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THE INFLUENCE OF SOME STIMULUS PARAMETERS ON HUMAN KINESTHETIC SENSITIVITY

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by

HOWARD LLOYD COHEN

A dissertation submitted to the Graduate Faculty
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ABSTRACT

THE INFLUENCE OF SOME STIMULUS PARAMETERS ON HUMAN KINESTHETIC SENSITIVITY

by

HOWARD LLOYD COHEN

Advisor: Professor William S. Battersby

Two experiments were conducted in order to parametrically evaluate kinesthetic sensitivity in four normal young adults. A highly precise system for the delivery of kinesthetic stimulation and for the measurement of angular displacement was used to assess sensitivity at the proximal interphalangeal joint of the index finger of the right hand. Sensitivity was measured as a function of angular velocity, angular displacement, and stimulus duration, and three starting positions of the joint and two directions of movement were investigated. Two psychophysical procedures--a combination of the methods of adjustment and constant stimuli, and the method of constant stimuli-- were employed, and two response measures--percent correct detection and response time--were used.

In Experiment 1, the kinesthetic stimuli consisted of all combinations of seven velocities (.15, .30, .80, 1.5, 3.0, 6.2, and 11.0°/ sec.) and two directions of movement (up, down). The stimuli were randomly presented, but were blocked across three starting positions of the joint (15°, 25°, and 35° from the vertical). The psychophysical procedure employed was a combination of the methods of adjustment and constant stimuli, in which the duration of each velocity - direction combination was increased to a maximum of 10 seconds. Upon detecting movement,

the subject pressed a telegraph key which terminated the stimulus and gave a measure of response time. A verbal response indicating the direction of movement was also required. A stimulus not detected within 10 seconds was considered a miss. Percent correct detection and response time were each plotted as functions of log angular velocity, for each direction and starting position, and threshold angular velocities (50% correct detection) were obtained. In order to assess the statistical significance of the effects of velocity, direction, and starting position on each of the dependent measures, individual 7 x 2 x 3 analyses of variance, with repeated measures on each factor, were performed on the group data. The results indicated that while the main effect of velocity was significant for each dependent measure, the main effects of direction and starting position were not.

The purpose of Experiment 2 was to obtain 1) a measure of passive movement sensitivity not confounded by the subject's response mode, 2) a true indicator of angular displacement sensitivity, and 3) a more accurate determination of the lower limits of passive movement sensitivity than was seen in Experiment 1. In Experiment 2, which used the same subjects and apparatus, the psychophysical procedure employed was the method of constant stimuli. The kinesthetic stimulu consisted of all combinations of six velocities (.05, .10, .15, .30, .80, and 1.5°/ sec.), six durations (1, 2, 4, 6, 8, and 10 seconds), and two directions (up, down). The starting position of the joint was kept constant at 25° from the vertical. Upon detecting movement, the subject gave a verbal response and also identified the movement direction. Percent correct detection was plotted as a function of both log angular velocity and stimulus duration. A 6 x 6 x 2 analysis of variance, with

repeated measures on each factor, was performed on the group data in order to assess the effects of velocity, duration, and direction on detection. The results indicated that each of the main effects, as well as the velocity by duration interaction, was significant. Next, each velocity - duration combination was multiplied, in order to obtain a range of angular displacements. Percent correct detection was then plotted as a function of log angular displacement, and threshold angular displacements (50% correct detection) were obtained.

The results of both studies indicate that passive movement sensitivity is influenced by both the angular velocity and angular displacement of the movement. There is additional evidence from Experiment 2, that differences in directional sensitivity at low angular velocities may be manifested when the joint is rotated near to its movement limit.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

> Though his eyes be shut, a man knows about the position and posture of his body, and whether its parts are moving or exerting effort in sustaining a weight or in pressing against resistance. If this be kinesthesis, then no philosopher can ever have doubted its existence.
>
> E. G. Boring (1942)

Investigations into kinesthetic sensitivity have generally proceeded along two lines of research: the elaboration of the physiological mechanisms through which joint afferent information is mediated, and its psychophysical assessment in the human observer. While much has been accomplished toward defining the kinesthetic contributions from joint, muscle, and cutaneous receptors and the mapping of central kinesthetic pathways, the psychophysical investigation of kinesthesis has suffered from a paucity of experimental findings, many of which have been inconsistent and even contradictory.

In the following psychophysical study, kinesthetic sensitivity is assessed via an electromechanical system designed to provide both more precise stimulus control and more accurate response measurement than have typically been used. In two parametric experiments, an attempt is made to resolve some of the differences reported in the earlier psychophysical studies, and to explain the results on the basis of possible physiological mechanisms. Reviews of the relevant psychophysical and physiological literature can be found in Chapters 1 and 2, respectively.

One technique by which kinesthetic sensitivity has been assessed is the passive movement procedure, wherein the parameters of movement, e.g., velocity, direction, angular displacement, starting position of the joint, etc., are manipulated by the experimenter. Psychophysical studies employing this technique have proceeded along several lines of research, among which are the determination of 1) physiological mechanisms mediating kinesthetic sensation, 2) threshold sensitivities of various joints, 3) effects of increasing angular velocity or angular displacement on threshold sensitivity, 4) differences between thresholds for movement detection and for direction identification, 5) threshold differences as a function of direction of movement, and 6) effect of starting position of the joint on threshold sensitivity.

Identification of the receptors responsible for kinesthetic sensation

Many psychophysical studies of kinesthetic sensitivity have attempted to define the relative contributions of joint, muscle, and cutaneous receptors (see Chapter 2). Goldscheider (1889) believed that kinesthetic sensation originated primarily, or even solely, from receptors in and around the joint capsule, and was due mainly to friction between the articulating surfaces and to pressure on the joint capsule. The basis for this belief was a series of studies in which Goldscheider found that faradic stimulation across a joint elevated its movement threshold. Muscles and tendons were assumed to make a minor contribution to kinesthetic sensitivity because thresholds were not significantly affected by the position of the limb, i.e., flexion or extension. Goldscheider's conclusion was criticized (Pillsbury,1901; Winter,1912) first, because there was no histological evidence for receptors in the articulating surfaces, and second, because faradic stimulation even distal to the joint under observation could increase threshold. For example, passing a current across the wrist joint elevated the passive movement threshold at the elbow as much as did stimulation across the elbow itself. Simultaneous stimulation of both the wrist and elbow joints raised the threshold even further. Since this effect could not have been the result of stimulating articular receptors, it was concluded that mediation of the effect could only have been through stretch receptors in the tendons and ligaments at the insertions of the muscles.

Threshold sensitivities of the various joints

Goldscheider (1889), acting as his own subject, ran over 4000 trials and tested the sensitivities of nine joints: the first and second interphalangeal, the metacarpo-phalangeal, the wrist, elbow, shoulder, hip, knee, and ankle, all on the left side. Threshold was defined as that angular displacement that was detected on 50% of the trials. It was found, in general, that threshold angle increased along a proximal - distal gradient. Thus, the threshold at the ankle joint was approximately twice that at the hip joint. In a similar study (Laidlaw & Hamilton, 1937b), passive movement thresholds were assessed at many of the same joints, but on both sides of the body. While there were no laterality differences in threshold, the proximal - distal gradient was again demonstrated, with the hip joint having the greatest sensitivity. The proximal - distal gradient of kinesthetic sensitivity is in contrast to that for cutaneous sensitivity (two point threshold), wherein the distal elements are more sensitive than are the proximal (Vierordt, 1869).

Effect of increasing either angular velocity or angular displacement on threshold sensitivity

As one increases either angular velocity or angular displacement, it would be expected that threshold angle would decrease and detection rate would increase. Unfortunately, these relationships have not been reliably demonstrated. For example, Winter (1912) used angular velocities of .75 to 5.26 mm. / sec., and instead of finding a systematic decrease in threshold angle as velocity increased, he found both increases and decreases. Cleghorn and Darcus (1952) found that, with a fixed angular displacement and over the range of velocities used (.05 to .25 deg./ sec.), detection was an increasing function of velocity up to a point of maximum performance (.20°/ sec.), beyond which there was a decrease in performance which they attributed to a decreased time factor. It was proposed that, at higher velocities, the movement becomes more of a jolt, which could have been missed with the slightest relaxation of attention. More recent studies (Gandevia & McCloskey, 1976; Kokmen, Bossemeyer, & Williams, 1977), however, have been more successful in demonstrating the expected relationships. The first study (Gandevia & McCloskey, 1976) assessed sensitivity at the distal interphalangeal joint and examined subjects under three conditions. Under the first two conditions, the joint was moved at angular velocities of 1° to 10°/ sec., through either a constant 10 displacement or for a constant 1.2 second duration. Under the last condition, the joint was moved at a constant 8°/ sec. velocity over angular displacements of 2.5°, 5.0°, 7.5°, and 10.0°. The results indicated that when the joint was moved over a constant angular displacement, or for a constant duration, detection was an increasing function of angular velocity. When velocity was held constant, detection was an increasing function of angular displacement. The second study (Kokmen, Bossemeyer, & Williams, 1977) measured sensitivity at both the metacarpophalangeal and metatarsophalangeal joints. A modified von Bekesy procedure was used, and both upper and lower thresholds were calculated for sinusoidal stimuli of .5 and 5.0 Hz., over angular displacements up to 10°. The thresholds obtained at both joints were found to be inversely related to the frequency of stimulation. The differences obtained were significant at $P<.001$.

Differences between thresholds for movement detection and for direction identification

There is much evidence to indicate that at threshold velocities, the detection of movement and the identification of direction do not occur simultaneously. Goldscheider (1889) reported that often, at the slowest velocities, there was only an awareness of movement, but not of direction. Cleghorn and Darcus (1952) found that while the detection rate for all stimuli presented at the elbow joint was 82%, that for the identification of direction was only 67%. Using an angular velocity of .20°/ sec. and a criterion of 80% correct detection, they found that while the threshold angle for movement detection was only .8°, that for the identification of direction was 1.8°. It has been pointed out (Cohen, 1958) that if one assumes that the same receptors mediate both sensations, it is logical to expect that a more precise sensation would replace a more vague one, as progressively more information is produced by the originally activated receptors.

Horch, Clark, and Burgess (1975), in a related study, used a variation of the passive movement procedure to assess sensitivity at the knee joints. The subject, seated, with both knees in the same starting position, was required to report when the movement of one limb produced a just noticeable difference in the alignment of the two limbs. While angular velocities of less than 1°/ min. produced no reliable sensation of movement, an angular displacement of 3° to 4° at this velocity resulted in a perception of altered position. On the basis of these findings, it was postulated that the knee joint contained two populations of receptors: a very slowly adapting, or even nonadapting type of position detector, and a rapidly adapting type of movement detector.

Threshold differences as a function of direction of movement

Research into whether the direction of movement has any effect on threshold sensitivity has generally produced contradictory results. Whereas Goldscheider (1889) found that at the elbow joint there was a greater sensitivity to flexions (upward movements), in contrast, both Winter (1912) and Cleghorn and Darcus (1952) found there was greater sensitivity to extensions (downward movements). Winter also found reversals in directional sensitivity as angular velocity increased. In contrast to the above, several studies have reported no directional differences (Browne, Lee, & Ring, 1954; Gandevia & McCloskey, 1976; Laidlaw & Hamilton, 1937b).

Effect of starting position of the joint on kinesthetic sensitivity

Although several studies have examined the effects of changes in starting position on threshold sensitivity, almost none appear to have done so in a systematic manner. Early studies (Goldscheider, 1889; Winter, 1912) reported contradictory findings. Whereas Winter (1912) found that changes in starting position produced appreciable threshold differences, Goldscheider (1889) found no such effects. Both sets of results were used to argue either for or against the contribution of muscle receptors to kinesthetic sensitivity.

As cited earlier, Cleghorn and Darcus (1952) found that, at the elbow joint, the detection rate for extension movements was significantly higher than that for flexions. While not specifically investigating the effects of changes in starting position, they did note, in a preliminary investigation, that the detection ratio between extensions and flexions varied systematically with joint position; the highest ratio at 10° from full extension, and then decreasing at 30° and again at 45° from the vertical. These results were attributed to differences in the pull of gravity which somehow modified the sensation of passive movement arising from the dorsal and ventral surfaces of the forearm.

As indicated in the aforementioned psychophysical studies, the results are often highly variable and even contradictory, i.e., the effects of direction, starting position, and angular velocity on threshold angle. Table 1 compares the results of five studies that examined passive movement thresholds at the elbow joint. If one examines the thresholds obtained in each of these studies, it is evident that while the largest threshold was obtained at the lowest velocity, threshold angle did not decrease systematically as angular velocity was increased.

It is quite probable that the paucity of replicable results is due to the fact that kinesthesis has rarely been investigated via standardized equipment and / or procedures. For example, there have been major differences in the way the kinesthetic stimulus has been produced, with diverse systems of stimulus delivery using hydraulic (Goldscheider, 1889; Horch, Clark, & Burgess, 1975), electromechanical (Browne, Lee, & Ring, 1954; Gandevia & McCloskey, 1976; Kokmen, Bossemeyer, & Williams, 1977), and even manual control (Laidlaw & Hamilton, 1937b).

TABLE 1

Summary of the Studies Measuring Passive Movement Thresholds at the Elbow Joint

Investigator	Range of Speed of Movement (deg./ sec.)	Range of Threshold
Goldscheider (1889)	.7 - 1.4	.40 - .76
Pillsbury (1901)	.33	.43 - .85
Winter (1912)	.08 - .56	.20 - 2.82
Laidlaw and Hamilton ((1937b)	) .16	.30 - 2.50
Cleghorn and Darcus (1952)	.05 - .25	.8 - 1.8*

* Smaller value is 80% correct detection of movement
Larger value is 80% correct identification of direction
Both values were obtained at an angular velocity of .20 deg./ sec.

Similarly, there have been wide differences in the precision of the methods used to measure angular displacement. These methods include reading the angular values from a scale (Browne, Lee, & Ring, 1954; Goldscheider, 1889; Laidlaw & Hamilton, 1937b), from an inkwriter deflection proportionate to the angular displacement (Gandevia & McCloskey, 1976; Horch, Clark, & Burgess, 1975), and from a minicomputer digital display (Kokmen, Bossemeyer, & Williams, 1977). Of equal importance with the differences in measurement technique is the fact that none of the systems used, has included a brake mechanism to terminate the stimulus. Without this control, it is possible because of both the inertia in the system and the elapsed time between detection and measurement, the nagular displacement measured is larger than the angular displacement detected.

