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RESEARCH ARTICLE

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Contribution of tactile information to accuracy in pointing movements

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Abstract We examined the contribution of tactile cues to accuracy during point-to-point movements. We used a task in which the experimenter guided either the left or right hand of the subject to a spatial location during the reference movement. During the subsequent test movement subjects were asked to point with the right hand to the remembered location without vision. Subjects contacted the target with their fingertip either during the reference movement, both the reference and test movements, or neither movement (i.e., the fingertip was held above the target surface). To differentiate between the contribution of tactile and proximal deep pressure information, the left index finger was anesthetized in a subsequent experiment. When subjects contacted the surface with the fingertip of the reference hand alone, error in movement direction decreased. When subjects made fingertip contact during the reference and test movements, gain error also decreased. Anesthesia of the fingertip degraded accuracy, suggesting that tactile information, independent of information from proximal deep pressure receptors, influenced movement accuracy. Thus, tactile information contributed to accuracy in pointing movements. We suggest that forces at fingertip contact may provide information regarding the orientation of the finger and forearm in space, which is used to replicate final arm posture. In addition, tactile cues at the beginning and end of the movement may be used to scale movement amplitude.

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Introduction

Accuracy of hand positioning based on integration of visual and proprioceptive inputs is more precise than that predicted by a model that simply adds the precision of visual and proprioceptive inputs (van Beers et al. 1999). This suggests that additional sensory information from other sources is either used to localize hand position in the workspace or potentiate existing proprioceptive inputs. Tactile cues may be an additional source of information for position sense, particularly when visual information is not available (Moberg 1983; Prochazka 1996; Slinger and Horsley 1906). During typing, for example, suppression of tactile information from the index finger (following digital nerve block) influences the terminal finger accuracy without altering the movement trajectory (Gordon and Soechting 1995). This suggests that tactile information may contribute to enhanced endpoint accuracy of the finger in space, at least when contour information (e.g., from the edge of the key) is available.

Tactile information from the fingertip may also contribute to position sense during pointing movements when contour information is not available. For instance, terminal accuracy of pointing movements was higher when subjects made contact with the target surface during adaptation to Coriolis force perturbations (Lackner and Dizio 1994). In addition, in an apposition task (when subjects pointed with the left hand to the remembered location of the passively positioned right hand without vision) the variability of movement endpoints was lower when subjects touched the target surface (Helms Tillery et al. 1994). In both of these studies, however, fingertip contact with the surface likely provided deep pressure information from proximal joints in addition to tactile information. Moreover, in the apposition task, touching the target surface primarily influenced variable error. Differences in constant error did not reach statistical significance, perhaps due to the small number of subjects (four) tested (Helms Tillery et al. 1994). Thus, it is not clear whether tactile cues from fingertip contact (independent of proximal deep pressure receptors) provide specific information regarding movement accuracy (direction and amplitude) or contribute to reduced variability in endpoint positioning.

Here we further examine the contribution of tactile cues to accuracy of pointing movements in the absence of vision. We adapted the task used by Helms Tillery et al. (1994) in which the experimenter guided either the left or right hand of the subject (whose eyes were closed) to a spatial location during the *reference* movement. During the subsequent *test* movement subjects were asked to point with the right hand to the remembered location without vision. This guided arm movement paradigm was chosen since active pointing of the reference arm would have required vision of the target, which is known to dominate over all other sources of feedback. Subjects made fingertip contact with the target surface either during the reference movement (which provided information about the target), both the reference and test movements (which provided information about the target and movement accuracy), or neither movement (i.e., the fingertip was held above the target surface). To differentiate between the contribution of tactile and deep pressure information, the left index finger was anesthetized in experiment 2. This methodology allowed us to ask the following questions: (1) does fingertip contact with the target surface influence movement direction and amplitude or variability? (2) What is the effect of suppression of tactile information on movement accuracy? (3) Does tactile information influence accuracy when kinesthetic information about target location is directly available (same hand used for reference and test movements) compared to movements in which kinesthetic information regarding target location is not directly available (different hand used for reference and test movements)?

Materials and methods

Subjects

Fourteen right-handed healthy subjects (age range 20–40 years) participated in the experiments after giving informed consent according to the declaration of Helsinki. Ten subjects (five males and five females) participated in experiment 1 and 3. Nine subjects (six males, three females) participated in experiment 2, including five subjects who participated in the other two experiments. The experiments were conducted approximately 1 month apart. Subjects participating in experiment 2 had no history of allergic response to local anesthetic. The study was approved by the Institutional Review Board at Teachers College, Columbia University.

Experimental setup and procedures

The experimental procedures were adapted from Helms Tillery et al. (1994) and were generally similar for all three experiments reported. Subjects sat 15 cm in front of a table with the index finger of both hands resting on a starting position located approximately 10 cm from the edge of the table along their body midline. Sixteen targets were arranged on a planar rectangular grid on the surface of the table. The targets (0.75 cm diameter) were drawn on a sheet of graph paper. The distance between targets was 10 cm in the anteroposterior plane and 15 cm in the mediolateral plane (see Fig. 1). An electromagnetic sensor (Polhemus Fastrak, Colchester, VT) was mounted on the dorsal aspect of the distal phalanx of the subjects' right index finger. The sensor was connected to a personal computer and interfaced with a data acquisition and analysis system (SC/ZOOM, Umeå University, Sweden). The sensor measured static position with an accuracy of 0.08 cm. Position data were sampled at 120 Hz and stored for offline analysis.

