

Predicted sensory feedback derived from motor commands does not improve haptic sensitivity

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Abstract Haptic perception is based on the integration of afferent proprioceptive and tactile signals. A further potential source of information during active touch is predicted sensory feedback (PSF) derived from a copy of efferent motor commands that give rise to the exploratory actions. There is substantial evidence that PSF is important for predicting the sensory consequences of action, but its role in perception is unknown. Theoretically, PSF leads to a higher redundancy of haptic information, which should improve sensitivity of the haptic sense. To investigate the effect of PSF on haptic precision, blindfolded subjects haptically explored the curved contour of a virtual object generated by a robotic manipulandum. They either actively moved their hand along the contour, or their hand was moved passively by the device along the same contour. In the *active* condition afferent sensory information and PSF were present, while in the *passive* condition subjects relied solely on afferent information. In each trial, two stimuli of different curvature were presented. Subjects needed to indicate which of the two was more “curved” (forced choice). For each condition, the detection and three discrimination thresholds were computed. The main finding is

that absence of efference copy information did not systematically degrade haptic acuity. This indirectly implies that PSF does not aid or enhance haptic perception. We conclude that when maximum haptic sensitivity is required to explore novel objects, the perceptual system relies primarily on afferent tactile and proprioceptive information, and PSF has no added effect on the precision of the perceptual estimate.

Keywords Efference copy · Forward models · Human · Multisensory integration · Proprioception · Tactile

Introduction

When humans explore an object in the environment with their hands, several sources of information are combined to arrive at a single, unified haptic percept of the object. Two of these sources, tactile and proprioceptive cues, are based on afferent sensory feedback from the periphery. A third potential sensory source for haptic perception is predicted sensory feedback (PSF), which is the information derived from a copy of the motor commands that give rise to the exploratory hand movements (the so-called *efference copy* or *motor command corollary discharge*). Thus, the motor acts necessary for moving ones’ fingers along the contours of an object are not only a prerequisite for haptic perception, but are also a potential source of information for estimating object properties (see Fig. 1).

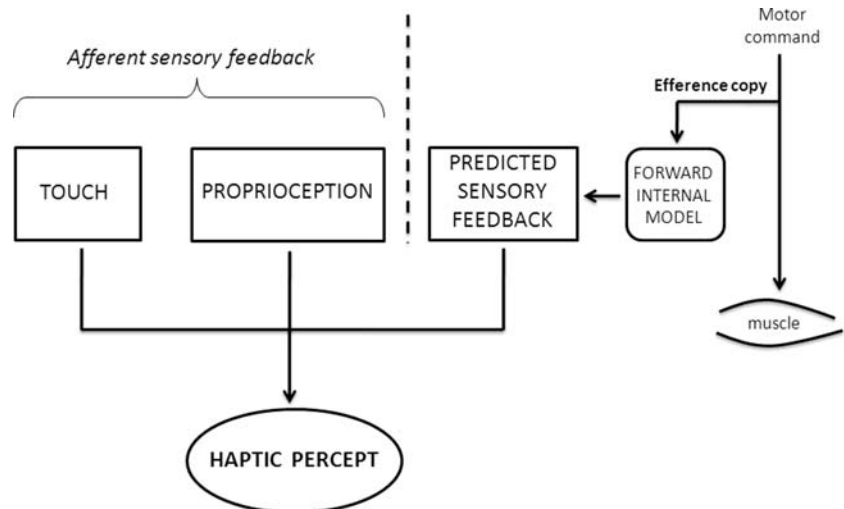
The fundamental importance of motor command corollary discharges has long been recognized (Von Helmholtz 1925; von Holst and Mittelstaedt 1950; Feinberg 1978). Efference copies are thought to be the input of forward internal models that can predict the sensory consequences of

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Fig. 1 Schematic diagram depicting the various sensory sources for haptic perception. Predicted sensory feedback derived from motor commands is one potential source of haptic information



the issued motor commands (Kawato 1999). This predicted sensory information has also been termed “internal feedback” (Evarts 1971). The benefit of internal feedback is that it enables the sensorimotor system to evaluate motor commands before the effectors have been actuated (MacKay 1966). Evidence for the existence of these corollary discharges has been found for both relatively simple, rigid systems (e.g., eye movements in fish and insects) and for complex motor behavior in humans (Feinberg 1978). Many behavioral (Miall et al. 1993; Wolpert et al. 1995; Flanagan and Wing 1997; Sarchilli and Vercher 1999; Mehta and Schaal 2002) and theoretical studies (Kawato et al. 1987; Jordan and Rumelhart 1992; Miall et al. 1993; Wolpert and Kawato 1998; Kawato 1999) have suggested that forward models are functionally and computationally critical for a broad repertoire of behaviors ranging from sensorimotor integration to higher cognitive function (Kawato et al. 2003).

