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RESEARCH ARTICLE

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Haptic localization and the internal representation of the hand in space

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Abstract As the hand actively explores the environment, contact with an object leads to neuronal activity in the topographic maps of somatosensory cortex. However, the brain must combine this somatotopically encoded tactile information with an internal representation of the hand's location in space if it is to determine the position of the object in three-dimensional space (3-D haptic localization). To investigate the fidelity of this internal representation in human subjects, a small tactual stimulator, light enough to be worn on the subject's hand, was used to present a brief mechanical pulse (6-ms duration) to the right index finger before, during, or after a fast, visually evoked movement of the right hand. In experiment 1, subjects responded by pointing to the perceived location of the mechanical stimulus in 3-D space. Stimuli presented shortly before or during the visually evoked movement were systematically mislocalized, with the reported location of the stimulus approximately equal to the location occupied by the hand 90 ms after stimulus onset. This pattern of errors indicates a representation of the movement that fails to account for the change in the hand's location during somatosensory delays and, in some subjects, inaccurately depicts the velocity of the actual movement. In experiment 2, subjects were instructed to verbally indicate the perceived temporal relationship of the stimulus and the visually evoked movement (i.e., by reporting whether the stimulus was presented "before," "during," or "after" the movement). On average, stimuli presented in the 38-ms period before movement onset were more likely to be perceived as having occurred during rather than before the movement. Similarly, stimuli in the 145-ms period before movement termination were more likely to be perceived as having occurred after rather than during the movement. The analogous findings of experiments 1 and 2 indicate that the same inaccurate representation of dynamic hand position is used to both localize tactual stimuli in 3-D space and construct the perception of arm movement.

Key words Hand · Movement · Somatosensory system · Internal representation · Spatial localization · Human

Introduction

The location of a single tactual stimulus can be described with respect to several behaviorally relevant coordinate systems. Previous investigations of the somatosensory system have usually focused on the ability to localize stimuli in perhaps the most fundamental of these frames of reference: a topographic representation of the body surface. However, a description of stimulus location in this somatotopic map is insufficient to drive behaviors that require a description in a higher-order coordinate system. One such behavior is the ability to localize a tactually perceived object in three-dimensional (3-D) space. As an example, consider the ability to use the right hand to brush away an unseen insect crawling on the left hand. For this behavior, somatotopic coordinates cannot sufficiently describe the location of the insect given that the left arm and hand may be in any of an infinite number of postures. To direct the right hand to the appropriate spatial location, the position of the left hand in space must also be considered. Thus, the brain must create a higher-order spatial coordinate system by combining the somatotopic map with an internal representation of the body's position in 3-D space. Using the definitions of Loomis and Lederman (1986), I refer to this higher-order coordinate system as a *haptic* one to distinguish it from the purely somatotopic *tactile* coordinate system. The general term *tactual* is used to refer to tactile, haptic, and kinesthetic perceptions, inclusively.

Although the example of swatting an insect is meant to provide only a general introduction to somatospatial coordinate systems, several detailed investigations have

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in fact examined this "wiping" ability in normal and spinal frogs. Spinal frogs can accurately direct wiping movements to the somatotopic locations of irritating stimuli (Fukson et al. 1980), but this ability breaks down if the target location is on a limb perturbed from its normal resting posture (Giszter et al. 1989). This suggests that brain structures above the level of the spinal cord are responsible for encoding a dynamic representation of limb position for use in haptic localization.

Past investigations of tactual localization abilities have varied little with respect to the task required of the subjects. For the most part, stimuli were applied to some stationary region of the body or limbs, and subjects were required to indicate the stimulated location by, for example, comparing it with some previous tactual reference, pointing to an analogous position on a drawing or model of the body, or pointing to it directly (Cole 1929; Boring 1942). Only this last response variation can be considered truly haptic, since the goal of the targeting movement must be computed by considering both the somatotopic location of the stimulus and the orientation of the body and limbs in space. In general, errors in this type of haptic localization task are somewhat larger than in a task requiring a tactile-tactile comparison (Cole 1929). However, this type of task only provides information concerning the somatotopic subcomponent of haptic localization, given that testing occurs with the stimulated region of the body in only a single, unchanging location in space.

The purpose of the present study was to investigate the accuracy of the other subcomponent of haptic localization, namely the internal representation of the body's orientation and location in space. Although other studies have assessed the accuracy of representations of body position under static (e.g., Paillard and Brouchon 1968; Horch et al. 1975) and dynamic conditions (e.g., Sittig et al. 1987; Cordo 1990), none have focused on the accuracy with which the brain uses this representation to construct a map of 3-D haptic space. In the present investigation, a brief tactual stimulus was applied to the right index finger of a subject shortly before, during, or after a visually evoked movement of the right hand; a second movement was performed to indicate the perceived 3-D location of the stimulus. With all stimuli applied to the same point on the body surface, any uncertainty in the somatotopic location was effectively eliminated. Thus, localization was a matter of knowing where the hand was at the time of the stimulus, with accuracy dependent mainly on the fidelities of the subject's internal representation of hand position and the perception of stimulus timing. An analysis of the localization errors revealed that the brain does not compensate for movement of the hand during somatosensory transmission and processing delays, and that the representation of hand in space moves, in some subjects, with a velocity less than that of the hand itself. In a second experiment, subjects verbally reported the temporal relationship of the stimulus and the movement. The resulting pattern of errors indicates that the perception of self-motion is derived from the same internal representation that is used for haptic localization. Short descriptions of preliminary findings have been presented elsewhere (Dassonville et al. 1993a, 1994).

Materials and methods

Four healthy human subjects (two women and two men, between 25 and 29 years of age) participated in the study. One subject was the author (P.R.D.) and two were members of the laboratory working on unrelated projects (J.K.B. and N.L.P.). Informed consent was obtained as per the protocol approved by the University of Minnesota Institutional Review Committee. Each subject was classified as right-handed according to the Edinburgh Inventory for Handedness (Oldfield 1971).

During each experimental session, the subject sat unrestrained in a chair facing a wall of the laboratory at a distance of approximately 80 cm. Two green light-emitting diodes (LEDs) were mounted on the wall along a horizontal axis at shoulder height, 26 cm left (LED 1) and right (LED 2) of the subject's midline, respectively (Fig. 1A). These LEDs, which had intensities well above visual threshold, served as visual targets for pointing movements in the tasks described below. Because the LEDs were placed out of reach, the subjects were instructed only to point in their directions, without attempting to make contact. This ensured that the subjects received no extraneous tactual stimulation during the experimental trials. As is expected from this spatial arrangement (Fig. 1A), visually evoked movements from one LED to the other had amplitudes less than the 52 cm separation of the LEDs, with the amplitudes somewhat dependent on the length and posture of the subject's arm.

The position of the right arm in 3-D space was monitored by a video-based motion analysis system (VP320; Motion Analysis Corporation) at a sampling rate of 200 Hz, with passive markers placed on the fingertip, wrist, elbow, and shoulder. A system calibration indicated, in the worst case, an error of 0.72 mm (SD 0.92) in computing the actual marker locations for the particular motion analysis configuration (i.e., camera locations, shutter speed, etc.) used in the present study. Experimental sessions were performed in the dim, red ambient light required by the cameras; however, subjects wore goggles with an affixed green filter gel that blocked this ambient light while allowing vision of the green LEDs when illuminated. Room lights were illuminated between trials (10 s) to prevent dark adaptation of the visual system, and to allow the visual and motor systems to remain calibrated throughout the experiment.

To present tactual stimuli to a subject's moving hand, a lightweight stimulator (80 g) was developed to be worn on the hand. The stimulator was constructed from a small 8-Ω audio speaker with the diaphragm removed and a metal probe (approximately 1-mm diameter) attached to the voice coil. The probe could be driven through a small hole in a finger plate mounted over the speaker's face by applying a short (5 ms) square-wave voltage to the speaker inputs. The speaker assembly was attached to a plastic handle that allowed the subject to comfortably grip the stimulator with the right hand. The right index finger was extended in a pointing fashion and rested upon the finger plate through which the metal probe protruded. Velcro straps were used to secure the stimulator to the hand, and the input leads were loosely strapped to the right arm from the wrist to the shoulder. The tactual stimulus in each trial consisted of a single mechanical pulse applied to the tip of the index finger; timing was under computer control and was synchronized to the frame rate of the motion analysis hardware. White noise and ear plugs were used to mask the faint sound emitted by the stimulator.

