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RESEARCH ARTICLE

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Haptic discrimination of object shape in humans: contribution of cutaneous and proprioceptive inputs

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Abstract Using two-dimensional (2D) angles composed of two straight, 8-cm-long arms that formed an angle, we investigated the importance of cutaneous feedback from the exploring index finger, and proprioceptive feedback from the shoulder (scanning movements made with the outstretched arm), to the human ability to discriminate small differences in the angles. Using a two-alternative forced-choice paradigm, subjects identified the larger angle in each pair explored (standard angle, 90°; comparison angles, 91° to 103°). Subjects were tested under four experimental conditions: (1) active touch (reference condition); (2) active touch with digital anaesthesia; (3) passive touch (a computer-controlled device displaced the angle under the subject's immobile digit); and (4) passive touch with digital anaesthesia. When only proprioceptive feedback from the shoulder was available (condition 2), there was a significant increase in discrimination threshold, from 4.0° in the reference condition (condition 1) to 7.2°, indicating that cutaneous feedback from the exploring digit contributed to task performance. When only cutaneous feedback from the finger was available (condition 3), there was also a significant increase in threshold from 4.2° in the active condition to 8.7°. This suggested that proprioceptive feedback from the shoulder, potentially from a variety of deep (muscle and joint) but also cutaneous receptors, contributed to the ability to discriminate small changes in 2D angles. When both sources of feedback were eliminated (condition 4), subjects were unable to discriminate even the largest difference presented (13°). The results suggest that this sensory task is truly an integrative task drawing on sensory information from two different submodalities and so, following the definition of Gibson, is haptic in nature. The results are discussed in relation to the potential neural mechanisms that might underlie a task that requires integration across two anatomically separate body parts and two distinct modalities.

Keywords Tactile shape discrimination · Two-dimensional angles · Active touch · Passive touch

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Introduction

When you manipulate an object in your hand with a view to identifying the object, sensory feedback is generated from multiple sources, including mechanoreceptors in the skin and also mechanoreceptors in deep structures (muscle, tendon, joint). This complex feedback, which we term haptic feedback here (following Gibson 1966), must be integrated across both space and time in order to define object shape. In the companion paper (Voisin et al. 2002), we reported on the development of a sensory task that allowed us to begin to evaluate, in a rigorous and parametric fashion, the human ability to discriminate simple two-dimensional (2D) shapes composed of two straight arms that formed an angle. The task was specifically designed so that both cutaneous feedback from the exploring index finger and proprioceptive feedback from the shoulder (movements made with the outstretched arm) could potentially contribute to defining the shape of the experimental objects.

Two important observations were made. First, performance of the 2D angle discrimination task was not modified by changing the orientation of one of the two angles that were presented in each trial (standard angle of 90° and comparison angles of 91°–103°). This observation indicates that subjects based their sensory decision on a central representation of the angle itself, and not the orientation of one arm of the angle, i.e. they analysed the shape of the experimental objects, as per the instructions given. Second, performance in the task, when expressed in terms of angular changes at the shoulder, was superior to that predicted from previous studies of static position sense at the shoulder, a range of 0.08° to 1.36° versus 1.4° to 4.7° (Cohen 1958a) or 0.6° to 1.1° (van Beers et al. 1998). This result strongly suggests that static position sense alone cannot explain the results. Two other sources of sensory feedback could have contributed. On the one hand, cutaneous feedback, generated when the finger was in contact with the angle of intersection, could have contributed to the high degree of precision found in this task. Such a suggestion is supported by the fact that a majority of subjects reported basing their sensory decision, at least in part, on cutaneous information from the angle of intersection, specifically the amount of compression of the finger at the angle. On the other hand, dynamic position feedback (movement sense) may also have contributed in the form of sensory reafference from the moving limb, possibly interpreted in relation with the motor command (Gandevia et al. 1993). Such a suggestion is consistent with Kelso's (1977) observation that anaesthesia of the hand and fingers, eliminating cutaneous feedback from the hand while preserving muscle spindle feedback from the long flexors of the digits, had no effect on the accuracy of voluntary finger movements.

The purpose of this study was to confirm our suggestion that both cutaneous feedback from the exploring digit and proprioceptive feedback from the shoulder contribute to the human ability to discriminate differences in 2D angles by scanning the angles with the index finger of the outstretched arm. This was addressed by measuring performance in the task under four conditions: (1) active touch, with both cutaneous and proprioceptive feedback available; (2) active touch with digital anaesthesia, so that only proprioceptive feedback was available; (3) passive touch, whereby a computer-controlled device displaced the angle under the subject's immobile digit so that only cutaneous feedback was available; and (4) passive touch with digital anaesthesia, so that neither source of feedback was available. The results support our hypothesis that both cutaneous and proprioceptive feedback contribute to 2D angle discrimination, since perceptual performance declined when either source was eliminated. Indeed, subjects were unable to perform the task when both sources of feedback were eliminated. Preliminary reports of the results have been published (Voisin and Chapman 2000, 2001).

Materials and methods

Subjects

The subjects were eight healthy adults (three women and five men; 21–27 years of age), all right handed for writing. Participation was voluntary, and remunerated. The institutional ethics committee approved the experimental protocol, and all subjects gave their informed consent prior to the experiments. Subjects participated in one (n=4), three (n=2) or four (n=2) experimental sessions. Each session lasted 3–4 h, and consisted of two blocks of 56 trials. The methods are described in Voisin et al. (2002). Below, there is a brief recapitulation of the methods and a description of the salient differences.