The role of efference copy signals for haptic perception is not clearly understood. While multimodal visuo-haptic information has been shown to be integrated following a maximum likelihood rule (Ernst and Banks 2002; Gori et al. 2008), the importance of PSF signals for haptic sensitivity is unknown. From a computational perspective an added sensory signal increases the redundancy of available information (Ernst and Banks 2002; van Beers et al. 2002), which should improve the precision of haptic estimates. However, we do not know whether internal feedback is interpreted in the same way as afferent feedback from the periphery. There is evidence that efference copy information may diminish kinesthetic sensations during active movement (Angel and Malenka 1982; Chapman et al. 1987) as afferent information may become suppressed (Voss et al. 2006). However, this suppression seems to affect kinesthetic perception only during the initial part of the movement. The perception of final limb position at the end of reaching or pointing movements is

often more accurate after active than passive motion (Adamovich et al. 1998; Laufer et al. 2001), which indirectly supports the view that PSF may enhance kinesthetic sensitivity of goal-directed actions. Yet, haptic exploration is qualitatively different from a goal-directed action. It is a serial process usually extending over several seconds, and the “goal” is the haptic percept not a target in space.

To investigate the effect of PSF on haptic precision, we designed a task in which blindfolded subjects explored the contour of a virtual object with their hand and estimated its curvature. The exploration was either actively performed or the hand was passively moved by a robotic device. During active exploration afferent sensory and PSF was available, while haptic perception was solely based on afferent inputs during passive motion. If perceptual estimation is improved by redundant internal feedback, one expects to find a higher haptic sensitivity during active exploration. Alternatively, PSF may have no impact or a degrading effect on haptic sensitivity. The first case implies that PSF is used to compensate for noise in the afferent sensory inputs. In the alternative scenario, efference copy information degrades haptic sensitivity possibly due to the suppression of peripheral afferent signals or it is a source of neural noise itself. The latter scenario is supported by recent evidence suggesting that isotonic contractions of antagonistic muscles decrease proprioceptive sensitivity to hand curvature (Lillis and Scheidt 2003). With respect to haptics, it has been shown that haptic detection thresholds are not systematically lower during “active touch” when compared to passive sensing (Konczak et al. 2008), which indicates that PSF may not improve haptic acuity. However, the above studies only investigated *detection* thresholds (i.e., the absolute sensitivity to detect a curved hand path) but not *discrimination* thresholds (i.e., just noticeable differences between two curved hand-paths). This distinction is important, because the role of internal feedback at levels

above detection (supra-threshold) may be quite different as the amount of afferent sensory noise increases with an increase in stimulus size (i.e., here the degree of curvature). Thus, PSF may become more important as a source of haptic information when afferent information begins to lose precision. Therefore, this experiment not only determined the *detection* threshold, but also evaluated the *discrimination* thresholds for three virtual objects of various curvatures.

Methods

Subjects

Eight healthy, right handed adults (6 males, 2 females, age = 28 ± 2.1) with no history of neurological or orthopedic disease participated in the study. They were naïve to the device and to the task. All participants gave their informed consent prior to testing. The study was approved by the local ethics committee.

Apparatus

The robotic manipulandum was a 2-degrees-of-freedom planar manipulandum with a large elliptical workspace (80×40 cm). The mechanical structure consisted of a very rigid parallelogram mechanism powered by two direct drive brushless motors. The manipulandum had low intrinsic mechanical impedance at the end-effector (inertia < 1 kg; negligible viscosity and friction). It provided a high level of back-drivability and a good isotropy (manipulability index = 0.23 ± 0.02 ; force/torque ratio = 2.21 ± 0.19 N/Nm) with a large available force level at the handle (continuous force > 50 N; peak force > 200 N) allowing for experiencing a wide range of haptic stimuli. The controller consisted of three nested loops with a 16-kHz sampling rate (current loop) and 1-kHz rate (impedance control loop), plus a 100-Hz virtual reality loop. Software environment was based on RT-Lab[®] and Simulink[®].

Procedure

Subjects sat comfortably on a chair in front of the robot manipulandum (see Fig. 2a). Their right shoulder (acromion) was aligned with the neutral position of the manipulandum (i.e., its horizontal position). To restrict upper body motion, the trunk was strapped to the seat by belts. 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. Seat position with respect to the manipulandum was adjusted in

such a way that the maximal arm displacement in the sagittal plane during testing did not exceed 80% of the individual's arm length.

