trial mean for each age group. Note the sharp peaks in the first trial of a new block (transition trials), indicating especially large deviations from the respective baseline trajectories. Age differences were clearly visible throughout the majority of trials, with the youngest children exhibiting the largest deviations and requiring more trials to adapt.

times did not vary significantly as a function of damping (Figure 5B). However, those data indicated that children in both groups required the most trials to compensate negative damping. The failure to reach significance was likely a consequence of the large between-participants variability, which is often seen in studies on motor development. It should be noted that our choice of a simple exponential model to capture the time of adaptation was an a posteriori decision primarily influenced by our data. Not all participants showed a gradual or stepwise adaptation in their trajectories. In those cases, an exponential model was actually not the best choice.

Because of the earlier mentioned limitation in determining the adaptation time, we implemented a second measure of time to compensation that was based on how fast participants were able to adjust their position at the end of the first movement unit to levels observed during their baseline performance (see Figure 6A). To distinguish that measure from the previous adaptation time variable, we refer to it herein as *trials to adaptation*.

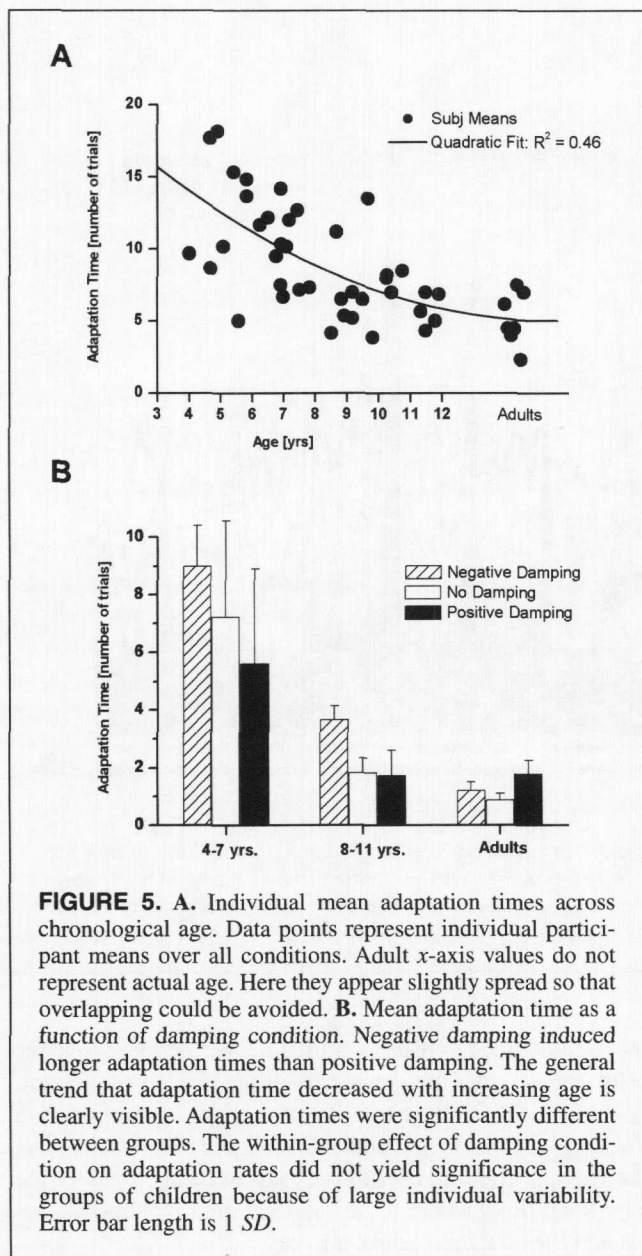
A 3 (age)  $\times$  3 (damping factor) repeated measures ANOVA on trials to adaptation yielded a significant main effect for damping factor,  $F(2, 86) = 6.45, p < .01$ , and for age,  $F(2, 43) = 10.58, p < .001$ . The Age  $\times$  Damping Factor

interaction failed to reach significance. Subsequent post hoc tests revealed that the younger children needed significantly more trials to adapt to a novel damping condition than did the older children or adults (see Figure 6B). On average, the younger children needed 4.4 trials to compensate for the new force field, whereas the older children required 3.0 trials and the adults 2.1 trials.