Experimental design and procedural differences have also contributed to many of the discrepancies reported. Among the factors that have differed include the psychophysical methods, e.g., limits (Browne, Lee, & Ring, 1954; Kokmen, Bossemeyer, & Williams, 1977) and constant stimuli (Cleghorn & Darcus, 1952), the use of catch trials (Browne, Lee, & Ring, 1954) or their exclusion (Kokmen, Bossemeyer, & Williams, 1977), and the response modes, e.g., verbal (Cleghorn & Darcus, 1952; Laidlaw & Hamilton, 1937b) or psychomotor (Browne, Lee, & Ring, 1954; Kokmen, Bossemeyer, & Williams, 1977).

The purpose of the present research was to assess kinesthetic sensitivity under conditions of more precise stimulus control, more accurate response measurement, and with more procedural rigor than has typically been employed. Measures were made on four normal human subjects. The two experiments that were conducted used two psychophysical procedures: a combination of the methods of adjustment and constant stimuli and the method of constant stimuli, and two response modes: psychomotor and verbal. Kinesthetic sensitivity was evaluated via two dependent measures: percent correct detection and response time. The effects of angular velocity, direction of movement, and the starting position of the joint were systematically evaluated for each dependent measure.

CHAPTER 2

LITERATURE REVIEW: THE PERIPHERAL AND CENTRAL MECHANISMS UNDERLYING KINESTHETIC SENSITIVITY

Joint Receptors

The joint capsule, which is ligamentous in nature, both surrounds and binds the joint. Its shape and thickness vary in order to conform to the demands placed upon the joint. The synovial membrane, a structure found within the capsule wall, secretes synovial fluid, which lubricates the articulating surfaces and reduces the friction between them (Howard & Templeton, 1966; Kelley, 1971). The joint receptors are a type of mechanoreceptor for which the adequate stimuli include changes in length, tension, compression, shear forces arising from the effects of gravity, the relative movement of body parts, and the contraction of muscle itself (Adams, 1977; Grigg, 1975; Howard & Templeton, 1966). There is general agreement that the joint receptors are of three major types: free nerve endings, Pacinian corpuscle - like encapsulated structures, and spray type endings. These spray endings are further classified as Ruffini - like receptors when situated in the joint capsule, and as Golgi tendon organs when situated in the ligaments (Skoglund, 1956; 1973). The morphological characteristics of these receptors show wide variability within and across species (Polacek, 1966).

The experimental determination of the response properties of these receptors has typically focused upon the articular nerves (posterior, medial, and lateral) in the knee joint of the cat, while a lesser number of studies in other species, e.g., monkey, and at other joints, e.g., wrist and elbow, have generally confirmed the findings in this preparation. On the basis of extracellular recordings, the Ruffini endings in the joint capsule and the Golgi tendon organs in the ligaments have been classified as slowly adapting receptors, while the Pacinian corpuscle, embedded in the deep tissue of the joints, has been classified as rapidly adapting (Boyd, 1954). The Ruffini endings are highly sensitive at threshold, tend to have narrow excitatory angles, and respond with an increased discharge frequency to either one or two directions of movement. They are not true position detectors, however, since they are also responsive to capsular changes produced by muscle (Adams, 1977; Eklund & Skoglund, 1960). The Golgi tendon organs in the ligaments, on the other hand, respond primarily to one direction of movement, are not influenced by changes in muscle tension, and maintain their discharges for prolonged periods. As such, these receptors seem to be exact indicators of both joint position and direction of movement (Skoglund, 1956). Because of their low sensitivity, they do not, presumably, signal velocity.

Stimulation of a slowly adapting receptor, e.g., Ruffini ending, produces an initial high frequency discharge, called the dynamic frequency (Adams, 1977), which is directly proportional to the velocity of movement. Following stimulus offset, this discharge frequency then decays to a tonic level which may persist for hours, and which presumably, therefore, reflects the position of the limb (Boyd & Roberts, 1953; Skoglund, 1956).

On the other hand, stimulation of a rapidly adapting receptor, e.g., the Pacinian corpuscle, produces a discharge frequency which appears to be unrelated to movement velocity, direction, or starting position of the joint (McCloskey, 1978). For this reason, the Pacinian corpuscle may be classified as a movement detector (either velocity or acceleration), or may simply act to signal the onset of movement (Burgess & Perl, 1973).

The classically accepted belief was that joint receptors provided continuous monitoring of joint angle. The earliest research suggested that each receptor had a limited range and a precise excitatory angle at which it discharged maximally (Cohen, 1955; 1956). These excitatory angles, which could be as narrow as 3° (Cohen, 1955), were considered to provide a specific signal for each successive joint position during movement (Adams, 1977), and to be more or less uniformly distributed throughout the entire range (Matthews, 1977). According to this view, each position of the limb apparently activated a new population of joint receptors. If true, this could be strong evidence that these receptors mediated the appreciation of both movement and direction. However, evidence from other sources questioned whether these receptors did, in fact, provide continuous signaling of joint angle (Grigg, 1975). Unit recordings from joint receptors have revealed that most slowly adapting receptors fire primarily at the extremes of flexion or extension (Boyd & Roberts, 1953; Burgess & Clark, 1969b; McCall, Farias, Williams, & BeMent, 1974; Skoglund, 1956), and that only a small population responds to the intermediate positions of the limb. Thus far, the specific response characteristics of this latter receptor type do not appear to have been defined.

Millar (1973) found that intermediate range receptors (present in about 50% of his cat elbow joint preparations) fired at high frequencies only when at the extremes of movement. In contrast, Burgess and Clark (1969b) and Clark and Burgess (1975) report for these receptors that it was necessary for the limb to be so near the extremes of flexion or extension that the stimulus could be considered nociceptive. In any event, the population of these receptors appears to be so small and variable that it is questionable whether they could accurately encode limb position and movement (Burgess & Clark, 1969b; Clark & Burgess, 1975).

In a series of studies using the cat knee joint preparation (identical to that of Boyd & Roberts, 1953), Grigg (1975; 1976) and Grigg and Greenspan (1977) have demonstrated that holding the tibia - femur angle constant at an intermediate position, and inducing an isometric contraction in the adjacent muscles by electric shock, could activate the joint afferents. This finding suggests that many of the joint afferents that respond to intermediate positions of the limb do so by virtue of the muscular connections to the joint capsule, and not because of the properties of the receptor itself. According to Matthews (1977), the finding that alterations in muscle tension can exert an influence on the joint capsule and, as a consequence, the firing rate of joint receptors, means that, " in order to interpret the discharge rate of joint receptor neurons, the prevailing level and distribution of motor activity would also have to be taken into account " (p. 138).

Further evidence that the relationship between joint receptors and kinesthesis is a complex one comes from two studies that attempted to relate the frequency of discharge to the direction of movement (Burgess & Clark, 1969b; McCall, Farias, Williams, & BeMent, 1974). Both of these studies initially reported a population of receptors that fired maximally at the extremes of either flexion <u>or</u> extension (single ended). Moreover, they also describe a population of receptors that apparently fired with the same discharge rate to the extremes of both flexion and extension (double ended). In the first study (Burgess & Clark, 1969b), double ended receptors far outnumbered the single ended. In the second study (McCall et. al. 1974), on the other hand, double ended receptors numbered half of the single ended ones and, with the limb positioned near either extreme of movement, the frequency of discharge, as a function of joint angle, was bell shaped. This indicated that there was a discharge rate, less than maximal, that was produced by two different limb positions. At present, the differences between the two studies remain unresolved and require further work.

Muscle Receptors

The question of whether the impulses arising from within the muscle itself can be consciously perceived has been debated since Bell (1826) proposed the existence of a separate " muscle sense " (p. 163). There are experimental results both for and against this concept. Against this concept stands the fact that kinesthesis can be lost when a joint is anesthetized via infiltration with a local anesthetic, while the muscles remain functional (Provins, 1958). Second, there is a lack of sensation produced by physically pulling on an exposed tendon (Gelfan & Carter, 1967). Finally, there is evidence indicating that stimulation of muscle receptors in human extraocular muscles does not produce conscious sensation of changes in eye position (Brindley & Merton, 1960). Others, however, have contested each one of the foregoing results. First, it was found that with anesthesia of both cutaneous and joint afferents in the index finger, it was still possible to detect movement, identify its direction, and identify the terminal position, e.g., up or down (Goodwin, McCloskey, & Matthews, 1972a). Second, it was reported (Matthews & Simmonds, 1974) that pulling on an exposed tendon so that the muscle was stretched but the appropriate finger was not moved, elicited sensations of movement referred to that joint. Finally, by using a forced choice technique, trained subjects, and a procedure that minimized both discomfort and stress, Skavenski (1972) demonstrated, reliably, the conscious awareness of passive displacement of the eye.

Regardless of these findings, if muscles are insentient, then a complete loss of kinesthetic sensitivity should result from any procedure which would eliminate the afferent impulses from joint receptors. Two lines of investigation on human subjects have demonstrated that this prediction is probably incorrect. In the first after complete removal of the joint capsule, postoperative testing with clinical techniques revealed kinesthetic sensitivity to be within normal limits (Cross & McCloskey, 1973). In another study (Grigg, Finerman, & Riley, 1973), several psychophysical procedures (detection, magnitude estimation, and magnitude production) were used to compare the sensitivity at the operated hip joint (joint capsulectomy) with that on the contralateral side. Although sensitivity was lower at the operated hip joint, the magnitude of the difference was statistically significant in less than half of the cases. While neither of the above authors cite these findings as conclusive evidence for the sensory contribution of muscle receptors, Cross and McCloskey (1973) feel that this is a strong possibility, and Grigg et al., (1973) postulate an " extracapsular sensory periphery " which would involve muscle receptors and perhaps cutaneous receptors as well.

The second line of investigation involves those studies in which either a local anesthetic (Browne, Lee, & Ring, 1954; Gandevia & McCloskey, 1976; Provins, 1958; Williams, Bossemeyer, & Kokmen, 1977) or a combination of local anesthetic and pressure cuffs (Goodwin, McCloskey, & Matthews, 1972a; 1972b; Williams, Bossemeyer, & Kokmen, 1977) was used to eliminate capsular function and cutaneous (touch) sensitivity. The level of cutaneous anesthesia was assessed via standard clinical testing (pinprick, pressure, and touch) at the joint under observation. When anesthesia was complete, kinesthetic sensitivity was then evaluated by general clinical techniques and found to be diminished, but clearly not absent. Both movement and direction could be identified, although it was necessary to increase either the velocity of the movement or the magnitude of the excursion. More interestingly, it was often possible to increase sensitivity by having the subject actively contract the muscles involved (Goodwin et al. 1972a). This latter result has been confirmed by some (Browne, Lee, & Ring, 1954; Gandevia & McCloskey, 1976) but not by others (Provins, 1958). However, it has been pointed out (Goodwin et al. 1972a) that the negative study used only one velocity of movement, and this might have been below threshold for the muscle receptors involved.

Two studies (Gandevia & McCloskey, 1976; Goodwin et al., 1972a) have taken advantage of the the fact that when the fingers are extended straight out and parallel, and the middle finger is then ventroflexed at the proximal interphalangeal joint, it is impossible to move the distal interphalangeal joint because the terminal portions of both flexor and extensor tendons are then slack, so that contraction of their muscles no longer influences the joint. This allows the assessment of kinesthetic sensitivity both with and without the contribution of muscle receptors. If tested psychophysically in this position, sensitivity is greatly diminished. If anesthetized in this position, the joint loses all position sense. When, however, the middle finger is then aligned with the adjacent fingers (the muscles having been essentially restored), kinesthetic sensitivity becomes greatly enhanced.

Cutaneous Receptors

The contribution of cutaneous receptors to kinesthetic sensitivity has been difficult to evaluate because digital nerves often supply both skin and joints (Kokmen, Bossemeyer, & Williams, 1977). As a consequence, any attempt to anesthetize one receptor type may interfere with normal function in the other (Moberg, 1972). While the anatomical findings are rather specific, both the clinical and experimental findings are generally contradictory. Whereas Ferrier (1876) reported that injuries to spinal or peripheral nerves resulted in deficits in both cutaneous and kinesthetic sensitivity, Head and Sherren (1905) reported that such deficits could exist independently of one another. The interpretation of the experimental findings from human subjects is also problematic. For example, two studies (Clark & Burgess, 1975; Clark, Horch, Bach, & Larson, 1979) have shown that local anesthesia of the skin overlying the knee produces no serious impairment in sensitivity. Other studies (Browne, Lee, & Ring, 1954; Goodwin et al. 1972a; Provins, 1958), however, have found that kinesthetic sensitivity of the toes and fingers was markedly decreased following anesthesia of both skin and joints, but no deficit was evident from interference with joint receptors alone (Cross & McCloskey, 1973; Goodwin et al., 1972a). This suggests a cutaneous contribution to the kinesthetic sensitivity of the fingers and toes, but not to that of the knee. A further problem that has yet to be resolved is the nature of the kinesthetic input, i.e., whether it is a specific signal of position and movement, or a central facilitatory effect on muscle and joint afferents (Gandevia & McCloskey, 1976). In summary, few studies have investigated the cutaneous contribution to kinesthetic sensitivity, and where they have done so, the findings are often contradictory.

Central Structures

Kinesthetic sensation is ultimately dependent upon the central projections of the appropriate receptors. However, because muscle nerves often course through articular nerves, and because the reverse is also true, one cannot be certain that the central response reflects the activation of a unitary type of kinesthetic afferent (McCloskey, 1978). This complication should be considered in the interpretation of studies of central kinesthetic responsivity.