Perceptual task

The angles, apparatus and task are described in the companion paper. In brief, subjects scanned pairs of angles, using the glabrous skin of the middle phalanx of the right index finger of the outstretched arm, and identified the larger angle of each pair by pressing one of two response buttons on a keypad with their left hand (first or second angle larger). Each angle was scanned with a single to-and-fro movement (sequence *a-b-c-b-a*, Fig. 1A). The angles were machined from 1-cm-thick Plexiglas (see Fig. 1A). Each arm was 8 cm long, and the first arm explored was identical for all angles. The angle at the intersection of the arms was 90° for the standard angle (four replicates used). The comparison angles (n=7) spanned a range from 91° to 103° (increments of 2°). The angles were firmly clamped in an apparatus (see Fig. 1B) instrumented to record contact force and digit position. The latter was monitored using the outputs of optical sensors, paired with light emitting diodes (LEDs) placed so that they were interrupted when the index finger was at the start position (a), the intersection (b) or the end position (c). The subject was comfortably seated beside the apparatus (vision and hearing occluded), which was placed at arm's length from the subject, at the level of the shoulder, 30° to the right of midline. During a trial, one standard angle and one comparison angle was presented. As in the companion paper, one of the two angles in each pair was slightly rotated towards the midline (4° shift in the vertical plane) to encourage subjects to evaluate the whole angle, and not simply the orientation of the second arm of the angle relative to horizontal. Subjects were not informed of the presence of the shift, or given any feedback on their performance. Each comparison angle was presented 8 times in a pseudorandom order for a total of 56 trials per block. The order of testing was counterbalanced for all relevant factors (shift on the first or second angle; standard angle presented first or second). The first block of trials in each session was preceded by several practice trials to familiarize the subject with the scanning movement (active or passive, depending on the experiment and the order of testing) and the perceptual task. Practice trials were repeated for the second block of trials in most cases, in order to allow the subjects the time to familiarize themselves with the changed experimental condition (after anaesthesia; passive instead of active scans). An exception was made for three subjects for which the second block was identical to the first (two blocks with local anaesthesia).

Experimental conditions

Condition 1: active touch with both cutaneous and proprioceptive feedback

Subjects made an active to-and-fro scanning movement, sliding the index finger over the angle. Subjects were specifically instructed to keep the arm (and digit) straight throughout the scan (nail up), limiting rotation to the shoulder. The sequence of events in a trial was: (1) the first angle was installed in the apparatus; (2) the experimenter guided the subject to position the index finger at the initial position (a in Fig. 1A); (3) the experimenter started data acquisition with a carriage return; (4) 300 ms later, a tone signalled the subject to begin the first scan; (5) the subject scanned the index finger over the angle (sequence, *a-b-c-b-a*); (6) after completing the scan, the subject withdrew the finger from the angle; (7) the second angle was installed in the apparatus; (8) steps 2–6 were repeated; and (9) the subject entered his/her response in the keypad. Note that subjects kept the upper limb rigid throughout the scan, so that the skin area in contact with the object varied as a function of the arm explored (radial side of the middle phalanx for *ab*; ulnar side for *bc*).

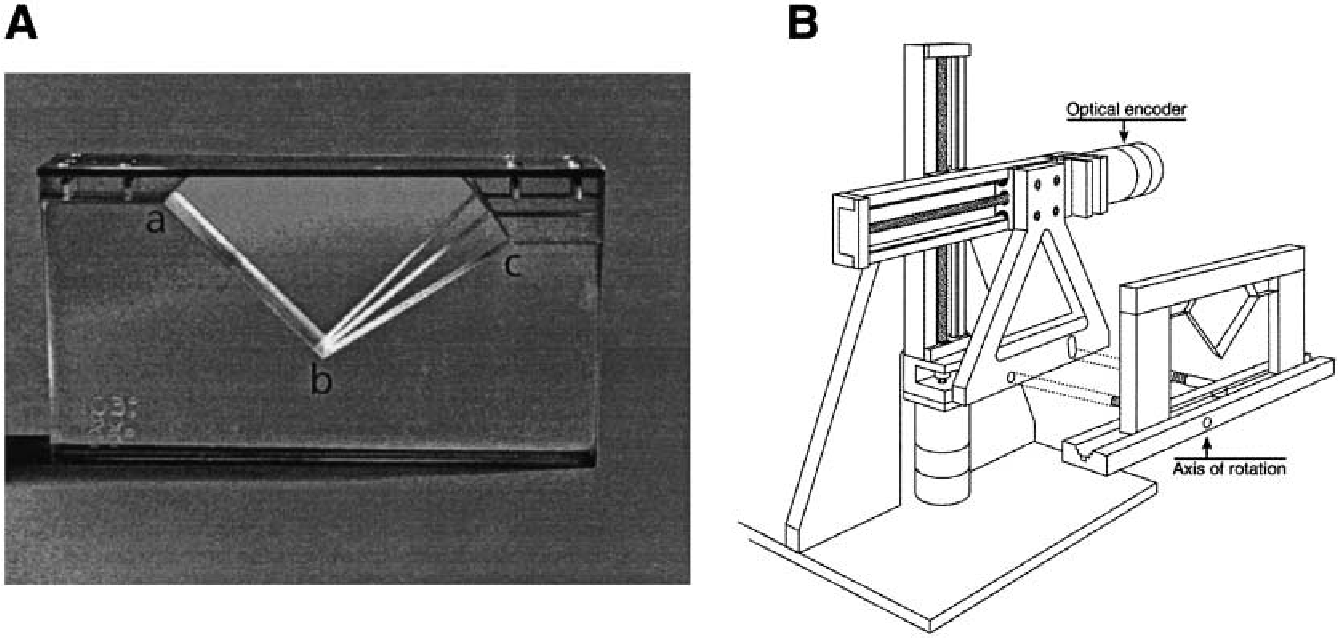

Fig. 1 **A** Photograph of the experimental objects showing, from back to front, the standard angle (90°) and two comparison angles (95° and 103°). All scans started with the index finger placed at position *a*. The sequence of movement was *a-b-c-b-a*, where *b* corresponds to the angle at the intersection and *c* was located at the end of the second of the two arms that formed the angle. **B** Setup for passive scanning of the angles, showing the x-y stage, optical encoders, and the method for attaching the experimental apparatus, into which the angles were clamped, onto the x-y stage. The apparatus could be rotated on the mounting (see axis of rotation)

