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14. ABSTRACT (Maximum 200 words)

We studied the capacities of human subjects to localize tactile stimuli in 3D space. For that purpose, five subjects (3 women and 2 men) were asked to make a pointing movement to a visual stimulus in otherwise complete darkness. At some random time before, during or after this initial movement, a tactile probe was presented to the tip of the subject's index finger. The probe (1-mm diameter, 0.75-mm extent, 5-ms duration) was applied by a lightweight (80 g) tactile stimulator worn on the subject's hand. To complete the task, the subject was required to point to the 3D spatial location at which the probe was applied. Hand position was monitored (200 Hz) by a video-based motion analysis system. In each subject, probes presented just before or during the initial movement were systematically mislocalized in the direction of that movement so that subjects perceived the probe to be at the location occupied by the hand 50 to 100 ms after probe onset. This mislocalization is likely to be important in dealing with objects in the dark, especially with obstacles encountered along a movement's path.

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Background and Significance.

A common feature of the visual and somatosensory systems is the use of topographic maps to encode the location of visual and tactile stimuli. However, because the receptor organs (i.e., the retina and skin, respectively) can move with respect to the body, these retinotopic and somatotopic representations are only useful to describe where on the retina (e.g., 10 deg left of the fovea) or skin (e.g., on the tip of the right index finger) the stimulus occurred. If the brain is to compute the location of the stimulant in 3D space, it must combine this topographic information with an internal representation of the direction the eyes are pointing or the location of the hand in space; this idea was first proposed by Helmholtz (1867) for the visual system (for a historical review, see McCloskey 1981). Because of this requirement, inaccuracies in the brain's knowledge of eye or hand position will lead to corresponding errors in target localization. Although this point has been addressed in studies of the visual and oculomotor systems (see below), it has been completely overlooked in the tactile and skeletomotor systems.

It has long been known that the brain does indeed maintain and use an internal representation of eye position (for a review, see Howard 1982). But how faithful is this representation? When a human subject makes a saccadic eye movement from one visual stimulus to another, the eyes may reach a peak angular velocity of more than 500 deg/s. Does the internal representation of eye position change with a similar velocity? Further complications are introduced by the long afferent processing delays of the retina and early visual structures - the internal representation must be delayed by a corresponding amount of time if the incoming retinal image is to be combined with a signal encoding the eyes' position at the time the image struck the retina. In several studies of visual perception (e.g., Matin and Pearce 1965; Mateeff 1978) and oculomotor control (Honda 1990; Dassonville et al. 1992a, 1992b, 1993b), subjects were required to localize brief visual targets presented near the temporal occurrence of a saccade. Although the subjects accurately localized the visual probes if presentation occurred well before or well after the intervening saccade, probes presented just before, during, or just after the saccade were consistently mislocalized. The pattern of errors suggests that visual perception and oculomotor localization are based on an internal representation of eye position that begins changing well before the saccade and has a velocity much less than that of the saccade.

The experiments performed in our laboratory over the past year were designed to provide a means to similarly examine the internal representation of hand in space used in the localization of tactile stimuli in 3D space. Briefly, subjects were required to make a pointing movement to a visual target. At some time before, during, or after this initial movement, a tactile

stimulus was applied to the index finger. The subject was subsequently required to make a targeting movement to the spatial location at which the probe was perceived. By examining the subject's ability to localize these probes, as in the visuomotor experiments described above, we were able to obtain a picture of the brain's internal representation of hand in space. The results from this experiment will be presented at the 1993 Society for Neuroscience Annual Conference (Dassonville et al. 1993a, attached).

Methods.

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Subjects.

Healthy human subjects (3 women and 2 men) were tested in a purely behavioral task. The protocol for the proposed study was submitted to and approved by the Institutional Committee on Human Subjects at the University of Minnesota. Four subjects were tested and remunerated at a rate of \$10.00/hr.

Arm position monitoring.

A video-based motion analysis system (Motion Analysis VP320) was used to monitor the subject's arm position at a sampling rate of 200 Hz. This system employed three cameras to track the motion of small spherical reflective markers in 3D space - light was provided by three camera-mounted banks of red light emitting diodes (LEDs). Markers were secured with adhesive to the subject's shoulder, elbow, wrist, and fingertip of the preferred arm (Figs. 1A). During the intertrial interval, the digitized position data was automatically transferred to a Sun SparcStation for storage and subsequent offline processing (Motion Analysis ExpertVision software).

Visual targets.

Green LEDs were used as visual targets for a portion of the pointing movements made by the subject. These targets were placed in a plane parallel to the frontal plane of the subject, located approximately 1 m from the subject's chest (i.e., out of the subject's reach). The timing of LED onset and duration was under computer control.

Tactile targets.