Subjects were asked to keep their eyes closed during data collection and to maintain their index finger extended with all the other digits flexed (as if pointing). Each trial began with the subjects' index fingers at the starting position. During the *reference movement* the experimenter lifted the subjects' hand off the table surface, guided the subject's left or right hand (by grasping the subject's wrist) to 1 of the 16 targets, held it there for 3 s, and then brought it back to the starting position. Subjects were asked to support the weight of the arm themselves (i.e., no mechanical support was given) and to let the experimenter guide the hand in a horizontal plane above the target. Care was taken to move the arm in a consistent manner (along a straight-line path from the start position to the target) from trial to trial. The experimenter ensured that the subject's finger was kept at an angle that would normally be used while making a natural pointing movement (~45° with respect to the table surface). During the subsequent *test movement*, subjects were asked to move their right hand to the remembered location and maintain the position for 2–3 s. Position data were collected once subjects had verbally indicated that they were at the remembered location. No temporal constraints were imposed on the task. After each trial, the experimenter repositioned the subject's hand to the starting position. Performance was tested under three conditions (A, B and C) in an order counterbalanced across subjects. Each condition consisted of a set of 64 trials (4 trials at each of the 16 targets).

In *condition A (no fingertip contact)* only kinesthetic information regarding target location was available during the reference and test movements. During the reference movement the index fingertip (left in experiment 1, right in experiment 3) was guided from the starting position and positioned approximately 1 cm *above* the target surface. During the test movement subjects were asked to bring the right index finger to the remembered location *above* the target.

In *condition B (reference fingertip contact),* fingertip contact was provided only during the reference movement, affording kinesthetic and tactile information regarding target location. The index fingertip (left in experiment 1 and 2; right in experiment 3) was positioned *directly on the target surface* by the experimenter. Care was taken to ensure that the fingerpad touched the target surface lightly, and that subjects still supported the weight of their arm without resting on the target. Subjects were asked to position the right index finger at the remembered location *above* the target surface during the test movement.

In *condition C (reference and test fingertip contact),* fingertip contact was available during both the reference and test movements, providing kinesthetic and tactile information regarding target location and movement accuracy. During the reference movement the index fingertip (left in experiment 1; right in experiment 3) was positioned *directly on the target surface* as described in condition B. During the test movement subjects were asked to position the right index finger at the remembered location and lightly *touch the target surface* (without using the target surface to support the weight of the arm).

Experiment 1: switched-limb movements

Subjects were asked to localize the position of the left hand and bring the right hand to the remembered location with their eyes closed. Performance was tested under all three conditions (A, B, and C described above) in a randomized order. Subjects performed 1 set of 64 trials under each of the three conditions (192 trials).

Experiment 2: switched-limb movements following digital anesthesia

This experiment examined the effect of suppression of tactile cues from the left index finger on movement accuracy. Since the effect of the anesthetic was relatively short (~25–45 min), only one experimental condition could be tested. Based on preliminary results of experiment 1, we chose condition B (reference fingertip contact). Procedures from experiment 1 were replicated. Performance was tested under control (no anesthesia) and experimental (anesthesia) conditions in a counterbalanced order. For the control condition subjects performed 1 set of 64 trials. For the experimental condition, a local anesthetic (0.3–0.5 ml 3% lidocaine solution) was injected by a physician under sterile conditions into each side of the base of the distal phalanx of the left index finger, suppressing tactile information from the distal phalanx. Once digital anesthesia had taken effect, as determined by light touch and pinprick, subjects performed 1 set of 64 trials. When the experimental (anesthesia) condition was performed first, subjects were tested on a different day under the control condition to prevent finger tenderness (from the needle) from influencing performance.

Experiment 3: single-limb movements

This experiment was conducted to examine whether tactile cues contributed to movement accuracy when kinesthetic information regarding target location was directly available from the reference movement. The right hand was used for both the reference and test movements. Performance was tested under all three conditions (A, B and C) in a randomized order. Subjects performed 1 set of 64 trials under each condition (total of 192 trials).

Data analysis

Mean x and y position was computed for all trials at each target location. Performance accuracy in all experiments was evaluated using four measures. To quantify the overall magnitude of error, we computed *radial error*, which is the two-dimensional analog of absolute error (Hancock et al. 1995). To quantify performance bias, two measures were computed in order to differentiate between error along the direction of movement (gain error) and error orthogonal to the movement direction (directional error) (see Vindras and Viviani 1998). *Gain error* was defined as the ratio between the response vector and the target vector, where the response vector was the distance from the start position to the final position and the target vector was the distance from the starting position to the target. *Directional error* was defined as the angle between the response vector and the target vector. In the analyses presented below, we report the unsigned magnitude of the directional error. Finally, *variable error* was computed from x, y position to provide a measure of consistency and was defined as the standard deviation of responses around the mean.

