

Motor commands in children interfere with their haptic perception of objects

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Abstract Neural processes of sensory-motor- and motor-sensory integration link perception and action, forming the basis for human interaction with the environment. Haptic perception, the ability to extract object features through action, is based on these processes. To study the development of motor-sensory integration, children judged the curvature of virtual objects after exploring them actively or while guided passively by a robot. Haptic acuity reached adult levels only at early adolescence. Unlike in adults, haptic precision in children was consistently lower during active exploration when compared to passive motion. Thus, the exploratory movements themselves constitute a form of noise for the developing haptic system that younger brains cannot compensate until mid-adolescence. Computationally, this is consistent with a noisy efference copy mechanism producing imprecise predicted sensory feedback, which compromises haptic precision in children, while the mature mechanism aids the adult brain to account for the effect of self-generated motion on perception.

Keywords Forward models · Human development · Haptic · Active perception · Passive perception

Introduction

From birth, humans interact with the world through their actions. The underlying processes of integration between motor and sensory information form the basis of this interaction by linking perception and action systems. Haptic percepts, such as perceiving object contours by exploring them with the hand, rely on these inter-sensory and motor-sensory processes. Consequently, the development of haptic perception may in part be understood as a process where inter-sensory and motor-sensory mechanisms mature and become functional, and where motor development determines the sequence in which haptic perceptual abilities unfold (Bushnell and Boudreau 1993). It is known that infants in their first year of life can already discriminate certain haptic properties such as hardness and softness (Rochat 1987). However, results from studies on haptic object recognition and orientation in school-age children indicate that this developmental process is not completed before middle childhood and may even last until adolescence (Morrongiello et al. 1994; Gori et al. 2008). To illustrate the interaction between motor and haptic development, consider that haptic acuity of size and orientation discrimination does not reach adult-like levels before the age of 8–12 years (Gori et al. 2008), which coincides with improved levels of object manipulation in children (Rentschler 2004).

It is further known that several childhood disorders, such as autism, are associated with deficits in haptic and kinesthetic perception (e.g. Teitelbaum et al. 1998; Mari et al. 2003), although our understanding of how the disorders affect perceptual processing is still not complete. One possible avenue to advance our understanding of haptic development and the possible pediatric disease states affecting haptics and proprioception is to consider the

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various forms of feedback that need to be processed by the brain.

Haptic percepts derive from the integration of external tactile and proprioceptive feedback with internal predicted sensory feedback (PSF). This *internal feedback* is derived from a copy of the efferent motor commands that give rise to the exploratory actions (von Holst and Mittelstaedt 1950; Evarts 1971). Computationally, PSF is thought to be the product of an internal feedforward dynamics model that uses motor commands as inputs (MacKay 1966; Kawato 1999). Its neural bases are likely cerebro-cerebellar networks (Miall et al. 1993; Wolpert and Kawato 1998). While forward dynamics models are known to play an important role for motor control, they also serve an important function for perception (Sciutti et al. 2010). In essence, the nervous system can use an efference copy to predict the sensory consequences of its planned movements and then subtract this prediction from the incoming stream of afferent signals to obtain an *exafferent* signal reflecting the state of the environment (von Holst 1954). While there is substantial evidence that many biological systems including humans use efference copy mechanisms to control a wide range of behaviors and functions (Kawato et al. 1987; Jordan and Rumelhart 1992; Miall et al. 1993; Wolpert and Kawato 1998; Kawato 1999), the neural mechanisms that link motor commands and sensory data and how these mechanisms develop in human ontogenesis have not yet been completely delineated.

To investigate the development of haptic perception and the underlying use of internal and external feedback, we employed a curvature perception paradigm that has been widely used in adult studies (Davidson 1972; Gordon and Morison 1982; Konczak et al. 2008; Wijntjes and Kappers 2009; Wijntjes et al. 2009; Sciutti et al. 2010; Squeri et al. 2012). Using a robotic manipulandum, we created boundary forces resembling a virtual curved contour. Children and adults either moved actively the handle of the manipulandum with their hand or were passively guided by the robot along these contours. Determining haptic precision during active versus passive haptic exploration subsequently allowed us to delineate how sensory and motor processes interact in the developing brain to achieve a unique haptic percept and to map the development of haptic acuity in childhood.

Methods

Thirty-three children between 6 and 14 years of age and 8 adults naive to the study and with no history of neurological disorders participated (total $N = 41$). All participants (or guardians/parents) gave their informed consent prior to

testing. The study was approved by the local ethics committee.