To verify the characteristics of the stimulator, measurements were made of the timing and extent of the probe's excursion through the finger plate. In tests performed without a finger positioned over the finger plate, the probe protruded for a duration of approximately 6 ms after a mechanical delay of approximately

1 ms. Electrical delays were found to be negligible, as were the errors in synchronizing the stimulator's trigger to the frame rate of the cameras. The maximum extent of the probe's protrusion was approximately 0.75 mm. Under experimental conditions, of course, the skin of the index finger provided a mechanical resistance to the probe, decreasing its maximum extent and, perhaps, its duration. Although the strength of the stimulus and the intensity of the accompanying tactual percept were not directly measured, it is clear that the stimulus was well above perceptual threshold: no subject ever reported a trial in which the stimulus was not perceived.

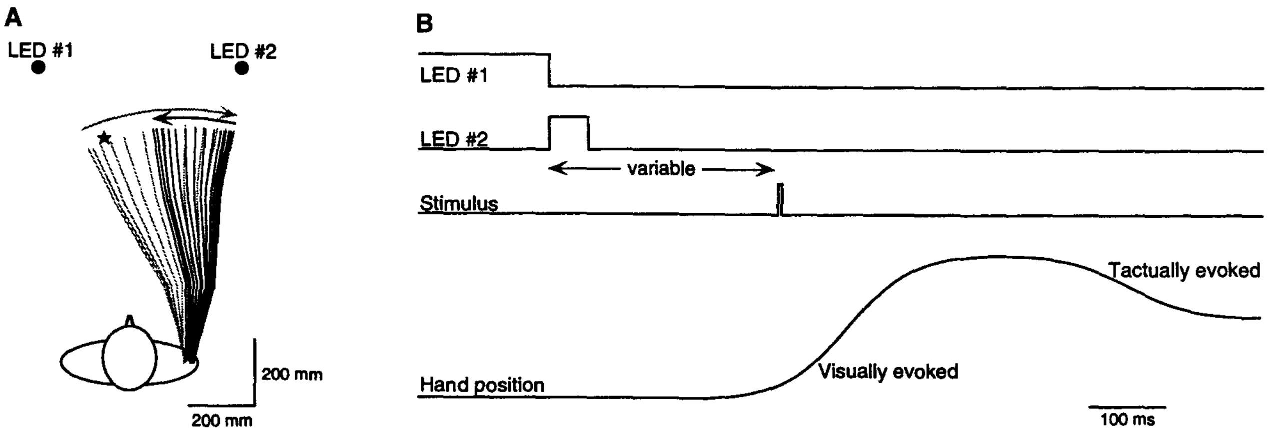
Experiment 1: haptic localization

Subjects were instructed to make fast movements with clear onsets and terminations (i.e., no slow, drifting movements) and were allowed several minutes before the experimental session to practice appropriate movements. During these practice trials, the experimenter provided guidance concerning movement velocity and consistency across trials, but gave no feedback concerning pointing accuracy. Subjects were encouraged to make the movements using a comfortable arm posture, with consistency across trials the only constraint. All subjects chose a posture in which the arm was fully extended or had only a slight elbow flexion (Fig. 1A), and this posture was approximately maintained throughout each trial. Pointing movements were made by rotating the shoulder joint almost exclusively, with very little (if any) involvement of the elbow, wrist, or finger joints.

Each trial began with the removal of the ambient light, followed 2 s later by the illumination of LED 1. The subject responded by pointing in the direction of this visual target with the unrestrained right hand and arm. After a random duration of 2–4 s, LED 1 was extinguished and replaced by LED 2, 52 cm to the right, for a duration of 50 ms (Fig. 1B). This was the signal for the subject to make a pointing movement of the right arm from the direction of LED 1 to that of LED 2 (this movement will be referred to as the *visually evoked movement* in the remainder of the text). After a variable delay (25, 125, 200, 275, 350, 400, 450, 500, 575, or 700 ms, pseudorandomly ordered) measured from the onset of LED 2, a tactual stimulus (6 ms duration) was applied to the tip of the right index finger by the stimulator worn on the subject's hand. The trial-to-trial variability of the delay allowed the stimulus to be presented either before (i.e., during the reaction time), during, or after the visually evoked movement and prevented the subject from anticipating the timing and corresponding spatial location of the stimulus. The subject completed the task by making a pointing movement back to the 3-D location at which the stimulus had been perceived (this movement will be referred to as the *tactually evoked movement*). Subjects were instructed to complete the visually evoked movement to LED 2 before starting the tactually evoked movement. After the tactually evoked movement was complete, subjects were to maintain the appropriate pointing posture until the end of the trial was signalled by a short tone accompanied by the simultaneous illumination of LEDs 1 and 2. For trials in which the tactual stimulus was perceived to have occurred after the visually evoked movement, no tactually evoked movement was necessary because the subject was already pointing at the perceived location. Under these circumstances, subjects were instructed to maintain the final position of the visually evoked movement until the trial's end. Throughout each trial, subjects could see nothing except the LEDs during their illumination, and these were extinguished at least 125 ms before the onset of the visually evoked movement. Thus, no feedback concerning movement accuracy or stimulus location was provided. Subjects were asked to verbally indicate trials in which the stimulus location was uncertain; these trials (1.6% of all trials) were excluded from subsequent analyses. Data from each subject were collected in four or five experimental sessions performed on separate days; 50 or 100 trials were collected in each session, with each subject performing a total of 350–400 trials. Eye movements were not monitored.

In an off-line analysis of the data, the position of the index finger was computed in x, y, z coordinates (ExpertVision software; Motion Analysis) and then filtered with a low-pass, finite impulse response filter (15 Hz cutoff; MacProbe software; Aristometrics). Although the movements were confined primarily to the horizontal axis of a frontoparallel plane, some displacement was obvious along the other axes. For this reason, the coordinate system was rotated on a trial-by-trial basis so that the starting and ending position of the visually evoked movement fell along a single axis. The position and error data shown in the tables and figures were calculated along the main axis of the visually evoked movement. The start and end of each movement were defined as the times at which velocity increased above or decreased below, respectively, a level of 0.05 m/s. If a tactually evoked movement was present in a given trial (e.g., Fig. 2A, trials a-d), its end point was considered to be the subject's perception of the stimulus location. If no tactually evoked movement was present (e.g., Fig. 2A, trial e), it was assumed that the subject perceived the stimulus to have occurred after the visually evoked movement; the end point of the visually evoked movement was used as a measurement of the perceived location in these trials. Excluded from analysis were any trials (4.1% of all trials) in which the visually or tactually evoked movement was followed by one or more corrective movements.

Fig. 1 **A** Spatial schematic of the subject's task. *Stick figure* shows arm trajectory (shown at a sampling rate of 40 Hz for illustrative purposes) for the visually evoked movement (*stippled*, moving rightward) from LED 1 to LED 2 and the subsequent tactually evoked movement (*solid*, moving leftward) to indicate the perceived spatial location of the stimulus (*star*, actual stimulus location). **B** Temporal schematic of the stimulus presentation and subject's response (*Hand position*). LED 1 duration 2–4 s; LED 2 duration 50 ms; stimulus duration 6 ms, with a variable onset delay (25–700 ms) timed to occur before, during, or after the visually evoked movement



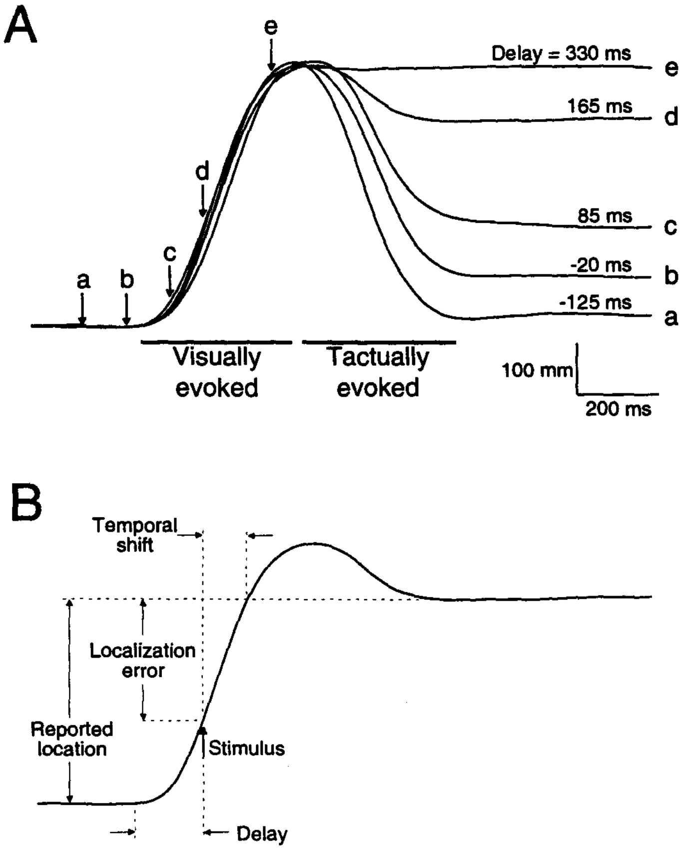


Fig. 2 **A** Position of the hand (*ordinate*) plotted with respect to time (*abscissa*) for five typical trials from experiment 1 (subject M.C.D.). The upward deflection of each trace shows the time course of the rightward visually evoked movement from LED 1 to LED 2; the downward deflection shows the subsequent tactually evoked movement. Trials have been aligned on the onset of the visually evoked movement. Labeled *arrows* (and delay values, measured from the onset of the visually evoked movement) indicate the onset time of the tactual stimulus in each of the corresponding trials. **B** Single trial (*d* in **A**) showing the derivation of the reported location (end of the tactually evoked movement), localization error (reported location minus actual location of the stimulus), and temporal shift (duration between stimulus onset and the time at which the hand occupied the reported location of the stimulus)