In experiment 1 and 3, all four dependent variables were analyzed using a 3 (experimental condition) × 16 (target) repeated measures analysis of variance (ANOVA). In experiment 2, the dependent variables were analyzed using a 2 (control vs experimental) × 16 (target) repeated measures ANOVA. The level of significance for all analyses was set at 0.05. Newman-Keuls post hoc tests were conducted as necessary.

In addition to performance accuracy, we examined the extent to which directional errors were correlated within subjects. We compared the directional errors across the three conditions within each experiment for each subject. We also compared directional errors within each condition across subjects to determine if all subjects demonstrated similar error patterns. Finally, we correlated the directional errors within each condition across experiment 1 and 3 for each subject to examine if the directional error patterns were similar for single-limb and switched-limb movements.

Results

Experiment 1: switched-limb movements

When using the right hand to point to locations specified by the left hand during the reference movement, subjects demonstrated fairly large errors (averaging 6.3 cm across target locations and conditions). Figure 1 shows the mean x and y error at each target and condition for two subjects. Target positions are indicated in each plot by the 16 open circles arranged in a rectangular grid. The filled circle located along the center of the target columns on the x-axis indicates the starting hand position.

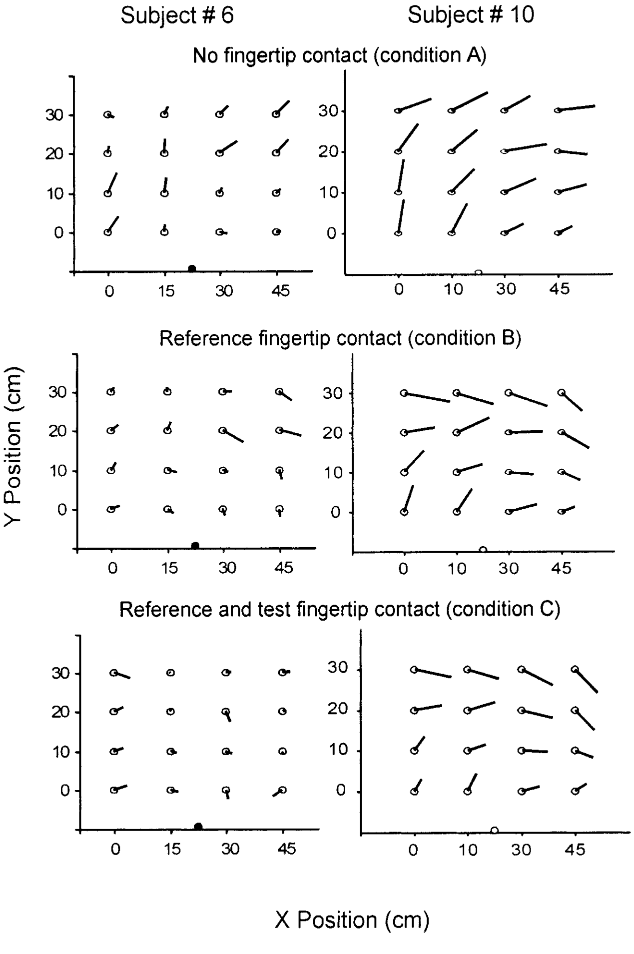

Fig. 1 The spatial pattern of errors in each condition is shown for two subjects for all three experimental conditions (*top panel* no fingertip contact, *middle panel* reference fingertip contact, *bottom panel* reference and test fingertip contact) for switched-limb movements. *The filled circle at the bottom center of each panel* indicates the starting position of the hand, which was aligned with the subject's mid-sagittal plane. *Open circles* indicate the targets and *the lines radiating from the target* indicate error in final hand location

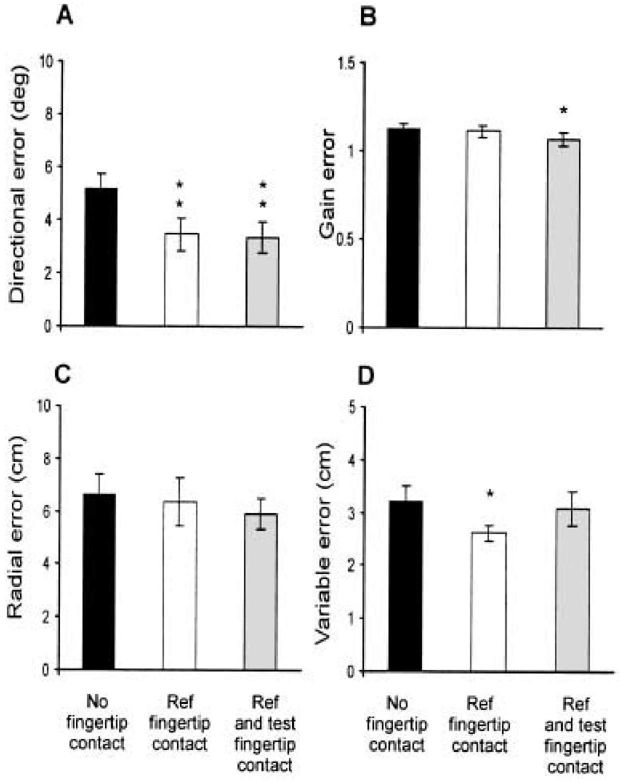

Fig. 2 Means (± SEM) for directional error **(A)**, gain error **(B)**, radial error **(C)** and variable error **(D)** for switched-limb movements (experiment 1). *Each panel* shows all three experimental conditions (*left column* no fingertip contact, *middle column* reference fingertip contact, *right column* reference and test fingertip contact). (* significance at 0.05 level, ** significance at the 0.01 level)

The lines radiating from the circles indicate the magnitude and direction of the mean error at each target location.

