RESEARCH ARTICLE

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Haptic shape discrimination in humans: insight into haptic frames of reference

Abstract This study investigates how a change in the physical relation between objects (two-dimensional, 2-D, angles) and a subject, as well as scanning conditions, modify the ability to discriminate small changes in 2-D shape. Subjects scanned pairs of angles (90º standard; 91º–103º comparison angles) with the right index finger of the out-stretched arm, identifying the larger of each pair. When joint rotation was restricted to the shoulder, the discrimination threshold significantly increased when the angles were explored with the shoulder in a more eccentric position rather than closer to the midline (60º versus 30º to the right). This result was attributed to changes in proprioceptive sensitivity, since explorations restricted to distal joints (wrist/second metacarpopha-langeal joint) showed no change with shoulder position. The results showed, moreover, that discrimination threshold was similar for distal and proximal joints when the delay between scanning the pairs of angles was long (15 s). This observation suggests that regional variations in proprioceptive acuity (proximal > distal) may reflect an adaptation to generate an invariant central representation of haptic shape. Using a shorter in-terscan delay (5 s), a position-dependent increase in discrimination threshold was revealed for distal explo-rations, an effect that disappeared when the head was turned in the direction of the unseen angle (vision oc-cluded). We suggest that these results can be explained by the existence of two competing egocentric frames of reference with different time courses, one of short duration that is centred on the arm/hand, and a second of longer duration centred on the head. At the short delay, the reference frames interacted to distort the haptic representation when they were misaligned. This distortion was resolved at the long delay, possibly through suppression of the arm/hand-centred reference frame.

Keywords Angle discrimination · Proprioceptive · Tactile · Cutaneous · Human psychophysics

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Introduction

Haptic touch, a term coined by Gibson (1966), refers to the ability to extract information about surface or object properties on the basis of combined feedback from cutaneous and proprioceptive mechanoreceptors. Evi-dence now suggests that haptic sensory abilities are more precise than sensory judgements based upon using sig-nals generated by a single somaesthetic modality. For example, by using a task in which subjects explored pairs of two-dimensional (2-D) angles by scanning the index finger of the out-stretched arm over the unseen objects (rotation thus limited to the shoulder), we showed that subjects can discriminate angular differences on the or-der of 4.7° (0.7°–12.1°) (Voisin et al 2002a). The corre-sponding changes in shoulder angle (mean, 0.54°; range, 0.08°–1.36°) were much lower than previous estimates of position sense at the shoulder (Cohen 1958; Hall and McCloskey 1983; Clark et al 1995), suggesting that perception is enhanced when both sources of sensory signals are available. This latter observation has recently been confirmed by Henriques and Soechting (2003). Using a different task whereby subjects judged curvature and trajectory orientation using a robot arm with added force feedback in order to generate virtual walls or

shapes, they estimated that shoulder joint acuity was ~0.2°. Together, these observations suggest that it is the integration of cutaneous and proprioceptive signals that is responsible for the apparently heightened sensitivity to position of the shoulder. Consistent with this, suppression of either cutaneous or proprioceptive feedback significantly increases 2-D angle discrimination threshold, with performance declining to chance levels when both sources of feedback are suppressed (Voisin et al 2002b).

The purpose of this study was to investigate physical factors that can modify the ability to discriminate differences in haptic shape. The results of Kappers and colleagues (Kappers and Koenderink 1999; Kappers 1999, 2002) suggest that the accuracy with which subjects can perform a haptic spatial matching task, reproducing the orientation of a bar (one component of shape), is modified by the spatial location of the bar and the exploration strategy (serial, unimanual versus simultaneous, bimanual). They found that errors increased as the horizontal distance between the reference and test bar increased, but interpretation of their results was complicated by the possibility that proprioceptive sensitivity varied across the different parts of the large workspace (up to 1.2 m) and that some conditions modified the skin area in contact with the bars across the workspace. Interestingly, Zuidhoek et al (2003) showed that the large distortions in matching the orientation of reference and test bars using bimanual explorations were decreased by adding a 10 s delay between the exploration and matching. This observation, inspired by similar observations in the visuomotor field (see Discussion), led the authors to suggest that the delay allowed subjects to switch from an initial egocentric (body-centred) frame of reference to an allocentric (external) frame of reference. It seems logical to expect that such a transformation was essential for their task, which required subjects to transfer and rotate the pattern of sensory impressions from one hand to the opposite one. It is less clear, however, whether such a suggestion can be extended to a consideration of unimanual, serial explorations that require no interhemispheric transfer or rotation.

There is also some evidence that these reference frames are modifiable. Zuidhoek et al (2004) demonstrated that performance in the bilateral haptic matching task is improved when the head/eyes are oriented towards the unseen reference bar, as compared to a neutral position, or oriented towards the contralateral hand, also unseen, manipulating the test bar. In addition, they found that noninformative vision (hands hidden) also improved performance when compared to a no vision condition (see also Newport et al 2002).