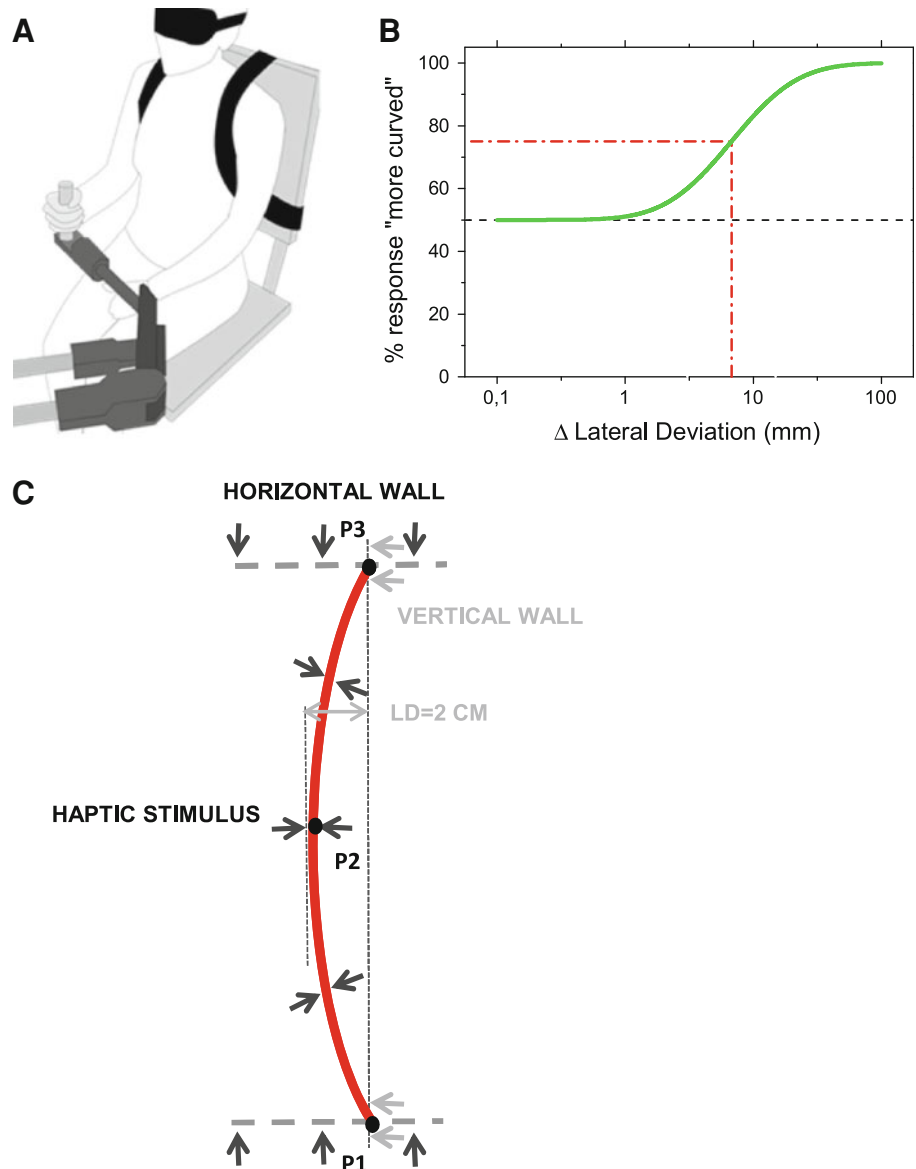
With vision occluded, participants haptically sensed with their hand a virtual curved contour, as if exploring the smooth surface of a round object with the hand, that was created by appropriate boundary forces of a robotic manipulandum. Subjects sat comfortably on a chair in front of a 2-degrees-of-freedom robotic manipulandum (for a detailed description, see Casadio et al. 2006) (Fig. 1a). Their right shoulder (acromion) was aligned with the neutral position of the manipulandum. Upper body motion was restricted by seat belts and by adjusting the seat position relative to the manipulandum in such a way that the maximal sagittal arm displacement during testing did not exceed 80 % of the individual's arm length. The center of the robot workspace was adjusted so that subjects assumed initial sagittal joint angles of approximately 90° for the elbow and 45° for the shoulder. To discern the possible effects of predictive sensory feedback, two experimental conditions were employed: subjects either actively moved the handle along the virtual contour or their hand was passively guided by the manipulandum along the same path. The hand motion consisted of a forward movement along the curved surface followed by a motion backward along the same path for each stimulus. The complete exploration of each curvature lasted about 3 s. In each trial, participants were exposed to the standard stimulus of fixed dimension (Lateral Deviation, $LD_s = 20$ mm) and a comparison stimulus of variable dimension and always bigger than the standard ($LD_c > LD_s$). The two stimuli were randomly presented. The correspondent curvature of the standard stimulus was 3.85 m^{-1} . The starting position of the manipulandum was identical for all trials. The protocol consisted of 40 trials (80 stimuli) for the children and 150 trials (300 stimuli) for the adult group.