The task required subjects to hold the handle and haptically sense a virtual curved contour (Fig. 2c), as if exploring the smooth surface of a round object with the hand. During testing, vision was occluded, so the contour could only be sensed haptically. To discern the possible effects of predictive sensory feedback two experimental conditions were employed: subjects either moved the handle actively along the virtual contour or the hand was moved passively by the manipulandum.

During each trial participants were randomly presented with a sequence of two haptic stimuli in a 2-interval, forced-choice procedure separated by a 500-ms interstimulus interval. Subjects were required to discriminate between the presentation of one fixed (*standard*) and one variable curvature (*comparison*). After each trial the participant indicated verbally which stimulus (contour) was more curved. Based on this judgment, the curvature of the virtual wall was adjusted in the subsequent trial using an adaptive procedure (QUEST algorithm, see Watson and Pelli 1983). The adaptive procedure assured that the sequence of curvature values converged to the threshold almost monotonically for all conditions. 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. Four different standard stimuli of various curvature were randomly presented (lateral deviations were LD = 0, 1, 2, 4 cm, corresponding to a straight line and to curvatures of 1.98, 3.85 and 6.9 m^{-1} , respectively; see Fig. 2d; for further details on stimulus presentation see “[Design and measurements](#)”). The linear path distance for all stimuli was 20 cm. The starting position of the manipulandum was identical for all trials. Before data collection, participants underwent a familiarization phase, in which they experienced the haptic forces during active and passive motion, by performing 15 curvature explorations in each of the two conditions.

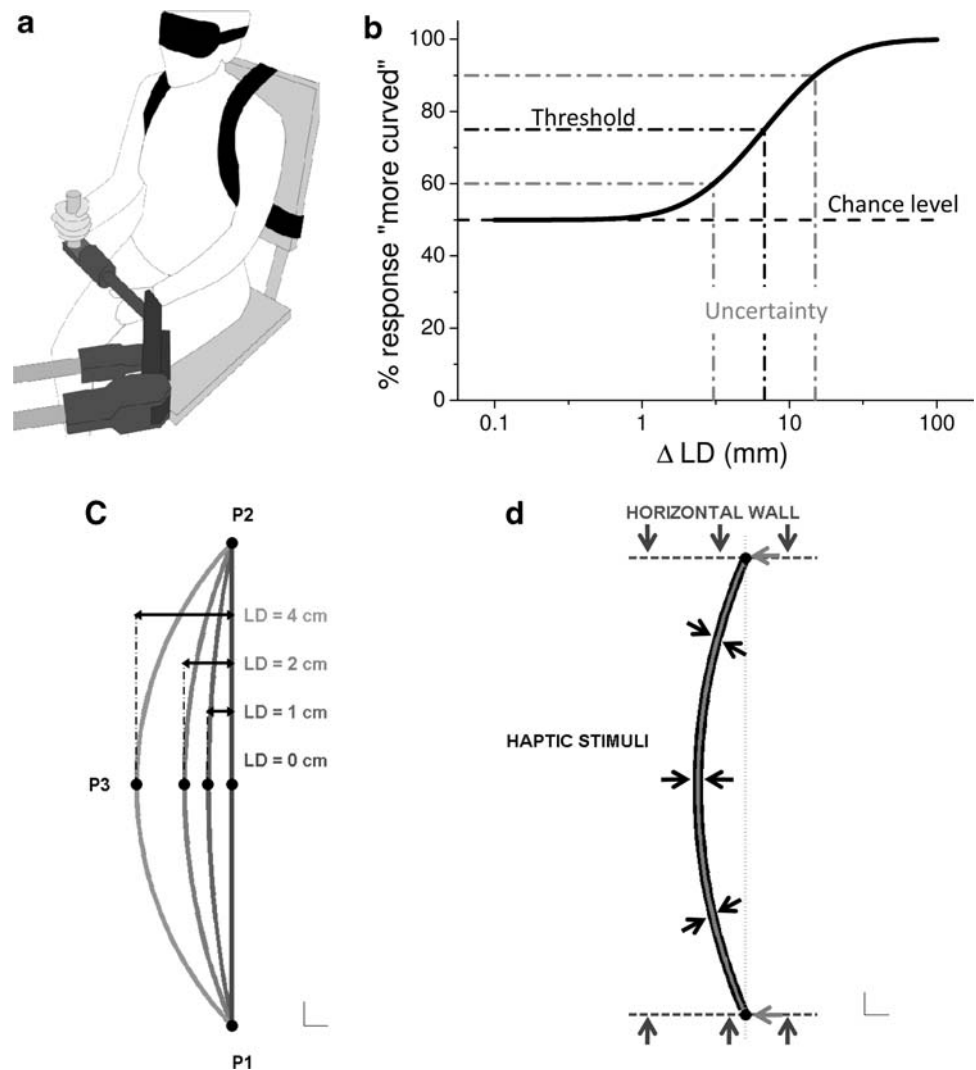
In general, the end-effector moved along an arc starting from point P1, passing through P3 and ending at P2 (Fig. 2c) and then returning to P1. The motion law is:

$$\begin{cases} X_{EE} = X_C + R \cos(\pi + \theta \cos((2\pi/T)(t - tStart))) \\ Y_{EE} = Y_C + R \sin(\pi + \theta \cos((2\pi/T)(t - tStart))) \end{cases} \quad (1)$$

where X_{EE} and Y_{EE} 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 $tStart$ is the begin of motion.

In the *passive condition* the robot delivered a two-component force field to the hand: an attractive force that

Fig. 2 **a** Experimental setup depicting the position of the participants with respect to the 2-degrees-of-freedom planar robot manipulandum. **b** Example of a psychometric function for haptic curvature perception. The *ordinate values* indicate the probability of perceiving the probe as more curved than the standard, the *abscissa* represents the differences in lateral deviation between probe and standard. The *threshold* was defined as the lateral deviation yielding 75% of correct responses. The *interval of uncertainty* was computed as the difference between the two lateral deviations corresponding to the 60 and 90% correct answer levels. **c** Dimensions of the curved virtual contour/path for discrimination experiments. The three standard curvatures are expressed in terms of maximum lateral deviation from a straight line (LDs: 1, 2, 4 cm). **d** Construction of the virtual path for active exploration. The hand path was constrained by three different virtual barriers: (a) two radial force fields, (b) two horizontal barriers as stops, and (c) a vertical wall that was activated when subjects attempted to move beyond $x = 0$



smoothly moved the hand along the virtual surface and a viscous force field for the stabilization of the arm (Eq. 2):

$$F = K \sqrt{|X_T - X_H|} \frac{(X_T - X_H)}{|X_T - X_H|} + \begin{bmatrix} B & 0 \\ 0 & B \end{bmatrix} \frac{dX_H}{dt}, \quad (2)$$

where X_H and X_T are, respectively, the actual coordinates of hand and target position at a precise instant, B is the derivative gain (10 N s/m) and K_H 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. The complete exploration of each curvature lasted 3 s and consisted of forward motion along the curved surface followed by a motion backward along the same path.

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 at a speed similar to the passive condition. To assure that the time to experience the virtual contour was comparable between the active and passive condition, subjects were trained and instructed to perform the active exploration in the same time as during passive motion (≈ 3 s). When subjects moved shorter than 2.4 s (20% decrease in movement time) they were notified by the experimenter and reminded to maintain the target movement time of 3 s (mean movement time for all subjects was 2.9 s; see "Results" for details). Knowing that speed cues are not a major contributor in the haptic sensing of shape (Soechting and Poizner 2005), we refrained from imposing further constraints in the active motion condition. The appropriate boundary forces were characterized by the following controller:

$$F = K(X_H - X_W) + \begin{bmatrix} B & 0 \\ 0 & B \end{bmatrix} \frac{dX_H}{dt}, \quad (3)$$

where the stiffness K and damping B were set to 2,500 N/m and 10 N s/m, respectively. The force field was active outside the boundaries depicted in Fig. 2d.

Design and measurements

In each condition (active vs. passive) subjects were exposed to one of the four standard values ($LD = 0, 1, 2, 4$ cm). Each standard was presented together with a comparison stimulus in blocks of 80 trials, yielding a total of 640 trials per subject. The order of presentation of the standard and the comparison stimuli in each trial was random, and thus not predictable for the subject. For determining the absolute sensitivity to detect curvature (detection threshold), the standard value was a straight line ($LD = 0$ cm), and the comparison stimulus had a convex curvature. The ability to discriminate between two curved contours (discrimination threshold) was examined at the three other standard values ($LD > 0$ cm). In this case, two different curvatures were presented in each trial, one fixed at a specific base value (*standard*) and the other variable, but always bigger than the base (*comparison*).

The percentage of trials where the probe was judged as more curved than the standard was computed for each of the four standard curvatures, and was fitted with a cumulative Gaussian function, yielding four psychometric sensitivity functions for each subject and condition (for an example, see Fig. 2b). Based on these sensitivity functions we derived eight haptic thresholds and *intervals of uncertainty* for each condition and standard stimulus (2 conditions by 4 standards). The threshold was defined as the lateral deviation for which the comparison value was correctly perceived as more curved than the standard at the 75% correct response level. Standard errors of the thresholds were computed using a bootstrap simulation (Efron and Tibshirani 1993). The *interval of uncertainty* for haptic estimation was computed as the difference of the two lateral deviation values at the 0.6 and 0.9 probability of giving a correct response (i.e., the 60 and 90% correct response level, see Fig. 2b). The interval of uncertainty provides a measure for the range of curvature values at which the subject could not reliably perceive a difference between the standard and the comparison stimulus.