Both subjects were more accurate when either the reference fingertip (condition B) or both reference and test fingertips (condition C) made contact with the target surface. In addition, each subject displayed an idiosyncratic pattern of errors (see Helms Tillery et al. 1994). For instance, subject 6 (left panels) was more accurate at proximal targets to the right of the starting position and distal targets to the left of the starting position. In contrast, subject 10 (right panels) was more accurate at proximal targets located to the right of midline. However, the pattern of directional errors within each subject was similar across the three conditions. Within-subject correlation of directional errors across the three conditions was high for nine out of ten subjects (mean of 0.80). For the tenth subject the mean correlation was 0.55. However, between subject correlation within each condition was very low (–0.06, –0.05 and –0.07 for conditions A, B and C respectively), indicating that each subject had a unique pattern of directional error within the workspace.

Figure 2 shows the average data for subjects tested in this experiment. Repeated measures analysis for the magnitude of directional error (Fig. 2A) revealed a significant main effect of condition ($F_{(2,18)}$=8.18, P<0.001). Post hoc analysis indicated that the magnitude of directional error was lower when subjects made fingertip contact with the surface either during the reference movement (condition B) or both reference and test movements (condition C). The difference between the two latter conditions, however, was not statistically significant. Analysis of gain error (Fig. 2B) also revealed a significant main effect of condition ($F_{(2,18)}$=4.00, P<0.05). Post hoc analysis indicated that gain error was lowest when the fingertip made surface contact during both the reference and test movements (condition C) as compared to the other two conditions. In addition, there was a significant main effect of target ($F_{(15,135)}$=9.76, P<0.001) for gain error indicating that accuracy of movement amplitude varied with target distance. Post hoc analyses demonstrated that, on average, subjects tended to overshoot proximal targets but were fairly accurate at distal targets.

Radial error (Fig. 2C) was slightly lower when the fingertip made surface contact during both reference and test movements (condition C), although the differences did not reach statistical significance. In contrast, we found a main effect of condition ($F_{(2,18)}$=5.46, P<0.01) and target ($F_{(15,135)}$=1.77, P<0.05) for variable error (Fig. 2D). Post hoc analysis indicated that variable error was lowest when subjects touched the target surface during the reference movement (condition B) compared to the other two conditions. Generally, variable error was lowest for the most proximal targets and highest for the distal targets. Thus, while subjects were more accurate at distal targets, they were much less consistent.

Experiment 2: switched-limb movements following digital anesthesia

Although the results of the previous experiment indicated that fingertip contact improved accuracy during switched-limb movements, it is not clear whether information from tactile receptors at the fingertip, proximal deep pressure receptors, or both contributed to improved accuracy. In order to examine the specific role of tactile cues, we anesthetized the distal phalanx of the left index finger. Data from two subjects are shown in Fig. 3, which shows the mean *x* and *y* response at each target location for the control and experimental (anesthesia) conditions. The magnitude of radial error was greater when the left index finger was anesthetized (bottom panels) as compared to the control condition (top panels). The average increase in the magnitude of error following anesthesia was ~25% and 20% for subjects 1 and 2, respectively.

As seen in the previous experiment, subjects demonstrated a unique pattern of directional error that was consistent across conditions. The within subject correlation of directional error was fairly high for eight out of nine subjects (mean 0.71), whereas the between subject correlation of directional error was 0.02 for the control condition and 0.07 for the experimental condition. Figure 4 shows that the influence of tactile cues described above

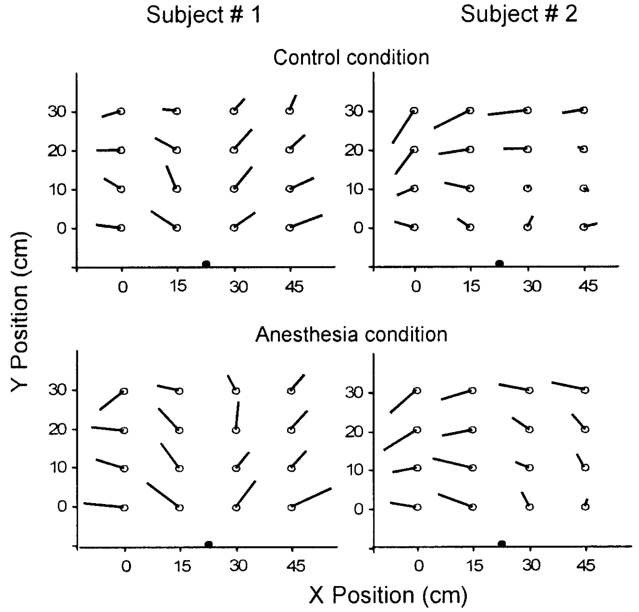

Fig. 3 Spatial pattern of errors is shown for two subjects for the control (no anesthesia) condition *in the top panels* and experimental (anesthesia) condition *in the bottom panels. The filled circle at the bottom center of each panel* indicates the starting position of the hand. *Open circles* indicate the targets and *the lines radiating from the target* indicate error in final hand location