Condition 2: active touch with anaesthesia (no cutaneous feedback)

Performance of the 2D angle discrimination task was tested in the absence of cutaneous feedback from the index finger in order to determine the ability of subjects to perform the discrimination using only proprioceptive feedback. The sequence of events in the trials was identical to that described for condition 1. The right index finger was anaesthetized under medical supervision using a ring block at the level of the proximal phalanx; up to 4 ml 2% lidocaine was injected subcutaneously at multiple sites distributed around the circumference of the proximal phalanx, just distal to the metacarpophalangeal joint. In three subjects, the ring block was repeated after the first block of trials, and a second block of trials with anaesthesia was recorded (pause of ~30 min between blocks). In one subject, 2.5 ml 2% mepivacaine was employed instead of the lidocaine. Light touch was abolished distal to the injection sites within 15–20 min. We verified the state of anaesthesia (abolition of light touch) at 20-min intervals during the session. Subjects reported that the effects of the local anaesthesia lasted for several hours after the end of the session.

Condition 3: passive touch (no proprioceptive feedback)

In order to assess the ability of subjects to perform the angle discrimination task using only cutaneous information, the angles were displaced passively, under servo control, over the glabrous skin of the outstretched, immobile index finger. As shown in Fig. 1B, the apparatus was mounted on a vertically oriented x-y stage (Thomson microstage, MS33-LXB-L300). Each axis was equipped with a DC servomotor (Aerotech, model 1017) and an optical encoder (Sumtak opticorder, LDA-051-800). The desired movement trajectory was controlled by a microcomputer using a FlexMotion-6C controller to operate a multiaxis linear servo amplifier (Servo Dynamics, SD2-412-45-2F). The trajectory was updated every 125 µs; examples of the up and down trajectories are shown in Fig. 4. The mounting on the x-y stage was adjustable so that the 4° shift in orientation could be imposed as in the active condition (axis of rotation shown in Fig. 1B). The sequence of events in a trial was identical to that described for condition 1 with the exception that the subject was now required to remain motionless throughout the angle presentation (position identical to the initial position in condition 1), all the while maintaining contact with the object. The angle was presented using the same movement sequence as in the active condition, *a-b-c-b-a*, with each angle and shift having its own unique point-to-point trajectory. The contact surface on the index finger was identical to that for condition 1, with the skin area in contact varying as a function of the arm presented (radial side for *ab*; ulnar side for *bc*). For each subject, the mean speed was chosen to match the subject's own movement parameters in the active task. This was calculated from the outputs of the optical sensors, using data collected either in the immediately preceding session (subjects 4, 6 and 7) or in the same session (subjects 8 and 9).

Condition 4: passive touch with anaesthesia (no cutaneous or proprioceptive feedback)

This control experiment addressed the possibility that subjects used some source of feedback other than cutaneous feedback from the index finger and proprioceptive feedback from the shoulder to perform the 2D angle discrimination. The right index finger was anaesthetized with 2.5 ml 2% mepivacaine (see condition 2 above). After light touch was abolished, performance of the 2D angle discrimination task was evaluated using passive touch, as described for condition 3.

Order of testing

Performance in condition 1 (active touch with cutaneous and proprioceptive feedback) served as the reference for two of the three modified experimental conditions, conditions 2 and 3. The reference data are, in part, a subset of those presented in the companion paper (Voisin et al. 2002). For condition 2 (active touch with anaesthesia), the reference condition was tested before anaesthesia, either in the same session (n=2) or in the immediately preceding session (1–3 days earlier; n=3). In the latter case, performance during anaesthesia was evaluated in two repeated blocks of 56 trials. For condition 3 (passive touch), the order of testing in the session was counterbalanced (three subjects, condition 1 first; two subjects, condition 3 first). For condition 4 (passive touch with anaesthesia), passive touch (condition 3) served as the "reference" condition; this testing occurred in the same session, immediately preceding the anaesthesia.

Data acquisition and analysis

The following data were recorded with each trial: the subject's response, the value of the angles scanned (including their order of presentation and the presence of the 4° shift), the contact force, and the times that the digit arrived at, and left, positions *a*, *b* and *c* during the course of the to-and-fro movement.

For each subject, discrimination performance was characterized by computing the proportion of correct responses for each comparison angle in each block of trials. The results were fitted to a logistic function, and discrimination threshold (75% correct) was computed from the logistic function. To assess the respective contribution of cutaneous and proprioceptive feedback to 2D angle discrimination, the effects of the exploratory condition on discrimination threshold were analysed with paired t-tests (condition 1 vs condition 2; condition 1 vs condition 3).

The scanning movements were characterized by calculating the scanning speed (output of the optical sensors), the length of time that the digit was in contact with the angle at the intersection (dwell-time) and contact force (output of the strain gauges). Paired t-tests were employed to determine whether the exploratory conditions were the same in the reference condition (1) and the modified conditions (2 and 3).