The purpose of the present experiments was to determine how changes in the physical relations between the explored angles and the subject and changes in the scanning conditions modify the ability to discriminate small differences in 2-D shape. The haptic explorations were limited to unimanual, serial explorations of 2-D angles (standard 90°; comparison, 91°–103°) using identical trajectories, allowing us to systematically investigate several key factors that could potentially contribute to the perception of haptic inputs from the immediate peripersonal space. We investigated the effects of changing the positions of the explored angles in space, using two different exploratory strategies: angles were explored with the index finger of the outstretched arm, and rotation was restricted to either proximal (shoulder) or distal joints (wrist and second metacarpophalangeal, mcp). This allowed us to address the potential contribution of changes in receptor sensitivity to the results when angles were explored at different locations using shoulder movements, and to compare performance at proximal and distal joints. Thus, we were able to determine whether known variations in position sense, proximal joints being more sensitive than distal joints (Hall and McCloskey 1983), lead to systematic changes in haptic shape discrimination. Finally, we investigated the influence of two factors known to modify performance in bilateral haptic matching tasks, extending these results to a strictly unimanual and serial exploration: the delay between successive scans of the pairs of angles, and the orientation of the head relative to the unseen angles.

Preliminary reports of the results have appeared (Voisin and Chapman 2003a, 2003b).

Methods

Subjects

Three women and three men (ages 21–27 years) volunteered to participate in experiment 1 (one experimental session). Eleven volunteers (5 women, 6 men; 22–50 years) participated in experiment 2 (one to four sessions per subject). Two subjects participated in both experiments. All but two subjects were right-handed for writing (one from each experiment). The experimental protocol was approved by the institutional ethics committee, and all subjects gave their informed, written consent before participating in the experiments. The duration of each experimental session was approximately 2 h for experiment 1, and 1 h for experiment 2.

Angles

A set of angles (Fig. 1B) was machined from 1 cm thick Plexiglass. These are described in detail in Voisin et al (2002a). Briefly, each angle was formed by the intersection of two 8 cm long arms. The first arm explored (*ab* in Fig. 1B) was identical for all angles; the second arm (*bc*) was modified to form a standard angle of 90°, or a comparison angle, 91°–103° (2° steps). The angles were clamped upright into an apparatus instrumented with three pairs of light-emitting diodes and optical sensors to record digit position at the start position, *a*, the intersection, *b*, and opposite extremity, *c* (see Fig. 2a in Voisin et al 2002a).
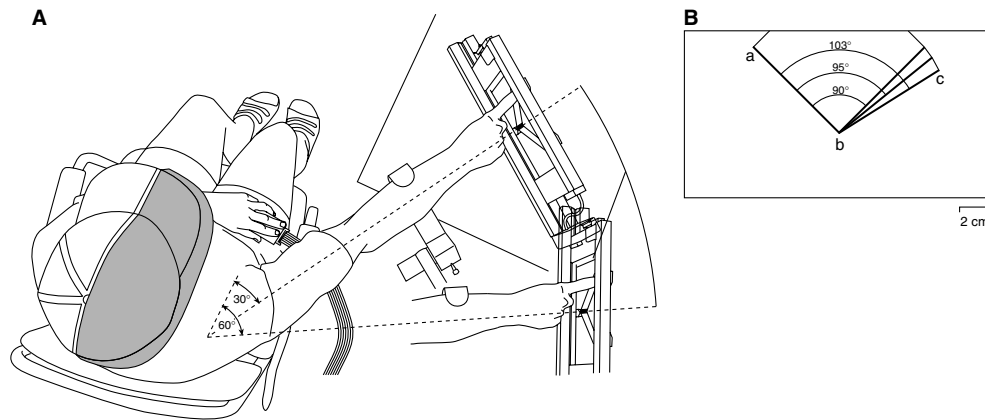
Fig. 1A–B A Subject position in the reference condition (apparatus 30° to the right) and the modified condition (60° to the right) for experiment 1. The index finger is shown at the start position (*a* in **B**). Vision of the objects was occluded by a mask over the right-hand side of the head (*shaded region*). The forearm support was used for all experiments involving distal joint rotations; it was removed for those using shoulder movements. **B** Schematic depiction of the 2-D angles from the point of view of the subject. The standard angle was 90°; the comparison angles ranged from 91° to 103°. The surface scanned by the finger is shown with a *thick line*. All scans began with the index finger positioned at *a*, and involved a to-and-fro movement (*abcba*). Note that the first arm of the angle, *ab*, was identical for all angles

Two-dimensional angle discrimination task

The methods have been described in detail elsewhere (Voisin et al 2002a). In brief, the subjects were seated in a chair with the apparatus positioned at arm's length and at the height of the shoulder (Fig. 1A). Vision was occluded, and white noise delivered through headphones. A two-alternative forced-choice task was used. The experimenter first guided the subject's finger to the start position (Fig. 1A). Subjects scanned the right index finger (D2) over the first angle using a single to-and-fro movement (*abcba*). After the subjects withdrew their finger from the apparatus, a second angle (90° or a comparison angle) was installed. After repositioning the finger at the start position, the second angle was scanned. The delay between successive scans within a trial was ~14 s for experiment 1 (Voisin et al 2002a); for experiment 2, the delay was either ~5 s or ~15 s (silent count). For convenience, these are referred to as delays of 5 and 15 s hereafter. After scanning the two angles, subjects identified the larger angle by pressing one of two response buttons on a keypad with the left hand (first or second angle larger, see Fig. 1A). No feedback on performance was given. One angle in each pair was slightly rotated towards the midline (4° shift in the vertical plane) to ensure that subjects evaluated the whole angle and not just the orientation of the second arm relative to horizontal (Voisin et al 2002a). The order of testing was counterbalanced for all factors (shift on the first or second angle, standard angle presented first or second, value of the comparison angle).