Subjects were also asked to perform several control trials in which no tactual stimuli were delivered. As in the main task, a visually evoked movement was made between LEDs 1 and 2, but, rather than a subsequent tactually evoked movement, subjects were instructed to make a movement back to the remembered location of LED 1. The accuracy of these movements was used as an indicator of the subject's knowledge of the hand's position at the start of the visually evoked movement. Trials of this type (n=15 in subjects J.K.B., M.C.D. and N.L.P.; n=10 in subject P.R.D.) were collected as the final five trials in two or three experimental sessions with the haptic localization task.

Experiment 2: temporal perception

In a variation of the task described above, the same subjects were instructed to focus attention on the timing of each tactual stimulus rather than its location, and to simply report whether the stimulus was presented "before," "during," or "after" the visually evoked movement. Verbal responses were recorded by the experimenter under three-alternative, forced-choice conditions. Subjects were explicitly instructed not to make a tactually evoked movement to the location of the stimulus. Trials were discarded (1.3% of total) only if the visually evoked movement was followed by one or more corrective movements. All other parameters and conditions were identical to those of the haptic localization task. Data from each subject were collected in three experimental sessions (100 trials each) performed on separate days after the localization experiments were complete.

Results

Experiment 1: haptic localization

Fig. 2A shows the visually and tactually evoked movements of five typical trials from a single subject. In each trial, the tactual stimulus was delivered at a different time with respect to the onset of the visually evoked movement, with the stimuli marked a and b presented before the movement, and those marked c, d, and e presented during the movement. For trials in which a tactually evoked movement was performed (e.g., trials a-d, Fig. 2A), the accuracy of the subject's response was assessed by comparing the reported location of the stimulus (i.e., the final position of the tactually evoked movement, Fig. 2B) with the hand's location at the time of stimulus presentation. In trial e, the stimulus was presented shortly before the end of the visually evoked movement and was therefore located very near to the hand's position at the completion of the movement. Because no tactually evoked movement was elicited, the reported location of the stimulus in this trial and others like it was assumed to be equal to the final position of the visually evoked movement. It seems unlikely that the absence of a tactually evoked movement would arise as a result of an uncertainty in the subject's perception of stimulus location, given that the subjects were instructed, and reminded often throughout each session, to verbally indicate trials in which there was any uncertainty.

Each of the four subjects displayed a similar pattern of errors in the attempt to localize the tactual stimulus in space (Fig. 3A). Stimuli presented just before or during the visually evoked movement were mislocalized in the direction of the movement; that is, each stimulus was perceived to be located to the right of its actual position in space. The largest errors, often greater than 200–300 mm in amplitude, occurred with stimuli presented shortly before the peak velocity of the movement. In contrast, accuracy was much better for stimuli presented more than 150 ms before the onset of the visually evoked movement, although some subjects localized these stimuli with a small rightward bias. Stimuli presented after the movement were also localized accurately; this was not unexpected, though, given that these stimuli required no tactually evoked movement to indicate the perceived location.

Errors were also evident when subjects attempted to perform a movement back to the remembered location of LED 1 in the control trials performed with no tactual

Fig. 3 A Localization errors for each subject. Error magnitude was computed, for each trial, by subtracting the position of the hand at stimulus onset from the end position of the tactually evoked movement (*ordinate*, positive values denote errors in the direction of the visually evoked movement). Location along the *abscissa* denotes the delay between the stimulus and the onset of the visually evoked movement (positive values denote stimuli occurring after movement onset). For comparison, the *solid curves* denote the mean time course of the visually evoked movements. *Open circles* denote trials in which the subject made no tactually evoked movement, like that depicted in Fig. 2A, trial e. *Dashed lines* indicate the magnitude of the bias in reporting the remembered location of LED 1 in control trials. **B** Same data as in **A**, replotted to show the absolute locations at which the subjects reported the tactual stimuli (*ordinate*). The *solid curve* denotes the mean time course of the visually evoked movements and therefore serves as an estimate of the actual stimulus location for any given delay

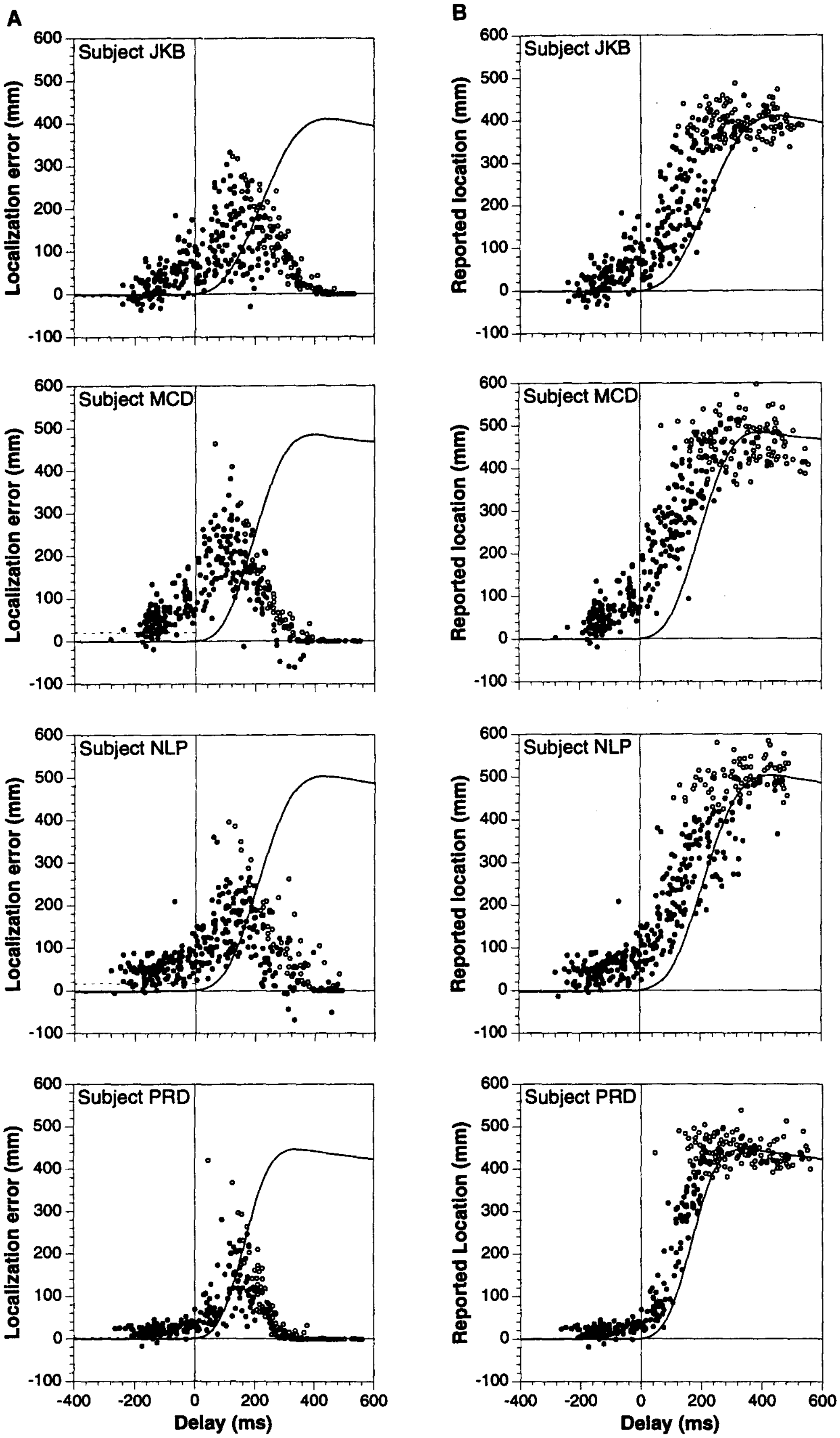


Table 1 Errors in the remembered location of LED 1. Positive errors indicate a mislocalization to the *right* of the actual position

Subject	Mean error±SD (mm)
JKB	−5.7±13.5[n.s.]
MCD	20.3±12.4[a]
NLP	16.8±23.1[a]
PRD	2.8±12.6[n.s.]