Finally, the trajectory of the index finger was recorded in the reference condition at the end of one of the experimental sessions in five subjects, using an Optotrak 3020 motion analysis system. A pair of small infrared light emitting diodes (IREDs) were placed on the proximal phalanx of the index finger. The spatial location of the IREDs was recorded with a precision of 0.5 mm and a sampling frequency of 100 Hz while subjects actively scanned the standard angle (90°) and several comparison angles (95°, 100° and 105°). These data allowed us to examine the active movement trajectories, and to calculate the mean speed profile.

In all analyses, the level of significance was fixed at $P<0.05$.

Results

Scanning movements

In these experiments, the active movement trajectory was constrained by the angles themselves and the 4° shift that was arbitrarily imposed on one angle of each pair presented. In all experiments, the standard angle was 90°, and the comparison angles spanned a range of 91° to 103°. The movements were also constrained by positioning the apparatus at arm's length from the subject, who was instructed to scan the angles using the glabrous skin of the middle phalanx of the index finger. In order to maintain contact between the middle phalanx and the angle, the subject had to limit joint rotation to the shoulder. This was monitored during the experiments by the optical sensors on the apparatus that were located behind the angle (from the subject's point of view), and were interrupted by the protruding distal phalanx of the index finger. At acquisition, trials in which the distal phalanx did not interrupt the LEDs in the pre-determined order, *a-b-c-b-a* (Fig. 1A), were aborted and repeated later in the session. These observations suggested that the relevant feedback for task performance was limited to two sources, cutaneous feedback from the glabrous skin of the index finger, and proprioceptive feedback from the shoulder. The relative contribution of each source of feedback to psychophysical performance was therefore assessed by selectively eliminating each source of information, separately and in combination.

Effects of eliminating cutaneous feedback from the finger (condition 1 vs condition 2)

We examined the contribution of cutaneous feedback from the index finger to the performance of the 2D angle discrimination task in five subjects by measuring performance in the reference condition (active touch with both cutaneous and proprioceptive feedback), and then again after anaesthetizing the index finger.

Following injection of the local anaesthetic around the base of the index finger, light touch distal to the injection site was abolished throughout the data acquisition period. Thus, sensory feedback during anaesthesia arose principally, if not entirely, from proprioceptors about the shoulder. The pooled results of five subjects are shown in Fig. 2A, along with the logistic curves fitted to the pooled data in each condition. When the smallest angular difference was presented (1°), performance was at the chance level for this two-alternative forced-choice paradigm. When larger angular differences were presented, performance improved in both testing conditions. Performance was, however, consistently poorer in the presence of anaesthesia. Consequently, the discrimination threshold (75% correct, shown in Fig. 2A) was increased in the presence of anaesthesia. This was consistent with the subject reports to the effect that they generally found the task more difficult during the anaesthetic block.

Discrimination threshold was calculated from the logistic functions fitted to the data of each subject and the results are presented in Table 1. All subjects showed an increase in threshold in the absence of cutaneous feedback, but the change was modest (P=0.03): mean discrimination threshold increased from 4.0° in the reference condition to 7.2° in the anaesthetized condition. Motor strategy was, in contrast, not significantly changed: there was no significant change in contact force, scanning speed or dwell-time at the intersection across the two testing conditions (see Table 2 for details). In the companion paper, we reported that subjects generally used a combination of two cognitive strategies to perform the task: mental images of the angles (whole angle strategy), and the pattern of cutaneous feedback from the angle of intersection (intersection strategy). During anaesthesia, most subjects found the discrimination more difficult because they were no longer able to rely on the cutaneous feedback from the angle of intersection. Instead, their decision was now based solely on

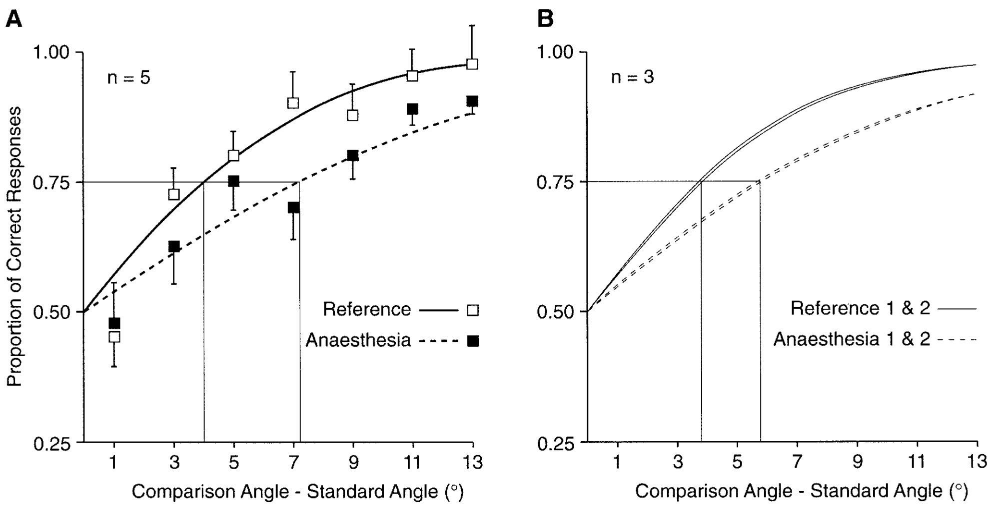

Fig. 2A, B Effects of digital anaesthesia on performance of the 2D angle discrimination task. The proportion of correct responses is plotted as a function of the angular difference between the comparison angle (91°–103°) and the standard angle (90°). **A** Pooled results of five subjects (means ± SEM) during the reference condition 1, active touch with cutaneous and proprioceptive feedback, and condition 2, active touch with no cutaneous feedback (anaesthesia). Logistic curves were fitted to the pooled data. Discrimination threshold (75% correct) is shown. **B** Results from three of the five subjects shown in **A**, who performed two repeated blocks of trials with anaesthesia in the same session, along with their performance in the reference conditions in the immediately preceding session and in the subsequent session. Note that the logistic functions for each condition (reference or anaesthesia) were closely similar