Experiment 1

The purpose of this experiment was to determine whether 2-D angle discrimination is modified by the position of the scanned angles relative to the subject's shoulder. In the reference condition, the apparatus was placed 30° to the right of a midsagittal plane running through the acromion, as shown in Fig. 1A (note that the forearm support shown here was removed). The position of the apparatus was adjusted so that the glabrous skin of the middle phalanx of D2 contacted the angle at the intersection (dotted line). Subjects scanned the angles with the glabrous skin of the middle phalanx of D2, forearm pronated and arm out-stretched, so that movement was restricted to the shoulder. In the modified condition, the apparatus was positioned 60° to the right (Fig. 1A). In order to ensure that the cutaneous contact (glabrous skin of D2) was identical to the reference condition, the orientation of the apparatus was adjusted so that it was perpendicular to the arm at the intersection (*b*, and see Fig. 1A).

Experiment 2

This series of experiments evaluated 2-D angle discrimination when the scanning movements were restricted to the distal articulations (mainly wrist, but also involving the second mcp joint). Subject position is shown in Fig. 1A. During the scans, the forearm rested on a support to ensure that the movements were restricted to the distal articulations. As D2 scanned over the angles, the skin in contact shifted distally at the two extremities of the scan, extending to the distal phalanx for subjects with smaller hands. As a consequence, the tip of D2 did not reliably interrupt the LED/optical sensors at positions *a* and *c* (Fig. 1B), and so we were unable to monitor movement kinematics (below). Four comparisons were made. First, we repeated the experiment described for experiment 1 (apparatus positioned at 30° or 60° to the right), but the angles were now explored using movements of the distal articulations. This modification sought to dissociate the effects related to the location of the explored angles from potential changes in receptor

sensitivity at the moving joint. Second, we compared 2-D angle discrimination performance when the angles were explored with either proximal or distal articulations (separate blocks of trials). In this case the position of the angles was as for the reference condition in experiment 1 (apparatus positioned at 30° to the right of midline, delay of 15 s). Third, we examined the effect of decreasing the delay between the end of the first scan and the start of the second from 15 s to 5 s, with the aim of determining whether the delay between the successive scans contributed to the results. The apparatus was explored in two positions, 30° and 60° to the right. Finally, with the apparatus located at 60° to the right of midline, we evaluated the influence of the orientation of the head on 2-D angle discrimination. Performance with the head pointing forward (for example, see Fig. 1A) was compared to that obtained when the subject was instructed to turn their head in the direction of the apparatus. In both situations, vision of the angles and the exploring arm was blocked; the interscan delay was 5 s.
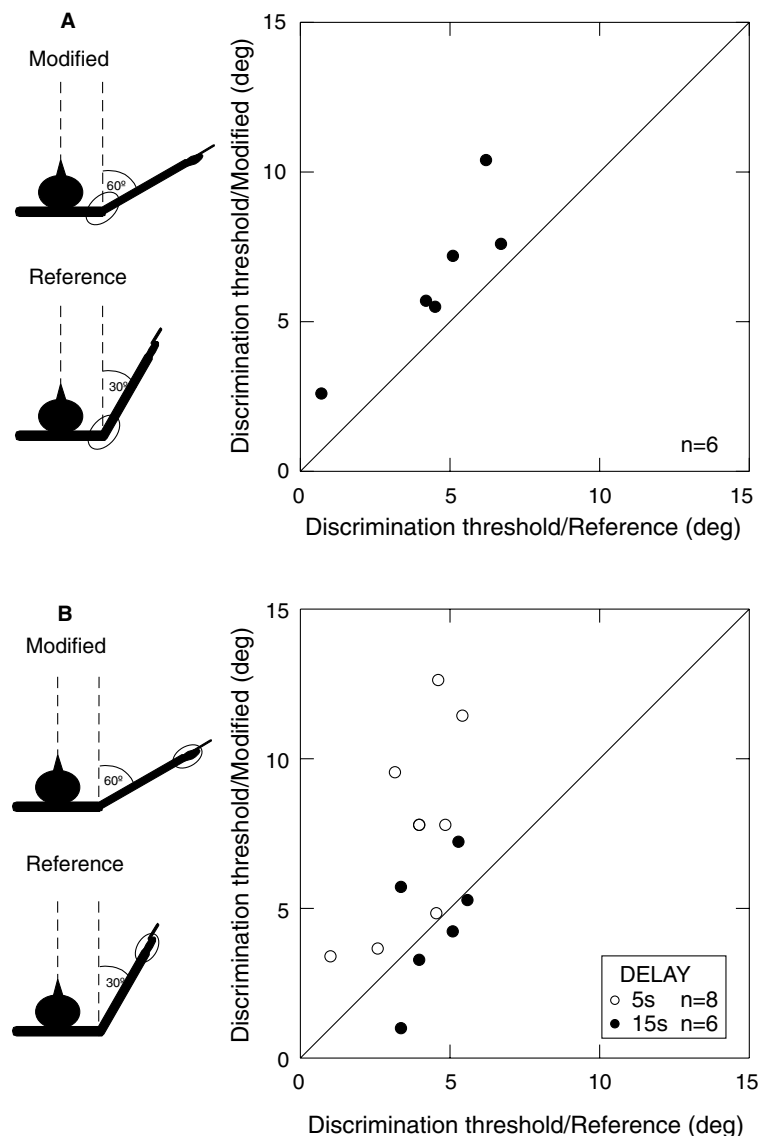
Experimental design