[a] Value is significantly different from zero (Student's *t*-test, $P<0.02$)

stimuli (Table 1), with two of the subjects (M.C.D. and N.L.P.) indicating the remembered position of the LED to be significantly to the right of its actual position. Qualitatively, the bias seen in the control trials (dashed lines in Fig. 3A) was similar to that for the localization of tactual stimuli presented well before the movement. For the three subjects (M.C.D., N.L.P., and P.R.D.) with rightward biases in the localization of tactual stimuli presented well before the movement, the remembered location of LED 1 was also biased to the right; the fourth subject (J.K.B.) had a small leftward bias in both conditions.

In Fig. 3B, individual data points show the absolute position at which the subjects reported each tactual stimulus, plotted with respect to the delay between the stimulus and the onset of the visually evoked movement. Taken in sum, the cloud of data points depicts the time course of the change in the reported location of the stimulus as it moves from LED 1 to LED 2. To quantify this time course, the logistic function

$$position = bias + (amp - bias)\cdot\frac{e^{\left(\frac{delay - T_{50}}{\tau}\right)}}{1+e^{\left(\frac{delay - T_{50}}{\tau}\right)}} \qquad (1)$$

was fit to the localization data of each subject. For each trial, *position* is the reported location of the tactual stimulus, *bias* is the mean bias (for that subject) in locating the remembered position of LED 1 in control trials (see above and Table 1), *amp* is the amplitude of the visually evoked movement, and *delay* is the stimulus delay with respect to movement onset. The values of T_{50} (the time, with respect to movement onset, at which the logistic function surpassed 50% of the final amplitude) and the time constant (τ) were computed through an iterative nonlinear regression (SPSS). This function was used only as a means to easily describe the data and was not intended to model any underlying brain functions. With its sigmoidal shape, the logistic function provided an excellent fit to the localization data and allowed a quantitative description of the data using only two dependent variables (T_{50} and τ). These values, as well as the coefficient of determination (R^2), are shown in Table 2 for each subject. For comparison, similar functions (with zero bias) were fit to the actual hand position data of the visually evoked movements; the corresponding T_{50}, τ, and R^2 values are also shown in Table 2.

The results shown in Fig. 3B and Table 2 indicate two obvious differences between the time course of the change in reported location and that of the actual movement of the hand (solid curves in Fig. 3B). First, the reported location begins to change well before the onset of the movement and, in fact, leads the position of the hand throughout the movement. The difference between the T_{50} values from the respective regressions (Table 2) in each subject gives an estimate of the temporal shift between the reported location and the actual movement. The mean temporal shift was found to be 98.7 ms (SD 25.7); values for individual subjects are shown in the final column of Table 1 (positive values indicate a change in reported location that leads the movement). Subject P.R.D., for example, reported each stimulus to be at the spatial position that the hand occupied approximately 64 ms after stimulus onset. Second, in three subjects (most notably M.C.D.), the reported location moves with a velocity that is significantly less than the velocity of the hand. This difference is made evident by comparing the time constants (τ) from the regressions of the reported locations and actual movements (Table 2; larger τ equals slower velocity). (The time constants serve as an indicator of velocity for a movement of a given amplitude only. For this reason, a comparison of time constants across subjects has little value.)

To quantify the time course of the reported location in a manner independent of the assumptions necessary for a nonlinear regression, temporal shift values were also determined on a trial-by-trial basis by computing the duration between stimulus onset and the time that the visually evoked movement passed through the eventual reported location (Fig. 2B). However, individual temporal shift

Table 2 Regression coefficients for the logistic function (Eq. 1) fit to the visually evoked movements and reported location data of experiment 1

Subject	Visually evoked movement			Reported location			Temporal shift
	T_{50} (ms)[a]	τ (ms)	R^2	T_{50} (ms)[a]	τ (ms)	R^2	$T_{50(\mathrm{VEM})}-T_{50(\mathrm{RL})}$ (ms)[b]
JKB	226.6	57.3	0.985	103.5[c]	69.7[c]	0.895	123.1
MCD	198.1	45.1	0.990	87.5[c]	70.2[c]	0.923	110.6
NLP	232.4	60.0	0.959	134.8[c]	82.0[c]	0.873	97.6
PRD	172.6	38.7	0.989	109.1[c]	37.0[n.s.]	0.956	63.5

[a] Measured with respect to movement onset

[b] Value indicates the difference in the T_{50} measurements from the visually evoked movement (VEM) and reported location (RL)

[c] Significant difference in T_{50} (or τ) values from movement and reported location data in the same subject (*Z*-score comparison using pooled standard error, $P<0.0005$)

Table 3 Mean temporal shift and regression coefficients for temporal shift versus stimulus delay (Fig. 4)

Subject	Regression coefficient			Temporal shift
	Intercept (ms)	Slope (ms/ms)	R^2	Mean±SD (ms)
JKB	131.0^a	–0.217^b	0.110	104.9±46.5^c
MCD	161.9^a	–0.492^b	0.725	96.1±46.3^c
NLP	144.0^a	–0.362^b	0.492	90.7±49.6^c
PRD	71.8^a	–0.118^b	0.102	59.7±21.5^c

[a] Intercept is significantly greater than zero (*t*-test, $P<0.0001$)

[b] Slope is significantly less than zero (*t*-test, $P<0.002$)

[c] Temporal shift is significantly greater than zero (Student's *t*-test, $P<0.001$)

values magnify to excessive levels the bias and variability in the subjects' localization of stimuli presented well before the movement. Additionally, stimuli that were reported to have occurred at the end of the visually evoked movement (i.e., no tactually evoked movements were made) have undefined temporal shift values. For these reasons, the calculation of individual temporal shift values was restricted to only those stimuli that were presented after movement onset and resulted in a subsequent tactually evoked movement. For each subject, the mean temporal shift was significantly greater than 0 (Table 3). A more detailed analysis reveals that the temporal shift values decrease throughout the duration of the visually evoked movement (Fig. 4), providing further evidence that the reported location moves with a velocity less than that of the actual movement. This difference in velocities resulted in a regression line with a slope significantly less than zero in each subject (Table 3). Although the mean temporal shifts measured in this manner have an approximate correspondence with the temporal shift values measured by nonlinear regression (Table 2), the former are somewhat smaller (87.9±19.7 ms vs 98.7±25.7 ms, averaged across subjects). This is most probably attributable to the reliance on only a subset of the total trials for the computation of the mean temporal shift values in Table 3. The values would have been greater had they included trials in which the stimulus was presented just before movement onset and whose reported location was greater than the magnitude of the early bias (e.g., stimuli presented less than 150 ms before movement onset in subjects J.K.B. and M.C.D.).

In Fig. 3B, the reported location of each stimulus was plotted with respect to the delay between the stimulus and

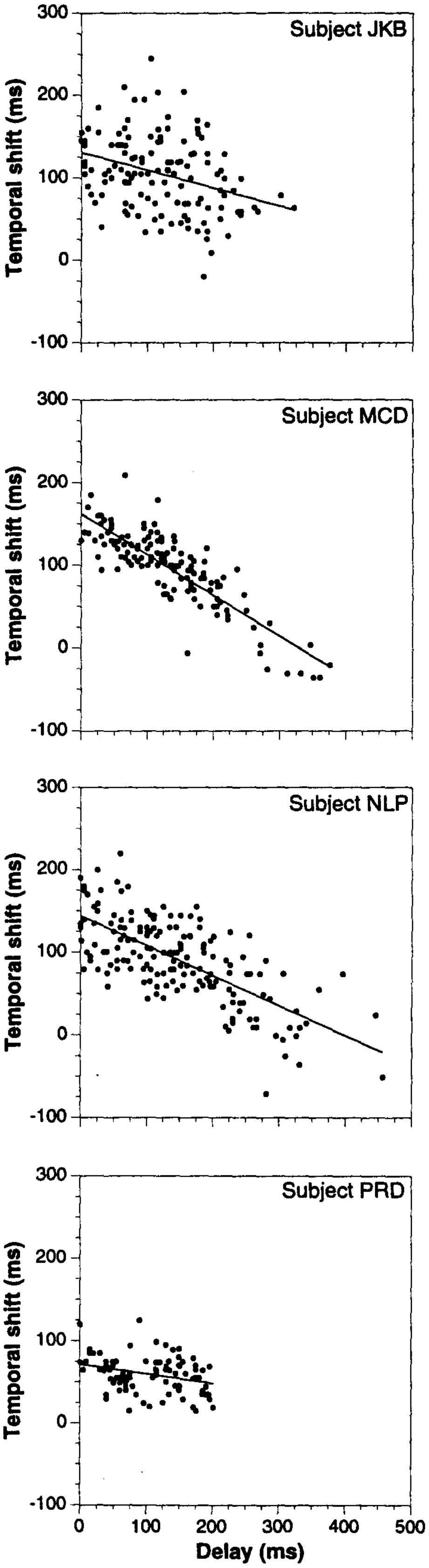


Fig. 4 Temporal shift values for individual trials (*ordinate*), plotted with respect to stimulus delay from movement onset (*abscissa*). For each trial, magnitude of the temporal shift is equal to the duration between stimulus onset and the time that the visually evoked movement passed through the eventual reported location (Fig. 2B). Data shown include only those trials in which the stimulus was presented after movement onset and resulted in a subsequent tactually evoked movement. Linear regressions (*solid lines*; parameters given in Table 3) show a larger temporal shift for stimuli presented shortly after movement onset (0 ms) than for those presented later, indicating a change in the reported location that moves with a velocity less than that of the actual movement