Table 1 Discrimination threshold (°) during the reference condition (condition 1) and the two modified conditions, anaesthesia and passive (respectively, conditions 2 and 3)

Subject	Reference	Anaesthesia	Reference (repeat)[a]	Reference	Passive
1	2.9	5.9	–	–	–
2	3.9	5.0	2.6	–	–
3	0.7	4.9	2.6	–	–
4	6.7	7.9	5.3	3.6	7.9
6	5.8	12.1	–	3.7	6.9
7	–	–	–	2.7	7.6
8	–	–	–	7.8	>13.0
9	–	–	–	3.3	8.0
Mean	4.0	7.2		4.2	8.7

[a] For subject nos. 2, 3 and 4, the reference condition was tested in the preceding session because the effects of anaesthesia were tested in both blocks of trials in the session. Here we give the thresholds from the subsequent session, showing that in all cases discrimination threshold during anaesthesia was higher than the estimates during both reference conditions

mental images of the angles or the movement trajectory. One subject (no. 3) reported that the discriminations were easy even during anaesthesia, but this subject reported using only a mental representation of the angles in the reference condition. Nevertheless, this subject's threshold was also increased during anaesthesia, suggesting that the cutaneous input likely contributed to the central representation of the angles.

In order to ensure that the observations were robust, we performed two blocks of trials with anaesthesia in the same session for three subjects, after repeating the ring block halfway through the session. Figure 2B plots the two logistic functions fitted to the data from each block (dashed lines). The functions were virtually indistinguishable, indicating that the effects of anaesthesia were indeed robust. For these subjects, performance in the reference condition was recorded in the immediately preceding session and in the subsequent session (solid lines). Using the data from a different session as the reference value for these experiments did not bias our estimate of the magnitude of the effect of anaesthesia because performance in the two reference conditions was almost identical.

Effects of eliminating proprioceptive feedback from the shoulder (condition 1 vs condition 3)

The contribution of proprioceptive feedback from the shoulder to 2D angle discrimination was determined by measuring performance in the reference condition, active touch with cutaneous and proprioceptive feedback, and

Table 2 Comparison of the movement-related parameters (± SEM) during the reference condition (condition 1) and the two modified conditions, anaesthesia (condition 2) and passive touch (condition 3)

	Reference (n=5)	Anaesthesia (n=5)	t-test (P)	Reference (n=5)	Passive (n=5)	t-test (P)
Speed (mm/s)	155±27	169±31	0.09	246±43	162±13	0.13
Dwell time (ms)	754±115	688±82	0.22	560±64	1,115±125	0.01
Force (N)	0.68±0.18	0.69±0.21	0.97	0.88±0.12[a]	0.78±0.10	0.81

[a] Force data available for only four subjects

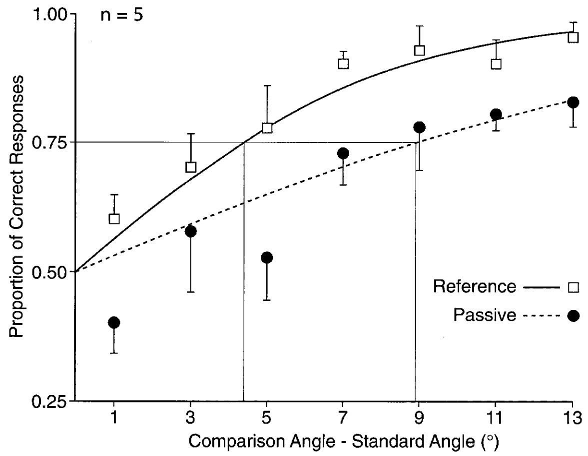

Fig. 3 Effects of eliminating proprioceptive feedback on performance of the 2D angle discrimination task. Pooled results of five subjects during the reference condition 1, active touch with cutaneous and proprioceptive feedback, and condition 3, passive touch with only cutaneous feedback. Plotted as in Fig. 2A

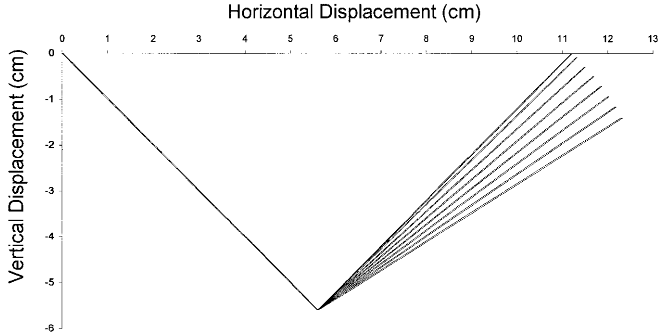

Fig. 4 Point-to-point trajectories described by the angles in condition 3, passive touch (no shift applied). Shown here are the trajectories from 56 to-and-fro scans: 28 repetitions of the standard, 90°, and 4 repetitions of each of the seven comparison angles, 91°–103°