In each experimental session, one block of trials was the reference condition, and the other was the modified condition (order counterbalanced across subjects). In experiment 1, each block contained 56 trials (eight replications of seven comparison angles, 91, 93, 95, 97, 99, 101 and 103°); this was reduced to 32 trials/block in experiment 2 (eight replications of four comparison angles, 91, 95, 99 and 103°). Each block was preceded by several practice trials to familiarize the subject with the experimental condition.

Data acquisition and analysis

Discrimination performance was characterized for each subject, in each block of trials, by computing the proportion of correct responses for each comparison angle. The results were then fitted to a logistic function, from

Fig. 2A–B Effect of changing the location of the explored angles on discrimination thresholds when subjects explored the angles with the outstretched arm: rotation was limited to either the shoulder (**A**) or the wrist/second mcp (**B**). As shown in the cartoons on the left, angle position relative to the subject in the reference condition was 30º to the right of a midsagittal plane running through the acromion (see *dotted line*); in the modified condition, the angles were presented in a more eccentric position, 60º to the right. The joint at which rotation occurred is encircled on the cartoons. Discrimination threshold in the modified condition (60º) is plotted as a function of threshold in the reference condition (30º), with the *diagonal line* corresponding to identical performance in both conditions. When exploration involved shoulder movements (**A**), all subjects showed an increased discrimination threshold in the more eccentric position (interscan delay, ~14 s). When joint rotation involved the wrist/second mcp (**B**, note that these were not the same subjects as in **A**), discrimination threshold was similar in both positions when the delay was long (15 s, *filled symbols*). When the delay was decreased (5 s, *open symbols*), threshold was higher at the eccentric position (60º)

which the discrimination threshold (75% correct) was computed (Voisin et al 2002a). If the estimated threshold was greater than the largest comparison angle presented, 103° (corresponding to an angular difference of 13° from the standard angle, 90°), then discrimination threshold was arbitrarily set at 13°. Paired *t*-tests were applied to the group data for each comparison made (reference versus modified condition). For experiment 1, the outputs of the optical sensors were used to characterize the scanning movements in terms of average speed and the length of time that the digit was in contact with the intersection (dwell-time at point *b*, Fig. 1B). For experiment 2, these data were not available (above). The level of significance for all analyses was set at $P < 0.05$.

Results

Experiment 1

Performance of the 2-D angle discrimination task

Data were collected from six sessions in six subjects. In this series of experiments, the angles were explored with D2, and movement was restricted to the shoulder by instructing the subjects to keep their out-stretched arm rigid throughout the to-and-fro scans. The movement trajectories themselves were defined by the angles (90°–103°), and were identical for both testing conditions. The data from the reference condition (angles positioned 30° to the right) have been described elsewhere (Voisin et al 2002a). In brief, a wide range of discrimination thresholds was found (0.7°–6.2°). Practice did not significantly improve 2-D angle discrimination. The only factor to change with practice was scanning speed: subjects were faster when testing was repeated. There was considerable variation in scanning speed and the length of time that the digit was in contact with the intersection (dwell-time) across subjects, but there was no evidence that either factor was systematically modified as a function of the value of the angle explored (Voisin et al 2002a).

60° versus 30°

In this comparison, we tested the effect of changing the position of the angles relative to the subject. Angles were scanned at either 60° or 30° to the right of a midsagittal plane passing through the right acromion. Movement trajectories, defined by the angles, were identical in both cases. The majority of subjects (4/6) found that the modified condition was similar in difficulty to the reference condition. Nevertheless, there was a systematic and significant increase in discrimination threshold in the more eccentric position, 60° (mean, 6.5°), as compared to the reference condition, 30° (4.6°, $P = 0.011$; Fig. 2A). The parameters of movement were also systematically changed in the eccentric position: mean scanning speed was faster (reference, 178 mm/s; modified, 190 mm/s, $P = 0.032$), and there was a parallel de-crease in dwell-time at the intersection (respectively, 825 ms and 767 ms, $P = 0.036$). Two factors may have contributed to the higher thresholds in the 60° position. On the one hand, the higher thresholds might be explained by cognitive factors, in particular the relative lack of familiarity of subjects with interpreting signals from the more eccentric location as compared to parts of the workspace closer to the midline. Alternately, it is equally possible that the proprioceptive feedback was modified by the change in position with, for example, recruitment of different populations of muscle spindle afferents, possibly differing in sensitivity to limb position in the two different test positions.

