

# PROPERTIES OF SLOWLY ADAPTING JOINT RECEPTORS DO NOT READILY PREDICT PERCEPTION OF LIMB POSITION

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## Abstract

A passive limb position recognition task was used to examine two predictions based upon a neurophysiological model of slowly adapting (SA) joint receptors. First we hypothesized that durations at target position coinciding with dynamic (3, 6 sec) and static (15, 30 and 150 sec) phases of SA joint response should be associated with different accuracy levels favoring the longer durations. Second, because of the greater density of SA joint receptors sensitive to extreme positions, we predicted greater accuracy there than at intermediate limb positions. Results did not support either prediction about recognition accuracy. Errors for brief and long target durations were not statistically different. Increasing limb angles led to increased errors negating our second prediction. These data conflict with recent theorizing on the behavioral significance of joint receptors and indicate that knowledge of limb position is not readily predicted from joint receptor firing functions.

Recently a number of articles have argued that perception of limb position cannot be based entirely on input from slowly adapting (SA) joint receptors. Both behavioral (Goodwin, McCloskey & Matthews, 1972; Roland, 1978) and neurophysiological (for review, Goodwin, 1976; Matthews, 1977) data have implicated cutaneous and muscle afferents as playing a role in perception of position. The authors of these studies attempt to manipulate the type of input

available to subjects by selective or total occlusion of joint, skin or muscle afferents; common techniques used have been reversible chemical (e.g., Roland, 1978) ischaemic (e.g. Kelso, 1977a) and thermal (e.g. Paillard & Brouchon, 1974) anesthesia of the hand and forearm. Additionally, there are several studies of patients who have had joints (and necessarily, joint receptors) surgically removed (Grigg, Finerman & Riley, 1975; Kelso, 1978a). The consensus of these studies is that under conditions of selective anesthesia, perception of limb position is not entirely lost and that other sources of kinesthetic information may contribute to position sense.

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Usually however, the conclusions of such studies are amended with the caution that the results obtained may not always be applicable to more normal conditions. Consequently, the belief that SA joint receptors may provide the normal basis for perception of limb position has been and continues to be fairly common (e.g. Adams, 1977; Marteniuk, 1976; Monster, Herman & Altland, 1973; Russell, 1976). This belief is based on a 'classical' model of SA joint receptor function described in several reviews (e.g. Skoglund, 1973; Somjen, 1972) and the accompanying assumption that understanding of neurophysiological characteristics of sensory receptors would permit some prediction of perceptual-motor behavior under normal conditions.

This paper provides an initial attempt to test the assumption that knowledge of SA joint receptor characteristics enables prediction of limb position recognition accuracy under relatively normal conditions. First, the 'classical' model of SA joint receptor characteristics is presented, followed by significant modification of that model necessitated by recent neurophysiological research. Then, on the basis of the revised model of SA joint receptor characteristics, two specific predictions are made about recognition accuracy in a passive limb positioning task.

## SA JOINT RECEPTOR CHARACTERISTICS

The 'classical' model has three features relevant to the idea that SA joint receptors are crucial to position sense:

1. The full range of limb positions is supposedly represented equally throughout the population of SA receptors at a joint.
2. The frequency responses of SA joint receptors are invariantly specific for a given angle.
3. The angle-specific frequency responses are attained very rapidly (less than 2 sec-

onds) and are steadily maintained as long as limb position is held.

More recent data challenge all three features of the classical model. In the first place, relatively few SA joint receptors fire at intermediate angles in cat and monkey (the common experimental animals); instead, most fire at full extension or flexion (Burgess & Clark, 1969; Clark, 1975; Grigg, 1975; Millar, 1975). Second, prior presentation of a joint angle influences subsequent receptor frequency responses to that angle. This hysteresis-like effect has been observed if a joint angle is maintained for as little as 30 seconds and may last as long as several minutes (McCall, Farias, Williams & BeMent, 1974; Millar, 1975). Finally, SA joint receptors display two separable response phases to movement toward a subsequently maintained joint position (Mountcastle & Powell, 1959; Skoglund, 1973; McCall *et al.* 1974). The initial, dynamic phase is sensitive to velocity and acceleration as well as to displacement; this phase lasts approximately 12-15 seconds in unanesthetized preparations; in anesthetized preparations, abnormally rapid rates of adaptation are observed (Mountcastle, Poggio & Werner, 1963) which may account for some reports of brief (1-2 sec) dynamic phase durations. The second, static (completely adapted) phase is position sensitive only; it has been observed to last as long as ten minutes.

