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DIFFERENTIAL ENCODING OF LOCATION CUES BY ACTIVE AND PASSIVE TOUCH

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ABSTRACT

The position of the index fingertip was used as a target for the reaching movement of the other hand in man. Systematic differences in the accuracy of pointing were interpreted as reflecting differential encoding of location cues involved in generating the reaching motor programs. Results showed that tactile information was differently encoded as location cues when combined with movement information of proprioceptive origin involved in active touching as contrasted with proprioceptive positional information about the resting position of a limb passively touched.

Keywords : Active touch. Position sense. Kinaesthesis. Dynamic and static proprioception. Location cues.

INTRODUCTION

The present study was initiated as a direct extension of a previous set of experiments on fingertip position sense that showed locating errors were significantly smaller when the target hand is actively moved than when passively displaced by external forces (ref. 8.10). The results were interpreted in terms of a differential contribution of articular and muscular proprioceptive afferents to the performance. This interpretation stems from the assumption that systematic differences in the accuracy of reaching may reflect some differences in the encoding of location cues which affects the central command to generate the motor program.

Tactile cues were used in these new experiments on localization pointing in which correcting feedback was prevented. Tactile stimulation of the fingertip was associated with either active or passive positioning of the target hand or with its stable position actively maintained or passively sustained.

Results confirm and extend those already presented in an earlier publication (ref. 1). They show that tactile information was differently encoded as location cues when combined with movement cues as contrasted with positional cues of proprioceptive origin.

METHOD

As in the preceding studies (ref. 1.8.10) the position of the right index fingertip is used as a target for the reaching movement of the left index finger. The subject is sitting, with head and trunk fixed before a sheet of Plexiglas set in the frontal plane about 40 cm away from him and carrying two parallel tracks 60 cm in length set vertically and symmetrically in relation to his mid-sagittal plane (see Fig. 1).