the onset of the visually evoked movement. This manner of data representation was chosen based on the assumption that the change in reported location would be time-locked to the onset of the movement. This assumption was drawn from the hypothesis that the brain computes the perceived location by sampling, at the time the stimulus is perceived, an internal representation of hand in space that is itself time-locked to the actual movement. However, one might conjecture a competing hypothesis in which the internal representation is time-locked to the onset of the visual target (i.e., LED 2) rather than the subsequent visually evoked movement. To test these hypotheses, the results of the nonlinear regression described above (Eq. 1) were compared with a similar regression performed using as an independent variable the delay between the tactual stimulus and LED 2 rather than that between the stimulus and movement onset. In each subject, the absolute residuals from individual trials were smaller for the regression using the delay between the stimulus and movement onset, reaching statistical significance in subjects M.C.D., N.L.P., and P.R.D. (Wilcoxon matched-pairs, signed-ranks test; $P<0.0001$). Thus, the change in the reported location had a more consistent temporal relationship to the onset of the visually evoked movement than to the onset of the visual stimulus.

Experiment 2: temporal perception

The results of experiment 1 indicate that haptic localization follows a time course that is somewhat different from that of the actual hand movement – the change in reported location leads the actual movement, with a velocity that, in some subjects, is slower than the actual velocity. This finding leads to a question concerning the subjects' perception of the temporal characteristics of the movement: specifically, would a subject's perception of when the movement began and ended be dictated by the time course of the change in reported location or the time course of the actual movement? For example, would subject M.C.D. perceive a stimulus that occurs 50 ms before the movement (i.e., at a time when the reported location is moving but the hand is not, Fig. 3B) as having occurred during the movement or before? Experiment 2 was designed to answer these questions.

The results of experiment 2 are shown in Fig. 5. For each subject, tactual stimuli presented shortly before movement onset were often misperceived as having occurred during the movement. To quantify this phenomenon in each subject, a logistic regression was performed on the subset of trials in which the subject reported that the stimulus had occurred "before" or "during" the movement; the independent variable was the time of stimulus onset, measured with respect to movement onset. This regression provided a measure (T_{start}; Fig. 5, Table 4) of the time at which the subject was equally likely to report a stimulus as having occurred "before" and "during" the movement. Stimuli presented before the T_{start} time were more likely to be reported as having occurred "before" the movement, whereas those presented after the T_{start} time were more likely to be reported as having occurred "during" the movement (the time constant τ_{start}, Table 4, is a measure of the rate at which this probability changed). Measured in this manner, the subjects' perception of movement onset was, on average, 37.8 ms (SD 27.1) in advance of the actual movement. A similar analysis revealed that the perceived end of the movement (T_{end}; Fig. 5, Table 4) occurred, on average, 144.8 ms (SD 21.7) before the actual end. Thus, it does seem that the subject's perception of the movement was temporally shifted in a manner similar to that of the reported location in the haptic localization task of experiment 1. Because the reported location in experiment 1 moved with a velocity less than that of the actual movement, one might further expect the perceived duration of the movement to be longer than the actual duration. In each subject, however, the perceived end of the movement was consistently shifted in time by a larger amount than was the perceived start, giving rise to a perceived duration (i.e., the elapsed time between the perceived start and end) that was significantly shorter than the actual duration. A possible cause of this apparent paradox will be presented in the Discussion.

Comparison of the results from experiments 1 and 2

Figure 6 provides a direct comparison of the results from the spatial localization and temporal perception experiments. The plots in Fig. 6A show, for each subject, the

Table 4 Coefficients for the logistic regressions of the temporal perception data from experiment 2

Subject	Perceived start		Perceived end		Temporal shift
	T_{start} (ms)[a]	τ_{start} (ms)	T_{end} (ms)[b]	τ_{end} (ms)	$(T_{\mathrm{start}}+T_{\mathrm{end}})/2$ (ms)
JKB	45.6[c]	27.0[c]	176.5[c]	24.0[c]	111.05
MCD	66.7[c]	21.0[c]	125.8[c]	35.8[c]	96.25
NLP	35.6[c]	41.3[c]	139.8[c]	44.1[c]	87.7
PRD	1.5[n.s.]	12.3[c]	136.9[c]	25.7[c]	69.2

[a] Measured with respect to movement onset (positive values denote time before onset)

[b] Measured with respect to movement termination (positive values denote time before termination)

[c] Regression coefficient is significantly different from zero (χ^2 of Wald statistic, $P<0.001$)