At the end of each trial, participants were required to report which of the two stimuli was more curved. Subsequently, the percentage of trials in which the comparison stimulus was judged as more curved than the standard was computed. Data were then fitted using a cumulative Gaussian function (Fig. 1b) to determine discrimination thresholds (σ) and standard errors. Standard errors of the thresholds were computed using a bootstrap simulation (Efron and Tibshirani 1993).

Each trial was initiated by the experimenter by pressing a button.

Time between trials was kept variable (~ 4 – 10 s), so that subjects could not predict the onset of the subsequent trial. Before data collection, participants underwent a familiarization phase, in which they experienced the haptic forces during active and passive motion, by performing 5 curvature explorations in each of the two conditions. In general, the end effector moved along an arc starting from

Fig. 1 Experimental setup, stimulus and exemplar psychometric function. **a** The experimental setup depicting the position of the participants with respect to the robot (Casadio et al. 2006). **b** Exemplar data of a psychometric function for haptic curvature perception. The ordinate values indicate the percentage of subject's responses indicating the probe as more curved than the standard stimulus. The abscissa represents the differences in lateral deviation (LD) between the probe and the standard. The threshold corresponds to the difference in lateral deviation yielding 75 % of correct responses. **c** The curvature stimulus. Shown is the construction of the virtual curved path for active exploration. The hand path was constrained by three different virtual barriers. For the passive movement condition, the hand was moved along the same trajectory by the robot



point P1, passing through P3 and ending at P2 (Fig. 1c) and then returning to P1. The motion law is described by:

$$\begin{cases} X_{EE}(t) = X_c + R \cos(\pi + \vartheta \cos(2\pi t/T)) \\ Y_{EE}(t) = Y_c + R \sin(\pi + \vartheta \cos(2\pi t/T)) \end{cases} \quad (1)$$

where $X_{EE}(t)$ and $Y_{EE}(t)$ are the moving end effector coordinates, X_c and Y_c are the coordinates of the circle center, R is the radius of the circle, ϑ is the central angle of the arc, T is the duration of the entire movement ($T = 3$ s) and t is the actual movement duration.

In the *passive condition*, the robot delivered a two-component force field to the hand guiding it along the prescribed contour without the need of muscular activation by the participant. An attractive force smoothly moved the hand along the virtual contour, and a viscous force field stabilized the arm (Eq. 2):

$$F(t) = K_P \sqrt{|X_T - X_{EE}(t)|} \frac{(X_T - X_{EE}(t))}{|X_T - X_{EE}(t)|} + \begin{bmatrix} B & 0 \\ 0 & B \end{bmatrix} \frac{dX_{EE}(t)}{dt} \quad (2)$$

where $X_{EE}(t)$ and X_T are, respectively, the actual coordinates of hand and target position (on the prescribed contour) at a specific instant of time, B is the derivative gain (10 Ns/m) and K_P is the stiffness (60 N/m). This control allowed for the generation of a stereotyped biological speed profile, characterized by a symmetric shape with a single velocity peak and an acceleration and deceleration phase, which mimicked the profiles seen during active motion in humans.

In the *active condition*, the range of curvatures and the dimensions of the hand paths were identical to the passive

condition. Participants actively moved their hand along a virtual contour. The robot generated the appropriate boundary forces that were characterized by the following controller:

$$F(t) = K_A(X_{EE}(t) - X_W) + \begin{bmatrix} B & 0 \\ 0 & B \end{bmatrix} \frac{dX_{EE}(t)}{dt}, \quad (3)$$

where X_W is the position on the contour closest to the current hand position $X_{EE}(t)$, K_A is the high stiffness of the virtual object (2,500 N/m) and B is the same slight damping coefficient of the passive condition. The force field was active outside the boundaries depicted in Fig. 1c.