## Model implications.

The revised model of SA joint receptors raises some questions about results of previous studies which have been interpreted in terms of theoretical notions of limb position accuracy that are based on older neurophysiological data (for review see Adams, 1977; Kelso, 1978b). For example, if one assumes that stronger receptor responses are related to perceptual accuracy, then the greater responsiveness of SA joint receptors to

extreme angles is not easily reconciled with findings that recognition of positions requiring greater movement extent is less accurate than recognition of positions at intermediate or short extents. Rather, one would expect greater accuracy at either extreme joint position than at intermediate locations. It may be that positioning studies have tended to use limb positions which were defined so that shorter (more accurate) movements were at extreme angles and longer (less accurate) movements were at intermediate angles. One hypothesis that the present study is designed to test is that smaller recognition errors should obtain for both extreme flexion and extension positions than for intermediate positions, since the relative density of SA joint receptors is higher at the ends of the motion range.

The existence of a dynamic as well as static response phase of SA joint receptors poses additional interesting problems for studies of positioning accuracy. With a single exception, previous positioning studies all have used durations on target of 0 to 12 seconds, a period well within the dynamic rather than static response range. One might argue that position accuracy at such brief target durations cannot logically be attributed to the capability of SA joint receptors for maintaining a steady firing frequency as long as position is held. Indeed, two studies (Monster *et al.* 1973; Paillard & Brouchon, 1968) that used durations coincident with the dynamic response phase reported increasingly negative constant error with increased target durations. Wallace and Stelmach (1975) and Stelmach and McCracken (1978) found changes in absolute error between 0 and 2 or 5 second durations but no difference between 2 and 5 seconds. DelRey and Lichter (1971) observed no changes in error scores with target durations of 2, 5, and 10 seconds. These results suggest highly variable position recognition for target durations selected from the 'dynamic' response phase

range of SA joint receptors. In contrast, the one study that used longer target durations (15, 60, 180 sec., which would coincide with the static SA joint receptor response phase) reported no difference in recognition errors over the three durations, as might be predicted from knowledge of the steady firing of receptors during that period (Horsch, Clark & Burgess, 1975).

However, no experimental comparison of position accuracy between target durations coincident with the dynamic and static response phases has yet been attempted. If the steady maintained frequency response of SA joint receptors provides optimal information about position, then one might predict greater accuracy for target durations coincident with the static phase. Receptor input arising from briefer target durations might be confounded with velocity and acceleration information. Thus, the second purpose of the present study is comparison of position accuracy for brief (3, 6 sec) and long (15, 30, 150 sec) target durations. If the dynamic/static response phase distinction of SA joint receptors has predictive value for perception of position, then accuracy differences between the two classes of target durations should obtain. Moreover, there should be no difference in accuracy among the three longer durations; that is, the findings of Horsch *et al.* (1975) should be replicated. The durations of 15, 30, and 150 sec were selected in part to test the latter notion. A period of 30 sec was chosen to provide a time at which reflex and mechanical-elastic responses of the muscles to the targeting movement should be minimal (Hayes & Hatze, in press). A 150 sec target duration was used as a time at which conscious awareness of position due to cutaneous inputs should be unavailable to subjects, since appreciation of constant skin indentation fades after one to two minutes (Horsch *et al.* Experiment 2, 1975). Thus, accuracy differences among these three durations might suggest that either muscle or cutane-

ous afferents might be contributing to position sense.