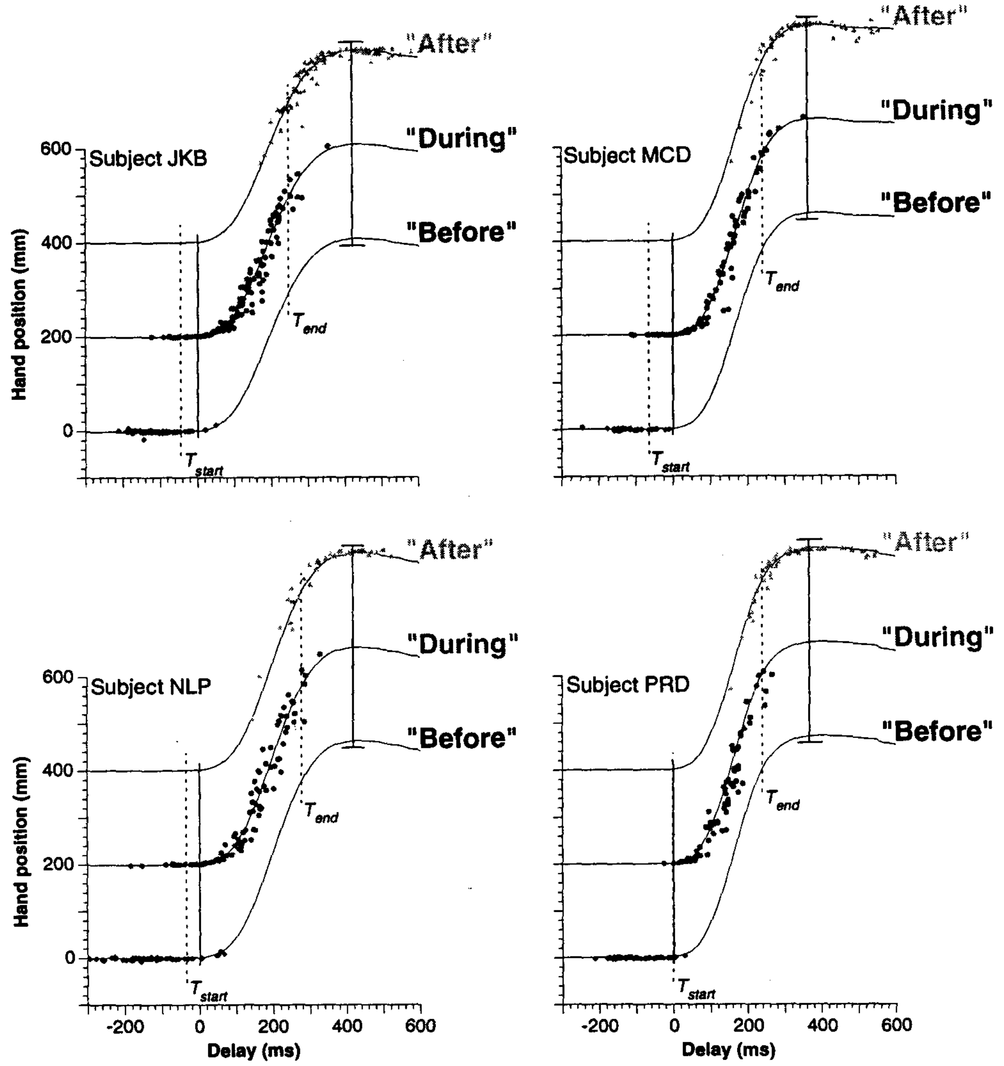


Fig. 5 Perceptual comparison of stimulus onset and movement times in each subject. Subjects were instructed to state whether each stimulus occurred "before," "during," or "after" the visually evoked movement. Each datum point shows the actual location of the hand (*ordinate*) at the time of stimulus onset (*abscissa*) for a single trial. For illustrative purposes, the amplitude and duration of each movement was normalized using the method of Atkeson and Hollerbach (1985), and the data have been translated upward by 200 mm and 400 mm for those trials in which the subjects reported the stimulus to occur "during" and "after," respectively. *Solid curves* represent the mean time course for all visually evoked movements. T_{start} (*left vertical dashed line*) shows the time at which the subject was equally likely to report "before" or "during," whereas T_{end} (*right vertical dashed line*) shows the time at which the subject was equally likely to report "during" or "after." The *solid vertical line* at 0 ms shows the actual start of the visually evoked movement. The *solid vertical line* to the *right* shows the mean time of movement termination ±SD (*horizontal bars*)

mean velocity profiles of the visually evoked movements (left) and of the change in reported location (right; computed as the derivative of the logistic function fit to the localization data, i.e., Eq. 1) as measured in experiment 1. The symbols in Fig. 6A depict the T_{start} (left in each plot) and T_{end} times (right in each plot) as measured in experiment 2. The left plot in Fig. 6A once again shows the perceptions of movement onset and termination to occur well in advance of the actual onset and termination of the visually evoked movement. Additionally, large inconsistencies were apparent across subjects in the velocity of the movement at the perceived termination. These inconsistencies were not apparent when the T_{start} and T_{end} times were compared with the velocity of the change in reported location (Fig. 6A, right plot). In each subject, the perceived onset occurred at the time the change in reported location reached a velocity of approximately 0.5 m/s. Similarly, the perceived termination occurred when the change in reported location dropped below a velocity of 0.5 m/s.

The temporal shift values of experiment 1 cannot be directly compared with the T_{start} and T_{end} values of experiment 2. Although each of these values serves as an estimate of the timing mismatch between the actual movement and the time course of the reported location or perceived movement, they estimate this mismatch at different times with respect to the movement. (The temporal shifts of the localization experiment measure this mismatch at the time that the reported location surpasses 50% of its final amplitude, whereas the T_{start} and T_{end} values estimate the mismatch at movement onset and termination, respectively.) However, if one assumes that the perceived movement has a velocity profile that is approximately bell-shaped (as do the actual movement and the change in the reported location; Fig. 6A), averaging the T_{start} and T_{end} values will yield a temporal shift value that estimates the mismatch between the perceived and actual movements at the time that the perceived movement surpasses 50% of its final amplitude (Table 4). This value can be directly compared with the temporal shift value measured in the spatial localization task of experiment 1 (Fig. 6B), with a high correlation evident between the shifts measured in the individual subjects (r=0.983). (Alternatively, one could estimate the tempo-

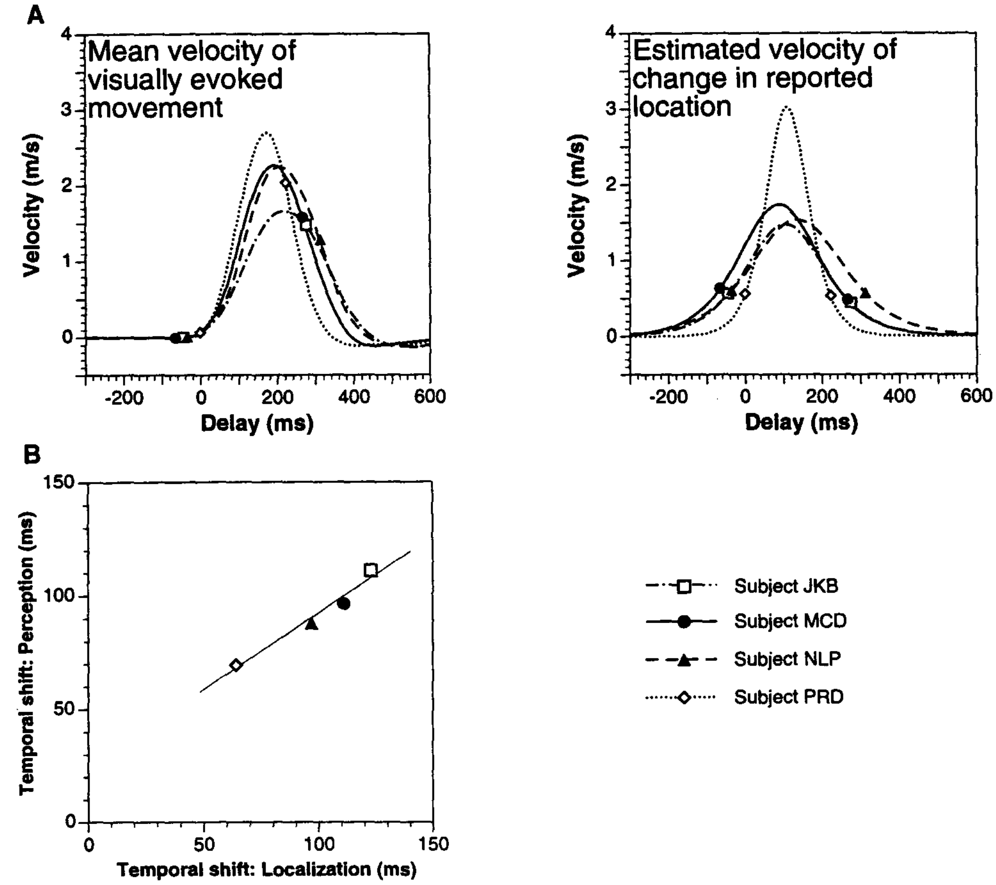


Fig. 6A, B Direct comparison of the results from the spatial localization and temporal perception experiments. **A** Symbols denote the T_{start} (*left* in each plot) and T_{end} (*right* in each plot) times derived from the temporal perception experiment, plotted with respect to the velocity profiles of the mean visually evoked movement (*left*) and the reported location data (*right*) as derived from the spatial localization experiment. Velocity profiles of the reported location data were computed as the derivative of the function (Eq. 1) fit to the localization data (Fig. 3B) from each subject. Temporal perception of the movement matches the time course of the reported location more closely than it matches the actual movement. **B** Comparison of the absolute temporal shifts measured in the temporal perception (*ordinate*) and haptic localization (*abscissa*) experiments (r=0.983), with values from the localization experiment computed using nonlinear regression (Table 2). Similar results (r=0.960) were obtained using the mean temporal shift calculated from individual localization trials (Table 3)

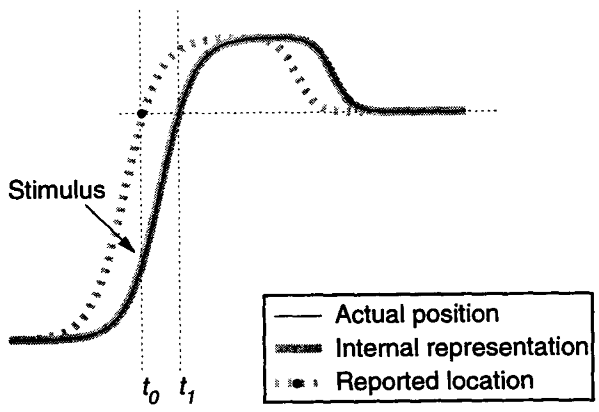


Fig. 7 Hypothetical trial in which the internal representation of hand position matches exactly the time course of the actual movement. The position trace of the hand (*solid curve*) shows the time course of the visually evoked (*left*) and tactually evoked movements (*right*) as depicted in Fig. 2; the hypothetical internal representation (*unbroken stippled curve*) is superimposed. The tactual stimulus is presented at time t_0, but somatosensory delays postpone the arrival of the accompanying neural activity until a later time, t_1. At time t_1, the internal representation indicates the current hand position rather than the hand position at stimulus onset (t_0); the reported location of the stimulus is therefore inaccurate. The *filled circle* depicts the reported location of the stimulus plotted with respect to the time of stimulus onset, as in Fig. 3B. If the reported locations of several stimuli at various onset times were similarly computed, the data points would fall along the dashed *stippled curve* that parallels the internal representation

ral shifts of experiment 1 at the start and end of the change in the reported location; these values would be directly comparable with the T_{start} and T_{end} times of experiment 2. However, variability in the localization data, as well as the bias present for stimuli occurring well before movement onset, make it impossible to accurately determine the start and end of the change in reported location.)