comparing this to performance in a modified condition, passive touch, in which case only cutaneous feedback was available. After subjects positioned their outstretched arm so that the glabrous skin of the middle phalanx of the index finger contacted the angle at the start position (*a* in Fig. 1A), the angle was then displaced, under computer control, underneath the immobile digit (glabrous skin of the middle phalanx). The movement sequence was identical to that used in the active condition. The pooled psychophysical results of five subjects are shown in Fig. 3. Performance was significantly poorer in the absence of proprioceptive feedback: mean discrimination threshold was 4.2° in the reference condition of active touch as compared to 8.7° during passive touch (P<0.0005). Consistent with this, the subjects generally reported the passive condition to be more difficult than the active condition. All subjects reported using the pattern of cutaneous feedback to perform the discrimination, both from the angle of intersection and during the passive scans of the two arms. Interestingly, three of five subjects (nos. 4, 7 and 9) used these inputs to generate mental images of the angles.

The passive testing conditions adequately reproduced the active testing conditions. The trajectories described by the angles during the passive scans were closely similar to the trajectories imposed by the angles themselves in the active condition. Figure 4 shows the superimposed traces for the to-and-fro passive scans of all eight angles (the standard, 90°, and the seven comparison angles, 91°–103°) in one block of trials. For simplicity, only the 'no shift' trials, corresponding to 56 to-and-fro scans, are plotted. The position control system was extremely precise. Inspection shows that each angle had its own unique point-to-point trajectory, with no overlap between angles. The traces for each individual angle are, in contrast, superimposed. Similar results were obtained when the data from the shifted angles (4°) were plotted (not shown). In addition, the mean scanning speed was identical in the two conditions (Table 2).

There were two differences in the testing conditions, but we have no reason to believe that these contributed to the results. First, the speed profiles were not identical during the scans. In the active condition, the movement analyses indicated that all subjects showed an approximately sinusoidally shaped velocity profile as each arm of the angle was explored. Examples from three subjects are shown in Fig. 5A. During the passive condition, we approximated this sinusoidal velocity profile in most subjects by imposing a ramp increase and decrease in velocity (subject nos. 2 and 6 in Fig. 5B), designed to reproduce the average duration of each segment of the movement. For subjects who used slower active scanning movements (subject no. 4, Fig. 5B), however, the ramp increase in velocity was followed by a period of constant velocity scanning before the ramp decrease that preceded the arrival at the end of the first or second arm of the angle. Since mean scanning speed was similar in the two conditions (above), we assume that subjects were able to collect comparable relevant sensory feedback during the angle scanning.

Second, in most cases we were unable to match the dwell-time at the angle of intersection due to the weight, and so the inertia, of the apparatus. Thus the digit remained at the intersection significantly longer in the passive condition (mean 1115 ms) as compared to the reference condition (mean 560 ms, Table 2). Thus, subjects had more time to collect information at the intersection during passive touch as compared to active. This did not appear to confer an advantage to the subjects because their performance was significantly poorer in passive touch. This apparent unimportance of dwell-time to performance of the 2D angle discrimination task is consistent with our previous observation that dwell-time did not covary with the cognitive strategy of the subjects (Voisin et al. 2002).

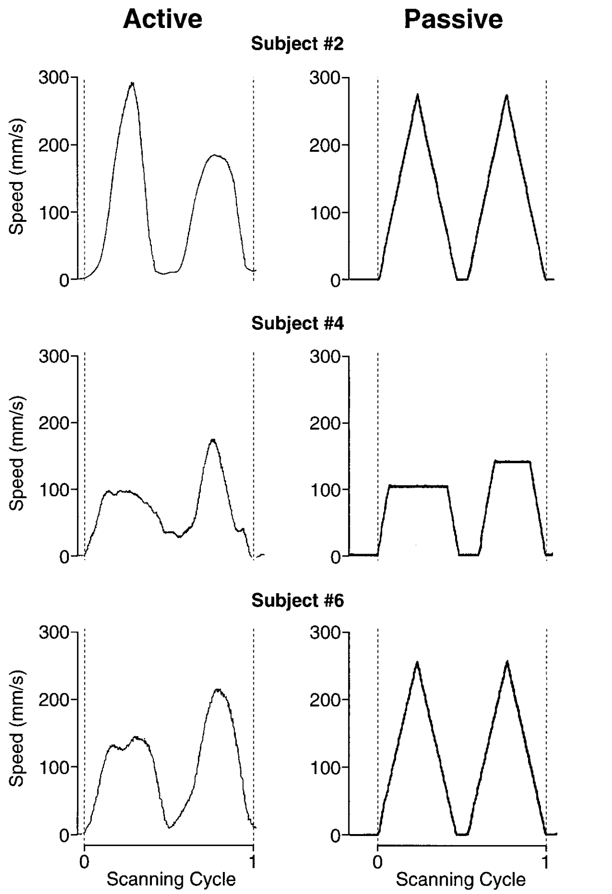

Fig. 5A, B Velocity profiles for the active and passive scans of three subjects, normalized to the duration of the scanning cycle (from *a*, initial position, to *c*, final position). **A** Mean velocity profile for four active trials (90°–105°). **B** Velocity profiles of 56 superimposed trials in the passive condition (90°–103°)