While kinesthetic impulses appear to be transmitted over several pathways (spino-reticular, spino-olivary, spinocervicothalamic, dorsal column - medial lemniscal, and the spinocerebellar), only the latter two will be considered, as they have been examined most extensively. The traditional view of the dorsal column - medial lemniscal system, as the primary pathway over which kinesthetic impulses are transmitted centrally, has been questioned by recent electrophysiological, neuroanatomical, and behavioral evidence. For example, it has been demonstrated that the pathways carrying both muscle and joint afferents are organized differently in fasciculus cuneatus (forelimbs) and fasciculus gracilis (hindlimbs). While many joint (Clark, Landgren, & Silfvenius, 1973) and muscle (Oscarsson & Rosen, 1963) afferents run the full length of fasciculus cuneatus to terminate in nucleus cuneatus, most fibers in fasciculus gracilis leave the dorsal columns before reaching the upper lumbar cord (Webster, 1977). Behavioral evidence in support of this electrophysiological finding comes from a study (Vierck, 1966) in which a monkey, conditioned to respond to the terminal position of the lower leg, showed no apparent deficit following a midthoracic dorsal column lesion. Extracellular recordings from both cat and monkey (Burgess & Clark, 1969a; Whitsel, Petrucelli, & Sapiro, 1969) found that less than 10% of the deep afferents in the knee joint project to upper cervical levels. Those projecting to cervical levels and, more centrally, to nucleus gracilis, were predominantly rapidly adapting and were incapable of signaling limb position (Williams, BeMent, Yin, & McCall, 1973). In the cat, hindlimb afferents appear to synapse in the Column of Clarke and leave the lumbar cord to enter the dorsal spinocerebellar tract (Webster, 1977). Many units in this tract are monosynaptically excited by group 1 muscle afferents (Oscarsson, 1973) and slowly adapting joint receptors, e.g., Ruffini endings (Lindstrom & Takata, 1972). The dorsal spinocerebellar tract then projects to nucleus Z, which lies just rostral to nucleus gracilis, in the floor of the fourth ventricle, and which contains units responding to muscle, or joint, or cutaneous stimulation (Johansson & Silfvenius, 1977). Nucleus Z in turn, projects to the thalamus.

While the elucidation of spinal and brainstem pathways is ongoing, there is, in contrast, overwhelming evidence that kinesthetic afferents from both hindlimbs and forelimbs course through the medial lemniscus to terminate in the contralateral ventrobasal (VB) complex of the thalamus (Mountcastle, 1974). An extensive investigation of the response properties of thalamic units (Mountcastle, Poggio, & Werner, 1963) demonstrated that, like joint receptors, they were maximally activated at the extremes of limb movement. Movement within the unit's excitatory angle produced an initial discharge frequency proportional to the movement velocity, and a tonic discharge frequency that was a function of limb position. Unlike joint receptors, however, these units were primarily single ended and frequently had excitatory angles extending over more than half the range of movement. As a result, units responding to opposite directions of movement shared overlapping excitatory angles. Such an arrangement was believed to facilitate the identification of direction. With the limb in an intermediate position, the discharge rate of both flexor and extensor neurons would be low. However, if for example, the limb was flexed, more flexor neurons would be recruited, their discharge rates would increase, and the discharge rates of extensor neurons would, in contrast, decrease markedly. An additional finding was that, for a large number of units, the relationship between discharge frequency and magnitude of angular displacement was best described by a power function. However, two major criticisms have been leveled at this study (Matthews, 1977). First are the difficulties in reconciling certain thalamic unit response properties, with the response properties of joint receptors. Second is the fact that the graded response to joint rotation may reflect either a partial or a total input from muscle afferents, rather than a total input from joint afferents, as Mountcastle et al. (1963) have proposed.

While the thalamus, cortex, and cerebellum each receive major kinesthetic inputs, it appears that only thalamic or cortical damage produces a kinesthetic deficit (Head, 1911; Holmes, 1917; Semmes, Weinstein, Ghent, & Teuber, 1960). The thalamocortical projection of kinesthetic afferents terminates in sensorimotor cortex. While it had previously been demonstrated in both cat and monkey (Mountcastle, 1957; Mountcastle & Powell, 1959) that cortical evoked responses could be elicited by contralateral joint rotation, it was not until more recently (Landgren & Silfvenius, 1969; Oscarsson & Rosen, 1963; Phillips, Powell, & Weisendanger, 1971) that such responses could be demonstrated following contralateral stimulation of both forelimb and hindlimb muscle afferents. The failure to establish such cortical projections had been used to argue against the contribution of muscle receptors to kinesthetic sensation.

Studies of cortical cytoarchitecture (Powell & Mountcastle, 1959) showed that primary somatosensory cortex (S 1) could be divided into four subdivisions, each having different functional properties. From anterior to posterior, these areas are 3a, 3b, 1, and 2 (Powell, 1977). While areas 3a and 3b receive a dense thalamic input, that to areas 1 and 2 is lighter and may represent collaterals from 3a and 3b afferents. Units in areas 3a and rostral 3b respond to electrical stimulation of both muscle and cutaneous nerves, while those in area 3b also respond to adequate cutaneous stimulation. Units in area 2 respond to joint rotation and to electrical stimulation of muscle nerves (Schwartz, Deeke, & Fredrickson, 1973), and units in area 1 have properties common to those in both areas 2 and 3 (Powell, 1977). Two adjacent areas to S 1 that also receive kinesthetic afferents are areas 5 and 4. Area 5 is posterior to S 1 and has a large population of units responding primarily to passive joint rotation on the contralateral side. Many units not responding to passive rotation will, in contrast, respond to active rotation on the contralateral side (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Area 4, which is primary motor cortex (M 1), contains units responding to joint rotation and, to a lesser extent, to muscle palpation and light touch (Lemon & Porter, 1976; Rosen & Asanuma, 1972). While it is most likely that kinesthetic sensibility is the result of complex cortical interactions, the nature of this interaction, the locus or loci, and even the necessary afferents, remain to be determined.

CHAPTER 3

GENERAL METHODS

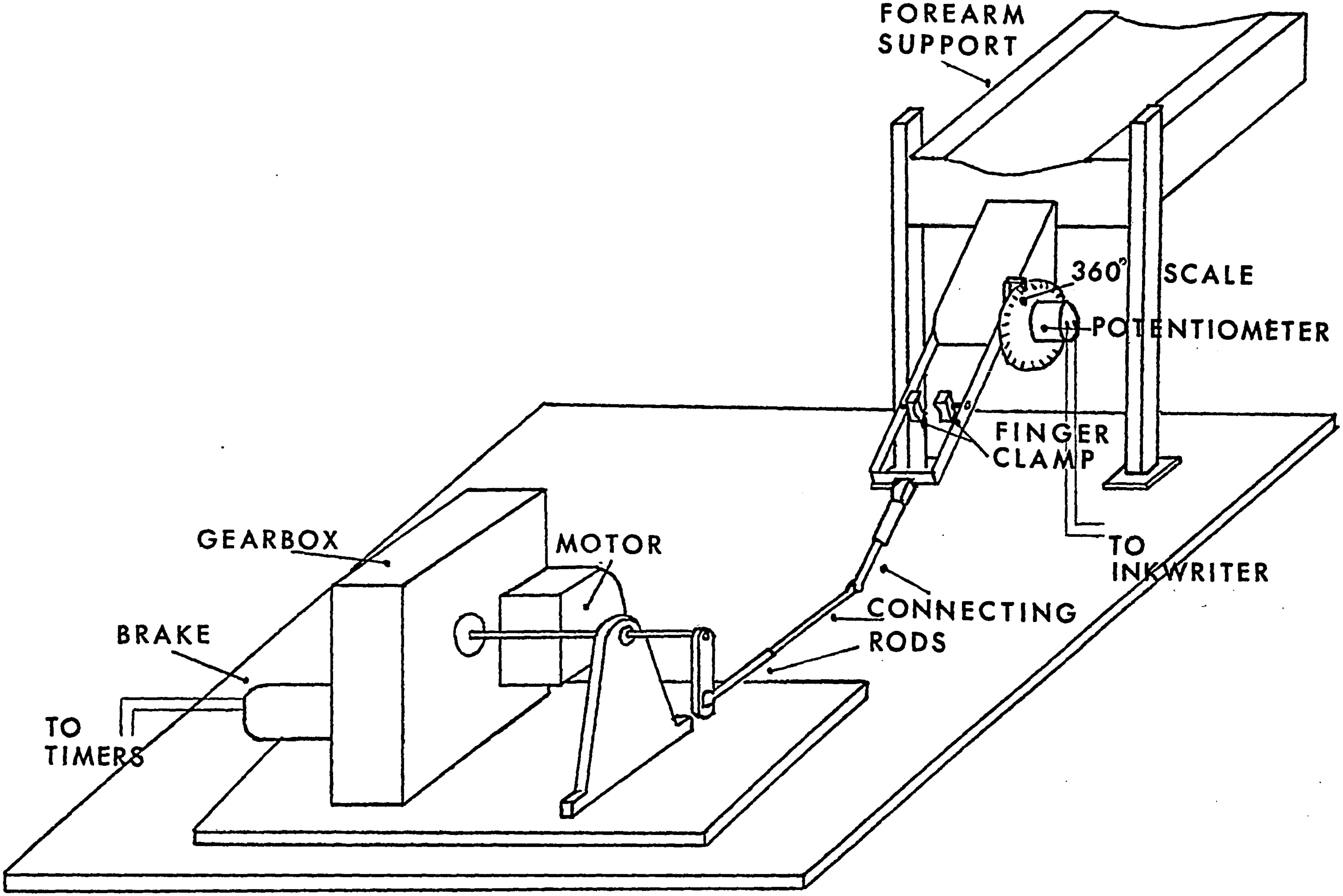
Subjects

The subjects were three graduate students and one postdoctoral student in the Department of Psychology at Queens College of The City University of New York. There were three females, ER, MG, and JB, and one male, RK, ranging in age from 24 to 37, and all were righthanded. They had all participated in previous psychophysical studies, but none had been tested for kinesthetic sensitivity. They were informed as to the purpose and design of the study, and each subject participated in the two main experiments. The subjects were paid at the rate of $ 2.50 per hour.

Apparatus

A system for the delivery of kinesthetic stimulation (see Fig. 1) was built around a multiple speed motor (Holtzer - Cabot CS - 147, 600 rpm, reversible synchronous motor, in conjunction with a Harvard Apparatus No. 600, multispeed transmission). A selector gear was used to engage any one of 12 possible speeds, and, in the neutral position, to disengage the output shaft of the motor. The part of the system that rotated, and was the source of the kinesthetic stimulus, was fitted with a padded, spring loaded finger clamp that, by exerting lateral pressures, secured the digit being tested. A pointer, mounted at one end of this moving arm, indicated angular displacement on a 360° scale. This scale, calibrated in one degree intervals, was mounted at the axis of rotation. Fitted through this axis was

Fig. 1 Diagram of the stimulus delivery system for kinesthetic stimulation.


FOREARM SUPPORT
360° SCALE
POTENTIOMETER
FINGER CLAMP
GEARBOX
MOTOR
TO INKWRITER
CONNECTING RODS
BRAKE
TO TIMERS

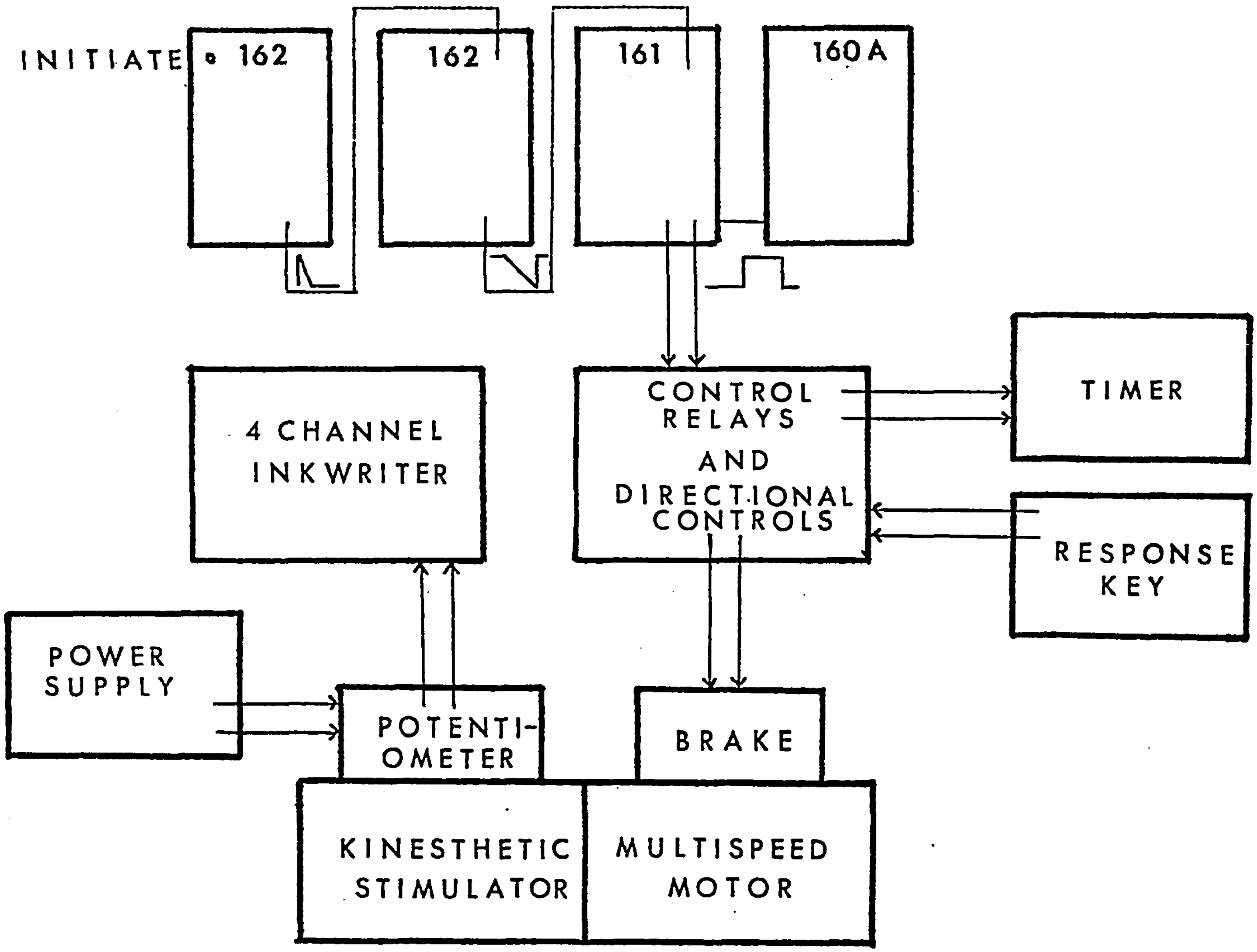
the shaft of a potentiometer (TIC Model S262 continuous turn, servomount, 3.5k ohms, .5% linearity). For the periodic calibration of the system, a voltage from a regulated power supply (Hewlett Packard 6216A) was placed across the potentiometer, and the output was fed into an inkwriter (Grass Type 5D, four channel polygraph). The angular displacement of the arm resulted in a proportional deflection of the inkwriter.