Experiment 2

Data were collected in 27 sessions from 11 subjects.

60° versus 30°

In order to determine if changes in proprioceptive feedback, specifically recruiting muscle spindles in different parts of the musculature controlling the shoulder movements, contributed to the results obtained in experiment 1, 2-D angle discrimination was tested when the exploratory movements were restricted to the distal articulations (mainly wrist but also involving the second mcp joint). The results are shown in Fig. 2B (filled symbols, $n = 6$). No change in discrimination threshold was observed across the two test positions (30°, 4.4°; 60°, 4.5°, $P = 0.983$). This finding supports the suggestion that the increased threshold seen when the exploratory movements were made using shoulder joint rotation was most likely explained by reduced proprioceptive sensitivity in the more eccentric position.

Proximal versus distal

Given the similarity of the results obtained with distal explorations in the reference condition to those obtained using shoulder movements in the reference condition (30°), we directly compared the abilities of six subjects to discriminate 2-D angles using proximal or distal (wrist/second mcp) movements. The angles themselves were placed at 30° to the right, and the delay between scanning the pairs of angles was set at 15 s. The results are presented in Fig. 3. There was no significant difference in the mean discrimination threshold for the distal explorations, 4.1°, as compared to the proximal explorations, 3.1° ($P = 0.532$). The lack of any difference was confirmed by pooling the data from all of the reference conditions performed with the angles located 30° to the right (including data presented in Voisin et al 2002a): mean threshold was 4.9° ($n = 19$) for the shoulder explorations, and 4.1° ($n = 20$) for the wrist/second mcp explorations (independent *t*-test, $P = 0.222$).

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Fig. 3 When tested in the same subjects, 2-D angle discrimination thresholds were similar for explorations made using either the wrist/second mcp (reference condition) or the shoulder (modified condition). Angle position, 30º to the right; interscan delay, 15 s. Plotted as in Fig. 2
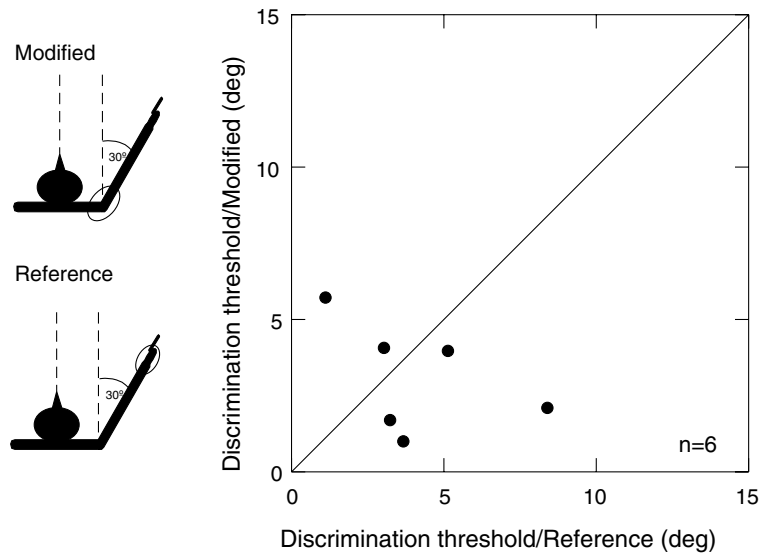
Effect of decreasing the interscan delay