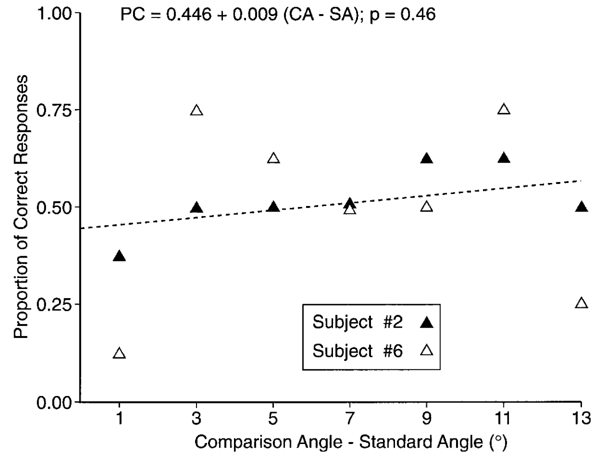

Fig. 6 Performance of two subjects in the 2D angle discrimination task as the angles were passively scanned under the anaesthetized index finger (condition 4). Subjects were not able to discriminate the angular differences. The constant of the linear regression shown here was close to the level of chance in this two-alternative forced-choice experiment (50% correct) (*CA* comparison angle, *PC* proportion correct, *SA* standard angle)

Effects of eliminating cutaneous and proprioceptive feedback (condition 4)

Two subjects (nos. 2 and 6) participated in a control experiment that aimed to determine whether any other sources of feedback might have potentially contributed to task performance. The right index finger was first anaesthetized. Once all tactile sensation was abolished, performance in the 2D angle discrimination task was tested using passive touch, as for condition 3 (Fig. 6). In this situation, neither subject was able to discriminate even the largest angular difference presented, 13°. A linear regression analysis applied to the pooled data indicated that the slope was not different from zero (P=0.46). Moreover, the constant for the equation, 0.45, was close to the level of chance performance in this task (50% discriminated). The inability of subjects to perform the discrimination under these conditions could not be explained by unfamiliarity with the test condition. Both subjects were able to perform the task in the presence of anaesthesia (Table 1). They were also able to discriminate angular differences in the passive condition (tested in the same session as condition 4). Together, these results suggest that 2D angle discrimination was entirely based on cutaneous feedback from the scanning digit and proprioceptive feedback from the shoulder.

Discussion

The present study has shown that the sources of salient input for 2D discrimination of macrogeometric angles are twofold: cutaneous input from the exploring index finger and proprioceptive input from the shoulder. No other source of sensory information contributed because performance fell to chance levels for this two-alternative forced choice paradigm when both inputs were eliminated. The results thus suggest that this sensory task is truly an integrative task drawing on sensory information from two different submodalities, and so, following the definition of Gibson (1966), is haptic in nature.

Two-dimensional angle discrimination in the absence of cutaneous feedback

We attribute the decreased performance with digital anaesthesia to the abolition of cutaneous feedback from the finger. It seems likely that all four types of cutaneous mechanoreceptors found in human glabrous skin (slowly adapting type I and II, rapidly adapting and Pacinian afferents; see review by Johnson 2001) were activated during the angle scans. This cutaneous feedback provided information about the pattern of contact between the skin and the experimental objects both while the digit scanned the two arms of the angle (stimulating first the radial and then the ulnar side of the middle phalanx) and also while the digit was at the intersection itself. As suggested in the companion paper (Voisin et al. 2002), it is likely that slowly adapting type I receptors may play a particularly important role because they can provide information about the precise pattern of skin contact with local contours (LaMotte and Srinivasan 1987a, 1987b; Wheat et al 1995; Goodwin et al. 1997).

Is it possible that joint receptors from the digit also contributed to the results, since their afferents would also have been blocked with digital anaesthesia? This seems unlikely for several reasons. First, the apparatus was positioned so that, with the arm outstretched, contact between the index finger and the object was limited to the glabrous skin of the middle phalanx of the index finger, i.e. a cutaneous surface. Second, the subject was required to maintain the distal and proximal interphalangeal joints, and the metacarpophalangeal (MCP) joint in full extension (0°). Careful observation during the experiments indicated that the subjects followed these instructions. In addition, the position of the distal phalanx was monitored throughout with optical sensors positioned behind the angle (see Fig. 2 in the companion paper). Finally, there is a fairly wide consensus that joint receptors do not contribute greatly to the appreciation of joint angles except at the extremes of the range of motion (reviewed in Matthews 1988; Jones 1994).

Interestingly, when we transformed the results from the anaesthetized condition (mean discrimination threshold of 7.2°) into angular changes at the shoulder angles (difference in position at the end-point of the second arm), the mean discrimination threshold was 0.83° (range 0.51°–1.46°). This falls within the range of published values for proprioceptive precision at the shoulder, 0.6° to 1.1° (van Beers et al. 1998). Thus our results provide independent confirmation of their results, and this using a different experimental paradigm (haptic exploration vs a whole-arm pointing task). In addition, this performance is less precise than that obtained when both sources of feedback, cutaneous and proprioceptive, were available (mean 0.54°; range 0.08° to 1.36°), i.e. during haptic exploration.

Two-dimensional angle discrimination in the absence of proprioceptive feedback

We attribute the decreased performance during the passive condition to a loss of proprioceptive feedback from the shoulder, although it is recognized that one other potential kinaesthetic signal was absent in this condition, namely the motor command (reviewed by Gandevia 1996). The importance of the latter is not clear, at least from the subjects' comments, because only one subject (no. 4) reported specifically using the movement trajectory to perform the task. The remaining subjects reported depending on sensations elicited during the scans. The proprioceptive feedback most likely included inputs from muscle receptors (especially primary and secondary endings of muscle spindles, although Golgi tendon organs may also have contributed) and perhaps joint receptors (reviewed in Matthews 1988). In addition, we cannot exclude a potential contribution from cutaneous feedback elicited by skin stretch at the shoulder since Cohen (1958b) found that position sense declined when position-related cutaneous feedback from the shoulder was distorted by applying tape to the skin overlying the joint. Consistent with this, Cohen et al. (1994) have shown that a proportion of cutaneous neurones in primary somatosensory cortex (SI) signal arm position during 2D whole-arm reaching movements.