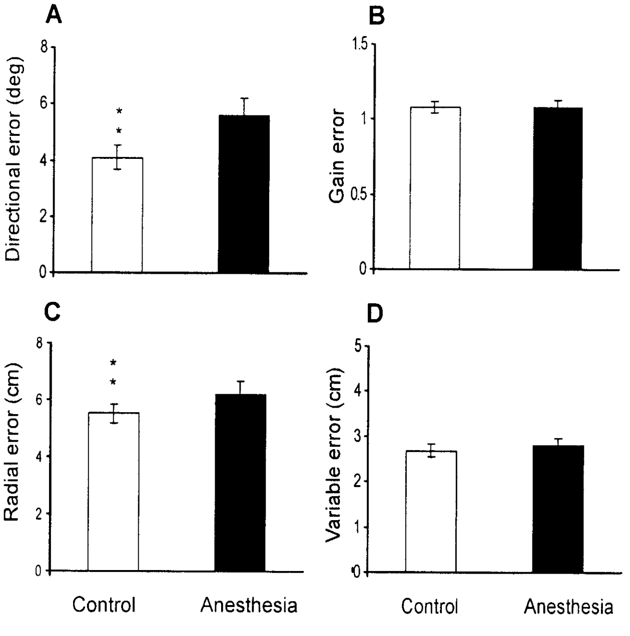

Fig. 4 Mean (± SEM) for directional error **(A)**, gain error **(B)**, radial error **(C)** and variable error **(D)** for experiment 2. The control condition is indicated by *the empty bar* and the experimental condition by *the filled bar*. (** significance at the 0.01 level)

was representative of all subjects. The magnitude of directional error (Fig. 4A) was higher when the left index finger was anesthetized ($F_{(1,8)}$=10.34, P<0.01). Gain error (Fig. 4B) was not influenced by digital anesthesia. However, radial error (Fig. 4C) was significantly higher following digital anesthesia compared to the control condition ($F_{(1,8)}$=11.26, P<0.01). No differences were seen for variable error.

In order to determine whether the increased error following anesthesia was a generalized effect (e.g., by causing a distraction), we asked two subjects to return and perform the procedure again. However, in this case, the finger adjacent to the reference finger (the middle finger) was anesthetized. The results did not demonstrate an influence of anesthesia to the middle finger on pointing accuracy, i.e., the dependent variables were similar across the control (C) and anesthesia (A) conditions as seen by the mean (standard deviation) values: [radial error 4.3 (1.18) cm for C and 4.5 (1.04) cm for A; gain error ratio 0.95 (0.03) for C and 0.98 (0.04) for A; directional error 27.1° (5°) for C and 22.7° (2.65°) for A; and variable error 2.2 (0.2) for C and 2.5 (0.2) for A]. Thus, anesthesia appears to influence pointing accuracy by suppression of tactile cues from the fingertip rather than from a generalized distraction produced by the anesthesia.

Experiment 3: single-limb movements

The switched-limb experiment (experiment 1) suggested that tactile cues from the left index finger improve directional accuracy of pointing with the right hand (when kinesthetic information regarding target location was not directly available). The present experiment was performed to determine whether tactile cues contributed to accuracy when kinesthetic information regarding the target was readily available from the same limb. The results suggest that tactile cues had less of an influence on the accuracy of single-limb movements. Figure 5 shows mean *x* and *y* position at all targets for two subjects. In general, both subjects demonstrated better accuracy when the reference and test fingertip (condition C) touched the target surface compared to the other conditions.

Each subject demonstrated a unique pattern of directional error that was consistent across conditions. Within-subject correlation across condition was fairly high for all subjects (0.74) whereas between-subject correlation was very low for all three conditions (–0.02, –0.04 and –0.04 for condition A, B and C respectively). Figure 6 shows the average data for all subjects. Repeated measures analysis demonstrated a main effect of condition ($F_{(2,18)}$=3.69, P<0.05) for directional error (Fig. 6A). Post hoc tests indicated that directional error was lower when subjects made fingertip contact during the reference movement (condition B). In addition, there was a main effect of condition ($F_{(2,18)}$=5.58, P<0.01) for gain error (Fig. 6B), which was lower when subjects made fingertip contact during both reference and test movements (condition C). Differences for radial error (Fig. 6C) and variable error (Fig. 6D) were not statistically significant across conditions.