For this series of experiments, we developed a lightweight (80 g) tactile stimulator that can be worn on the subject's moving hand. The stimulator consists of a small 8 ohm speaker with the diaphragm removed to minimize sound production (white noise from a second small speaker located in front of the subject will be

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used to mask the remaining sound). A small metal probe (approximately 1 mm diameter) was attached to the voice coil of the speaker; by applying a short square-wave voltage to the speaker inputs, this probe can be driven through a small hole in a finger plate mounted over the face of the speaker. The probe excursion above the finger plate surface is approximately 0.75 mm for a duration of 5 ms. (Measurements were made by focusing a laser parallel to the surface of the finger plate; during its extent, the probe interrupted the beam, preventing it from reaching a photodiode.) The subject's index finger is positioned on the finger plate, and the entire stimulator is securely strapped to the hand; the input leads are lightly strapped to the subject's arm from the hand to the shoulder. Timing of the stimulator pulse was under computer control.

Experimental Design.

To characterize the time course of the internal representation of hand in space under normal conditions, the subject was required to point to the spatial location of various visual and tactile events. To prevent the subject from using vision to solve the task, room lights were extinguished 2 s before the onset of each trial, and re-illuminated 2 s after the end of each trial (the red light from the 3 banks of red LEDs used by the motion detection system was blocked by requiring the subject to wear goggles on which a dark green filter gel had been mounted). The presence of the room lights between trials served two purposes: it prevented the dark adaptation of the subject's visual system, and allowed the visual and motor systems to remain in calibration throughout the experiment.

To begin each trial, a single visual stimulus (LED1) was illuminated. This green LED was clearly visible through the goggle-mounted filter gel, although not bright enough to provide vision of the arm. The subject was instructed to point toward LED1 with the index finger that was strapped to the tactile stimulator. After a random duration (2 - 4 s), LED1 was extinguished and replaced with another (LED2, 50-ms duration, approximately 0.75 m from LED1). This served as the trigger for the subject to initiate a pointing movement (*initial movement*) from the direction of LED1 to that of LED2. At some randomly selected delay, a tactile probe was presented to the index finger of the moving hand; the delays were appropriately selected (i.e., between 25 and 750 ms after the onset of LED2) so that the probe was issued either before, during, or after the initial arm movement. The task then required the subject, after completing the initial movement, to make a second movement (*targeting movement*) to the location in space at which the probe was presented. No feedback was ever given concerning the actual spatial location of the probe or the magnitude of localization errors.

Analysis of results.

Velocity and acceleration profiles were computed for each trial from the 3D position information (smoothed using a digital Butterworth filter with a low-pass cut-off of 15 Hz) collected by the motion analysis system; this allowed accurate detection of the start and end of each movement. The subject's spatial localization of the tactile probe was assessed as the position of the arm at the end of the targeting movement; if no targeting movement was detected, the subject's localization of the probe was considered coincident with the end of the initial movement. Fig. 1B shows the localization errors for a single subject in our investigation, plotted with respect to the delay between probe and initial movement onset. Because the task of localization requires the subject to combine information concerning the somatotopic location of the probe (which was always correctly perceived by the subject to occur on the index finger) with information concerning the location of the hand in space, these errors must be attributable to an inaccurate representation of the initial movement's time course. By plotting the perceived location of the probe in 3D space with respect to the delay between probe and movement onset (Fig. 1C), the time course of the internal representation of arm position can be observed.

Discussion.

The results shown in Fig. 1 demonstrate a timing mismatch between the brain's internal representation of hand in space and the actual location of the hand during the movement. Specifically, the subject perceived the tactile probe to be at the location occupied by the hand approximately 50 ms after probe onset, suggesting an incorrect compensation for sensory and motor processing delays. Similar timing mismatches were seen in 3 other subjects; in one of these subjects, it was additionally noted that the internal representation moved with a velocity much lower than that of the actual movement. Further investigations and analyses of the timing and velocity differences between an actual movement and its internal representation will allow us to draw conclusions regarding the neural source of the internal representation as well as the manner in which this representation is used to map the locations of tactile stimuli in 3D space.

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Figure 1

A. Stick figure represents arm trajectory (40 Hz sampling rate for illustrative purposes) for the initial (stippled, moving left to right) and targeting movements (solid, moving right to left) in an actual trial. Tactile probe presented when the arm was at the location indicated; subject's localization of the probe indicated by the cross. B. Errors associated with the task described. Each datum point represents the error in localization of the tactile probe (ordinate, mm) plotted with respect to the delay between probe representation and initial movement onset (abscissa, mm). Solid curve represents the time course of the initial movement. C. Time course of the internal representation of arm position. Each datum point represents the subject's localization of the tactile probe in 3D space (ordinate, mm) plotted with respect to the delay between probe presentation and initial movement onset (abscissa, mm). Solid curve represents the time course of the initial movement; the internal representation leads the movement by approximately 50 ms.