There is an additional difficulty in comparing errors in position accuracy when target durations vary. As both Wallace and Stelmach (1975) and Horsch *et al.* (1975) pointed out, central as well as peripheral explanations can be used to account for similarities or differences in positional accuracy associated with varied target durations. Amount of time to attend to target position, or to rehearse recognition of the position will increase with increased target duration. Without some control for potential rehearsal or attention effects, there is no empirical reason to choose either the peripheral (receptor) or central hypothesis concerning accuracy changes with varied target duration. In the present experiment, an attempt was made to control for the amount of time that subjects could pay full attention to a target position. A secondary, masking task was performed with the left arm during passive positioning of the subject's right arm by the experimenter. One group of subjects (nonmasked) performed the secondary (mirror tracing) task only during movements toward and away from the target position. The other group of subjects performed the tracing task during movements and also throughout the target duration, except for the final three seconds when they were cued to pay attention to the position of the right arm. Thus, subjects in the masked group were restricted to 3 seconds during which they could give undivided attention to the target position; subjects in the nonmasked group were free to attend fully to the target position for the entire target duration. There is no reason to suspect that the mirror tracing task was wholly adequate in blocking subjects' attention to arm movement or position. However, emphasis on accuracy in the tracing task (which was performed with the non-preferred hand) was strong, the task was continuous, and it required integration of visual-proprioceptive input. The combi-

nation of these three characteristics of the secondary task made mirror tracing a reasonable choice of a task that required attention and that should interfere structurally with the information required for the positioning task.

The primary task consisted of an angular, horizontal positioning movement involving the right elbow joint with vision of the positioning device excluded. Individuals were asked to indicate verbally the position of the right elbow which had previously been presented as a target. The sensitivity of this technique has been demonstrated in previous work (Kelso, 1977b). A passive mode of presenting both target and recognition positions was adopted. In active movements, central and peripheral modulation of SA joint receptor inputs would be more likely than in passive movements. Therefore, the passive task should maximize the contribution of SA joint receptor input to the perception of limb position.

## METHOD

### Subjects

Thirty right-handed, adult volunteer subjects were assigned in alternating sequence to one of the two experimental groups. There were 8 males and 7 females in each group.

### Apparatus

The angular positioning device, placed in the horizontal plane, had angles marked off along the periphery in one degree increments ( $0^\circ$  at base left,  $180^\circ$  at base right). A padded lever arm pivoted freely about a shaft centered at the base of the device. The apparatus was hidden from the subject's view by a curtain, with an opening in the curtain large enough for the subject's right arm. Above the base of the lever a sling was suspended; the sling stabilized the position of the subject's upper arm, allowing the arm to pivot at the elbow. Two velcro straps

maintained forearm position on the lever. A height-adjustable stool was used for seating. The subjects were situated such that the right arm was at its full extension ( $180^\circ$ ) on the lever arm when the arm pointed to  $145^\circ$  at the periphery, with the arm abducted  $90^\circ$  from the body without shoulder protraction or retraction. The range of motion used in the experiment was from  $45^\circ$  to  $135^\circ$  ( $10^\circ$  to  $135^\circ$  respectively on the device). The relatively large 'extreme flexion' angle of  $45^\circ$  was selected because in pilot work it was found that several persons were uncomfortable with greater degrees of flexion. Errors in the task were recorded to the nearest  $0.5^\circ$ .

A mirror-tracing task (star-shaped) was used for the secondary masking task. The tracing apparatus was placed at a right angle to the left edge of the positioning device. The subjects performed the star-tracing task left-handed, with the eyes and head turned toward the tracing apparatus at about  $45^\circ$  to left of body center. They were instructed to maintain this head position throughout the experiment. Performance was measured as the number of times off target (measured by an electronic counter) per star traced for each block of trials.

A stopwatch was used to time all durations within the experiment. All experimenter-produced movements were timed, to permit maintenance of a constant average velocity of  $10^\circ$  per second.

### Procedure

The subjects were told that the experiment tested their ability to perform as well as possible on two different tasks. Instructions emphasized that optimal performance required full attention on one task at a time and that dividing attention would lead to poorer overall performance. A bonus of \$5 was used to motivate subjects to maximize performance in both tasks; the bonus was awarded to the subject with the best combined score from the star-tracing and the position recognition tasks. Following verbal

presentation of the instructions for the two tasks, all subjects received practice trials until they demonstrated an ability to keep the right arm relaxed and to follow the experimenter's commands correctly; no subject required more than four practice trials.