Results

Figure 2 shows the discrimination thresholds of all subjects for the active and passive movement conditions. Average movement time was 2.93 ± 0.08 s (mean \pm SD) for the active and 2.92 ± 0.01 s for the passive condition. The corresponding average hand speed was 0.125 ± 0.005 m/s (mean \pm SD) for the active and 0.116 ± 0.001 m/s for the passive condition. A subsequent 2-way ANOVA with age and condition (active/passive) as factors revealed no significant main effects ($p = 0.19$ and $p = 0.07$ respectively). In both conditions, thresholds decreased with increasing age during childhood and became comparable to adults at about 13 years of age. Most noteworthy, the thresholds during middle childhood (6–11 years) were consistently higher during active exploration than during passive motion ($p = 0.03$), but not after this age ($p = 0.07$).

The thresholds obtained during passive movement can be seen as the developmental state of the external feedback system receiving afferent proprioceptive and tactile inputs, while the active exploration thresholds can be seen as the developmental state when the combined contributions of the external and internal feedback systems are present. To quantify the time frame of haptic development, an exponential decay function of the following form was fitted to each data set:

$$T = \beta_1 e^{\text{AGE}/\beta_2} + \beta_3, \quad (4)$$

where T is the haptic threshold in mm, AGE is the chronological age in months, and β_1 (mm) β_2 (months) β_3 (mm) are estimated constants. Estimated parameters were as follows: active: $\beta_1 = 650$, $\beta_2 = -2.2$, $\beta_3 = 6.8$; passive: $\beta_1 = 350$, $\beta_2 = -2$, $\beta_3 = 5.37$.

In order to quantify the effect of internal feedback on σ during active sensing, we computed the difference between the active and passive thresholds:

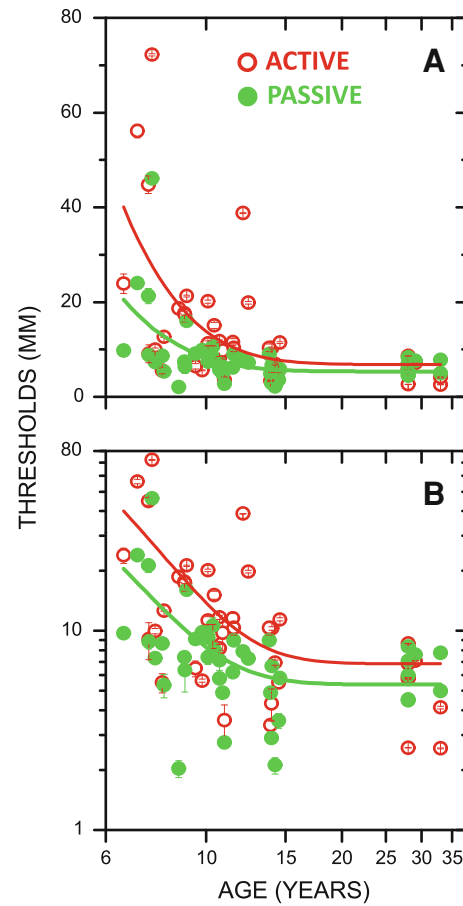


Fig. 2 Haptic discrimination thresholds (σ) during active and passive sensing as a function of age. **a** Each data point represents a particular subject threshold. Exponential decay functions were fitted to data of each condition. The estimated parameters were as follows: active: $\beta_1 = 650$, $\beta_2 = -2.2$, $\beta_3 = 6.8$; passive: $\beta_1 = 350$, $\beta_2 = -2$, $\beta_3 = 5.37$. **b** The same as Fig. 2a shown in logarithmic scale to illustrate that the relative difference between σ_{active} and σ_{passive} persisted throughout development

$$N_{\text{internal}} = \sigma_{\text{active}} - \sigma_{\text{passive}} \quad (5)$$

Figure 3a shows the developmental trajectory of this component highlighting that the difference between active and passive acuity diminished with age but persisted until approximately 13 years of age. This represents the perceptual “noise” due to internal feedback (N_{internal}). That is, it expresses the effect of PSF on haptic sensitivity, reflecting the maturity of the internal feedback system. To quantify the effect of internal feedback on σ during active sensing an exponential decay function of the form (4) was fitted to the threshold differences (N_{internal}). The resulting parameters were: $\beta_1 = 169$; $\beta_2 = -2.9$; $\beta_3 = 0.8$. The amplification factor of the input noise due to presence of active motion can be computed as relative difference between active and passive thresholds (expressed as its ratio k , see inset *D* in schematic diagram in Fig. 4:

$$k = \sigma_{\text{active}} / \sigma_{\text{passive}} \quad (6)$$

Based on the linear fits of the children and adult data, it can be seen that the difference ratio k was approximately 2 until about 11 years of age (see Fig. 3b), meaning that active thresholds tend to be twice as high as passive thresholds for those ages. In contrast, k was ≈ 1 for the adult data. Thus, while the absolute effect of active motion on haptic sensitivity diminished with age, the relative difference between active and passive movement thresholds remained nearly constant and twice as high as in adults throughout much of middle childhood. Quantifying the relationship between active and passive movement thresholds allowed us to estimate the active movement thresholds with respect to the corresponding passive movement threshold for all developmental ages by computing:

$$T_a = T_p \times k, \quad (7)$$

where T_a is the active threshold, T_p is the passive thresholds and k is the ratio estimated from the function fit of the observed data (see black curves in Fig. 3c).

To understand if this result was due to differences in the smoothness of the movement trajectory between active and passive condition, we analyzed hand trajectory jerk for each age group. To obtain jerk data for each age group, we first averaged the jerk time-series data obtained for each movement, then the mean jerk for all the movements performed by each child, and finally, we averaged subject mean jerks for each age. Not surprisingly, jerk during active movement was largest in the youngest group and decreased with increasing age. When expressing active motion jerk of children in relation to adult active motion jerk ($\text{jerk}_{\text{active}} / \text{jerk}_{\text{activeAdults}}$), the resulting jerk ratio became stable and adult-like, especially between 9 and 11 years of age (7 years = 2.31, 9 years = 1.26, 11 years = 0.93, 14 years = 1.03; adults = 1.0). Adult jerk was not significantly different with respect to the 7-year-old- and the 9-year-old group (p 's > 0.05). In contrast, haptic thresholds reached adult levels after 14 years of age (see Fig. 3c), indicating that hand trajectory formation and haptic acuity had different developmental time courses.

To determine when the precision of internal and external feedback systems reached levels comparable to adults, we considered the age at which children's thresholds fell within one standard deviation from the adult mean as the time of maturity. Using this criterion, we derived that passive haptic perception precedes the development of the active haptic sensing by approximately 2 years.

These results allowed us to outline a processing model of haptic perception (see Fig. 4) to understand and explain the observed development of haptic precision. According to the model, haptic perception is the result of combining the output of external and internal feedback systems. Both systems rely