Results

To evaluate the effect of PSF on haptic acuity of curvature perception, we compared detection and discrimination thresholds and uncertainty intervals for the *active* and *passive* condition. The mean active motion duration across all subjects and conditions was 2.9 ± 0.9 s, indicating that

the time to haptically sense the virtual contours was very comparable between conditions (passive movement time was constant at 3.0 s).

Haptic thresholds

To gain an understanding about the distribution of thresholds for both conditions, Fig. 3a shows the thresholds of all subjects for the four standards, with each individual's active threshold being plotted against his/her passive threshold. Most data points are distributed along the line of equality, indicating that neither condition led to consistently higher or lower thresholds. Fitting a linear function of the form $y = ax$ to these data yielded an angular coefficient of $a = 0.94$ (95% confidence bounds 0.81–1.08; $R^2 = 0.33$). This value was not significantly different from $a = 1$ (i.e., a 45° slope). To determine to what extent active sensing differed from passive sensing in each subject, all active thresholds were expressed as a percentage of the corresponding passive threshold (passive threshold = 100%). We found that 47% (15/32) of the individual subject thresholds during active motion were lower than the corresponding passive thresholds (range >3.5–56%), while 53% (17/32) were higher (range <–3.6 to –117%), indicating that there was no systematic bias for either condition. Only for the highest base value ($LD = 4$ cm), we could find a trend that active sensing was inferior to passive sensing (6/8 subjects showing lower thresholds in the passive condition).

A corresponding repeated measures (2 conditions by 4 standards) Analysis of variance procedure for threshold yielded no significant main effect for condition ($P > 0.05$) but a significant main effect for standard ($P = 0.0012$). A subsequent Tukey–Kramer post-hoc test revealed that the discrimination threshold for the 1-cm standard was significantly lower than those of detection ($LD = 0$ cm; $P < 0.05$) and discrimination with standard 4 cm ($P < 0.01$). The two-way interaction (condition \times standard) did not reach the level of significance ($P > 0.05$). The corresponding mean threshold values are shown in Fig. 3a (bottom panel). When sensitivity is expressed as the maximum lateral deviation of the curved contour, the mean detection thresholds were computed as 8.3 ± 0.9 mm for the active and of 6.8 ± 1.0 mm for the passive condition (corresponding to curvatures of 1.65 and 1.35 m⁻¹, respectively). For both active and passive conditions, the mean thresholds for all four standards graphically represented characteristic ‘dipper’ functions. ‘Dipper’ functions are indicative of facilitation effects that are observed when two stimuli close to the detection threshold are to be discriminated. Here, the discrimination thresholds for $LD = 1$ cm were approximately 30% lower than the corresponding detection thresholds.