Discussion

In the experiments described here, a tactual stimulus was presented to the right index finger before, during, or after a visually evoked movement of the right hand. Because the spatial location of the stimulus was equivalent to the spatial location of the index finger at the time of stimulus presentation, movement of the hand and variability in stimulus timing caused the stimulus location to vary from trial to trial. This was true despite the constant somatotopic location of the stimulus (i.e., always on the tip of the right index finger). Subjects were asked to indicate the spatial location of the stimulus (experiment 1) or the temporal relationship of the stimulus with respect to the movement (experiment 2). In experiment 1, subjects made large errors when indicating the perceived spatial locations of tactual stimuli presented near the time of the movement: Each stimulus was reported to have occurred at the location occupied by the hand approximately 90 ms after stimulus onset. Experiment 2 demonstrated a misperception of the temporal relationship between stimulus and movement, with stimuli presented 0–40 ms before movement onset perceived as having occurred during the movement and those presented 0–140 ms before movement termination perceived as having occurred after the movement. A comparison of the results from both experiments showed a high correlation in the spatial localization and temporal perception errors from individual subjects, suggesting a common underlying cause.

It is perhaps most parsimonious to assume that the brain locates a tactual stimulus in space by noting the position of the hand (or other body part) upon the arrival of neural activity denoting the presence of an object touching the skin. A localization mechanism such as this obviously necessitates the maintenance of an internal representation of hand (or other body part) in space. The perceived location of a tactual stimulus is therefore equivalent to the contents of the representation at the time of stimulus detection. Localization errors, then, can result from a faulty encoding of the stimulus's somatotopic location, a faulty detection of stimulus onset, or a faulty representation of the movement. Each of these possible error sources will be discussed in turn (see Matin and Matin 1969; Matin et al. 1970; and Dassonville et al. 1993b for similar discussions of visual localization and the internal representation of eye position).

Somatotopic representation as a source of error

The spatial resolution of the somatotopic map is known to vary widely with respect to the parts of the body tested, with the fingers, lips and tongue among the most sensitive regions. Of particular interest in the present study is the resolution of the pad of the distal segment of the index finger, which has a point localization threshold of less than 2 mm (Weinstein 1968). In the experiments described here, the tactual stimulus was always presented to the distal pad of the right index finger, and subjects never reported perceiving otherwise. For these reasons, it can be assumed that the errors of somatotopic localization were minimal.

Stimulus detection as a source of error

Clearly, the brain is faced with temporal errors in stimulus detection due to the transmission delays of the somatosensory system. For any tactual stimulus presented to the fingertip at some time t_0 (Fig. 7), 14–20 ms elapse while the resulting neuronal activity is transmitted to the central nervous system (Desmedt and Cheron 1981). Central processing of this activity undoubtedly delays this signal further before it finally reaches, at time t_1, the brain site responsible for integrating the somatotopic sensory information with a representation of hand position. Figure 7 shows a hypothetical example in which the internal representation matches exactly the time course of the movement. When the neural activity that encodes the somatotopic location of the stimulus arrives at the appropriate brain site (time t_1), it is combined with an internal representation that reflects the hand's current position rather than its position at the time of the stimulus (time t_0). Thus, the stimulus will be inaccurately perceived to have occurred at the position occupied by the hand at time t_1, with the resulting error in the same direction as the visually evoked movement. Obviously, if the stimulus is presented well before or well after the movement, the difference between the hand's position at the corresponding times is negligible, and the localization error would be small. The overall pattern of errors, then, would look much like that displayed by the subjects tested in the present experiment (Fig. 3A), with the largest errors occurring for stimuli presented shortly before the movement reaches peak velocity.

Figure 7 is also useful for demonstrating why the change in reported location leads the movement of the hand (Fig. 3B). The filled circle in Fig. 7 is plotted in the same manner as each of the data points in Fig. 3B. Spatially, this datum point depicts the perceived location of the tactual stimulus (*ordinate*), which, in turn, reflects the value of the internal representation at time t_1. However, this spatial value is plotted with respect to the time of stimulus onset (*abscissa*) rather than the unknown time t_1. Thus, although useful in showing where the subject perceived a stimulus presented at any given time, data plotted in this manner are shifted in time with respect to the internal representation by an amount equal to the somatosensory delay.

Investigators in several laboratories have examined the ability of human subjects to detect the presence of a tactual stimulus applied to the skin around the time of a movement (Dyhre-Poulsen 1975, 1978; Coquery 1978; Chapman et al. 1987; Feine et al. 1990; Schmidt et al. 1990a,b; Post et al. 1994). Each of these investigators found an increase in the perceptual threshold of detection during movement of the finger or arm being stimulated, with the increase beginning 100–200 ms before movement onset (Dyhre-Poulsen 1975, 1978; Coquery 1978). Milne et al. (1988) and Post et al. (1994) have also demonstrated that the subjective intensities of suprathreshold stimuli are reduced during movement. In the present study, stimuli were clearly above threshold (i.e., no subject ever reported any trial in which the stimulus was not detected), so an increase in detection threshold would have played no role in the haptic mislocalizations reported here. However, it is possible that a decrease in subjective intensity would be accompanied by an increase in tactual processing delays. For several reasons, though, it is doubtful that an effect such as this would play a large role, if any, in the current findings. First, subjective intensity decreases only 10–15% for stimuli presented during movement (Milne et al. 1988; Post et al. 1994). Any associated increase in processing delays would be small in comparison to the temporal shifts demonstrated here. Second, the magnitude of the decrease in subjective intensity is dependent on the spatial proximity of the stimulus and the moving joint, with stimuli presented near the joint more affected than those presented further from the joint (Post et al. 1994). In the present investigation, stimuli were applied to the fingertip, quite distant from the moving shoulder joint. Finally and most convincingly, the results of Post et al. (1994) indicate no increase in the response time necessary to judge the intensity of stimuli presented during movement, giving rise to doubts that the movement-related decrease in subjective intensity is accompanied by an increase in tactual delays.

Internal representation as a source of error

Whereas the presence of transmission and processing delays in the somatosensory system are well established, another possible source of localization errors – the fidelity of the internal representation – can only be addressed speculatively. There are two possible ways in which the internal representation might inaccurately depict the actual movement (i.e., misrepresentations of timing and/or velocity), and these will be addressed in turn.

Misrepresentation of timing

There is no *a priori* reason to expect the internal representation to be exactly coincident with the movement as is depicted in Fig. 7. Indeed, depending upon the physiological source of the internal representation, it could lead or lag the movement by a significant duration. Because of the transmission delays of the motor system and inertia of the arm, an internal representation based on a corollary discharge of the motor command (McCloskey 1981) would presumably lead the movement. Conversely, transmission and processing delays of proprioceptive and kinesthetic feedback from the moving arm (Gandevia and Burke 1992) would cause an internal representation based on these signals to lag the movement.

As was demonstrated in Fig. 7, delays in stimulus detection cause the change in the perceived spatial location of the stimulus to lead the internal representation. If, in turn, the internal representation leads the actual movement, the change in reported location will lead the movement by a period equal to the lead of the internal representation plus the duration of the somatosensory delays. A lagging representation, on the other hand, will cause the change in reported location to lead the movement by less than the duration of the somatosensory delays. Because of the additive manner in which these temporal factors combine, the temporal shift values presented in Tables 2 and 3 are equal to the delays of somatosensory transmission and processing, plus the lead (or lag) of the internal representation. Unfortunately, the duration of the somatosensory processing delay is unknown, making it impossible, with these methods, to determine the temporal disparity between the movement and its representation.

Interestingly, if the internal representation were to lag the movement by a duration equal to the somatosensory delays affecting the tactual stimulus, the errors would cancel and accurate localization would be achieved (see also Matin and Matin 1969; Matin et al. 1970; Dassonville et al. 1993b). However, because the change in reported location leads the movement in each of the subjects tested, it is obvious that the brain does not maintain an internal representation that lags the movement by an amount appropriate to compensate for the somatosensory delays.

Misrepresentation of velocity

It is also possible that the internal representation inaccurately encodes the velocity of the movement. Indeed, the experiments presented here offer evidence that this is the case, with the internal representation moving at a velocity significantly less than that of the movement in at least three of the four subjects (Tables 2, 3). However, one can envision at least three scenarios that would lead to these results. First, the internal representation might move with a velocity independent of the actual velocity of the movement, resulting in an underestimation of the velocities for fast movements and an overestimation of the velocities for slow movements. Second, the internal representation might accurately depict the velocity of slow movements, but saturates and falls behind movements of greater speed. Third, the velocity of the internal representation might be roughly scaled for different movements, underestimating the actual velocity of each. Preliminary testing of these hypotheses, using visually evoked movements with a wide range of velocities (Nagode and Dassonville 1995; Dassonville and Nagode 1995), has indicated the third scenario to be the most likely.