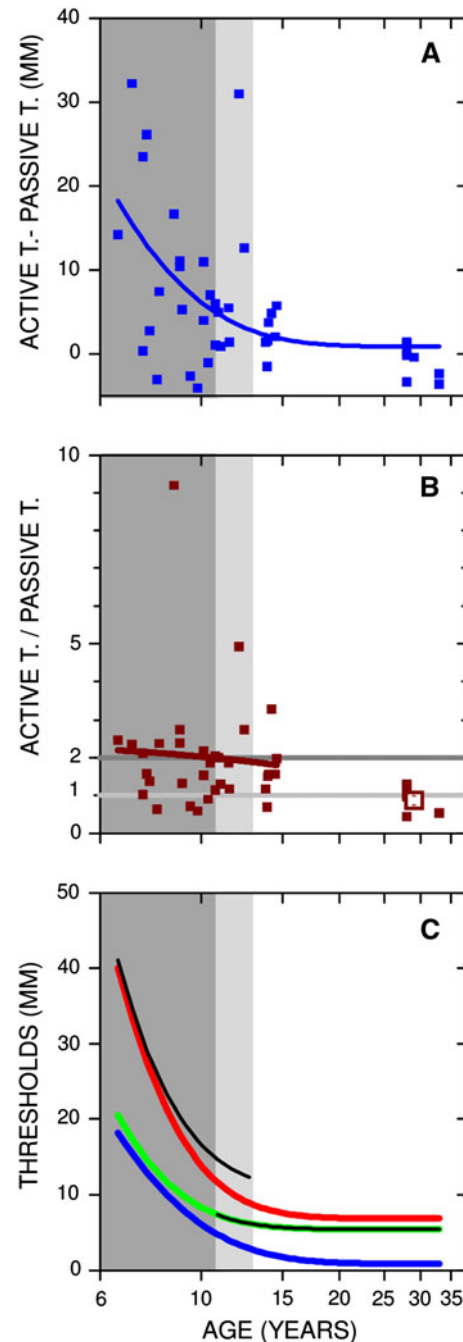


Fig. 3 Active versus passive haptic sensitivity. **a** Threshold differences (N_{internal}) between the active and passive conditions for each participant. A function of the form (4) was fitted to the data. Estimated function parameters were as follows: $\beta_1 = 169$; $\beta_2 = -2.9$; $\beta_3 = 0.8$. **b** Ratio k between active and passive thresholds for each participant with the respective function fit (for children). The *open dot symbol* represents the average threshold for adults. **c** Comparison between the fitted functions based on the observed data and the prediction of the model. Passive threshold fit (*green*), active threshold fit (*red*) and their difference (*blue*). The black line represents the prediction of the model (see “Methods” section). The *dark gray bar* in all the three panels indicates the time at which the external feedback system is developed, and the *light gray bar*, the delay associated with the development of the combined internal and external feedback system (see “Results” section for more details)

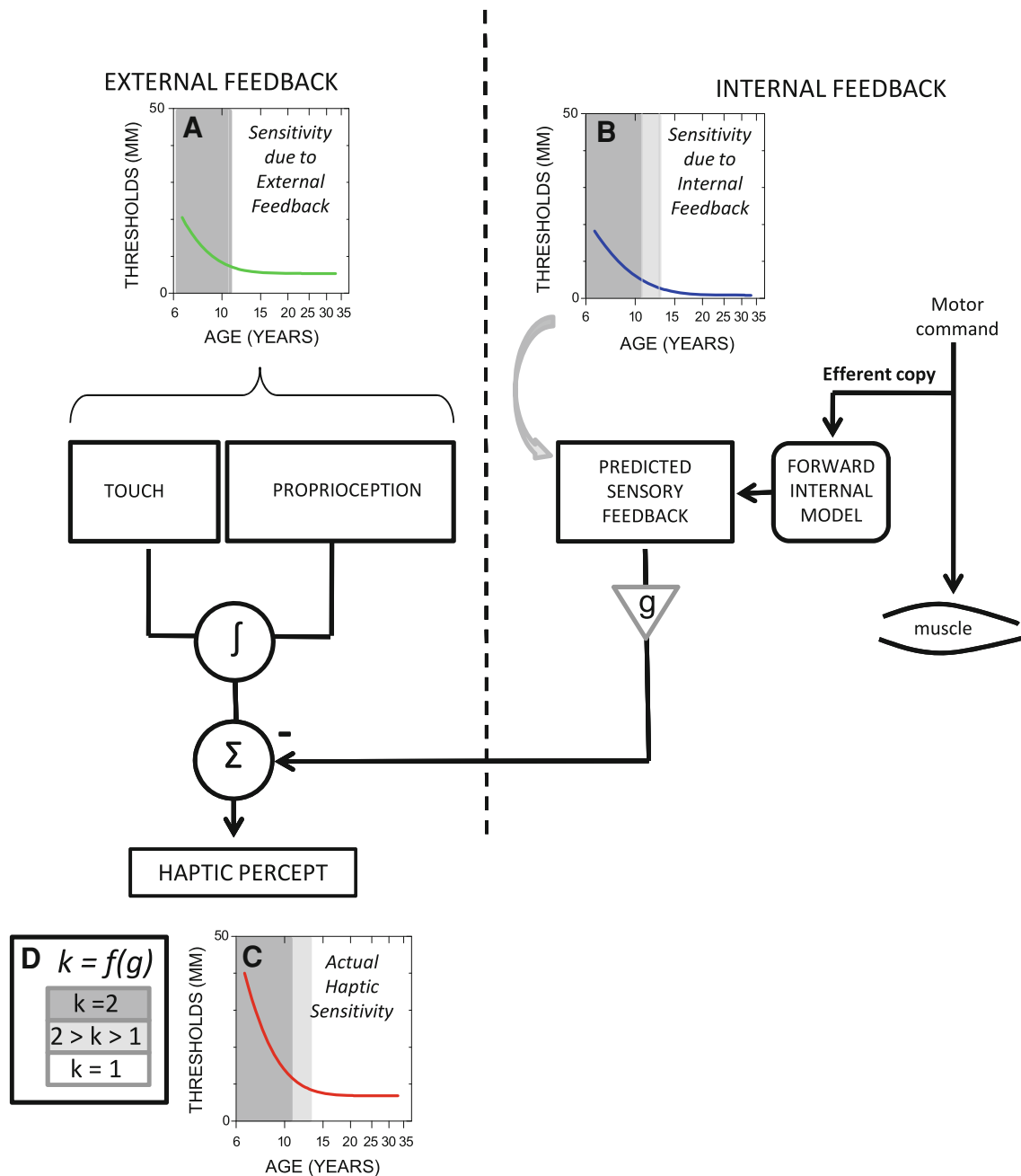


Fig. 4 Computational diagram depicting the underlying processes of haptic perception. Haptic perception is the result of combining the outputs of external and internal feedback systems. The external feedback is based on the integration of afferent touch and proprioceptive information (a). Internal feedback system is based on a forward dynamic model that generates a *predicted sensory feedback* signal (b). Predicted sensory feedback is subtracted from the external