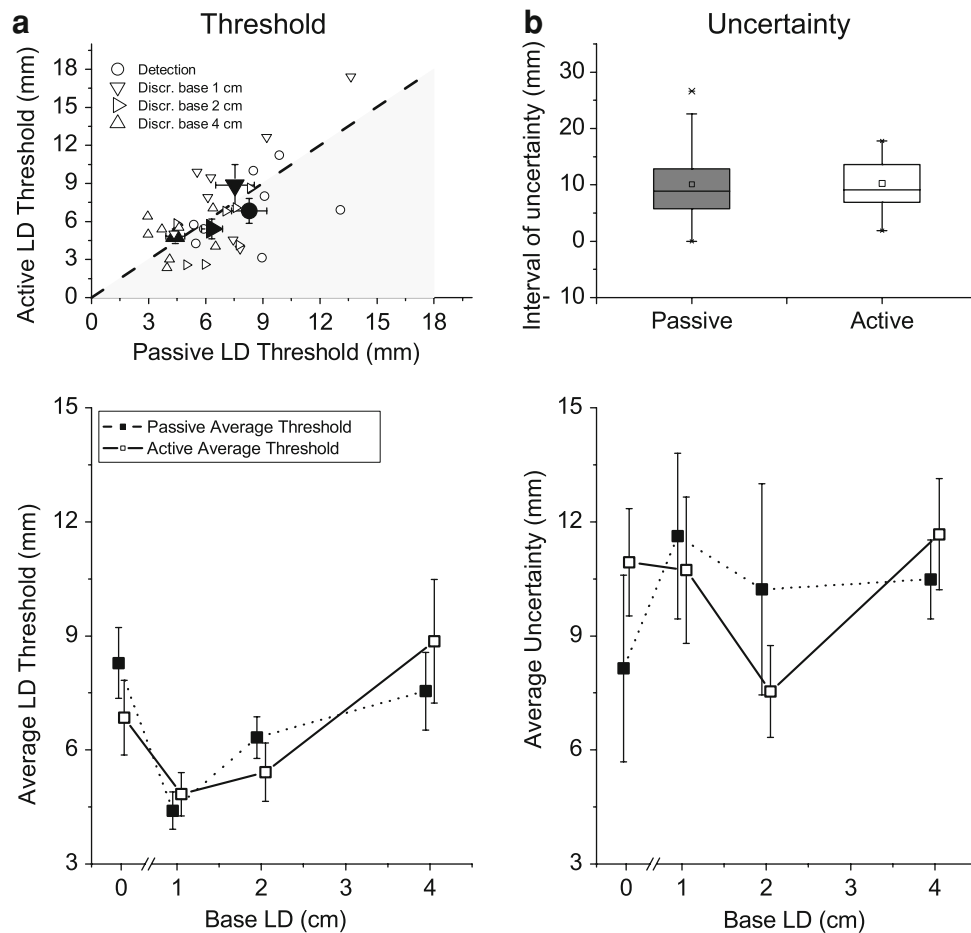


Fig. 3 **a** *Top panel* active versus passive curvature thresholds of each subject and standard (LD = 0, 1, 2, 4 cm). Different symbols represent different standards. A data point located in the shaded lower right side of the graph indicates that a subject had a higher passive threshold when compared to the active threshold, thus indicating a lower haptic acuity during passive sensing. The opposite would hold for a point in the upper left side of the graph (white background). The dashed line represents the line of equality, where the thresholds measured during active and passive exploration of the

same curvature were identical. Each of the four black symbols represents the average threshold for the corresponding task. Error bars represent group standard error. *Bottom panel* average active (solid line) and passive (dashed line) thresholds for the complete sample ($N = 8$). **b** *Top panel* box plot of intervals of uncertainty distributions in passive and active conditions. *Bottom panel* average active (solid line) and passive (dashed line) intervals of uncertainty for the complete sample ($N = 8$)