The overall timing control for the stimulus (see Fig. 2) was provided by a waveform generator (Tektronix Type 162). This unit triggered a second waveform generator (Tektronix Type 162) which, in turn, provided the timebase for a pulse generator (Tektronix Type 161). The pulse generator, acting through a series of relays, initiated three events. First it deenergized an electromagnetic brake (Simplatrol Model CB - 50 clutch brake) which was externally mounted around the extended motor gearshaft, and which, when energized, prevented any rotational motion in the system. Next it activated the moving arm at a preset velocity, in a given direction (up or down), for up to 10 seconds duration. Lastly, it activated a timer (Standard Electric) that read to .01 seconds. The subject responded to the detection of movement by pressing a telegraph key. This action energized the brake, terminated the kinesthetic stimulus, and stopped the timer, so that response time could be recorded. If the subject did not detect movement within 10 seconds of stimulus onset, the offset of the timing pulse resulted in energizing the brake, terminating the stimulus, and stopping the timer.

Procedure

Kinesthetic sensitivity was assessed at the proximal interphalangeal joint of

Fig. 2 Block diagram of the complete system for stimulus delivery, response measurement, and calibration.


INITIATE
162
162
161
160A
4 CHANNEL INKWRITER
CONTROL RELAYS AND DIRECTIONAL CONTROLS
TIMER
RESPONSE KEY
POWER SUPPLY
POTENTIOMETER
BRAKE
KINESTHETIC STIMULATOR
MULTISPEED MOTOR

the right index finger. The subject was seated beside and slightly behind the stimulus delivery system, and he either wore a blindfold or averted his eyes from the equipment. The right forearm was placed perpendicular to the upper arm, and was supported by a horizontal wooden armrest, with a shallow trough running down the middle. The hand was ventroflexed at an angle of about 45°, and the palm and fingers were placed upon another wooden rest and were secured with an elastic bandage. The right index finger was extended and was strapped down between the metacarpophalangeal and the proximal interphalangeal joints. The clamp was then applied to the lateral surfaces of the finger between the proximal and distal interphalangeal joints. The forces securing the joint were applied perpendicular to the plane of movement, permitting the finger to pivot freely around the proximal interphalangeal joint.

CHAPTER 4

EXPERIMENT 1

Procedure

Each subject participated in 12 test sessions that were blocked into 3 series of 4 sessions each. Within each series, the starting position of the joint was held constant at either 15°, 25°, or 35° from the vertical. The sequence of starting positions was assigned to each subject in a quasi-random manner. The kinesthetic stimuli consisted of all combinations of seven velocities (.15, .30, .80, 1.5, 3.0, 6.2, and 11.0 deg./ sec.) and two directions (up, down). The psychophysical method employed was a combination of the methods of adjustment and constant stimuli in which the duration of each velocity - direction combination, was increased to a maximum of 10 seconds. A single session consisted of 84 trials given in 4 blocks of 21 trials each. The stimuli were randomly presented, and within the 10 stimuli at each of the seven velocities, there were equal numbers of upward and downward movements. The 14 remaining trials were catch trials in which the gears were placed in the neutral position, the motor was activated for 10 seconds, and no movement occurred. The subject was instructed that, upon detecting movement, he was to press the telegraph key situated under his left hand. A verbal response, identifying the direction of movement, was also to be given. To initiate a trial, the experimenter gave a verbal ready signal and the subject responded verbally when ready. This foreperiod was of 3 to 10 seconds duration. Following the detection of movement, or the timing out of the stimulus pulse, the experimenter recorded the response time and direction. Feedback as to the direction and / or velocity of the stimulus was given following an undetected movement, an incorrect identification of direction, a successful detection of a catch trial, or a false alarm. The inter-trial interval was approximately 20 seconds; the interblock interval, from 3 to 4 minutes.

Data Analysis

The assessment of kinesthetic sensitivity was accomplished via two measures, percent correct detection and response time. Response time (in seconds) is defined as the sum of two temporal components: the duration of joint rotation necessary for movement detection, and the reaction time of the keypress response.

Each dependent measure was plotted as a function of log angular velocity (see Table 2), for each direction and starting position. Threshold angular velocities (50% correct detection) were then determined by graphic interpolation. The statistical significance of the effects of velocity, direction, and starting position on each dependent measure was assessed via separate 7 x 2 x 3 analyses of variance, with repeated measures on each factor, performed on the group data. Post hoc tests were then conducted on each significant main effect and interaction.

Results and Discussion

Fig. 3 presents percent correct detection as a function of log angular velocity (in deg./ sec.)[1] at a starting position of 15° for each subject.[2] The solid line represents upward movements; the broken line, downward movements. Figs. 4 and 5 present, in a similar manner, the functions obtained at starting positions of 25°

TABLE 2

Angular Velocities Used in Experiments 1 and 2 and Their Logarithmic Equivalents

	Angular Velocity (deg. / sec.)	Logarithm	
	11.0	1.04	
	6.2	.79	
	3.0	.48	
Experiment 1	1.5	.18	
	.8	-.10	
	.3	-.52	Experiment 2
	.15	-.82	
	.10	-1.0	
	.05	-1.3	

Fig. 3 Percent correct detection as a function of log angular velocity (deg./ sec.), for both upward (solid line) and downward (broken line) movements, at a starting position of 15° for subjects ER, RK, MG, and JB.

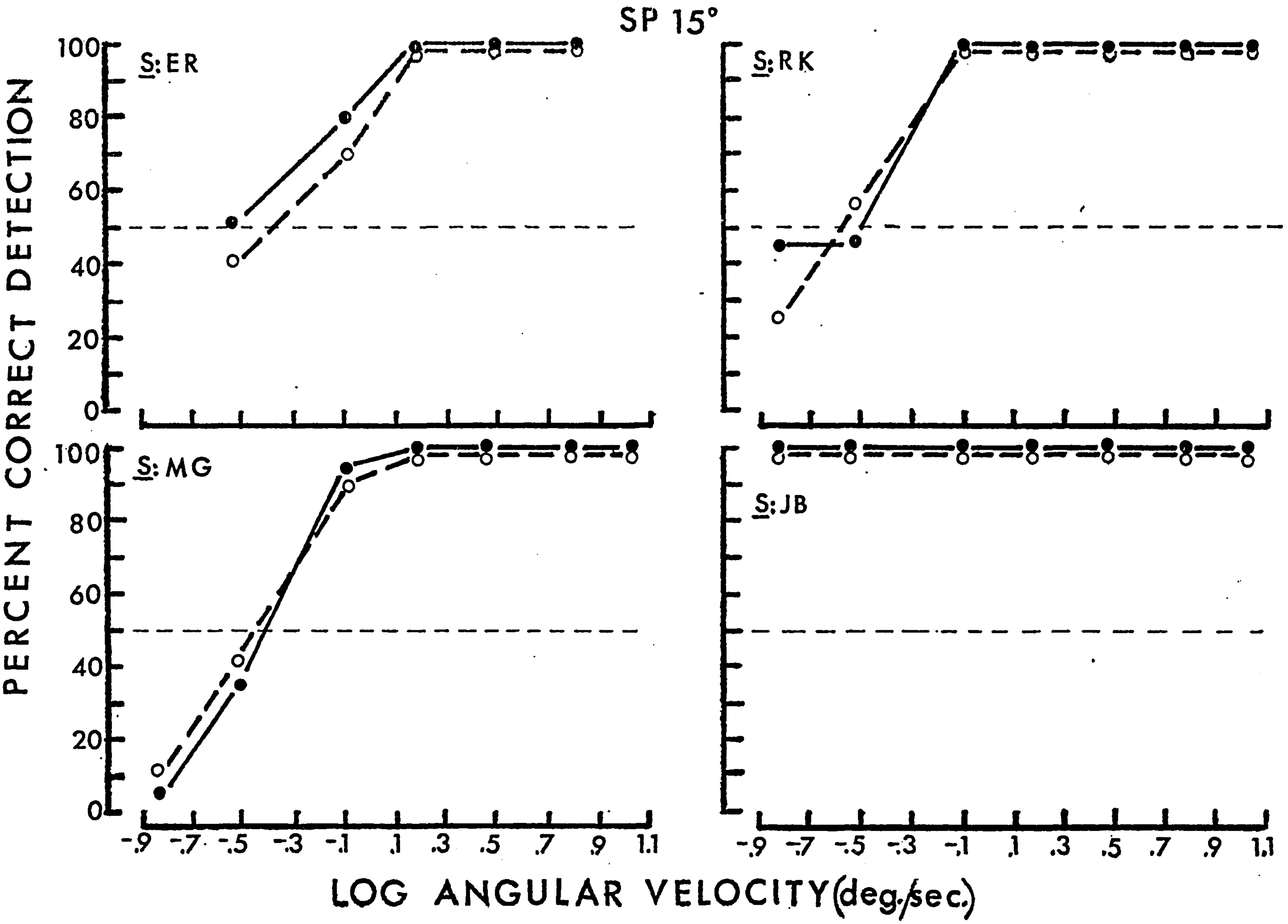

SP 15°
S: ER
S: RK
S: MG
S: JB
PERCENT CORRECT DETECTION
0
20
40
60
80
100
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY(deg/sec)

Fig. 4 Percent correct detection as a function of log angular velocity (deg./ sec.), for both upward (solid line) and downward (broken line) movements, at a starting position of 25° for subjects ER, RK, MG, and JB.

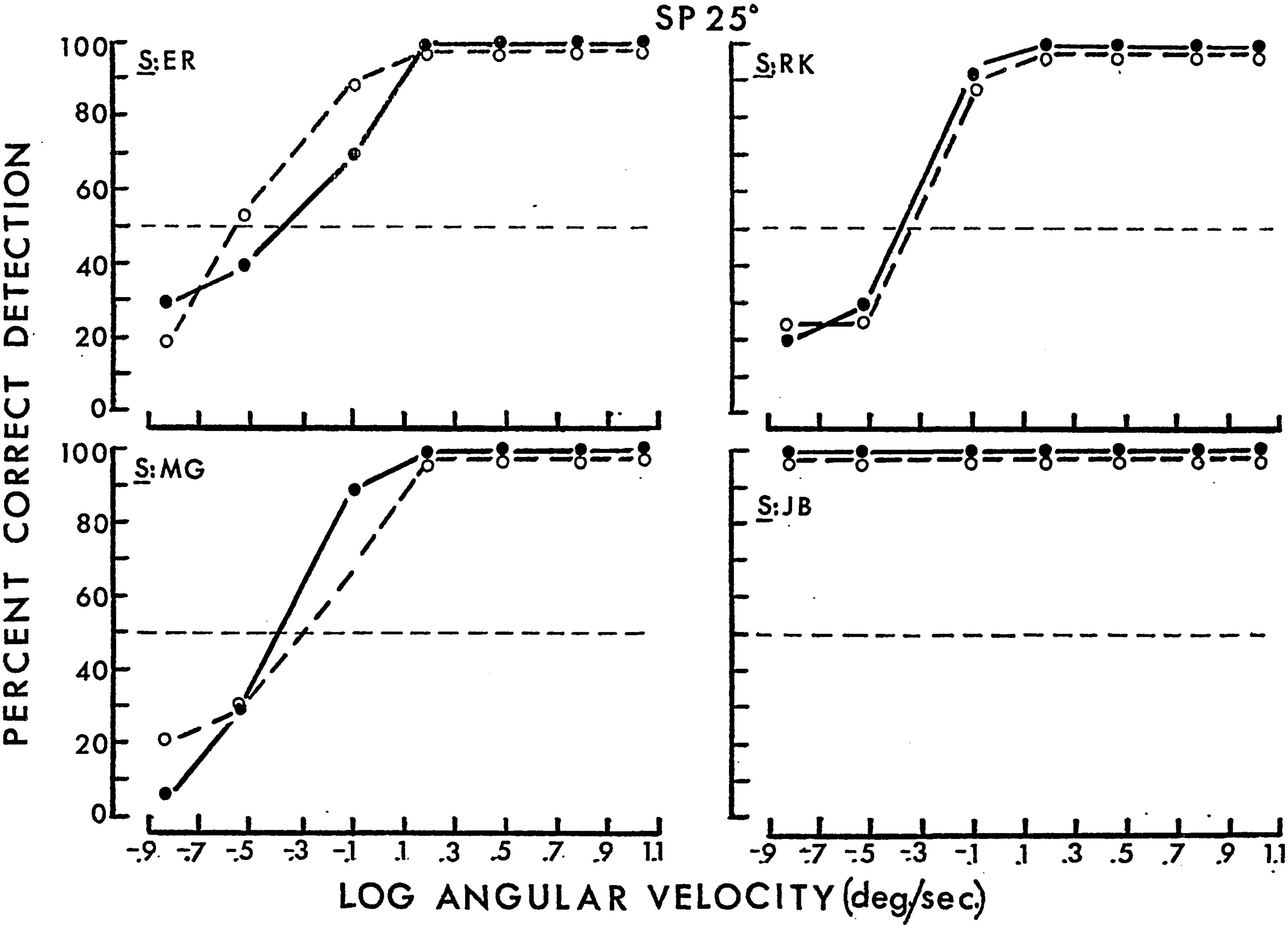
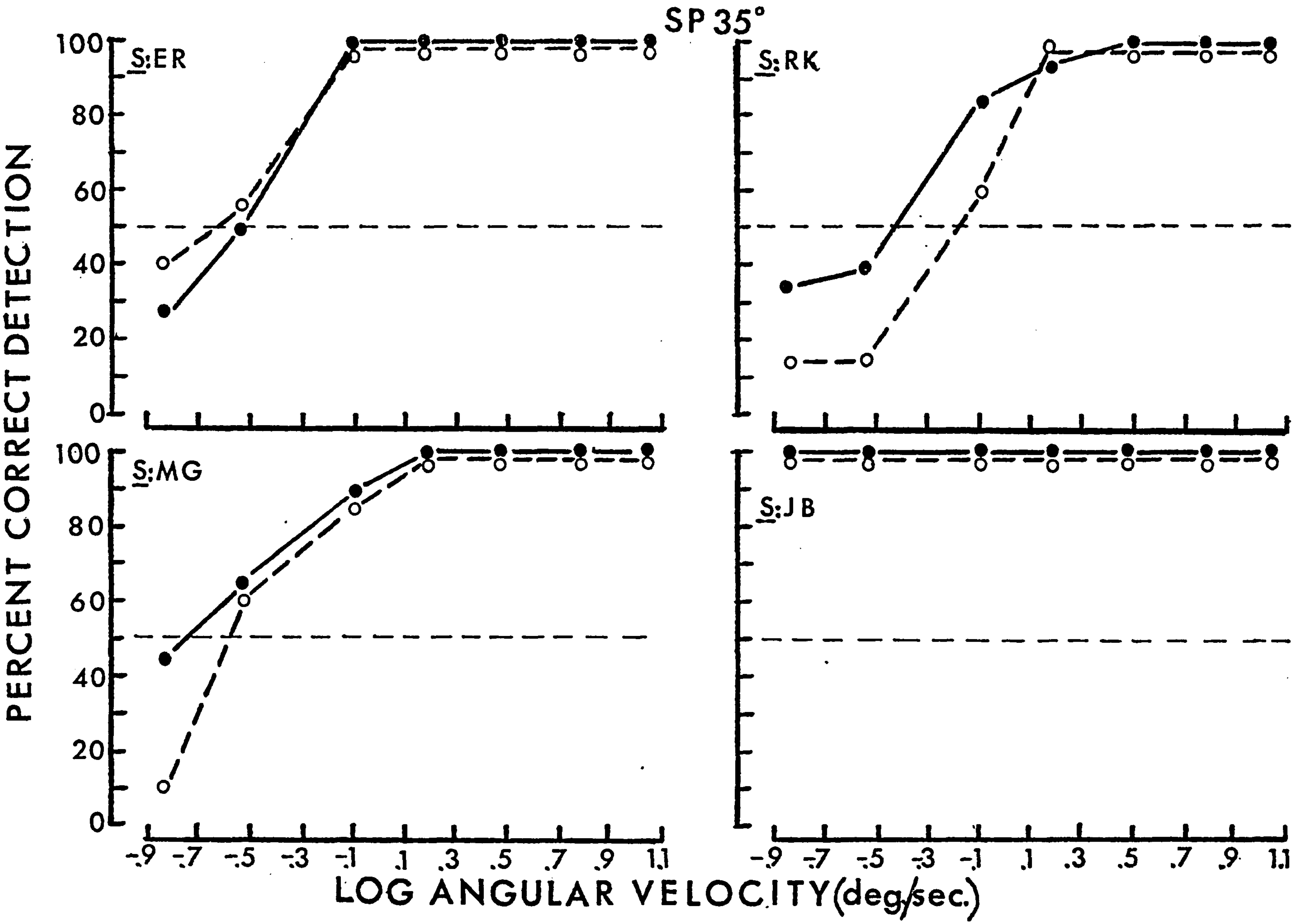