The subjects began each trial with the arm at  $45^\circ$  (flexed position) and with their eyes shut. On the command 'ready', subjects opened their eyes; one second later they were told to begin tracing. After 5 seconds, the experimenter began moving the subject's right arm to the target location, while the subject continued the tracing task.

### *Non-masked group*

When the target angle was achieved, subjects in the nonmasked group were told, 'stop, attention arm'; at this point timing of the target duration began. This command meant that the subject should stop tracing, close his/her eyes, and quickly shift attention to the position of the right arm. The subject was instructed to sit quietly and to continue paying attention to the arm position until hearing the command 'trace again'. This command was given 1 second prior to completion of the target duration; at completion of the duration, when the subject had resumed tracing, the experimenter moved the arm back to the start position at  $45^\circ$ . After 15 seconds from the beginning of the return movement, the experimenter said, 'stop, recognize', at which time the subject again closed his eyes, stopped tracing, and attended to his right arm which the experimenter immediately began to move from the start position toward the target location. When the subject felt his arm was in the same position that he had attended to during the criterion presentation, he indicated recognition by saying, 'stop'. The subjects were instructed to tell the experimenter to move the arm forward or back, if the experimenter had not stopped in the position which the subject had indicated. After the

experimenter recorded the angle which the subject indicated, the subject's arm was moved back to the start position. An inter-trial interval of 15 seconds was adopted.

### *Masked group*

For subjects in the masked group, procedures were essentially the same except that they continued tracing during all but the last 3 seconds of the target duration. Three seconds before the end of the target duration, they were told to attend to the arm; two seconds later they were told to 'trace again'. At the completion of the target duration, the experimenter moved the arm back to the start position. The remainder of the trial was exactly the same for the masked group as for the non-masked condition.

### **Design**

A mixed  $2 \times 3 \times 5$  factorial design was used,

with repeated measures on the second two factors. Secondary task activity (masked, non-masked) was the between groups variable. Response sector (flexion, extension, and intermediate) and target duration (3, 6, 15, 30, 150 seconds) were the within subject variables. Absolute, constant and variable error (AE, CE, and VE respectively) were the dependent measures. The subjects in each group ( $n = 15$ ) received 60 trials on the passive, angular recognition task; four trials were given in each response sector for all five target durations. Four blocks of 15 trials were presented to the subjects in two sessions which were at least 24 hours apart. In every block, all five target durations were presented three times in randomized order; each duration was matched with one angle for each response sector. There were 12 criterion angles, 4 per response sector (flexion =  $55^\circ$ ,  $58^\circ$ ,  $61^\circ$ , and  $64^\circ$ ; intermediate =  $106.5^\circ$ ,  $109.5^\circ$ ,  $112.5^\circ$  and  $115.5^\circ$ ; exten-

**Table 1**

**Mean absolute, constant, and variable error (in degrees) for masked and non-masked groups under different target durations**

| Group             | Duration (seconds) |                 |                 |                 |                 |
|-------------------|--------------------|-----------------|-----------------|-----------------|-----------------|
|                   | 3                  | 6               | 15              | 30              | 150             |
| <i>Masked</i>     |                    |                 |                 |                 |                 |
| AE                | 8.34<br>(3.95)*    | 8.82<br>(3.01)  | 9.06<br>(3.52)  | 9.37<br>(3.64)  | 9.68<br>(4.34)  |
| CE                | -5.40<br>(5.20)    | -5.03<br>(4.75) | -5.44<br>(4.99) | -6.05<br>(5.06) | -6.02<br>(6.23) |
| VE                | 4.78<br>(2.07)     | 5.19<br>(2.80)  | 5.17<br>(2.46)  | 5.45<br>(2.83)  | 4.33<br>(2.06)  |
| <i>Non-Masked</i> |                    |                 |                 |                 |                 |
| AE                | 7.46<br>(3.06)     | 8.48<br>(3.20)  | 7.59<br>(3.45)  | 7.32<br>(3.55)  | 6.20<br>(3.49)  |
| CE                | -4.37<br>(4.46)    | -5.33<br>(4.14) | -4.26<br>(4.34) | -4.51<br>(4.46) | -2.28<br>(4.87) |
| VE                | 4.89<br>(1.94)     | 5.29<br>(2.69)  | 4.72<br>(1.95)  | 4.27<br>(2.01)  | 4.49<br>(2.21)  |