feedback producing a signal representing the haptic percept (c). In the adult, PSF helps to improve the haptic estimate by removing the effect of ego motion (the reafference) from the total afferent input. During development, PSF has a higher noise level affecting haptic precision. The amount of noise is expressed by the amplification factor k (see Eq. (6)), which decreases with age (d)

on afferent signals from the periphery. The external feedback system integrates afferent touch and proprioceptive information (see \int in Fig. 4). The status of this system was tested in our passive motion condition. The internal feedback system is based on a forward dynamics model that performs a motor-sensory transformation to yield PSF. Predicted

sensory feedback is then subtracted from external feedback system to account for the effect of ego motion on perception, yielding a signal representing the haptic percept (see Σ in Fig. 4). The effect of the internal feedback system on haptic precision can be inferred from the difference between the active and passive motion conditions.

Discussion

The neural processes of sensory-motor and motor-sensory integration link perception and action systems, forming the basis for human interaction with the environment. Haptic perception, the ability to extract object features through exploratory actions of the hands or body, is based on these processes. How the haptic system develops during childhood is still not fully understood, although several childhood disorders such as autism have been associated with deficits in haptic and kinesthetic perception (Vilensky et al. 1981; Hughes 1996; Teitelbaum et al. 1998; Mari et al. 2003). This study measured haptic thresholds of children during active and passive haptic exploration, allowing us to map the haptic development and the maturation of motor-sensory integration processes. Our findings demonstrate that haptic precision does not reach adult levels before adolescence. There are at least three factors that may explain this long developmental process.

First, it is known that sensory and motor developments are two interdependent processes in human ontogenesis. This may be especially relevant for haptic perception because it relies on the exploratory movements of a limb or body system (in our case, the precise movement of the hand). While it is documented that by the age of 3 years normally developing children perform non-compliant, goal-directed reaches with the same kinematic consistency as adults (Konczak et al. 1997), it is quite plausible that the motor control for performing *compliant* motion like moving precisely along an object contour develops later. That is, a lack of motor control in youngest children necessarily would influence haptic development. We therefore checked whether the exploratory movements adopted in this task showed kinematic features of that nature. We found that the hand velocity profiles of the children during active motion were consistently bell-shaped. That is, they were similar to those typical of reaching movements and to the one experienced during the passive condition. However, the hand trajectories of the youngest children were less smooth than those of the older children. While such lack to perform compliant motion may have influenced their haptic acuity, it also became apparent that the development of haptic acuity and the underlying motor development had different time courses. Movement smoothness as measured by trajectory jerk reached adult-like levels between 9 and 11 years of age in our sample, while haptic thresholds did not show adult levels before 14 years of age. Thus, the lack of compliant motor control likely contributed the lack of haptic precision in early and middle childhood. Yet, it does not fully explain the time course of haptic development, indicating that other non-motor-related processes influence haptic development.

Second, central processing of external feedback throughout childhood produces imprecise input for sensory integration. That is, until adolescence, the afferent proprioceptive and tactile signals are too noisy or the networks of inter-sensory integration are not mature to yield precise haptic estimates comparable to adults. This claim is consistent with recent findings showing that multisensory integration develops late during childhood (Gori et al. 2008; Nardini et al. 2008; Barutchu et al. 2009, 2010) and that that unisensory signal processing needs to be developed before multisensory integration can occur (Gori et al. 2008). For the haptic system, tactile and proprioceptive afferent signals must provide sufficiently precise sensory data before inter-sensory integration processes may yield perceptually meaningful results. With respect to haptic perception, it is known that the spatial acuity of proprioceptive and tactile systems continue to develop until late childhood (Visser and Geuze 2000; Goble et al. 2005; Pickett and Konczak 2009; Mackrout and Proteau 2010) and that the age-related improvements in proprioceptive acuity during development contribute to the improvement in sensory-motor performances (Contreras-Vidal et al. 2005; Bo et al. 2006; Contreras-Vidal 2006; King et al. 2009). Thus, it is plausible and consistent with our passive motion data that multimodal haptic development lags unimodal proprioceptive and tactile development.