Short-term memory as an additional source of error

In experiment 1, subjects were instructed to complete the visually evoked movement before responding with a tactually evoked movement to the spatial location of the stimulus. This requirement imposed a delay between stimulus presentation and the onset of the localization movement, with longer delays for stimuli that occurred early in the trial. Because of this, stimulus location information had to be stored in short-term memory, where it may have been subjected to a time-dependent degradation in accuracy similar to that demonstrated by Gnadt et al. (1991) for remembered visual targets of saccadic eye movements. In the present study, however, trials with the longest memory delays (i.e., those with stimuli presented well before movement onset; Fig. 3A) were associated with relatively small localization errors, a pattern very different from that shown by Gnadt et al. (1991). It would seem, then, that any memory-related errors in the haptic localization task are small in comparison with the errors associated with the inaccuracies of the internal representation and stimulus detection.

Errors in temporal perception

In experiment 2, subjects were asked to compare the timing of a tactual stimulus with that of a visually evoked movement. As with the localization task of experiment 1, it seems reasonable to assume that the subjects performed this task by comparing the perceived time of stimulus onset with an internal representation of the movement. Given this, the ability to perform the task should be subject to the same sources of error described in the preceding sections, and, indeed, the temporal shifts (Fig. 6B) in the two experiments were found to be highly correlated. Furthermore, a comparison of the temporal perception data with the velocity profile of the change in reported location (Fig. 6A, right) proved highly consistent across subjects, with the perceived onset and termination of the movement corresponding to the times at which the velocity of the internal representation crossed a threshold of approximately 0.5 m/s. This method of determining the movement's perceived onset and termination may be necessary in order to minimize the false alarms that might otherwise occur due to a representation of movement that is susceptible to noise. As can be seen in Fig. 6A (right), the representation does move a small amount before the threshold velocity is surpassed (and after the velocity again drops below the threshold), providing an explanation for the paradox concerning the shorter duration of the perceived movement as compared to that of the change in reported location.

Two previous studies focused on the temporal perception of movement onset, but methodological differences make detailed comparisons with the results of the present investigation difficult. McCloskey et al. (1983) asked subjects to compare the timing of a voluntary movement (toe, foot, jaw, or arm/hand) with that of an electrical stimulus applied to the ankle. Averaged across subjects, the electromyographic (EMG) activity of arm or hand movements had to begin 107 ms before the electrical stimulus for the two to be considered simultaneous. With the experimental design of the present study, one would expect an even larger duration between the start of EMG activity and a stimulus perceived to be coincident with movement onset, given that stimuli presented to the finger should have shorter afferent transmission delays than those presented to the ankle. Although EMG activity was not measured in the present study, it can be assumed to have begun 50–100 ms before movement onset. Thus, EMG onset probably occurred 12–62 ms before the mean T_{start} time from the subjects tested, somewhat less than the expected value based on the results of McCloskey et al. (1983). This discrepancy is probably attributable to one or several of the differences in the stimulation and movement parameters of the two studies. Jirsa et al. (1992) asked subjects to compare the timing of a button press movement with that of an audible click presented to the right ear. Across subjects, the click was required to be 62.5 ms before the button press to be considered simultaneous. However, Jirsa et al. (1992) did not report the time it took for subjects to move the 1.5 cm distance between the finger's starting position and the surface of the button, making a direct comparison between their results and those presented here impossible. Neither McCloskey et al. (1983) nor Jirsa et al. (1992) assessed the perception of movement termination or duration.

Intersubject differences

The subjects tested in the present investigation did show a surprisingly large variation in the magnitudes of the effects described. Admittedly, the results of subject P.R.D. (the author) fell furthest from the mean, with a change in the reported location of the stimulus that most closely matched the timing and velocity of the movement. Obviously, this more accurate performance might have arisen due to the author's non-naive expectations. However, the decision to include the results from subject P.R.D. was a conservative one, since exclusion of these more accurate results would have served only to increase the mean estimates of the temporal shift and velocity differences.

In spite of the obvious quantitative variability across subjects, there were several qualitative similarities. In each subject, the reported location of the stimulus led the actual movement by a highly significant duration (temporal shifts; Tables 2, 3). In three of the four subjects, the reported location moved with a velocity significantly less than that of the movement; in the fourth subject (P.R.D.), the comparison was inconclusive, with one test indicating the velocity of the reported location to be significantly less (Table 3), whereas another showed no significant difference (Table 2). In each subject, the perceived onset and termination of the movement appeared to rely on a comparison of the internal representation's velocity with a threshold of approximately 0.5 m/s (Fig. 6A, right). Furthermore, the intersubject variability of the spatial localization task was consistent with that of the temporal perception task, as evidenced by the high correlation between the temporal shift measurements in the two experiments (Fig. 6B). It remains to be determined whether this variability resulted from intersubject differences in tactual processing delays, differences in the time course of the internal representations, or both.

Single or multiple representations of hand in space

The high correlation between the temporal shifts in the experiments presented here suggest that a single representation of hand in space is used for haptic localization and movement perception. Although other brain processes require a representation of movement, these processes may use a representation different from the one described here. Several laboratories have shown that the brain uses a representation based on proprioceptive input from the moving limb to coordinate the timing of cyclic (e.g., locomotion; Andersson and Grillner 1983) and noncyclic (e.g., throwing; Cordo et al. 1994) movement sequences. In the case of noncyclic movements, the representation apparently encodes the velocity of the movement in addition to the position of the joint (Cordo et al. 1994). The velocity component of the representation is necessary to compensate for the transmission and processing delays of the proprioceptive signal, allowing the brain to "predict" the current location of the hand. Because subjects could perform the task of Cordo et al. (1994) with great accuracy, the internal representation used to coordinate various movement components appears to have a better fit to the actual movement than does the representation used for haptic localization.

Similarities to the internal representation of eye position

In perceptual (e.g., Matin and Pearce 1965, Bischof and Kramer 1968) and oculomotor (e.g., Honda 1990, Dassonville et al. 1992) investigations analogous to the present one, several researchers have examined the ability of subjects to localize brief visual targets flashed near the time of saccadic eye movements. The internal representation of eye position was found to have inaccuracies similar to those described here for the representation of hand in space. Specifically, the representation of eye position underestimates the velocity of the eye movement and fails to compensate for the movement that occurs during the visual afferent delays. These discrepancies lead to large systematic errors in the ability to localize visual targets presented near the time of a saccade.

In an investigation similar to our experiment 2, Volkmann and Moore (1978) asked subjects to compare the temporal occurrence of a flashed visual stimulus with the occurrence of a saccadic eye movement. Stimuli presented in a duration from 100 ms before saccade onset to 250 ms after saccade termination were judged to have occurred during the saccade (these values are the times at which the subjects judged the flash equally likely to have occurred before or during and during or after the saccade, as approximated from Figs. 28.3 and 28.4 of Volkmann and Moore 1978). Although Volkmann and Moore did not directly compare these results with the time course of the internal representation of eye position, some subjects have been described as having internal representations that roughly match this perceived duration (Matin and Pearce 1965).

Further questions

The results presented here raise the question as to why these large haptic mislocalizations and temporal misperceptions are not more obvious under normal situations. Most of a person's movements are made under an ambient illumination that provides vision of the arm, which may yield a relatively accurate visual representation of hand position that supplements, or even supersedes, the nonvisual representation investigated in the present study (Rock and Harris 1967; Prablanc et al. 1979; Lackner and Taublieb 1984; Shimojo 1987; however, see also Dassonville and Georgopoulos 1994). Additionally, an illuminated environment is also likely to provide a visual image of the object that was responsible for the tactual stimulus. Perhaps a person's ability to localize the object based on the visual image overrides the faulty ability to localize the object based on tactual cues and knowledge of arm position; a similar type of visual capture has been demonstrated for situations in which an object's perceived visual and auditory locations are in conflict (Pick et al. 1969, Matin et al. 1982). It is also possible that the mislocalizations are specific to the type of movement made by the subjects in the present study; indeed, the movements were quite predictable in direction, amplitude, and velocity. Perhaps this predictability leads the brain to only roughly estimate the change in hand position, whereas more complicated movements, such as those made under normal circumstances, may require the brain to more closely monitor hand position so that the activity of several interacting muscles can be more accurately orchestrated (Cordo et al. 1994). Ongoing investigations in this laboratory are aimed at addressing these possibilities, as well as further quantifying the time course of the internal representation.

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