In comparing single and switched-limb movements (Figs. 2, 6), it is interesting to note that gain error was

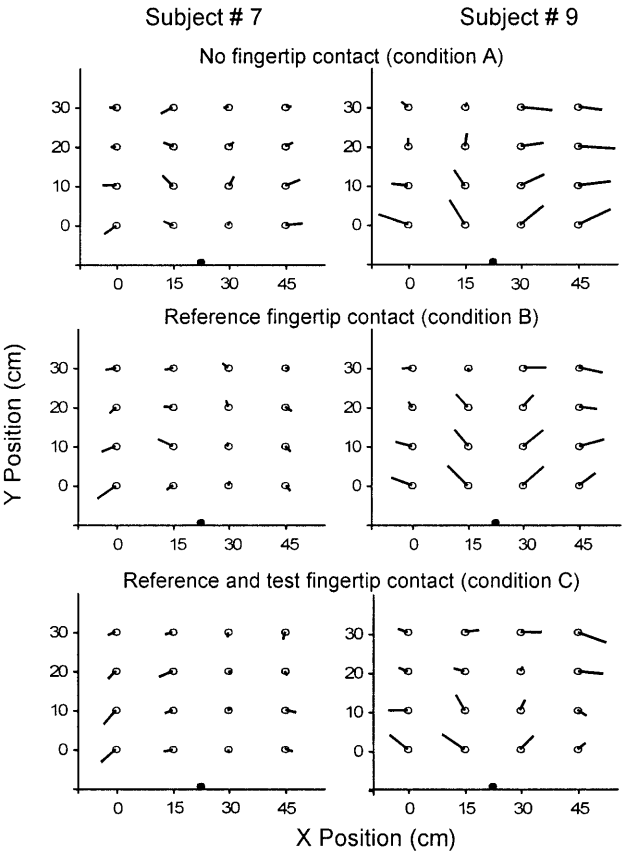

Fig. 5 The spatial pattern of errors in each condition is shown for two subjects for all experimental conditions (*top panel* no fingertip contact, *middle panel* reference fingertip contact, *bottom panel* reference and test fingertip contact) for single-limb movements

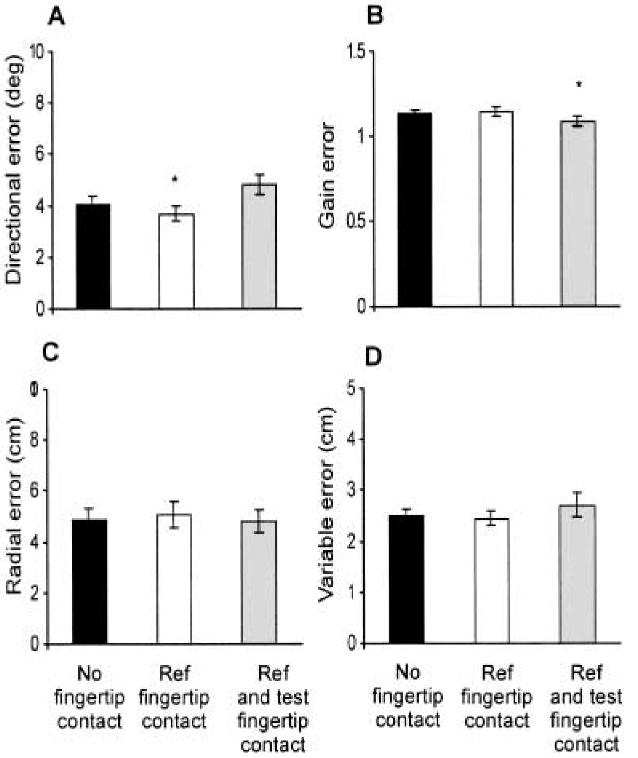

Fig. 6 Mean (± SEM) for directional error **(A)**, gain error **(B)**, radial error **(C)** and variable error **(D)** for experiment 3. *Each panel* shows all three experimental conditions (*left column* no tactile contact, *middle column* reference tactile contact, *right column* reference and test tactile contact). (* indicates significance at the 0.05 level)

similar for single-limb (1.10) and switched-limb (1.12) movements. Radial error was slightly higher for switched-limb movements (6.29 cm, compared to 4.90 cm for single-limb movements, averaged across conditions), although this difference did not approach statistical significance. No reliable differences were seen for variable error, which was slightly lower for single-limb compared to switched-limb movements (2.55 cm vs 2.97 cm, averaged across conditions). Directional error was higher for switched-limb movements compared to single limb movements, although the differences were accounted for primarily by condition A (no tactile contact). Taken together these results indicate that there were no reliable differences across single-limb and switched-limb movements.

Discussion

Our results extend previous findings (Helms Tillery et al. 1994) and indicate that tactile afferent information from the fingertip contributes to accuracy during pointing movements. Tactile information primarily influenced performance bias (direction and gain error) rather than consistency (variable error). Following digital anesthesia of the index fingertip, movement accuracy was degraded compared to the control condition, indicating that information from tactile receptors at the fingertip, independent of proximal deep pressure information, contributed to pointing accuracy. In addition, the influence of tactile information was more pronounced during switched-limb movements as compared to single-limb movements.