SP 25°
S: ER
S: RK
S: MG
S: JB
PERCENT CORRECT DETECTION
0
20
40
60
80
100
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec.)

Fig. 5 Percent correct detection as a function of log angular velocity (deg./ sec.), for both upward (solid line) and downward (broken line) movements, at a starting position of 35° for subjects ER, RK, MG, and JB.


SP 35°
S:ER
S:RK
S:MG
S:JB
PERCENT CORRECT DETECTION
0
20
40
60
80
100
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec.)

and 35°, respectively.

On visual inspection it can be seen that while subjects ER, RK, and MG generated monotonically increasing psychometric functions, those generated by subject JB demonstrated a 100% detection level across all velocities, directions, and starting positions. Because of this atypically high degree of sensitivity, it was decided to exclude subject JB's data from any subsequent functional analyses, and to place them in a separate appendix (Appendix 2). All statistical analyses were conducted both with and without these data but the significance of only a single interaction changed.[3] Therefore, only the results of the three subject analyses are reported.

For subjects ER, RK, and MG, detection was an increasing function of log angular velocity, reaching 100% at an angular velocity of 1.5°/ sec. (log angular velocity = .18). With the exception of a single miss by subject RK, each subject maintained a 100% detection level for all angular velocities beyond 1.5°/ sec.

Neither the direction of movement nor the starting position of the joint appears to have appreciably influenced detection rate. Inspection of each pair of directional functions reveal that their slopes are nearly parallel, and the differences between them are small and nonsystematic. A similar description applies to the comparisons made across starting positions.

Overall detection rates per starting position and per direction of movement are presented in Table 3, per subject. The overall measure of group performance across each starting position and direction of movement shows a 79.9% detection rate, with the individual overall rates ranging from 78.0 to 83.1%. These similarities in performance are also reflected in the threshold (50% correct detection) angular

TABLE 3

Percent Correct Detection Per Direction and Starting Position Per Subject.

Subject	Direction	Starting Position 15	25	35	Overall
	Up	86.0	79.2	82.1	83.1
ER	Down	82.0	84.2	85.0	
	Difference	4.0	-5.0	-2.9	
	Up	84.3	77.8	79.3	78.6
RK	Down	82.8	77.1	70.0	
	Difference	1.5	.7	9.3	
	Up	76.4	75.0	85.7	78.0
MG	Down	77.1	74.3	79.3	
	Difference	-.7	.7	6.4	
	Up	82.2	77.3	82.4	79.9
GROUP	Down	80.6	78.5	78.1	
	Difference	1.6	-1.2	4.3	

velocities calculated by graphic interpolation per subject, per condition (see Table 4). The mean threshold velocity across all subjects and conditions is .37°/ sec., with the individual overall thresholds ranging from .33°/ sec. to .41°/ sec.

In order to evaluate the statistical significance of the effects of velocity, direction, and starting position on detection, two 7 x 2 x 3 analyses of variance, with repeated measures on each factor, were performed on the group data. Both percentages and arc sin transformations[4] of the percentages were used in the separate analyses. Because there were no differences in the significance of any main effect or interaction as a consequence of the separate analyses, only the latter findings are reported. The results indicated that while the main effect of velocity was significant, $\underline{F}$ (6, 12) = 213.86, $\underline{p} < .001$, the main effects of direction, $\underline{F}$ (1, 2) = .94, $\underline{p} > .05$, and starting position, $\underline{F}$ (2, 4) = .37, $\underline{p} > .05$, were not (see Table A1 - 1 in Appendix 1). Post hoc analyses using the Scheffe Test assessed the significance of the differences among the mean detection rates across levels of velocity and found that 9 of the 21 comparisons were significant ($p < .05$) (see Table A1 - 2). These differences were found primarily between the four highest velocities and the two lowest velocities. Thus, over the aforementioned range of starting positions, directions of movement, and angular velocities, percent correct detection as a measure of kinesthetic sensitivity was significantly influenced only by the latter.

Response Time

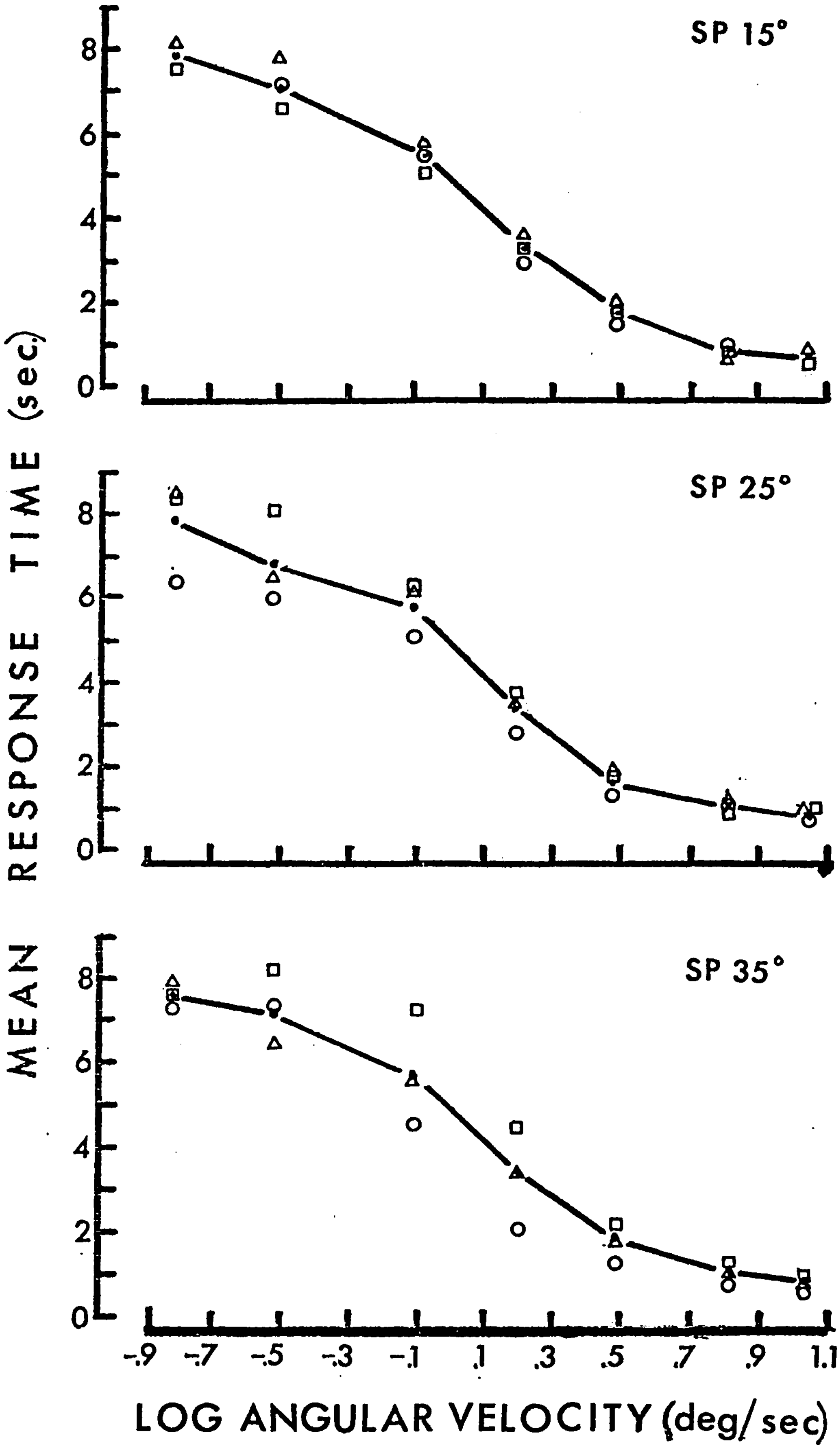
Response time (seconds) plotted as a function of log angular velocity (deg. / sec.) at starting positions of 15°, 25°, and 35°, is presented in Fig. 6 for the in-

TABLE 4

Threshold Angular Velocity (deg. / sec.) Per Direction and Starting Position, Per Subject.

		Starting Position			
Subject	Direction	15	25	35	Overall
ER	Up	.30	.42	.30	.33
	Down	.42	.26	.28	
	Difference	-.12	.16	.02	
RK	Up	.33	.41	.38	.41
	Down	.27	.44	.64	
	Difference	.06	-.03	-.26	
MG	Up	.39	.42	.18	.35
	Down	.38	.49	.26	
	Difference	.01	-.07	-.08	
GROUP	Up	.34	.42	.29	.37
	Down	.36	.40	.39	
	Difference	-.02	.02	-.10	

Fig. 6 Response time (sec.) as a function of log angular velocity (deg./ sec.) at starting positions of 15°, 25°, and 35° for the combined data of subjects ER (circle), RK (square), and MG (triangle). The function represents the mean of the individual data points, while the data points represent the mean response times for correct detections.