'To determine whether the delay between scanning the first and second angle of each pair contributed significantly to our results, we repeated the 60° versus 30° comparison (distal movements), decreasing the interscan delay from 15 s to 5 s. As shown in Fig. 2B (open symbols), there was a significant increase in threshold in the more eccentric position (60°, 7.6°; $P = 0.005$) as compared to the less eccentric position (30°, 3.8°). Since six of the eight subjects participated in both delay conditions, we were also able to determine that delay had no effect on discrimination threshold when the angles were located closer to the midline (5 s versus 15 s delay, $P = 0.442$). The results indicate, first of all, that the memory requirements of the task whereby subjects had to retain the memory of the first angle and compare this to the second did not—within the tested range—contribute to the results, since performance was similar for the two delays, at least when the angles were explored in the less eccentric position. The decreased performance with a short delay at the more eccentric location, on the other hand, is consistent with the possible existence of two separate frames of reference, one evident at a short delay and the other at the longer delay.
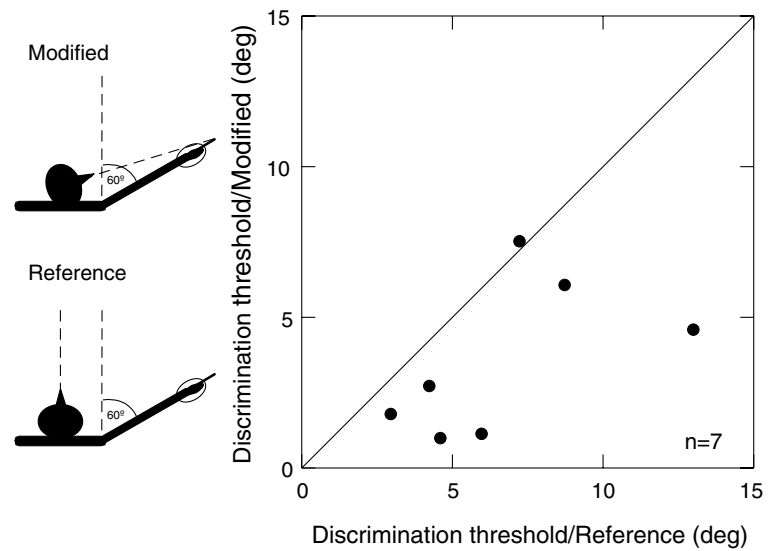
Effects of head orientation

To further explore the nature of the frame(s) of reference used to interpret haptic signals, we then repeated the latter experiment (distal explorations, angles located eccentrically) under two conditions—with the head pointing straight ahead (as in all experiments), and then with the head turned in the direction of the unseen angles (vision occluded as in all testing). We hypothesized that the higher threshold at the more eccentric position might reflect the existence of a head-centred reference frame, given that previous experiments showed that haptic perception is modified by head orientation (Zuidhoek et al 2004). A short interscan delay, 5 s, was employed so that threshold was elevated in the reference condition (head forward). All of the subjects ($n = 7$) also participated in the experiment evaluating the effects of changing the interscan delay on 2-D angle discrimination, and identical results were obtained on retesting under the same conditions (paired t-test, $P = 0.71$). Figure 4 shows that discrimination threshold was significantly decreased when the head was oriented toward the scanned angles (head forward, 6.7°; head turned, 3.6°; $P = 0.028$); in other words, performance improved. This finding suggested that the position of the angles relative to the shoulder was not the key factor modifying 2-D angle discrimination. Instead, it appeared that the orientation of the head relative to the arm/hand was the determining factor.

Figure 5 summarizes the results from all of the experiments (1 and 2), plotting mean discrimination threshold as a function of the eccentricity of the apparatus, and so the angles, relative to the orientation of the head. Data from the different delays are plotted separately. This shows, first of all, that variability was relatively constant across the different testing conditions despite considerable intersubject variation in threshold. Second, when considering only the data collected with the short delay (Fig. 5b), it can be seen that when the eccentricity of the angles relative to the head was small (0°, corresponding to the head turned position in Fig. 4), then discrimination thresholds were as low as those seen with the head forward, and the angles located closer to midline (30°). Together the results are consistent with the existence of conflicting head- and arm/hand-centred reference frames at short delays. The conflict appears to be resolved at longer delays, possibly in favour of a head-centred reference frame, because arm/hand position was no longer a factor.

Fig. 4 When the angles were explored in the more eccentric position (60º to the right) using wrist/second mcp rotation and a 5 s interscan delay, discrimination threshold showed a marked decrease when the head was turned in the direction of the unseen angles (modified condition) as compared to the head forward position (reference condition, same head position as in all other experiments). Plotted as in Fig. 2

Subject reports

Overall, subjects reported no systematic changes in difficulty across the different conditions tested in experiment 2. Interestingly, the subject who showed no change in the head orientation experiment (closely adjacent to the equality line) was the only subject to report that the head turned position was uncomfortable, and to report that the task was more difficult in the head turned position. Most subjects estimated the range of angles explored as ranging from 90° to 120°–125°. Thus, subjects correctly identified the use of a 90° angle, but they tended to overestimate the actual range of angles explored (90°–103°).

Fig. 5A–B Summary plot of mean discrimination thresholds (± SEM) as a function of the joint at which rotation occurred (**A**, shoulder; **B**, wrist/second mcp) and the eccentricity of the angles themselves relative to the head (nominal angular difference between the spatial location of the angles and the direction in which the head was pointing). Data are grouped according to the interscan delay (5 or 15 s). **A** Summary of the results of 18 blocks of trials (11 subjects) from experiments 1 and 2. **B** Results of 40 blocks of trials (11 subjects) from experiment 2
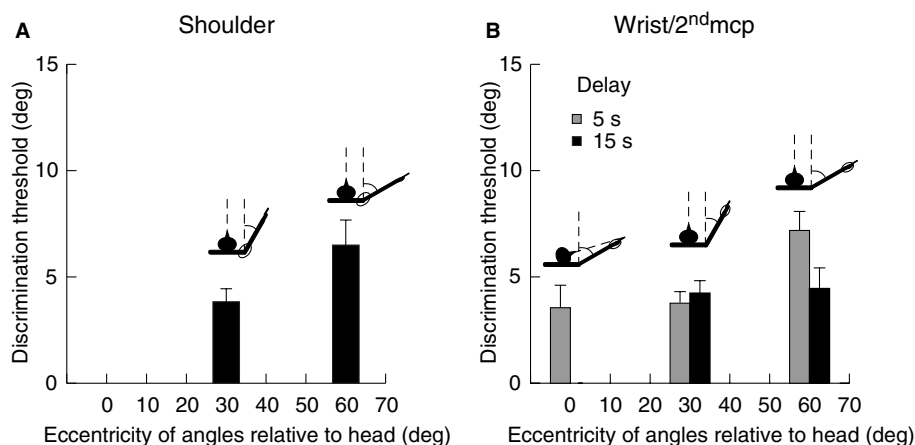
Discussion