AE = Absolute Error, CE = Constant Error, VE = Variable Error

\* Standard deviations of error scores are in parentheses

sion = 161°, 164°, 167° and 170°). Consequently, in each block of trials three angles were repeated once. Two conditions were imposed on these repetitions to minimize possible hysteresis-like effects on joint receptors adapted responses:

1. At least four trials intervened between repeated angles.
2. In no block was a repeated angle presented first at the 150 seconds duration.

## RESULTS

### Recognition errors

Although errors for the non-masked group were generally lower than those for the masked group, the difference reached significance only for AE,  $F(1,28) = 5.62, p < 0.05$ . Mean absolute, constant, and variable errors for groups are presented as a function of target duration in Table 1.

The main effect for duration at target did not reach the 0.05 level of significance for AE, CE, or VE,  $F(4,112) = 0.87, 1.30$ , and  $1.35$  respectively. Thus the hypothesis that the times associated with the dynamic and steady adapted response phases of receptors would be associated with differential error levels was not supported.

However, the duration by groups interaction was significant for AE,  $F(4,112) = 4.32, p < 0.01$ , and for CE,  $F(4,112) = 3.54, p < 0.01$ , though not for VE,  $F(4,112) = 1.24, p > 0.05$ . Newman-Keuls comparisons between the groups for each duration revealed a significant difference between groups only at 150 seconds for AE,  $q(10,50) = 3.48, p < 0.01$ . For CE, none of the individual group by duration comparisons reached the 0.05 level of significance. As may be seen in Table 1, AE and CE showed essentially the same pattern. Errors were higher generally for the masked group, and differences between groups tended to increase for the longer durations.

Mean absolute, constant and variable errors are presented as a function of target

sector in Table 2. The sector main effect was highly significant,  $F(2,56) = 56.09, p < 0.01$ ,  $F(2,56) = 158.04, p < 0.01$ , and  $F(2,56) = 20.87, p < 0.01$  for AE, CE and VE, respectively. The range effect was clearly evident, with overshooting characterizing the flexion sector ( $M = 2.30^\circ$ ), moderate undershooting for the intermediate sector ( $M = -5.68^\circ$ ), and highest negative error for the extension sector ( $M = -10.37^\circ$ ). AE increased from flexion to intermediate to extension sectors ( $M = 4.53^\circ, 8.91^\circ$ , and  $11.21^\circ$  respectively). For VE, the flexion sector showed the smallest average error ( $M = 3.63^\circ$ ), the intermediate sector showed the largest average error ( $M = 5.63^\circ$ ), and the extension sector slightly lower VE than the intermediate sector ( $M = 5.31^\circ$ ). Thus, VE was the only error score showing better performance in both extreme sectors. However, since overall accuracy (AE) indicated that errors increased as target angle (and, movement extent to the target) increased, the data on VE must be deemed insufficient as evidence for greater accuracy at extreme limb positions.

The sector by group interaction was significant only for CE,  $F(2,56) = 3.80, p < 0.03$ . For each sector, errors were closer to 0° for the non-masked than the masked group. The duration by sector interaction failed to reach the 0.05 level of significance for AE, CE, or VE,  $F_s(8,224) < 1$ . The three-way duration by sector by groups interaction was significant for AE,  $F(8,224) = 2.61, p < 0.01$ , and for CE,  $F(8,224) = 2.41, p < 0.05$ ; neither of these interactions was readily interpretable.