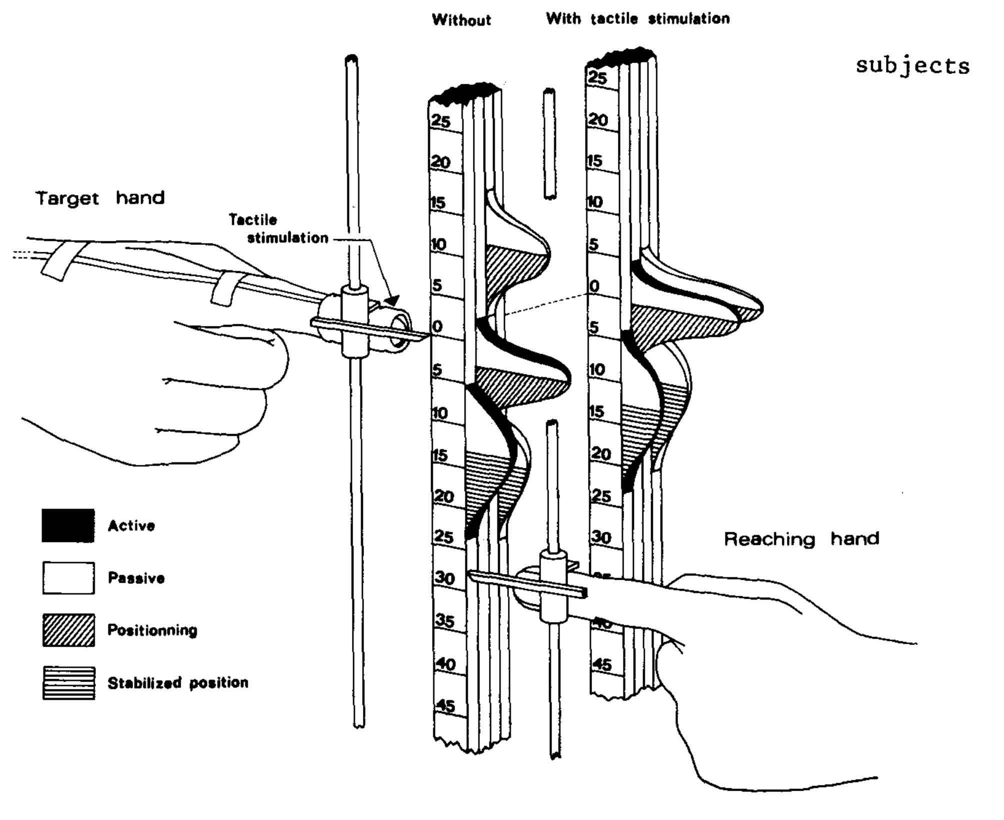

Fig. 1 Schematization of the experimental device (see text). Note that with regard to the central scale numbered in millimeters the size of the hand has been reduced for clarity of the drawing. The amount of error or reaching during each trial is indicated by the difference in position of the two slides measured on the central scale. Each distribution curve represented along the scale cumulates the results obtained on 13 subjects and represents each from 325 to 900 measures depending on the situation. The mean error of each distribution characterizes a locus of reaching as defined by the combination of the afferences encoded as location cues. See comments in the text.

Each of the subjects' index finger can operate a movable slide along one of the tracks. The subject moves his right hand at a speed freely adopted by him along the right track and terminates his movement or his hand is passively displaced in a similar manner through a device controlled by the experimenter and stopped at different heights, on each trial.

The final position attained by the displaced limb is either actively stabilized by the subject or passively sustained.

The tip of the left index finger is surrounded with an adhesive strip putting a pair of metallic electrodes into contact with the skin surface. An electrical stimulation is delivered by an electronic stimulator as a single rectangular pulse of 1 ms wide and whose intensity is adjusted at a level sufficient for detection of a light tactile shock but without any unpleasant component.

The stimulation was either triggered by the experimenter at the end of the active or passive positioning movement of the target hand or introduced at least 15 seconds after stabilization of the target arm actively maintained in its final position or passively supported.

Nine subjects took part in the former experiment and 4 in the present experiment. Each subject performed all the experimental conditions according to a balanced order.

RESULTS

When compared with the performances of reaching observed when only proprioceptive information is available (see Fig. 2) :

1°) additional tactile information clearly improves the accuracy of pointing when cutaneous stimulation is associated with the end of the kinetic phase of positioning regardless whether it was actively or passively achieved (see Fig. 1), error in both cases was not significantly different from null-error;

2°) additional tactile cues do not seem to be taken into account to locate the actively or passively stabilized position of the target finger. Errors in locating the fingertip in those conditions were essentially the same as those observed without tactile stimulation;

3°) tactile stimulations of other parts of the body (arm or limb) did not alter performance in either of the other conditions.

DISCUSSION

The most striking result of the present experiment is that phasic tactile information combined with kinesthetic proprioceptive information causes a definite improvement in the accuracy of reaching in the passive positioning condition. The performance was not significantly different from null-error and there was no difference between the active and the passive conditions. In contrast tactile information combined with statesthetic information about the stabilized target position does not add to the localizing property of static proprioceptive information. This finally led to the conclusion that cutaneous afferents take a localizing value only when combined with phasic joint afferents. Moreover, muscular afferents whether phasic or static do not seem to add anything to the localizing value of cutaneous afferents.

It appears from the present study that information about static position of joints and information about joint movement can be differentially processed. This processing can take place not only in subjective judgments relative to "position sense" and "kinesthesia" as already stressed by Mc Closkey (4) but, as well, in the encoding of location cues used at a subconscious level to generate spatially oriented motor programs.