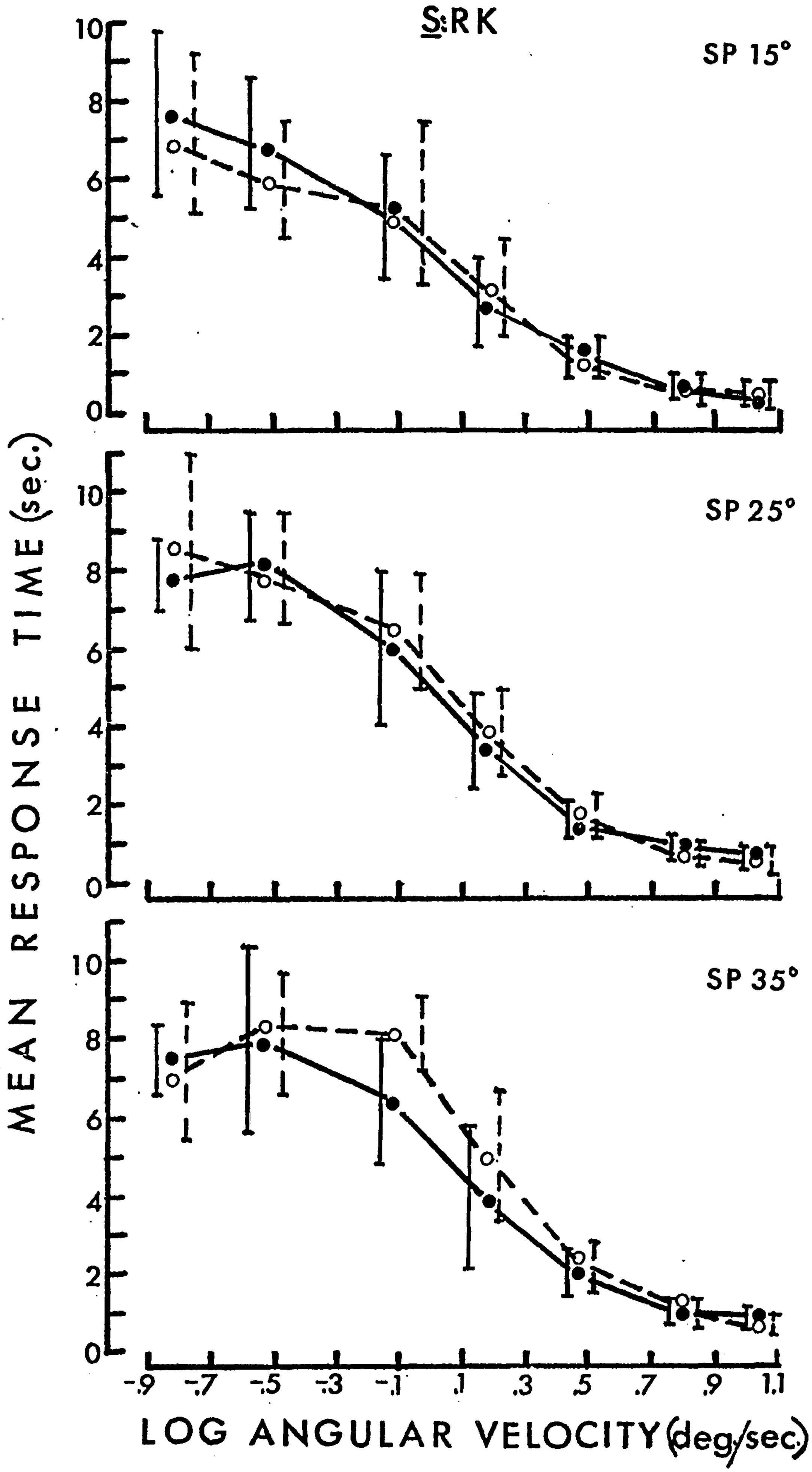

SP 15°
SP 25°
SP 35°
MEAN RESPONSE TIME (sec)
8
6
4
2
0
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec)

dividual and group data. Each data point represents mean response time for correct detections for each combination of subject and velocity. The line fitted through the data points connects the means of the mean response times. Fig. 7 presents the response time functions at starting positions of 15°, 25°, and 35°, generated by subject RK as representative of the individual functions. Response time (seconds) is plotted as a function of log angular velocity (deg./ sec.) for upward (solid line) and downward (broken line) movements. Each data point represents the mean response times for each combination of velocity and direction. The variability measure around each data point is $\pm$ 1 SD. Figs. A1 - 1 and A1 - 2 present, in the same manner, the data for subjects ER and MG, respectively.

The relationships obtained indicate that, in general, response time is a decreasing function of log angular velocity. However, exceptions sometimes occurred at velocities of .15°/ sec. and .30°/ sec. (log angular velocity -.82 and -.52, respectively), where the lower angular velocity produced a shorter mean response time than did the higher angular velocity. In general, however, the functions generated by each subject appear to be negatively accelerating, decreasing functions. Comparison across the subjects shows that the variability among them is greater at the lower velocities, while at the higher velocities they are quite similar, appearing to asymptote at the same level. On further inspection there appear to have been no pronounced effects on either the form of the function or in the actual response times attributable to changes in either direction or starting position.

In contrast to the functions generated by subjects ER, RK, and MG, those generated by subject JB were almost linear, having a sligh negative slope (see Fig.

Fig. 7 Response time (sec.) as a function of log angular velocity (deg./ sec.) for both upward (solid line) and downward (broken line) movements at starting positions of 15°, 25°, and 35° for subject RK. Each data point represents a mean for correct detections. The variability measure is ± 1 SD.


S:RK
SP 15°
SP 25°
SP 35°
MEAN RESPONSE TIME (sec.)
0
2
4
6
8
10
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec)

A2 - 1). While her response times to the higher velocity stimuli were similar to those of the other subjects, her response times to the lower velocity stimuli were approximately twice as fast. However, as was true for the other subjects, neither starting position nor direction of movement had any demonstrable effects on the form of the function.

One interpretation of the data generated by subjects ER, RK, and MG, is that as angular velocity increased, the subject's response requirements changed. At velocities below 1.5°/ sec., the primary emphasis appeared to be on stimulus detection. The generally lower detection rates and the more variable response times attest to the difficulty of the task. In contrast, at velocities of 1.5°/ sec. and higher, where the detection rate was almost 100% and the response times were short, with little variability, the emphasis appeared to be on how quickly the response could be made, making the situation analagous to that in a simple reaction time experiment. However, while the mean response time functions (see Fig. 6) approach an asymptote at about 770 msec., this value is anywhere from 5 to 6 times longer than the generally accepted values for kinesthetic reaction time (Chemikoff & Taylor, 1952; Vince, 1948). Possible reasons for this disparity include differences in stimulus production methods, the response mode, and the joints tested.

In order to assess the statistical significance of the effects of velocity, direction, and starting position on response time, a 7 x 2 x 3 analysis of variance, with repeated measures on each factor, was performed on the group data. The results indicated that while the main effect of velocity was significant, F (6, 12) = 297.96, $p < .001$, the main effects of direction, F (1, 2) = .02, $p > .05$, and starting position, F (2, 4)

= .02, $p > .05$, were not (see Table A1 - 3). A post hoc analysis using the Scheffe Test assessed the significance of the differences among the mean response times across levels of velocity and found that 13 of the 21 comparisons were significant ($p < .05$) (see Table A1 - 4). These differences were primarily between the response times at the 3 highest velocities and the 4 lowest velocities.

Angular Displacement

An attempt was made to derive an angular displacement measure of kinesthetic sensitivity. It was believed that this could be accomplished by multiplying the previously obtained response times (sec.) by the angular velocities (deg./ sec.) at which they were obtained. These displacements, like correct detections and response time would then be plotted as a function of log angular velocity. However, the relationship obtained by this procedure can only be described as an artifact because it is not valid to multiply a dependent variable by an independent variable and then plot the product as a function of that same independent variable.

False Alarms

Table 5 presents the individual false alarm rates per starting position, and per direction of movement. The mean false alarm rate was 16.2%, while the individual overall rates ranged from 13.7% to 20%. Chi square tests were performed on the false alarm rates across starting position, and on the percentages of upward and downward movements attributed to the false alarms, per subject. None of the individual false alarm rates were significantly affected by starting position, and only subject MG showed a significant bias in the directions attributed to the false alarms.

TABLE 5

Percent False Alarms Per Starting Position, the Percentage Ratio Between the Directions Attributed, and the Chi Square Values Across Starting Position and Direction, Per Subject.

						Chi Square	
Subject	15	25	35	Overall False Alarm Rate	Ratio of Up to Down	Starting Position	Direction
ER	19.6	20.8	19.6	20	43.8 : 53.1	.97 n.s.	.32 n.s.
RK	17.8	14.3	12.5	14.9	48.0 : 52.0	.66 n.s.	.18 n.s.
MG	10.7	17.8	12.5	13.7	21.7 : 78.3	1.14 n.s.	18.9 ($p < .001$)
			GROUP	16.2			

n.s. = not significant

However, this bias influenced neither the detection of upward and downward movements, nor the identification of their direction.

FOOTNOTES

1. Log angular velocity, rather than angular velocity, was used in order to expand and more clearly display those portions of the function representing angular velocities of less than one degree per second.

2. Subject ER was the first tested, and her initial data came from a starting position of 15°. Based upon visual inspection of the functions obtained for each of the dependent measures, it was decided that, in order to define these relationships more completely, the range of velocities should be extended in both directions. Thus, velocities of .15°/sec. and 11.0°/sec. were added. ER was not presented with these velocities until the third session of her second experimental condition (starting position of 25°). Each of the other subjects received the entire range of velocities.

3. The velocity by direction interaction in the three subject analysis of variance for response time was not significant, $F(6, 12) = 2.92$, $p > .05$, while that in the four subject analysis of variance, $F(6, 18) = 2.66$, $p < .05$, was significant.

4. An arc sin transformation ($2 \arcsin \sqrt{X}$, where X is the proportion of correct responses) was used to normalize the data and stabilize the error variance. Where proportions of 100% or 0% were obtained, Batlett's correction factors were substituted for X ($1 - 1/4n$ or $1/4n$, respectively).

CHAPTER 5

EXPERIMENT 2

The purpose of this study was to obtain 1) a measure of passive movement sensitivity not confounded by the subject's response mode, 2) a true indicator of angular displacement sensitivity, and a more accurate determination of the lower limits of passive movement sensitivity than was seen in Experiment 1. The first two objectives were accomplished by giving the subjects discrete rather than continuous stimuli, e.g., an upward movement at a velocity of .30°/ sec. for four seconds. Subjects were then required to give a verbal response as to both detectability and direction of the stimulus, within three seconds of the trial's termination. The third objective was accomplished by lowering the range of stimulus angular velocities to between .05°/ sec. and 1.5°/ sec., in contrast with the range of .15°/ sec. to 11.0°/ sec. used in Experiment 1.

Procedure

Experiment 2 used the same subjects and apparatus as in Experiment 1. Here, however, the starting position of the joint was kept constant at 25 from the vertical, and the subjects received stimuli consisting of all combinations of six velocities (.05, .10, .15, .30, .80, and 1.5°/ sec.), six durations (1, 2, 4, 6, 8, and 10 seconds), and two directions (up, down). The psychophysical procedure employed was the method of constant stimuli.

Each subject participated in four test sessions. A single session consisted of 108 trials presented in 4 blocks of 27 trials each. Catch trials with the same durations as the true movements (1, 2, 4, 6, 8, and 10 seconds) were randomly presented. While the total percentage of catch trials was 15.7%, this value varied slightly from session to session.

To initiate a trial, the experimenter gave a verbal ready signal to which the subject responded in kind, when ready. This foreperiod was typically of 3 to 10 seconds duration. Feedback as to the direction and / or velocity of the stimulus was given following an undetected movement, an incorrect identification of direction, a successful detection of a catch trial, or a false alarm. The intertrial interval was approximately 20 seconds; the interblock interval from 3 to 4 minutes.

Data Analysis

Percent correct detection was initially plotted as a function of both log angular velocity (deg./ sec.) and of stimulus duration (sec.). The statistical significance of the effects of velocity, duration, and direction on percent correct detection was assessed via two 6 x 6 x 2 analyses of variance, with repeated measures on each factor, performed on the group data. As in Experiment 1, the analyses used both percentages and arc sin transformations of the percentages. Becuase there were no differences in the significance of any main effect or interaction resulting from the two analyses, only the findings of the latter are reported. Post hoc tests were then conducted on the significant main effects and interactions.

Next, each stimulus velocity (deg./ sec.) was multiplied by each stimulus duration (sec.), to obtain a range of angular displacements (deg.). Percent correct detection was then plotted as a function of log angular displacement. In order to obtain a best fit function, each percentage between 10% and 90% was converted to a Z value, and a least squares solution was calculated. The obtained Z values were converted back into percentages and then plotted, and chi square tests were performed to assess the goodness of fit. Angular displacement thresholds (50% correct detection) were then obtained for each subject.

Results and Discussion

The results of this experiment appear to demonstrate the relationship between percent correct detection and angular displacement. When duration is held constant and velocity is increased, or the reverse, the effect is to increase the angular displacement. In general, the functions generated show that percent correct detection is an increasing function of log angular displacement. An additional finding, not in the results of Experiment 1, is that there was a significant directional difference favoring the detection of upward movements. While the difference between the upward vs. downward detection rates was only 4.8%, the direction of the difference was consistent across subjects and was significant at, $\underline{F}$ (1, 2) = 63.2, $\underline{p} < .001$.

Percent correct detection as a function of log angular velocity (deg./ sec.) per stimulus duration (sec.) is plotted in Fig. 8 for subjects ER, RK, and MG. Typically, when stimulus duration was kept constant, percent correct detection increased as a function of log angular velocity. As stimulus duration was increased, both the slopes of the functions and the detection rates increased. As a consequence, there was a continuous decrease in the threshold angular velocities (50% correct detection).

Percent correct detection as a function of stimulus duration (sec.) per angular velocity (deg./ sec.) is plotted in Fig. 9 for subjects ER, RK, and MG. In general,

Fig. 8 Percent correct detection as a function of log angular velocity (deg./ sec.) for movements of one second (open circle, dotted line), two seconds (open suare, broken line), four seconds (open triangle, solid line), six seconds (filled circle, dotted line), eight seconds (filled square, broken line), and ten seconds (filled triangle, solid line), for subjects ER, RK, and MG.