### Discussion

The ability to adapt is one of the central mechanisms of development, because changes in physical structure require adaptation. Our data documented the proposal that children as young as 4 years of age will reveal such adaptive behavior as they learn to compensate forces that they have rarely or never experienced before. However, our data also demonstrated that the ability to adapt to novel force fields is a developmental achievement. In general, the youngest children, between 4–7 years of age, were most affected by changes in damping, followed by the older children, who, in turn, were more affected than the adults.

All children showed kinematic features characteristic of the existence of neurally represented inverse dynamics models. Their arm trajectories became distorted after they switched to another damping condition. In addition, the



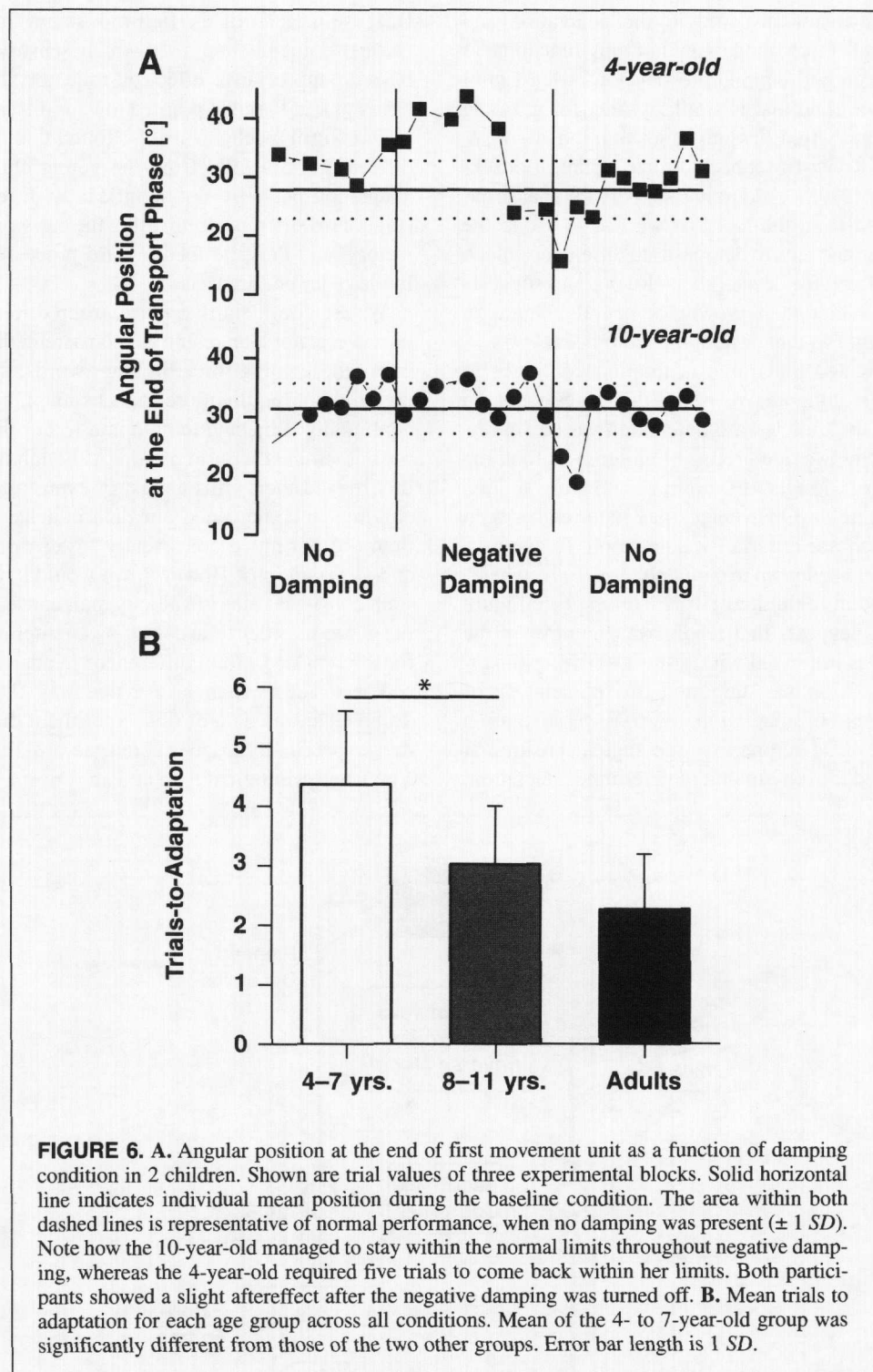
path deviation was in the direction opposite to the previously applied force. Such a kinematic aftereffect can be explained by an inverse dynamics model that continues to generate a motor command that compensates the arm dynamics as well as the no longer existing damping force (Kawato, 1999; see Figure 1B).