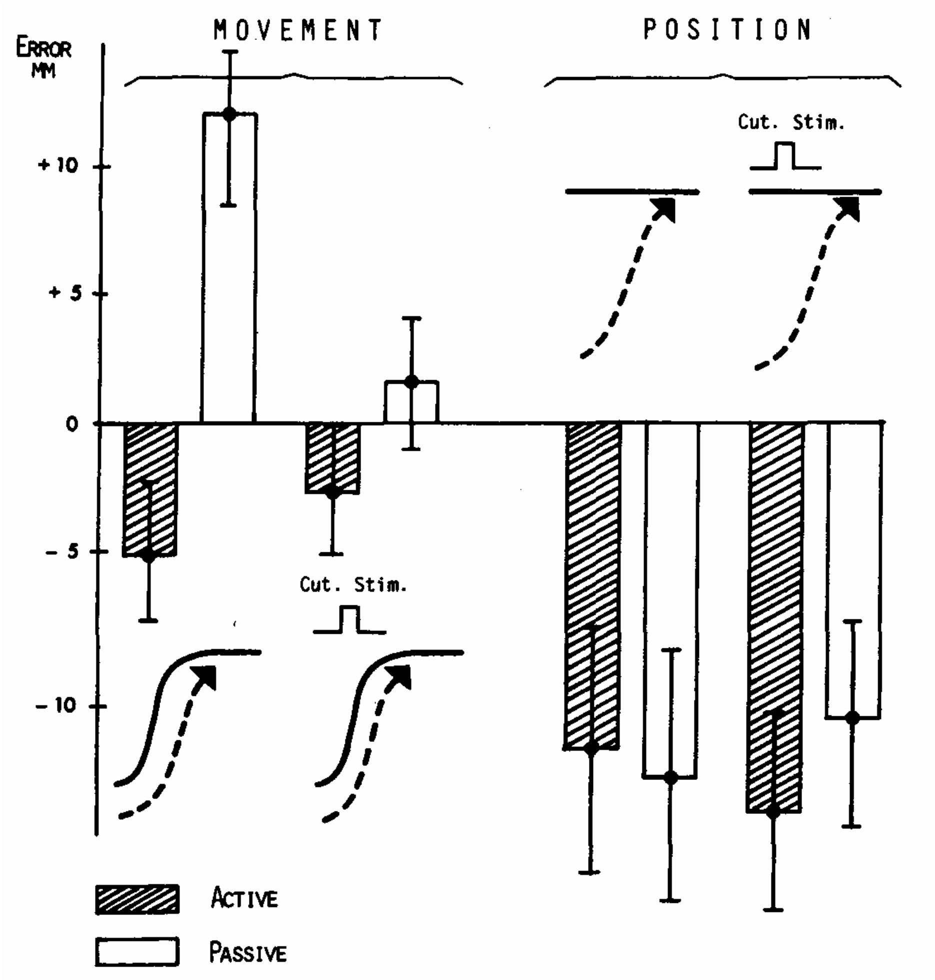

Fig. 2 Median and interquartile range of errors in locating the position of the target hand with the reaching hand. Black curves in the lower left symbolize the time course of positioning movement and black straight lines in the upper right the resting position of the target hand 15 sec after a positioning movement. The stripped curves indicated the timing of the pointing performance and the square wave those of the cutaneous stimulation.

The following table tentatively summarizes the different sources of information involved in our 8 experimental conditions.

	Positioning Movement				Stabilized Position			
	Active		Passive		Active		Passive	
Joint phasic	+		+		0		0	
Muscul. phasic	+		0		0		0	
Joint static	0		0		+		+	
Muscul. static	0		0		+		0	
Motor outflow	+		0		+		0	
Skin	0	+	0	+	0	+	0	+
Mean errors (in mm)	-5 *	-2,5 NS	+12 ***	+1,5 NS	-11,5 ***	-14 ***	-12,5 ***	-10,5 ***
	NS		***		NS		NS	

Motor outflow which could be involved as a possible explanation for the difference between active and passive condition of positioning does not seem to interfere in any of the conditions where cutaneous cues are available.

Recent observations by Millar (5) in cat and Grigg and Greenspan (3) claims that many joint afferent neurons, specially those measuring to intermediate angles which are silent in passive movement, could be excited by activation of muscles which, by virtue of their coupling to the joint, could directly stretch the joint capsule.