Contribution of tactile cues to movement accuracy

Subjects made appreciable errors in reproducing spatial locations when they were required to use only kinesthetic cues during single-limb and switched-limb movements. The magnitude of errors, on average 4–7 cm, was comparable to that in previous reports (Larish and Stelmach 1982; Helms Tillery et al. 1994). A high magnitude of errors is seen when target locations are specified by passive (rather than active) movements and subjects locate the target subsequently using active movements (Paillard and Brouchon 1974). Thus, our paradigm of guided reference movements may have resulted in added noise to the proprioceptive system. However, care was taken to ensure that all reference movement conditions were performed in an identical manner. Despite the added noise, in both single- and switched-limb movements, fingertip contact with the reference hand (condition B) generally influenced directional error, whereas fingertip contact with the reference and test hands (condition C) also influenced gain error. Thus movement direction was influenced by information about target location before the movement, whereas movement gain was influenced by information both before the movement (about target location) and after the movement (about movement accuracy).

Tactile information may potentiate proprioception (see Helms Tillery et al. 1994). Prior work has suggested that tactile information from the fingertip contributes to kinesthetic accuracy at more proximal joints of the fingers. For example, in a task requiring matching of PIP joint angles, kinesthetic acuity at the PIP joint was impaired even when the anesthesia was restricted to the distal phalanx (Clark et al. 1986). Skin strain patterns during hand movement may also convey information about joint movement (Edin and Abbs 1991; Edin and Johansson 1995). In the present study, however, skin strain patterns from the dorsal aspect of the hand (due to changes in finger joint positions) were unlikely to contribute to movement accuracy in space since the hand posture was maintained consistent during data collection. Therefore how might tactile information from the fingertip contribute to pointing accuracy?

While we did not measure shear forces at the fingertip, it is likely that when the fingerpad was positioned on the target at the end of the reference movement, skin strain patterns from small shear forces provided information regarding orientation of the fingertip and forearm in space. It is possible that information regarding orientation may have been used to replicate final posture of the arm during subsequent trials. Given the rich innervation of tactile afferents in the fingertip that are sensitive to the direction of mechanical stimuli (Goodwin et al. 1989; Johansson 1978; Srinivasan et al. 1990), skin strain direction may be represented in the population response of afferent fibers. Contact force at the fingertip has been shown to provide information regarding the direction of body sway in subjects standing either in a normal bipedal stance (Clapp and Wing 1999) or in the Romberg stance (Jeka and Lackner 1994; Rabin et al. 1999). Our finding that fingertip contact reduced directional error is consistent with this hypothesis.

It is also conceivable that fingertip contact with the table surface may have attenuated postural sway, thereby improving movement endpoint accuracy. Fingertip contact has been shown to stabilize postural sway in standing subjects despite the fact that the contact force at the fingertip was not enough to provide mechanical stability (Clapp and Wing 1999; Jeka and Lackner 1994; Rabin et al. 1999). However, this was unlikely since subjects in the present study were seated through the data collection process and their back was supported for pointing to proximal target locations. Given the oscillatory nature of postural sway, it is likely to influence variability in endpoint position rather than performance bias. Moreover, one would expect greater variability at the distal compared to proximal targets, given the lack of back support for distal targets. Analysis of variability across target locations (distal versus proximal) did not demonstrate any consistent patterns across experiments reported in this paper. In fact, tactile cues influenced directional and gain error more systematically than variable error.

Finally, fingertip contact with the surface provided deep pressure information from proximal joints (in addition to tactile cues), which may have contributed to pointing accuracy. However, we excluded this possibility by administering anesthesia to the left index fingertip (experiment 2). Following anesthesia, which attenuated tactile information, errors in magnitude and direction increased appreciably despite the presence of proximal deep pressure information (see Fig. 4). Thus, accuracy clearly improved due to tactile cues from the fingertip independent of deep pressure information.

Gain error (in contrast to the directional error) decreased only when the fingertip made contact during both the reference and test movements (condition C). Fingertip contact at the starting position and target provided discrete information regarding the beginning and end of movement, which may have been used to scale movement amplitude (Gentilucci et al. 1997). It has previously been shown that subjects are able to accurately discriminate movement amplitude using only kinesthetic cues (Bevan et al. 1994). The addition of tactile cues (via fingertip contact) to kinesthetic information may serve to enhance the estimate of movement amplitude.

Comparison of single-limb and switched-limb movements

Radial, gain and variable errors were not significantly different across single and switched-limb movement, suggesting that these movements may share common processes during planning. In reaching toward objects, for example, Tresilian and Stelmach (1997) have reported that critical parameters such as grip aperture and arm transport evolve similarly over time in both unimanual and bimanual movements. Furthermore, in pointing movements the endpoint distributions in three-dimensional space were similar irrespective of the arm used for specifying the target (Baud-Bovy and Viviani 1998). The shape and orientation of the confidence ellipsoids (based on the distribution of endpoints) were similar for single-limb and switched-limb movements. Despite obvious biomechanical differences in these movements, the similarities suggest that common processes may be employed.