When exposed to novel damping forces, the arm trajectories of the youngest children showed the greatest amount of spatial deviation (see Figure 4). Such behavior can be indicative of a neural controller with imprecise neural estimations of the true limb dynamics. However, such false estimation of a limb dynamic parameter (e.g., stiffness) at the neuronal level does not necessarily affect the overt kinematic variability of the limb. If one or more parameters of a child's IDM did not reflect the actual dynamics but remained largely constant, the deviations from the desired

trajectory would be systematic but would not increase movement variability. In other words, the actual trajectories would reveal some consistent error with respect to the planned trajectories (e.g., consistent hypometria, if limb inertia were underestimated).

Our finding that the kinematic errors were larger in our children but were also variable between trials can be explained by a temporally unstable neural representation of the inverse dynamics model. Here, the term unstable does not indicate the failure of the system to converge or remain bounded but instead refers to a developmental instability of the model. Other possible sources of motor variability are changes in muscle properties with age, poor sensory data from the periphery, or inaccurate motor planning (see Figure 1B). With respect to muscle properties, little is known about how the damping characteristics of muscles change during childhood; therefore, one cannot exclude that factor as a possible source of the observed motor variability. With respect to kinesthetic development, we know that muscle spindles are functional at birth, that myelin deposits of peripheral sensory nerves are at 90% of the adult level by the end of the 3rd post-natal year and that nerve conduction velocities for musculo-cutaneous, median, and ulnar nerves that innervate arm muscles have reached 93%–100% of the adult niveau by the age of 3 years (Baer & Johnson, 1965; Brody, Kinney, Kloman, & Gilles, 1987; Fehrmann, 1970; Gamstorp, 1970; Kinney, Brody, Kloman, & Gilles, 1988). Therefore, one can assume that the children in our study received reasonably accurate proprioceptive information from the periphery, which is essential for force adaptation. Thus, the poor peripheral sensory data hypothesis does not seem to be very feasible. With respect to a poor motor planning hypothesis, we argued that in our task spatial planning was obviously constrained and did not allow for extra degrees of freedom. That is, the demands on a planning system were relatively benign because there was no joint redundancy involved and specification of elbow angle uniquely determined the endpoint position, and vice versa. That assessment was true for even the youngest children in our study. Four-year-olds are clearly capable of performing motor skills that involve multiple joints. Even before that age, children have sufficiently mastered to compensate for joint interaction torques and perform arm movements with consistent kinematic profiles (Konczak, Borutta, Topka, & Dichgans, 1995; Konczak & Dichgans, 1997). Although one cannot exclude the possibility that inaccurate planning mechanisms (e.g., for computing inverse kinematics) contribute to movement variability, an internal model with false and fluctuating estimations of the true dynamics would clearly be a large source of kinematic variability. Such an IDM is not likely localized in a single specific region of the central nervous system but can be thought of as a distributed representation encompassing neural networks in the cerebellum and the motor cortex (Schweighofer, Arbib, & Kawato, 1998; Wolpert, Miall, & Kawato, 1998). Finally, it must be acknowledged that the observed kinematic variability in the later portions of the tra-





jectories were likely the result of feedforward and feedback mechanisms that operate in parallel (see Figures 1B and 2B).