Grigg and Greenspan (3) suggest that our previous observation on the distinction between active and passive positioning (ref. 10) could be explained by such an effect. However, we formerly discussed this point (ref. 8) and discarded such an explanation on two grounds : first, active and passive resting posture of the target hand might likely be differentiated for the same reason. Active maintenance of a position involves a muscular load assumed to stretch the joint capsule that is not occurring in a passively supported limb. The performance is nevertheless identical in both conditions. However it could be argued here that phasic joint receptors could be more sensitive than the static one to this effect.

A second argument is more convincing : cooling or vibrating the muscles of the target limb, without changing the muscular load, dramatically suppresses the superiority of active positioning over passive positioning in our experimental conditions. Such a result led us to conclude that there is a critical contribution of spindle afferents in the phenomena (ref. 10).

The addition of tactile cues to proprioceptive one revealed another experimental condition in which the distinctive effects of passive and active positioning is suppressed. Mountcastle and Powell (6) found in the sensori-motor cortex convergence of joint and cutaneous afferents in similar cells which were inhibited by afferent cutaneous volleys. Convergence of articular, muscular and cutaneous afferents in area 3 of the precentral cortex are now well documented as well as in the posterior parietal association cortex where they seem to be involved in operations within extrapersonal space (ref. 7). It has been recently found that relay cells of the thalamic ventrobasal complex transmitting kinesthesia (identified as "joint movement" cells) were inhibited by cutaneous electrical stimulation in the medial lemnis in the cat (ref. 13). Moreover Rosén (11) showed that in ventrobasal relay cells activated by Group I afferents IPSP's were evoked by cutaneous nerve stimulation. This could explain the prevalence taken by cutaneous information in locating the target when associated with proprioceptive movement cues in passive or active positioning of the target hand.

In contrast, following the electrical stimulation of fast pyramidal tract fibers, facilitations of all joint movement cells and inhibition of cutaneous relay cells in the ventrobasal complex, via collaterals projecting in the thalamic nuclei, have been reported (ref. 13). This led the authors to suggest that "when voluntary movements of limbs are initiated by pyramidal tract impulses, preference of transmission in the ventrobasal relay cells may shift from the cutaneous sense to kinesthesia as a consequence of pyramidal tract induced facilitation". They also conclude that "during the resting state of animals cutaneous sensory transmission in ventrobasal complex is given preference over kinesthetic transmission".

This sounds in opposition to our results showing that positional proprioceptive cues seem to prevail over tactual cues in the resting state of the target hand. Several possible explanations might explain this discrepancy.

First a more precise distinction between movement and positional articular afferents needs to be made to identify their interference with phasic or static muscular afferents; correspondingly the same distinction needs to be made when studying their interference with cutaneous afferents. Secondly some special "hair units" corresponding to the distal end of the forearm-forepaw have been described in the cat (ref. 13) as activated and not inhibited during active movement, thus indicating some functional differences among cutaneous afferents. Moreover, gating of cutaneous afferents through the efferent command (ref. 2) is likely to occur when it is possible to anticipate the skin contact which generally terminates an intended reaching act.

Finally (as already suggested by Brouchon and Hay (1)) our results point, by analogy to that has been found in the visual system (ref. 12), to the evidence of a double somesthetic system respectively for identifying and locating function : first, identification of patterns could be based on the analysis of the relative position of the points stimulated on the skin surface; second, location of a stimulated point could be based on a space coordinated system relative to the body postural reference (ref. 9). The separability of the first system is basically dependent upon the "acuity" of the receptive surface (as testable by a two point discrimination procedure). The second system is dependent on the encoding of cutaneous afferents as locations cues in a body-centered reference system (as testable by a pointing localization procedure). Thus, the mapping of the tactual space may proceed differently in each system. Active touch may carry out different functions when exploring objects by digital palpation compared to when locating them. Further studies along these lines could help to elucidate the specific nervous mechanisms involved in these dual sensori-motor process.

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