### Star-tracing errors

For the secondary task, measures of error rate (number of errors divided by the number of stars completed per block) were compared on the first and fourth blocks of trials, using *t*-tests for correlated means. These comparisons were performed to

**Table 2**

Mean absolute, constant, and variable errors (in degrees) within three target sectors for masked and non-masked groups

| Group             | Flexion         | Target Sector<br>Intermediate | Extension        |
|-------------------|-----------------|-------------------------------|------------------|
| <i>Masked</i>     |                 |                               |                  |
| AE                | 4.85<br>(2.26)* | 10.16<br>(4.10)               | 12.04<br>(4.71)  |
| CE                | 2.60<br>(3.72)  | -8.24<br>(6.06)               | -11.12<br>(5.95) |
| VE                | 3.90<br>(1.90)  | 5.40<br>(2.96)                | 5.66<br>(2.49)   |
| <i>Non-masked</i> |                 |                               |                  |
| AE                | 4.21<br>(2.44)  | 7.65<br>(3.59)                | 10.39<br>(4.07)  |
| CE                | 1.99<br>(3.53)  | -4.83<br>(5.05)               | -9.61<br>(4.79)  |
| VE                | 3.36<br>(1.68)  | 5.87<br>(2.66)                | 4.96<br>(2.13)   |

\* Standard deviations of error scores are in parentheses

ensure that subjects had improved across blocks of trials, on the assumption that improvement would indicate that subjects were indeed continuing to pay attention to the tracing task. The differences proved significant for both the masked and non-masked groups ( $t(14) = 5.25$ ,  $p < 0.01$ , and  $t(14) = 2.27$ ,  $p < 0.025$  respectively). For the masked group, error rate scores showed a consistent decrease with blocks ( $M_1 = 15.19$ ,  $M_2 = 7.5$ ,  $M_3 = 6.06$ ,  $M_4 = 4.57$  errors/star). For the non-masked group, there was a similar trend, except that block 3 (the first block of the second session) had slightly higher errors than block 2 ( $M_1 = 11.85$ ,  $M_2 = 7.07$ ,  $M_3 = 7.70$ ,  $M_4 = 6.29$  errors/star).

## DISCUSSION

The data of this study did not support the hypothesis that accuracy in recognition of a passively presented limb position might be

predicted from known neurophysiological characteristics of slowly adapting joint receptors. The first prediction, that errors should be smaller for the flexion and extension sectors than the intermediate sector was not confirmed. It is beyond the scope of these data to speculate on the nature (either central or peripheral) of the processes which might cause increased error with increased distance moved to a target position (but see Weiss, 1954; Wilberg, & Girouard, 1975). What is clear is that knowledge that most SA joint receptors respond to extreme but not intermediate joint angles did not enable accurate prediction of recognition errors in the positioning task used in this study.

The second hypothesis, that times corresponding to dynamic and static phases of SA joint receptor responses would be associated with different error levels, was also largely unsupported by the data of this experiment. There was no evidence that



target durations (presumed to coincide with the static, steady adapted response phase) allowed subjects to more accurately recognize the target position. The dynamic/static response phase dichotomy evident in neurophysiological studies was apparently without a behavioral counterpart under the conditions of low velocity, passive movements used in this study. However, as Burgess and Perl (1973) pointed out, for displacements of low acceleration or velocity the dynamic response of mechanoreceptors provides a relatively undistorted position signal. That is to say, the movement velocities used in this study may have been too small to elicit a dynamic phase response large enough to significantly disrupt positional information in the receptor response. A more appropriate test of the behavioral significance of the dynamic and static response phases would be to use movements of high acceleration or velocity. However, within the restricted velocity rate used in the present study, knowledge of dynamic and static response phases was not predictive of perceptual accuracy for limb position.