Most children attain their motor milestones (e.g., reaching, crawling, standing, and walking) within the first 12–18 postnatal months. It is obvious that the achievement of those milestones requires some form of feedforward control (Metta, Sandini, & Konczak, 1999; Shadmehr & Mussa-

Ivaldi, 1994). Our findings indirectly support the view that children at 4 years of age effectively compensate novel external forces, which implies that the formation of a neural representation that captures the limb dynamics had happened earlier in their ontogenesis. Although such representations (inverse dynamics models) are basically operational in early childhood, however, the data of our study demonstrated that

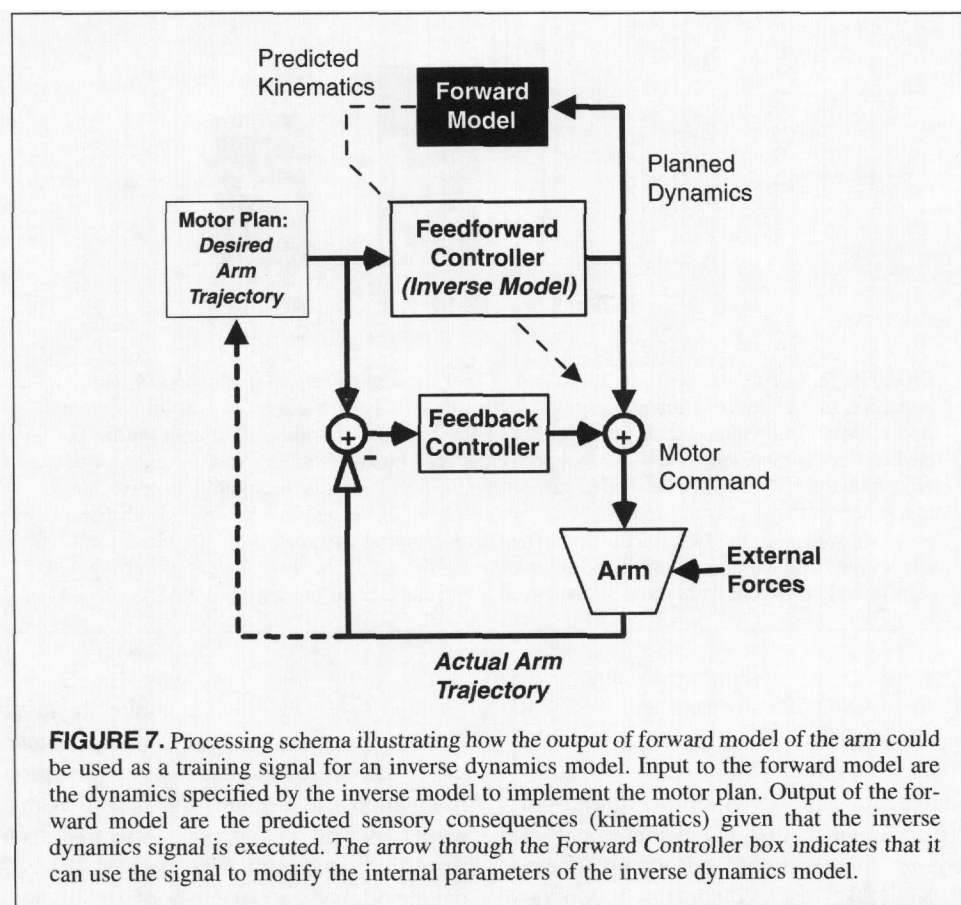
the neural mechanisms involved in the adaptation and updating of internal motor models are not fully functional in 4-year-old children and continue to develop at least until late childhood—a trend that is similarly seen for grasping and reaching (Forssberg, Eliasson, Kinoshita, Johansson, & Westling, 1991; Kuitz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998). Additional support for that argument was derived from the fact that we had to group the children in 4-year age bins to demonstrate differences. Such bin size is very large for developmental work and suggests that experience rather than growth or neural maturation alone is a key factor in that developmental process.