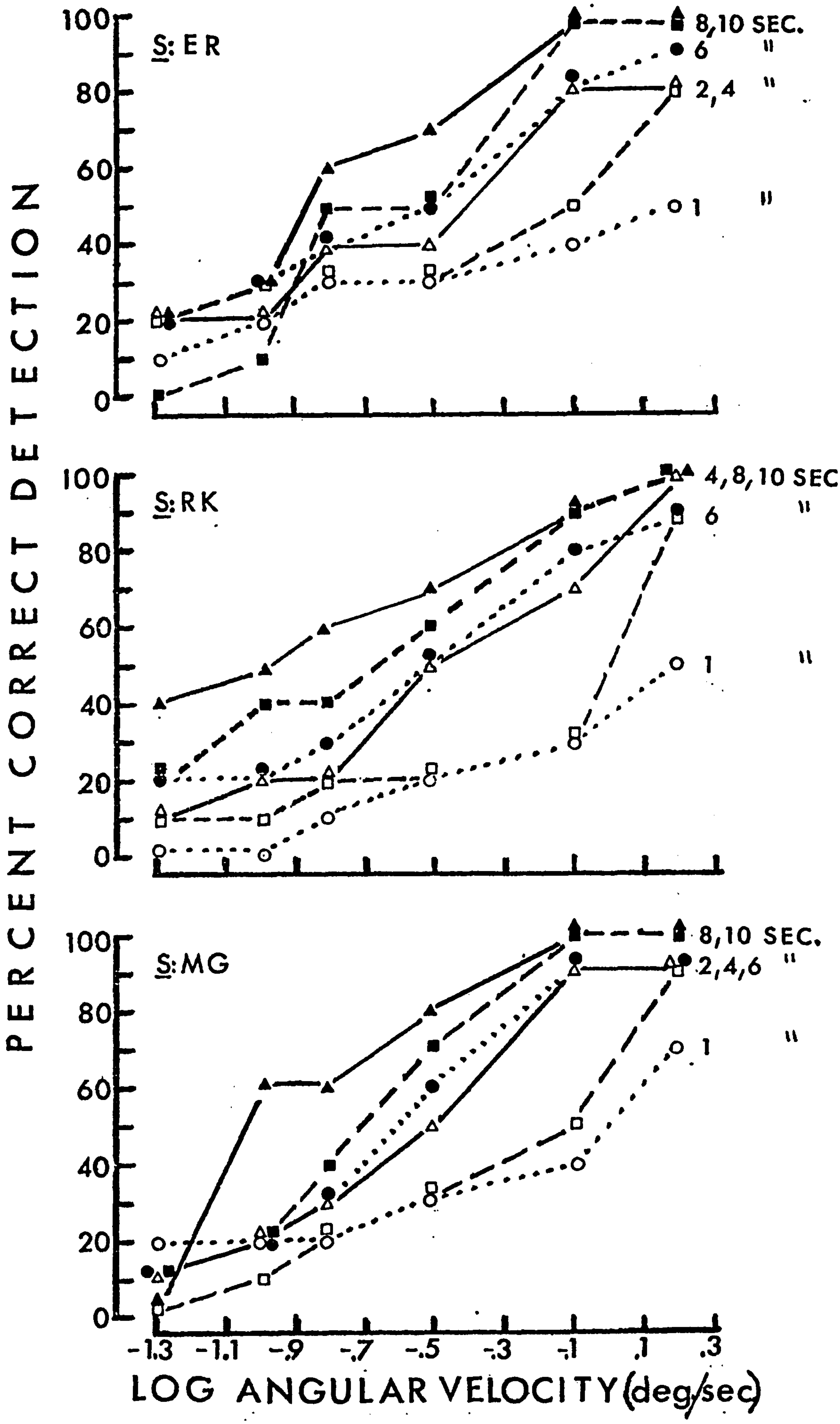
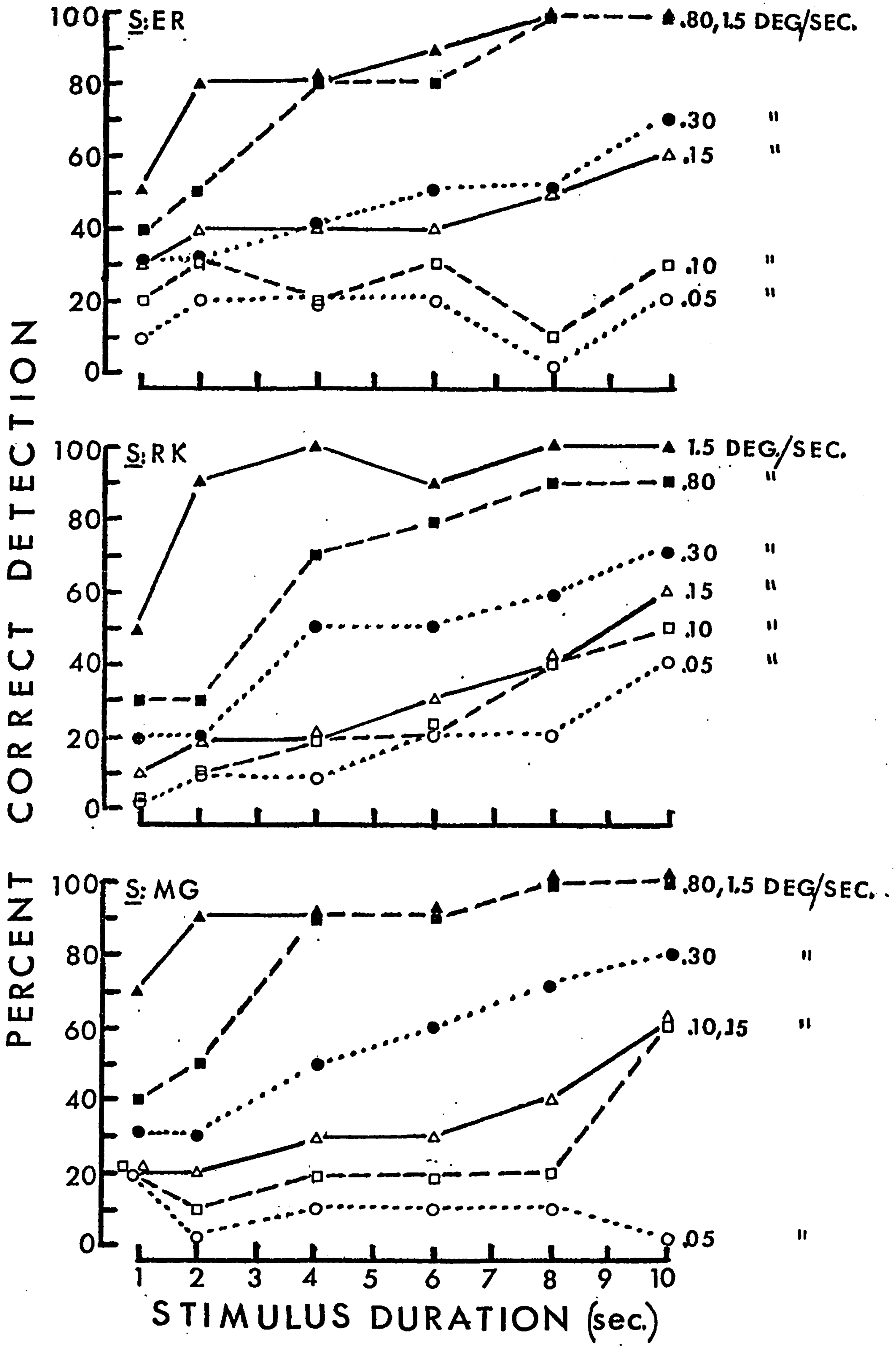

PERCENT CORRECT DETECTION
S: ER
S: RK
S: MG
0
20
40
60
80
100
8,10 SEC.
6 "
2,4 "
1 "
4,8,10 SEC.
6 "
1 "
8,10 SEC.
2,4,6 "
1 "
-1.3
-1.1
-.9
-.7
-.5
-.3
-.1
.1
.3
LOG ANGULAR VELOCITY (deg/sec)

Fig. 9 Percent correct detection as a function of stimulus duration (sec.) for movements at .05°/ sec. (open circle, dotted line), .10°/ sec. (open square, broken line), .15°/ sec. (open triangle, solid line), .30°/ sec. (filled circle, dotted line), .80°/ sec. (filled square, broken line), and 1.5°/ sec. (filled triangle, solid line) for subjects ER, RK, and MG.


PERCENT CORRECT DETECTION
S: ER
S: RK
S: MG
0
20
40
60
80
100
.80, 1.5 DEG/SEC.
.30 "
.15 "
.10 "
.05 "
1.5 DEG./SEC.
.80 "
.10, .15 "
1
2
3
4
5
6
7
8
9
10
STIMULUS DURATION (sec.)

when angular velocity was kept constant, percent correct detection increased as a function of stimulus duration. As velocity was increased, both the slopes of the functions and the detection rates increased, but much more gradually than when duration was increased (see Fig. 8). While subjects RK and MG failed to reach threshold (50% correct detection) with stimuli presented at a velocity of .05°/ sec., subject ER failed to reach threshold with stimulus velocities of both .05°/ sec. and .10°/ sec.

The individual detection rates per direction of movement are presented in Table 6, per subject. The measure of group performance indicates a 46.7% detection rate, with individual overall rates of 47.2%, 44.7%, and 48.0%, for subjects ER, RK, and MG, respectively. This is a marked decrease in sensitivity from the 79.9% detection rate in Experiment 1, reflecting the decrease in the range of stimulus velocities presented here. The consistent difference in the detection rates for upward vs. downward movements may also be seen.

Percent correct detection is plotted as a function of log angular displacement in Fig. 10 for subjects ER, RK, and MG, respectively. The range of angular displacements was obtained by multiplying each combination of angular velocity and stimulus duration. These products may be seen in Table 7. Multiple data points at the same angular displacement indicate that two or more velocity - duration combinations yielded the same displacement. Subscripts for the data points refer to the column - row entries in Table 7. While the relationship between percent correct detection and log angular displacement is a monotonically increasing one, there are some individual differences. The data generated by subject RK fall rather smoothly

TABLE 6

Percent Correct Detections of Upward and Downward Movements, Per Subject.

Subject	Direction of Movement		Percent Difference
	Up	Down	
ER	49.4	45.0	4.4
RK	47.2	42.2	5.0
MG	50.1	46.1	4.0
GROUP	48.9	44.4	4.5

Fig. 10 Percent correct detection as a function of log angular displacement (deg.) for subjects ER, RK, and MG. The subscripts for each data point represent the velocity - duration products indicated in Table 7. Multiple data points at a given displacement indicate that two or more velocity - duration combinations yielded the same product.

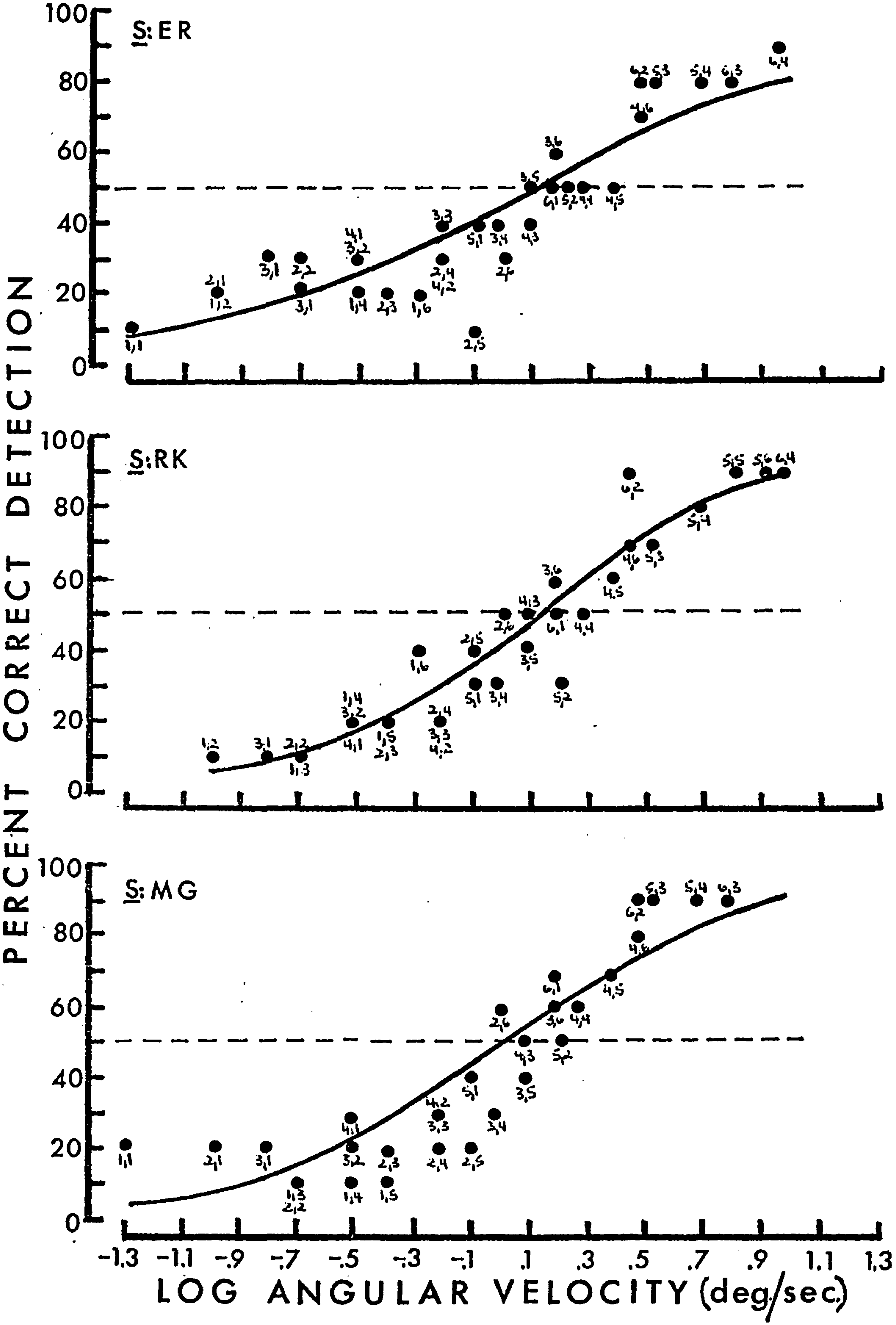

S: ER
S: RK
S: MG
PERCENT CORRECT DETECTION
0
20
40
60
80
100
LOG ANGULAR VELOCITY (deg/sec)
-1.3
-1.1
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
1.3

TABLE 7

The Angular Displacements (deg.) Obtained From Each Combination of Duration and Velocity.

Duration (seconds)	Velocity (deg. / sec.) .05	.10	.15	.30	.80	1.5
1	.05	.10	.15	.30	.80	1.5
2	.10	.20	.30	.60	1.60	3.0
4	.20	.40	.60	1.20	3.20	6.0
6	.30	.60	.90	1.80	4.80	9.0
8	.40	.80	1.20	2.40	6.40	12.0
10	.50	1.00	1.50	3.00	8.00	15.0

along a log normal ogive, while the data generated by subject MG, and to a lesser degree, ER, are negatively skewed and more scattered at the lower end. Chi square tests performed on the least squares solutions indicated that these best fit curves are acceptable at the .05 level of significance. The threshold angular displacements (50% correct detection) obtained for subjects ER, RK, and MG, are 1.20°, 1.32°, and 1.00°, respectively. Another indication of the greater sensitivity of subject JB is the angular displacement threshold of .07° obtained under the same conditions (see Fig. A2 - 4).