In this study, we demonstrated that haptic discrimination of 2-D angles is independent of the motor strategy (specifically the joints at which rotation occurs) when the angles are explored at a position near the midline. 2-D angle discrimination was also independent of the spatial location of the angles (30° versus 60°) when the delay between scanning the standard and comparison angles was long (15 s). In contrast, spatial location was a significant factor at a shorter interscan delay (5 s), but this effect was suppressed when the head was subsequently oriented towards the unseen angles. Together, the results provide insight into the central frames of reference used to represent haptic shape.

Spatial location and haptic angle discrimination

When the angles were explored in a more eccentric position, 2-D angle discrimination threshold was significantly increased for explorations made using shoulder

joint rotation. We initially interpreted this observation as suggesting that haptic discrimination is better in spatial locations closer to the midline, where most explorations in daily life are carried out (Graziano et al 2004). However, spatial location had no effect on 2-D angle discrimination when the explorations were restricted to distal joints (wrist/second mcp joint). Thus changes in proprioceptive sensitivity at the shoulder in the two test positions were most likely responsible for the effects seen when exploration was restricted to the proximal joint. Our finding that haptic angle discrimination is independent of spatial location, within the tested range (30°–60°), is consistent with Henriques and Soechting's (2003) recent report of no change in haptic appreciation of geometric shapes within a relatively constrained horizontal workspace located directly in front of the subject. Although Kappers and colleagues (Kappers and Koenderink 1999; Kappers 1999) found that haptic judgments of bar orientation are less precise as the horizontal, but not the vertical, distance from midline is increased, our results are consistent in that our experimental manipulation generated relatively large changes in the "vertical" location of the angles (within a horizontal plane relative to the subject's midline and running through the shoulder), and minimal changes in the horizontal location.

Proximal versus distal articulations

Previous studies of position sense at proximal and distal articulations have shown that proprioception is better at proximal joints than at distal joints (reviewed in Clark and Horch 1986). The present finding of similar performances with proximal and distal explorations under optimal conditions (15 s interscan delay, Fig. 5) argues in favour of an invariant central representation of object shape independent of the joints involved in the exploration, a conclusion that is necessarily limited to the 2-D angles investigated here. The acuity of the underlying proprioceptive signals, on the other hand, must logically follow the proximal-distal gradient previously described. Explorations with the distal joints necessarily required larger angular excursions than did explorations with the shoulder joint, given the difference in the length of the lever arm. This leads to the suggestion that regional variations in proprioceptive acuity may reflect an adaptation to generate an invariant central representation of haptic shape.

Frame(s) of reference

Much of our knowledge about spatial frames of reference comes from studies of visuomotor control. Such studies have provided evidence that multiple reference frames are used, depending upon task conditions. As recently reviewed by Cohen and Andersen (2002), these can be related to the subject or they can be related to external world coordinates. A variety of egocentric reference frames have been identified, including eye-, head-, limb- and hand-centred reference frames. Intermediate combinations have also been described (Soechting and Flanders 1993; Flanders and Soechting 1995).

Studies in the visuomotor system suggest that the initial processing of the spatial location of visual stimuli is relatively rapid and precise, and is based upon an egocentric frame(s) of reference, presumably facilitating interactions with the motor systems. This representation degrades over time, and is replaced by an allocentric reference frame, presumed to be more involved in perceptual functions (Milner and Goodale 1995). Thus, when a delay is introduced between the end of a visual stimulus and the initiation of movement towards the stimulus, subjects generally show increased errors (Bridgeman et al 1997; Rossetti 1998). Subjects with "blindsight" (preservation of the dorsal processing stream for action, with loss of the ventral stream for perception) show greater accuracy when the delay between the stimulus and the motor response is short (Rossetti 1998). Lesions that damage the dorsal processing stream have the opposite effect (Milner et al 1999).

Interestingly, however, and different from the visual system, our results suggest that the representation of haptic stimuli does not necessarily degrade over time. Indeed, performance in one condition (60°) improved when the delay was longer. In addition, low discrimination thresholds were obtained with short and long delays when the angles were explored at the more central location, 30°. A direct comparison is likely not warranted as the studies in the visual system concentrated mostly upon visuomotor performance, and so reflected errors in both sensory processing and motor planning/execution. In contrast, the present study focused only on sensory performance.