Our data indicated that force adaptation continues to develop during childhood. We based that assessment on our finding that the time toward adaptation varied significantly between the two age groups of children. It took the younger children longer to compensate for sudden changes in force fields. On average, they required between 4–7 trials to reach our criteria for adaptation. In contrast, the older children needed approximately 2–3 trials, whereas many of the adults exhibited 1-trial learning (see Figure 5). That finding suggests that feedforward control in the older children was improved with respect to their younger peers. That conclusion was supported after the analysis of our second measure of adaptation, the trials to adaptation variable. In that variable, one uses the angular position at the end of the first movement unit to determine adaptation.

Because the end of the first movement unit was about the earliest point in time after which sensory feedback could have an appreciative effect on trajectory formation, differences in that variable pointed toward differences in feedforward control mechanisms. We found that the older children differed significantly from the young children in trials to adaptation but were not significantly different from adults (Figure 6B), demonstrating that the early portions of the trajectory, and thus the feedforward processes, had improved in the older children.

We are confident that those group differences in adaptation were not the result of consistent differences in the imposed damping force. In other words, the youngest children did not require more trials to adapt, because they were continually subjected to damping forces that were too high given their smaller arm inertia. Although the youngest children flexed their arms as fast or even faster than the older children in some trials, our data indicated that those children did not move consistently faster throughout all trials and all conditions. However, we would have had to observe such consistent bias in velocity and, consequently, in damping force in order to accept it as an alternative explanation for the reported group differences in adaptation rate.

The exact mechanism for updating IDMs is unknown. To be clear, the data of this experiment did not allow us to make specific inferences about the possible nature of such a neurophysiological mechanism. From a systems point of



view and as suggested by previous findings on human adults (Thoroughman & Shadmehr, 1999), a feedback error signal could be used by the brain to update the IDM (see Figure 1B). However, signals from a neural forward model that computes the expected kinematics on the basis of the planned dynamics (output of the IDM) could yield similar results (see Figure 7) without the need for online peripheral feedback. That is, those two different processes of neural computation could yield similar behavioral results—consistent kinematic responses under changing dynamic conditions.

When we compared the adaptation rates in our experiment with those reported previously, it was obvious that the length of an adaptive process depends on the complexity of the experienced force field. Adults required over 750 trials to compensate two-dimensional viscous force fields in a two-joint arm movement task (Gandolfo et al., 1996), whereas our one-dimensional field hardly posed a challenge to adults. Further empirical evidence suggests that certain dynamic parameters are easier to compensate than others. For example, humans reliably adapt to new inertial loads within one trial (Bock, 1993; Weeks, Aubert, Feldmann, & Levin, 1996). Although those results are not incongruent with the notion that inverse motor models of the limb dynamics form the basis of a neural forward controller, they pose a challenge to researchers in explaining how specific and how many motor models are needed for controlling limb motion (Wolpert & Kawato, 1998).

In summary, the findings of this study and their interpretation within a systems framework point to IDMs as a potentially important central source of movement variability. The notion that the neural IDMs in children are imprecise and temporally unstable neural representations of the actual limb dynamics can explain why motor variability is higher during infancy and childhood than in adults. The paucity of feedforward control also provides a reason why younger children rely heavily on feedback control mechanisms during goal-directed reaching and grasping. However, imprecise or noisy feedforward controllers should not be thought of as the sole source of motor variability in children. Clearly, peripheral and central mechanisms other than feedforward control contribute to kinematic variability in ontogenesis.

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