Overall, there was a slightly larger increase in discrimination threshold in the passive condition (4.5°) as compared to the anaesthetized condition (3.2°). On considering the results obtained in the two subjects that were tested in both modified conditions (subject nos. 4 and 6, Table 1), it seems most likely that this difference was not meaningful. Subject no. 6 showed approximately the same relative increase in threshold in both modified conditions (×2.1 and ×1.9 for anaesthesia and passive, respectively). Subject no. 4 showed a larger increase during the passive condition than with anaesthesia, yet discrimination threshold in the two modified conditions was identical, 7.9°. Taken together, we suggest that cutaneous feedback from the finger and proprioceptive feedback from the shoulder both contributed in equal measure to 2D angle discrimination. This suggestion is consistent with the reported cognitive strategies of the subjects, the majority of whom reported using both sources of information to perform the sensory discrimination.

Two-dimensional angle discrimination is an integrative task

The present results suggest that our 2D angle discrimination task is truly an integrative task drawing on sensory information from two different submodalities, cutaneous and proprioceptive, originating from anatomically separate body parts, the finger and the shoulder. Subject performance was best with both modalities available, and diminished when either of the two sources of information was removed. As discussed in the companion paper (Voisin et al. 2002), sensory performance in this task was superior to what was expected from previous studies of, for example, position sense in isolation. Mean discrimination threshold was 4.7° (range 0.7° to 12.1°) when scanning objects using the index finger of the outstretched arm (both cutaneous and proprioceptive feedback available). When these results were expressed in terms of shoulder angles (difference in position at the end-point of the second arm), the mean discrimination threshold, 4.7°, corresponds to a change in shoulder position of 0.54° (range 0.08° to 1.36°). These values are lower than previous estimates of static position sense at the shoulder (see “Introduction”). This finding is not an isolated observation since John et al. (1989) reported that the ability to discriminate differences in the thickness of plates using a precision grip (cutaneous + proprioceptive feedback available) is far superior to what could have been expected from previous studies of joint position sense in the fingers (approximately 10°, Ferrell and

Smith 1988). John et al. (1989) reported that their subjects could resolve differences in joint angle with a precision of about 0.1° at the proximal interphalangeal joint or about 0.05° at the MCP joint. Taken together, these observations suggest that integrative tasks that can call upon both movement-related reafference (inputs from muscle, joint and skin receptors) and also the motor command reveal that sensory acuity is superior to that found using traditional tests. It is suggested that such integrative tasks, apart from being of more functional relevance, may be much more sensitive than traditional sensory tests to early changes in somaesthetic function that can, for example, herald the development of peripheral neuropathies (e.g. overuse syndromes, diabetic neuropathies).

Central mechanisms underlying 2D angle discrimination

The really intriguing point raised by the present results is to understand how subjects managed to integrate information from two anatomically separate body parts and two distinct modalities, cutaneous and proprioceptive, into a central representation of 2D shape. In the first case, the central representations of the hand and the shoulder within the parietal somatic sensory areas are largely separate. It is only in parietal association regions like the secondary somatosensory cortex (SII) and the posterior parietal cortex (areas 5 and 7b) that one finds large receptive fields that encompass both regions. In the second case, convergence of the two modalities, cutaneous and proprioceptive, is rare in the four areas that together comprise SI cortex, areas 3a, 3b, 1 and 2 (Hyvärinen and Poranen 1978; Chapman and Ageranioti-Bélanger 1991; Ageranioti-Bélanger and Chapman 1992; Iwamura et al. 1993; Salimi et al. 1999) and in several of the parietal association regions, including SII and area 7b (Robinson and Burton 1980). As for area 5 in the posterior parietal cortex, Sakata et al. (1973) reported that about one-third of cells are responsive to bimodal inputs, but these results have not been confirmed in other studies that found only a few area 5 cells responsive to both cutaneous and proprioceptive inputs (Duffy and Burchfiel 1971; Seal et al. 1982).

Although substantial convergence between the two modalities may not occur until the signals arrive in regions that are hierarchically superior to those investigated to date (e.g. parietal operculum), other factors also need to be considered. The proportions of haptic cells may have been underestimated in previous studies, given the difficulty in receptive field testing particularly in awake unrestrained animals. Further to this, it is known that SI neurones receive widespread convergent and yet subliminal inputs (Zarzecki and Wiggin 1982; Kang et al. 1985). Such inputs may become liminal in conjunction with other factors. One important factor might be the pattern of stimulation. For example, Iwamura et al. (1985) described neurones in area 2 that did not appear to have a somatic receptive field, and yet discharged when specific shapes were held in the monkey's hand. More recently, these findings have been extended to include posterior parietal cortex (Taira et al. 1990; Gardner et al. 1999). Another factor may be the behavioural context of the testing. Thus, Tremblay et al. (1996) reported that some area 2 neurones, with no identifiable receptive field, signalled differences in texture when tested in a texture discrimination task. Similar results have been obtained in SII (Sinclair and Burton 1993). An alternate suggestion is that, as in the visual system (Engel et al. 1997), coactivation of cutaneous and proprioceptive inputs may elicit some form of temporal binding so that the two inputs are interpreted together to generate a central representation of haptic shape. Such a mechanism is particularly attractive as this could bind together inputs from different modalities and different body regions into the emergent property of shape.

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