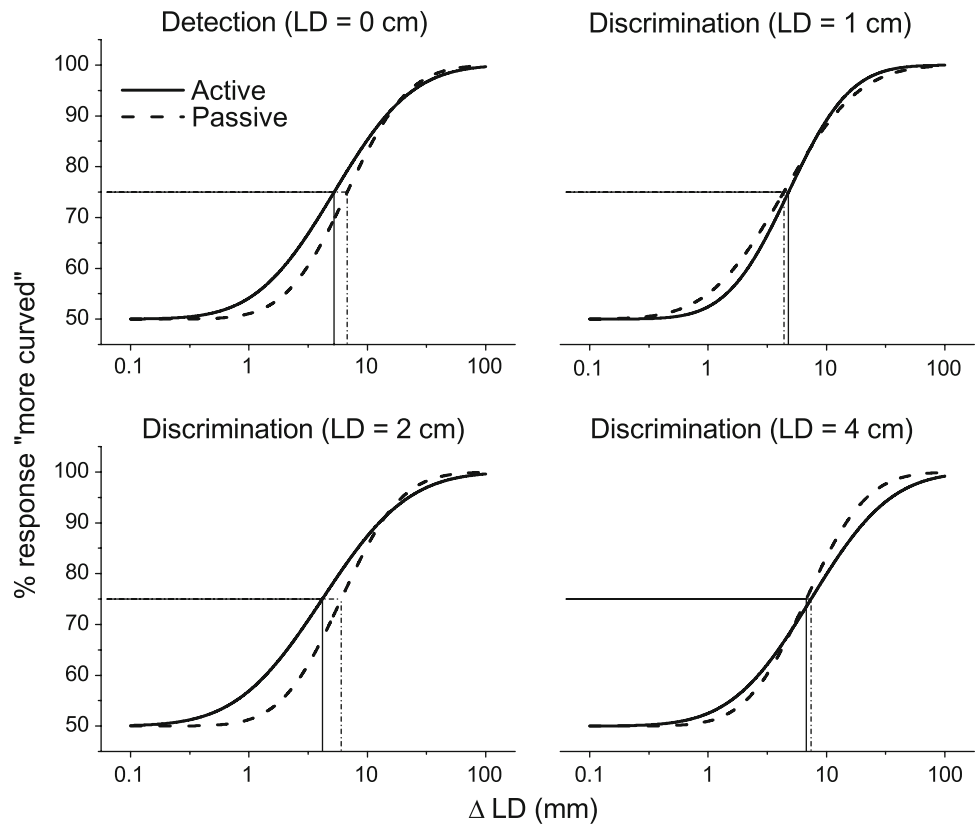
Intervals of uncertainty

To understand whether subjects exhibited different levels of uncertainty between the active and passive condition we computed the intervals of uncertainty. Figure 3b shows the distribution of the uncertainty intervals in the two conditions. The two distributions were not statistically different from each other as confirmed by a Kolmogorov–Smirnov test ($P > 0.05$). A corresponding repeated measures (2 conditions by 4 standards) analysis of variance procedure yielded no significant main effect either for condition ($P > 0.05$) or for standard ($P > 0.05$). Also the two-way interaction (condition \times standard) did not reach the level of significance ($P > 0.05$). The corresponding mean uncertainty values are shown in Fig. 3b (bottom panel).

Derived sensitivity functions

In a final analysis step, we used the pooled responses of all subjects to obtain general sensitivity functions representing the complete sample population. Figure 4 shows the two fitted psychometric functions for each condition. Each sensitivity function is based on pooling the responses of all the eight subjects for a particular standard (LD = 0, 1, 2, 4 cm; total $N = 5,120$ trials) and was obtained by fitting a cumulative Gaussian function. As can be seen the thresholds and intervals of uncertainty (i.e., the slope of each function) are rather similar. There was no discernible trend that thresholds or uncertainty level varied systematically between conditions (active vs. passive) and standard stimuli (LD = 0, 1, 2, 4 cm).

Fig. 4 Derived sensitivity functions for the active (*solid line*) and passive (*dashed line*) conditions for the four different standards (LD = 0, 1, 2, 4 cm). Each psychometric curve was obtained by pooling the responses of all the eight subjects for each condition (active/passive) and standard. The *solid* and *dashed thin lines* indicate 75% correct response level thresholds. The derived sensitivity functions reveal no discernible trend that active haptic sensing is superior to passive sensing



Discussion

In everyday life, there are many situations in which we rely on haptic information to recognize familiar or to explore new objects. Haptic exploration is a sequential process in which information is acquired serially over time and stored in working memory before a stable percept is formed (Henriques and Soechting 2005; Ehrich et al. 2008). Haptic perception constitutes a special case of perception because it is based on the integration of multisensory feedback (see Fig. 1).

This experiment investigated the potential role of PSF derived from a motor efference copy on haptic sensitivity. Participants experienced virtual round object contours during active manual exploration and when their hands were being passively guided. In contrast to the general prediction that increased sensory redundancy leads to an improved perceptual estimate, our results showed that performing an active exploration does not systematically improve precision of the haptic perception of object curvature. We found that with increasing base curvature haptic sensitivity deteriorated in the same way for both passive and active curvature evaluation. While such deterioration in sensitivity is consistent with the Weber–Fechner Law (Fechner 1889), the finding also excludes the possibility that PSF assumes a noise reduction role for haptic perception. On the contrary, our results are suggestive that

passive evaluation is associated with slightly lower thresholds when the objects curvatures become larger (see Fig. 3a bottom panel, for LD = 4 cm). These results are corroborated by earlier findings showing that haptic sensitivity of older healthy adults and patients with Parkinson's disease did not benefit from active motion (Konczak et al. 2008), and that proprioceptive acuity may actually decrease during active motion (Lillis and Scheidt 2003).

Computational models of perception have demonstrated that visuo-haptic information is integrated in a statistically optimal fashion, and that the redundancy of perceptual information improves perceptual precision (Ernst and Banks 2002; van Beers et al. 2002; Gori et al. 2008). Our results suggest that this may not be the case for internal feedback, because the presence of PSF did not increase haptic acuity. This implies that PSF may be an integral part of the motor control system, where it can aid various functions such as improving execution or reducing motor errors (von Holst and Mittelstaedt 1950; Jordan and Rumelhart 1992; Flanagan and Wing 1997; Wolpert and Kawato 1998; Kawato 1999), but it does not contribute or enhance haptic precision. That is, PSF is used by the nervous system as a sensorimotor signal, yet it may play little or no role for the perceptual estimation of object properties.