In the present study we specified target locations using either the left hand (for switched-limb movements) or the right hand (for single-limb movements) and subjects always responded with the right hand, similar to Baud-Bovy and Viviani (1998). Manipulating the limb used to specify target location during the reference movement did not influence movement accuracy during the test movement. This suggests that spatial information regarding target location may be represented in an effector-independent map of space for generating arm movements. Since tactile information enhanced movement accuracy, it is likely that tactile cues improved the fidelity of kinesthetic information regarding arm and hand posture within this map. However, the role of tactile information was less pronounced for the single-limb movements, likely because kinesthetic information regarding target location with respect to the pointing arm was readily available. The similar magnitude of the directional errors following right or left arm target presentation without tactile cues is in agreement with this notion. Thus, the proprioceptive information directly available during single-limb movements may already saturate the resolution capability of the CNS.

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References

Baud-Bovy G, Viviani P (1998) Pointing to kinesthetic targets in space. J Neurosci 18:1528–1545

Bevan L, Cordo P, Carlton L, Carlton M (1994) Proprioceptive coordination of movement sequences: discrimination of joint angle versus angular distance. J Neurophysiol 71:1862–1872

Clapp S, Wing AM (1999) Light touch contribution to balance in normal bipedal stance. Exp Brain Res 125:521–524

Clark FJ, Burgess RC, Chapin JW (1986) Proprioception with the proximal interphalangeal joint of the index finger: evidence for a movement sense without a static-position sense. Brain 109:1195–1208

Edin BB, Abbs JH (1991) Finger movement responses of cutaneous mechanoreceptor in the dorsal skin of the human hand. J Neurophysiol 65:657–670

Edin BB, Johansson N (1995) Skin strain patterns provide kinesthetic information to the human central nervous system. J Physiol 487:243–251

Gandevia SC, Burke D (1992) Does the nervous system depend on kinesthetic information to control natural limb movements? Behav Brain Sci 15:614–632

Gentilucci M, Toni I, Daprati E, Gangitano M (1997) Tactile input of the hand and the control of reaching to grasp movements. Exp Brain Res 114:130–137

Goodwin AW, John KT, Sathian K, Darian-Smith I (1989) Spatial and temporal factors determining afferent fiber responses to a grating moving sinusoidally over the monkey’s fingerpad. J Neurosci 9:1280–1293

Gordon AM, Soechting JF (1995) Use of tactile afferent information in sequential finger movements. Exp Brain Res 107:281–292

Gordon J, Ghilardi MF, Ghez C (1994) Accuracy of planar reaching movements. I. Independence of direction and extent variability. Exp Brain Res 99:97–111

Hancock GR, Butler MS, Fischman MG (1995) On the problem of two-dimensional error scores: measures and analysis of accuracy, bias and consistency. J Motor Behav 27:241–250

Helms Tillery SI, Flanders M, Soechting JF (1994) Errors in kinesthetic transformations for hand apposition. Neuroreport 6:177–181

Jeka JJ, Lackner JR (1994) Fingertip contact influences human postural control. Exp Brain Res 100:495–502

Johansson RS (1978) Tactile sensibility of the human hand: receptive field characteristics of mechanoreceptive units in the glaborous skin area. J Physiol 281:101–123

Lackner JR, Dizio P (1994) Rapid adaptation to Coriolis force perturbations of arm trajectory. J Neurophysiol 72:299–313

Larish D, Stelmach GE (1982) Spatial orientation of a limb using egocentric reference points. Percept Psychophys 32:19–26

Messier J, Kalaska JF (1997) Differential effects of task conditions on errors of direction and extent of reaching movements. Exp Brain Res 115:469–478

Moberg E (1983) The role of cutaneous afferents in position sense, kinaesthesia, and motor function of the hand. Brain 106:1–19

Paillard JR, Brouchon M (1974) A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. Brain Res 71:273–284

Prochazka A (1996) Proprioceptive feedback and movement regulation. In: Rowell J, Sheperd JT (eds) Handbook of physiology. American Physiological Society, Bethesda, MD

Rabin E, Bortolami SB, Dizio P, Lackner JR (1999) Haptic stabilization of posture: changes in arm proprioception and cutaneous feedback for different arm orientations. J Neurophysiol 82:3541–3549

Slinger RT, Horsley V (1906) Upon the orientation of points in space by the muscular, arthrodial and tactile senses of the upper limb in normal individuals and in blind persons. Brain 24:1–27

Srinivasan MA, Whitehouse JM, LaMotte RH (1990) Tactile detection of slip: surface microgeometry and peripheral neural codes. J Neurophysiol 63:1323–1332

Tresilian JR, Stelmach GE (1997) Common organization for unimanual and bimanual reach-to-grasp tasks. Exp Brain Res 113:283–299

van Beers RJ, Sittig AC, van der Gon DJJ (1999) Localization of a seen finger is based exclusively on proprioception and on vision of the finger. Exp Brain Res 125:43–49

Vindras P, Viviani P (1998) Frames of reference and control parameters in visuomanual pointing. J Exp Psychol Hum Percept Perform 24:569–591