Third, the efference copy mechanism needed to produce internal feedback is lacking precision. The haptic system requires not only inter-sensory tactile-proprioceptive integration, but also a process of motor-sensory integration. Because haptic perception involves movement, the integration between motor and sensory signals is an essential process to determine the effect of ego motion on perception (von Holst and Mittelstaedt 1950; von Holst 1954). By computing a *reafferent* signal based on the motor commands (i.e., predicted sensory feedback), a precise *efference* (i.e., the net effect of external sensory inputs) is obtained, and thus the precision of haptic estimates can be increased.

Like inter-sensory integration, a process of motor-sensory integration relies on the quality of its input signals. With respect to the motor signals, it is obvious that these become increasingly consistent and fine-tuned during development leading to improved coordination and increased spatiotemporal precision of voluntary motor acts. For example, as children start to perform their first goal-directed reaches around 4–5 months of age (von Hofsten 1991; Konczak et al. 1995), their early arm trajectories are jerky, lack coordination, and are associated with unwanted co-contractions of agonist and antagonistic muscles (Konczak and Dichgans 1997). This lack of control is consistent with a neural controller lacking precise estimations of the limb dynamics (Nori et al. 2009) and is

believed to contribute to the limited haptic abilities of infants (Bushnell and Boudreau 1993). Yet, by 3 years of age, children perform reaches with the same kinematic consistency as adults (Konczak and Dichgans 1997), and by 6 years of age, they show the ability for generalized adaptive learning, suggesting that a sufficiently precise inverse model of limb dynamics has been acquired (Jansen-Osmann et al. 2002). Such an internal model of the limb dynamics can function as a controller generating motor commands which can then be transformed by a forward dynamics model to generate internal sensory feedback, that is, a PSF signal. Given that reductions in movement variability and kinematic errors during adaptive motor learning are observed at least until 10 years of age (Jansen-Osmann et al. 2002), it can be concluded that inverse models continue to develop until late childhood.

Consequently, any forward model receiving its input from a noisy efference copy of the motor commands must be noisy until that age, producing imprecise *reafferent* or PSF signals. It is then plausible that noisy PSF in children leads to less precise estimations of the *exafference*, in our case to less precise estimations of curvature. In contrast, if the arm was moved passively and no voluntary motor commands were issued, no PSF was generated and the impact of an imprecise efference copy mechanism on perception was removed. The fact that active haptic sensing was consistently associated with inferior precision when compared with passive haptic sensing until the end of childhood is thus compatible with the computational view of a forward model of the body that produces noisy PSF. Until early adolescence, this type of internal feedback interferes with afferent signals that already can produce a higher haptic precision in the absence of efferent motor signals (see Fig. 4).

With respect to gaining an understanding of the development of the underlying neural processes, a picture emerges that reflects the working of several developmental processes: unimodal sensory development, the development of inter-sensory processes and the development of motor-sensory integration. All three processes are interdependent and have different time scales. Our data indicate that unimodal proprioceptive and tactile development “drives” haptic development. That is, the improved precision of sensory data enables networks of inter-sensory integration to become functional. In our data, this is reflected by the rapid improvements in haptic acuity during passive haptic sensing between the age of 5–11 years (see Fig. 2a). Our results also show that the development of motor-sensory integration lags with respect to the development of inter-sensory integration, which is documented by the differences between active and passive haptic sensing (see Fig. 3a). The reason for this lag in development may be owed to the fact that obtaining a precise PSF

signal requires multiple sensory-motor and motor-sensory transformations. That is, afferent sensory signals are needed to train motor networks (i.e., inverse dynamics models), which in turn train forward models involved in sensory prediction.

In summary, adults are capable of canceling the effects of motor-based signals on haptic perception, but young children cannot. The adult nervous system can utilize a motor corollary discharge mechanism to precisely predict sensory states, which will enhance the precision of haptic estimates. In contrast, the same mechanism in children produces a signal that effectively constitutes a form of noise for the perceptual system (Fig. 4). We conclude that haptic development cannot be understood solely as a process of sensory development or of the development of inter-sensory integration. Instead, it must be conceived as a complex developmental process of combining external with internal feedback and of motor development impacting on perceptual development.

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