For the haptic system, Zuidhoek et al (2003) proposed that bar orientation is initially represented in an egocentric frame of reference, and that this switches to an allocentric reference frame when a 10 s delay is added between the exploration and the subsequent matching. The initial egocentric representation was suggested by Kappers (2002) to be based on an intermediate reference frame derived from a hand-centred and an allocentric (fixed in space) representation of bar orientation (see also Flanders and Soechting 1995). Zuidhoek et al (2004) subsequently showed that the initial representation was modifiable. Specifically, they found that bimanual bar matching improved when the head was oriented towards the reference bar, and away from the test bar. The present study confirmed the latter findings, extending the observation to show that head orientation modifies the performance of a unimanual, haptic discrimination task.

Can the transformation of reference frames invoked for haptic bar orientation be applied to the present results? Certainly the data obtained using short delays strongly suggest that 2-D angles are initially represented

in some form of egocentric reference frame, be it head-centred and/or arm/hand-centred (Fig. 5B). As spatial location was not a factor at longer delays between scans, one might then postulate that this reflected a transformation to an allocentric frame of reference. This does not, however, appear likely. Here it is useful to recall the sequence of events in the trials: the first angle was scanned, the result stored temporarily and then recalled for comparison either during the second angle scan or immediately thereafter. For optimal task performance, the central representation of the first and second angles must logically be in the same frame of reference. Any transformation of the initial representation during the delay period would be expected to degrade perceptual performance, not improve it. This reasoning thus argues against a transformation from an ego- to an allocentric reference frame.

An alternate explanation for our results is that at least two distinct and competing egocentric frames of reference exist. We suggest that one reference frame is arm- or hand-centred, based on the observation that angle position was a significant factor in some experiments (short delay). A second frame of reference appears to be head-centred, although we cannot exclude the possibility that this may be gaze-related. (Note: No instructions about the direction of gaze were provided, and the subjects' vision of the angles was blocked at all times.) We suggest that these two egocentric reference frames co-exist, given that both are evident at short delays. When the misalignment between the head and arm/hand was small, then the angles were accurately encoded and threshold was low. When the misalignment was large (in other words there was a large angular difference between the direction in which the head was pointing and the position of the arm/hand, see Fig. 5b), the two reference frames interacted to distort the haptic representation.. At short delays, the net result was an increase in discrimination threshold. At longer delays, the incongruence was resolved by the suppression of the arm/hand-centred reference frame, a suggestion consistent with the observation that angle position was not a significant factor at long delays. The notion of a limited duration, initial egocentric frame of reference is consistent with observations in the visuomotor system (see above).

While this suggestion of two competing egocentric frames of reference appears to contradict the suggestion of Zuidhoek et al (2003) (above), the cognitive demands of their bar matching task were very different from this task of 2-D angle discrimination. In the present study, all shapes were explored in the same spatial location (within each experiment), with subjects discriminating very slight changes in 2-D angles. Thus there was definitely an advantage for the standard and comparison stimuli to be stored and compared within the same frame of reference. In contrast, the bar matching task involved transposing one pattern of stimulation sensed in one spatial location onto another spatial location; and the bimanual condition—in which case delay was a significant factor—required a transformation into the mirror image on the opposite hand. Thus, the requirements of the behavioural task can influence the nature of the haptic frame of reference.

Our suggestion that the reference frames are in part dependent on head position appears, at first glance, to be counter-intuitive. There is, on the other hand, some evidence that neck proprioceptive inputs can modify haptic perception (Guerraz et al 2000). Given the present results, one possible suggestion is that the neck proprioceptive feedback may have served to either enhance the head-centred reference frame, or alternately to suppress the competing arm/hand-centred representation. Another interpretation of the results is that the importance of head position for haptic angle discrimination may reflect the link between vision and haptics. Indeed, one can argue that vision is the dominant modality for object shape identification, and that touch serves as a back-up system for situations in which vision is inadequate (like when searching for an object in the dark). Moreover, several studies have suggested that visual imagery contributes to haptic object recognition (Zangaladaze et al 1999; Amedi et al 2001). Consistent with this, most subjects in the present experiments reported creating mental images, including visual, of the angles (Voisin et al 2002a). In addition, the results of imaging studies show that there is a common central representation of object shape, haptic and visual, involving areas in the occipital cortex associated with the ventral visual stream (Amedi et al 2001; James et al 2002). Thus, while the underlying neuronal mechanisms remain to be determined, head orientation relative to the explored angles may help to direct attention towards the haptic stimuli (Zuidhoek et al 2004), and so enhance the central neural representation of the angles (Meftah et al 2002). Certainly there is considerable evidence that spatial attention can enhance tactile perception, and that cross-modal links between modalities exist, including vision and touch (Spence et al 2000; Meftah et al 2002). Taken together, it is therefore not too surprising that head orientation influences haptic shape representation.

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