These results may be compared with those of other studies which have also used low or moderate velocity movements in positioning tasks. For the durations associated with the dynamic response phase, the data from this study were consistent with those of Del Rey and Lichter (1971), Wallace and Stelmach (1975), and Stelmach and McCracken (1978); that is, no difference between recognition errors for 3 and 6 seconds were observed. These results contrast with those of Paillard and Bouchon (1968) and Monster *et al.* (1973) who reported a consistent tendency of constant error to become more negative when time at target was increased from zero to 12 seconds. Those authors suggested that the constant error effect might be related to the decay of the velocity-sensitive dynamic response of slowly adapting joint receptors. That hypothesis seems somewhat questionable since the studies

noted above did not find the constant error effect. More probably the discrepancy is related to a difference in experimental procedures. Both Paillard and Bouchon (1968) and Monster *et al.* (1973) used a task in which the vertical position of one limb was matched by the opposite limb. The current study and those by Del Rey and Lichter (1971), Wallace and Stelmach (1975), and Stelmach *et al.* (1975) all used a horizontal task in which the criterion and reproduction movements were performed with the same limb in the horizontal plane. Either the difference in the plane of movement or in the use of the same or opposite limb to match the criterion position might account for the discrepancy in results.

The data showing statistically equivalent errors at longer 'static phase' target durations are in agreement with those reported by Horsch *et al.* (1975). The argument that rehearsal time might have been a critical factor in equating the three durations was not substantiated, for errors did not change significantly with durations for both the masked and non-masked groups. Moreover, one cannot attribute the superiority of the non-masked group simply to the longer time available to attend to limb position. Were attention time *per se* crucial, two results should have been observed. First, the superiority of the non-masked over the masked group should have increased consistently with longer durations. This prediction received only marginal support, in the one significant difference between groups at 150 sec (AE). Second, within the non-masked group, errors should have decreased significantly with increased time on target; some decline was noted, but it was not significant. An alternative explanation for the differences between the masked and non-masked groups may be that the secondary tracing task interfered with the recognition task, possibly by fatiguing subjects, especially for the long durations. An overall fatigue factor does not seem supported, for error differ-

ences at 3 and 6 secs between the two groups were very small.

As noted in the introduction, the present study represented an initial attempt to test directly the notion that perception of position can be predicted from knowledge of slowly adapting joint receptor firing functions. It would be useful to perform additional, more stringent tests of the relationship between receptor properties and perception, for example by using movements of higher velocity, or by monitoring muscle activity to ensure passivity, or by recording nerve impulse volleys from joint receptors during a positioning task. However, within the limitations of this study, the main conclusion was clear: there was not a straightforward relationship between accuracy of limb position perception and the two specified neurophysiological properties of SA joint receptors even under 'passive' conditions.

This conclusion may not be surprising, since available neurophysiological data are based on experiments with subhuman species. Firing functions for human SA joint receptors have yet to be studied. It also seems likely that higher processes could modify receptor input or the interpretation of receptor input significantly according to the needs of the information processing system. For example, accuracy of limb position perception can be improved with knowledge of results (for review see Newell, 1977); presumably, receptor input remains basically unchanged but utilization of that information is improved with learning.

Given the problems with extrapolating from neurophysiological properties of receptors in subhuman species to human perceptual behavior, it is intriguing how investigators frequently attribute findings to the functioning of specific receptors. A case in point is the often replicated finding that memory for limb position or 'location' is superior to memory for movement amplitude of 'distance' (for review see Stelmach &

Kelso, 1977). The fact that there are SA joint receptors which could signal location but not distance is often cited as a reason for the difference in memory for these two qualities. The present data as well as other evidence (Kelso, 1978b for review) suggest that it is time to reconsider such an interpretation. Similarly accounts of other active movement behaviors like motor timing based solely on the properties of SA joint receptors (Adams, 1977) seem unrealistic. At least for accuracy in discrete positioning movements, the need for peripheral input is greatly reduced under active conditions (Grigg *et al.* 1973; Kelso, 1977a; 1978b, Polit & Bizzi, 1979). Hence, if even passive position sense cannot be predicted readily from knowledge of SA joint receptor properties, then it seems unlikely that active movement behavior should be attributable entirely to these receptors' functional properties.

Despite the problems inherent in trying to make behavioral predictions from a neurophysiological model of receptor function, such attempts may be justified in at least two ways. First, data from studies making deliberate predictions can reveal how proposed neurophysiological explanations of behavior may be overly simplistic. Second, such studies may lead to potentially more accurate models interfacing behavioral and neurophysiological levels of description, for they can indicate which behaviors can be explained with reference to receptor level events and which cannot, thereby suggesting the need for more complex explanatory models.

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