Before accepting this conclusion, one needs to examine whether alternative explanations are equally plausible. First, is it possible that differences in attention between

active and passive sensing mask a potential benefit of PSF? There is no evidence to support this argument. In fact, previous research demonstrated that added attentional demands such as backward counting or performing a movement sequence had no appreciative impact on proprioceptive sensitivity (Collins et al. 1998; Lillis and Scheidt 2003). Second, is it possible that PSF was not useful for improving haptic precision, because the task was novel and the nervous system had not yet obtained a precise forward model of the hand-object dynamics? This explanation cannot be refuted by our data. Recent research has demonstrated that the haptic perception of complex shapes is influenced by experience and expectations (Ehrich et al. 2008). Although our virtual objects were symmetric and thus rather simple in shape, we cannot exclude the possibility that movement and perceptual experience regarding these virtual contours would improve sensitivity as part of a learning process. Based on our results we can only conclude that the ability to discriminate small differences of haptic stimuli is likely a prolonged learning process exceeding the 80 trials subjects experienced in this experiment.

Finally, is it possible that during active exploration “noise” from the innervated muscles degrades proprioceptive signals necessary for haptic perception? Because active exploration is necessarily associated with muscular activation, and many proprioceptive sensors are embedded or are part of the musculo-skeletal system (e.g., muscle spindles, Golgi tendon organs), it is plausible that neural activity associated with muscle innervation actually increases noise or biases the haptic system. There is evidence suggesting that active motion biases limb position sense leading to an overestimation of position during the early portion of a planned movement and to underestimation during the final movement phase (Wolpert et al. 1995; Lönn et al. 2000; Gritsenko et al. 2007). Such behavior is consistent with a system that relies on state estimation at the beginning of the movement, and mainly uses afferent delayed feedback during the later part of the movement (Wolpert et al. 1995; Vaziri et al. 2006). However, when human participants were deprived of efference copy information during passive motion, the overestimation of the early motion persisted (Gritsenko et al. 2007) casting doubt that efference copy-derived PSF was responsible for the perceptual bias. Given that our data did not reveal a consistent bias during either the active or passive condition, we have no indication to assume that PSF influenced haptic sensitivity in our task. Yet, the absence of a perceptual bias does not negate the possibility that muscle activation is associated with increased sensory noise. There is indeed evidence indicating that muscle activity can degrade proprioceptive sensitivity. The study by Lillis and Scheidt (2003) examined human sensitivity to hand path deviation

from a straight line using a similar setup as in this experiment. They found that the presence of isotonic contractions of antagonistic muscles (i.e., those acting against the intended movement direction) decreased the sensitivity of hand path curvature perception while agonistic activity had no effect. In contrast to Lillis and Scheidt (2003, Experiment 2), subjects actively moved the handle in our experiment. That is, the muscular activation determined the motion of the hand, not an external force. In addition, the arm movements in our experiment were not associated with a strong isotonic activation. Therefore, the effect of muscle activity on our data cannot be inferred from the results of Lillis and Scheidt (2003). However, it is known that increases in movement amplitude are associated with increased muscle activation (longer duration and/or fiber recruitment). This increased motor signal intensity leads to higher variability of the corresponding central nervous signals, which in turn can affect centrally generated signals such as predicted sensory feedback (PSF, see Fig. 1). If PSF has any influence on haptic perception, one would expect that noisy PSF would lead to a reduced haptic sensitivity. That is, noise due to central motor commands could affect perception. With respect to our experiment, this “motor noise” hypothesis implies that when movement amplitudes and muscular innervations levels increase, haptic acuity should decrease at a higher rate during active touch than during passive sensing. In fact, this is what we found: at the largest curvature standard (LD = 4 cm), which was associated with the longest hand paths, the differences between passively guided and active motion were most pronounced, and the mean threshold for active motion was 19% higher than passive threshold (see Fig. 3a). However, this finding alone is not sufficient to prove the “motor noise” hypothesis.

In summary, human haptic perception of hand path curvature is highly precise both during active exploration and passive touch; on average, a lateral deviation around 7 mm over a 200 mm linear distance was sufficient to distinguish a curved line with respect to a straight line. When asked to discriminate between two curved contours, haptic sensitivity decreased as the base curvature increased—a finding consistent with the Weber–Fechner law (Fechner 1889). The main finding is that absence of efference copy information did not systematically degrade haptic acuity. This indirectly implies that PSF does not aid or enhance haptic perception. There is some evidence that active motion actually might compromise haptic acuity, a finding consistent with earlier studies (Lillis and Scheidt 2003; Konczak et al. 2008). We conclude that in situations where a high degree of haptic sensitivity is required to explore novel objects, the perceptual system relies primarily on the integration of afferent sensory information (tactile and proprioceptive). PSF may become beneficial

for recognizing and manipulating known objects. That is, its role for haptic perception may become enhanced with perceptual experience. However, this claim requires systematic study, and this experiment did not systematically investigate the issue of perceptual experience.

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