The results of the analysis of variance indicated that the main effects of velocity, $\underline{F}(5, 10) = 93.6$, $\underline{p} < .001$, duration, $\underline{F}(5, 10) = 29.3$, $\underline{p} < .001$, and direction, $\underline{F}(1, 2) = 63.2$, $\underline{p} < .001$, as well as the velocity by duration interaction, $\underline{F}(25, 50) = 4.40$, $\underline{p} < .001$, were each significant (see Table A1 - 5). A post hoc analysis using a Scheffe Test assessed the significance of the differences among the mean detection rates across levels of both velocity and duration. The number of significant comparisons was 3 of 15 for velocity and 0 of 15 for duration. In the former, the differences were found between the detection rates at the two highest velocities (.80°/ sec. and 1.5°/ sec.) and the two lowest velocities (.05°/ sec. and .10°/ sec.) (see Table A1 - 6). The Scheffe Test for simple main effects on the velocity by duration interaction showed that detection was significantly influenced by the two highest velocities (.80°/ sec. and 1.5°/ sec.) across all durations, and by the four lower velocities (.05, .10, .15, and .30°/ sec.) at durations beyond four seconds (see Table A1 - 7).

False Alarms

The mean false alarm rate across all subjects and conditions was 22.7%, while the individual rates were 18.0%, 22.2%, and 27.8%, for subjects ER, RK, and MG, respectively (see Table 8). The ratio of upward to downward movements attributed to the false alarms typically favored one direction or the other, but chi square tests indicated that the difference was significant only for subject RK.

TABLE 8

Percent False Alarms, the Percentage Ratio Between the Directions Attributed, and the Chi Square Values Across Direction, Per Subject.

Subject	False Alarm Rate	Ratio of Up to Down[a]	Chi Square
ER	27.8	60 : 30	2.28 n.s.
RK	22.2	68.8 : 18.8	5.29 ($p<.025$)
MG	18.0	38.5 : 61.5	.76 n.s.
GROUP	22.7		

n.s. = not significant

[a] The percentages do not total 100% because some of the false alarms were reports of movement for which the direction was not identified.

CHAPTER 6

DISCUSSION

The results of the present study show that both measures of kinesthetic sensitivity evaluated--percent correct detection and response time--were significantly influenced by the angular velocity of the movement; percent correct detection as an increasing function, response time as a decreasing function. In addition, percent correct detection was also shown to be an increasing function of angular displacement. The direction of movement produced contradictory effects, showing no significance in Experiment 1 but a significant favoring of upward movements in Experiment 2. Starting position produced no significant differences. As discussed below, these findings are of significance with respect to previous psychophysical studies and also to the physiological mechanisms underlying kinesthetic sensitivity.

Comparisons to Prior Psychophysical Studies

At the outset it should be noted that, as a consequence of both the paucity of psychophysical studies and various methodological differences, it is sometimes difficult to generalize the present findings and make meaningful comparisons.

In comparison with earlier studies, the present investigation of passive movement sensitivity was accomplished via a system that provided precise control over angular velocity, stimulus duration, and movement direction, and that also allowed both angular displacement and temporal response measurements to be made with a degree of accuracy not previously used. Moreover, use of the proximal interphalangeal (PIP) joint of the index finger helped to simplify the manner in which the joint was secured, and minimized the directional cues produced by supporting and rotating the joint from below. Finally, two psychophysical procedures were used (a combined method of adjustment and constant stimuli, and the method of constant stimuli), with one presenting automatically timed presentations of movement (Experiment 2); the other using subject terminated movements (Experiment 1). In the latter procedure (but not the former) there is a confounding effect of reaction time. In all cases, performance and reliability were enhanced by using a warning signal and by permitting the subject to control foreperiod duration.

The increasing relationship between percent correct detection and log angular velocity found in both Experiments 1 and 2 (see Figs. 3 to 5, 8) is consistent with the results of several other studies (Cleghorn & Darcus, 1952; Gandevia & McCloskey, 1976; Winter, 1912). In addition, the functions presented in Figs. 9 and 8 demonstrate that percent correct detection increases either when the duration of a constant velocity stimulus is increased, or when the velocity of a constant duration stimulus is increased; the latter finding consistent with that of Gandevia and McCloskey (1976).

The threshold angular velocities (50% correct detection) determined in Experiment 1 were .33, .41, and .35 deg°/ sec. for subjects ER, RK, and MG, respectively, and represent the mean values across both direction and starting position. However, interpreting the magnitude of the thresholds is made difficult because only two other studies (Gandevia & McCloskey, 1976; Goldscheider, 1889) even assessed sensitivity at an IP joint, and because methodological differences prevent making direct comparisons. In one study (Goldscheider, 1889), the joint was rotated at a constant angular velocity in order to determine a threshold angular displacement. The present study, in contrast, used a range of angular velocities to determine a threshold angular velocity (50% correct detection). In the other study noted above (Gandevia & McCloskey, 1976), sensitivity was assessed at the distal IP joint, in contrast to the proximal IP joint examined in the present study. Although comparison of thresholds cannot be made because of methodological differences, comparison of group mean detection rates can be. In one of a series of experiments (Gandevia & McCloskey, 1976), angular velocity was varied (1°/ sec. to 10°/ sec.) over a fixed duration (1.2 sec.), making it analagous to the procedure used in the present Experiment 2. Detection rates of 30% and 60% (for angular velocities of 1°/ sec. and 2°/ sec., over 1.2 sec.) were reported, and those compare favorably with the rates of 36.7% and 56.6% for angular velocities of .80°/ sec. and 1.5°/ sec., over 1 sec., found in the present study. Considering that these two digital joints are functionally similar and immediately adjacent, it is not surprising that they should have similar sensitivities.

The increasing relationship between percent correct detection and log angular displacement is in agreement with the findings of several other studies (Cleghom & Darcus, 1952; Gandevia & McCloskey, 1976; Grigg, Finerman, & Riley, 1973). The angular displacement thresholds determined here were 1.20°, 1.32°, and 1.00°, for subjects ER, RK, and MG, respectively. However, because of procedural differences, it is again difficult to interpret the magnitude of these thresholds in the context of the previous studies at the IP joint (Gandevia & McCloskey, 1976; Goldscheider, 1889). In one of those studies (Goldscheider, 1889), an approximately constant velocity of 12.4°/ sec. to 12.8°/ sec. produced threshold displacements of .72° to 1.05°. While the threshold magnitudes are comparable, the angular velocities are not. Whereas Goldscheider used an approximately constant angular velocity, the present study used a much lower range of velocities, presenting them over a series of varying durations. The methodological differences between the present study and the Gandevia and McCloskey study prevent comparisons between either thresholds *or* detection rates.

While the preceding discussion has concerned itself with the effects of either angular velocity *or* angular displacement, these parameters along with stimulus duration are interdependent, and one cannot exist without the other. For this reason, it may be extremely difficult to determine which parameter is more important for the appreciation of passive movement. However, in the present study, both stimulus duration and angular velocity are seen to be positively correlated with angular displacement (see Figs. 8 and 9). As such, the magnitude of angular displacement is therefore the best single predictor of the appreciation of passive movement. While not directly addressing itself to this problem, one technique has succeeded in evaluating the effect of angular displacement, independent of angular velocity. Horch, Clark, and Burgess (1975) rotated the knee joint so slowly as to preclude any sensation of movement. Yet, they produced a sensation of altered position when a displacement of 2° to 4° had been attained. Such a technique could be used to determine " pure " displacement thresholds over the entire mobility range of any given joint, or to reassess the proximal - distal gradient of decreasing kinesthetic sensitivity (Goldscheider, 1889; Laidlaw & Hamilton, 1937b).

The effect of movement direction on detection rate produced contradictory results in Experiments 1 and 2, just as it has done in previous studies. The lack of a significant effect in Experiment 1 is consistent with the findings of Browne, Lee, and Ring (1954), Gandevia and McCloskey (1976), and Laidlaw and Hamilton (1937b), while the significant favoring of upward movements in Experiment 2 is in agreement with Goldscheider (1889). However, both present findings are in contrast to those of Cleghorn and Darcus (1952) and Winter (1912), who found a significant favoring of downward movements.

In this study, starting position of the joint had no significant effect on any of the dependent measures. This result is consistent with that of Goldscheider (1889) but in contradiction to Winter (1912) and to a preliminary finding by Cleghorn and Darcus (1952). A possible methodological factor in this lack of significance is that the range of starting positions investigated may have been too narrow. However, this range was determined by both the resting position of the hand and the mechanical limitations of the kinesthetic stimulator. A consideration of all of the aforementioned psychophysical findings, in the context of their underlying physiological mechanisms, will be undertaken in a later section.

While comparison of detection rates and threshold angular velocities and displacements indicates generally similar sensitivities among three subjects, it also indicates the superior sensitivity of subject JB and emphasizes the need to examine the possible reasons for these differences. Several previous studies (Browne, Lee, & Ring, 1954; Laidlaw & Hamilton, 1937b) noted a small number of individuals whose atypical performance was the result of markedly decreased sensitivity. In one study (Laidlaw & Hamilton, 1937b), the thresholds of a group of elderly subjects (ages 50 to 85) were observed to be several times higher, and more variable, than the thresholds of two groups of young adults (ages 17 to 35). These differences might have been expected, as deterioration of the joints with age is a common phenomenon (Kelley, 1971). Another study (Browne, Lee, & Ring, 1954) reported that 12% of its subjects had thresholds almost four times higher than the group average. However, while half of this atypical group would be considered clinically impaired, none was aware of any deficit. It is probable that passive movements occurring during normal activities are several times faster, and of greater magnitude, than those occurring under experimental conditions. It was also noted that those subjects had no impairment in the detection of active movements, and their passive movement thresholds could be brought into the normal range by active contraction of the appropriate muscles.

In the present study, subject JB, a 24 year old female, was the same age as subject RK, and while athletic, was no more athletic than either subjects ER or MG. JB did not wear a blindfold, but averted her eyes from the equipment, as did subjects ER and MG. To test the possibility that she used visual cues, she was blindfolded for several blocks of trials, but the results remained the same. The use of auditory cues was also excluded because there was no discernible difference in motor noise either when the stimulator was operated at different speeds, or when catch trials were presented. The only other possible explanation for her superior sensitivity is that she may have had a higher degree of muscle tone. Testing of this hypothesis could be accomplished in two ways. In one, baseline electromyograms

(EMG) would be obtained for each subject, and on - line monitoring of the EMG would take place during all testing sessions. In the other, thresholds would first be obtained with muscles relaxed. These data would then be compared to the thresholds obtained with the muscles voluntarily tensed and producing a known force. As will be noted later, voluntary increases in muscle tension are generally associated with enhanced kinesthetic sensitivity (Browne, Lee, & Ring, 1954; Goodwin, McCloskey, & Matthews, 1972a).

Physiological Mechanisms Underlying Kinesthetic Sensitivity

Evidence for the physiological mediation of velocity sensitivity exists at several levels of the nervous system. Peripherally, velocity sensitive responses have been recorded from each kinesthetic receptor type. First, the dynamic discharges of slowly adapting joint receptors, e.g., Ruffini endings, within their excitatory angles have been shown to be proportional to movement velocity (Boyd & Roberts, 1953; Skoglund, 1956). Both the annulospiral endings (primary muscle spindle receptors) and flowerspray endings (secondary muscle spindle receptors) have shown velocity sensitivity, with the former demonstrating superior sensitivity to dynamic stimulation (Hunt, 1974; Matthews, 1974). Lastly, two types of cutaneous receptors, identified as a Pacinian corpuscle (PC) and a type II slowly adapting receptor (SA II), have demonstrated dynamic sensitivity to both skin stretch and indentation, and may possibly provide information about both movement velocity and direction (Hulliger, Nordh, Thelin, & Vallbo, 1979). At higher levels, slowly adapting units with response properties similar to those of peripheral joint receptors have been identified in both thalamus (Mountcastle, Poggio, & Werner, 1963) and cortex (Mountcastle & Powell, 1959). At each locus, the magnitude of the discharge over the unit's excitatory angle was proportional to the movement velocity. Hence one would expect psychophysical thresholds to vary with angular velocity.

There is much evidence to indicate that the physiological mediation of angular displacement sensitivity, like that of angular velocity, occurs at several levels of the nervous system. Peripherally, the tonic discharges of each kinesthetic receptor type appear to reflect the magnitude of the angular displacement. When slowly adapting joint receptors were studied with the muscular attachments to the joint capsule surgically severed, displacement sensitivity was primarily found at the extremes of movement (Burgess & Clark, 1969; Clark & Burgess, 1975; Grigg & Greenspan, 1977). Thus, the role of joint receptors in the mediation of displacement sensitivity is questionable. While on one hand, some (Clark & Burgess, 1975) suggest that the role of joint receptors may be to subserve sensitivity only at the extremes of movement, others (Goodwin, 1976; McCloskey, 1978) believe that under normal physiologic conditions, where all muscle attachments to the joint capsule are intact, the tensions developed by the muscles may significantly alter joint receptor responsivity to include intermediate positions. One experiment that tested this hypothesis (Grigg, 1975) found only minimal differences in the excitatory angles of units evaluated under both conditions. Additionally, for the aforementioned hypothesis to be true, the muscular forces would have to be sufficiently high (Grigg, 1976; Grigg & Greenspan, 1977), and the CNS would have to be able to interpret a joint receptor discharge that, for a fixed angular displacement, varied with changes in muscle tension (Goodwin, 1976; McCloskey, 1978).

The discharge frequencies of both the muscle spindle primaries and secondaries are a function of the amount of stretch of the muscles in which they are located (Hunt, 1974; Matthews, 1977), and are linearly related over a wide range of muscle lengths (Hunt, 1974; Vallbo, 1974). In the relaxed state, additional spindles can be recruited as joint rotation stretches the muscle (Vallbo, 1974). There, it appears that the recruitment of additional spindles, combined with the increased stretch induced discharge, may mediate the appreciation of both the direction of movement and the magnitude of its displacement. However, complicating this rather direct relationship is the fact that the muscle spindle discharge not only reflects the degree of passive stretch of the muscle but the fusimotor discharge of the gamma efferent system as well. Human investigations have shown that muscle spindle discharges increase during increased isometric contraction (Vallbo, 1974), which means that the CNS would then have to interpret which part of the discharge reflected stretch induced activity, and which part reflected the increased fusimotor tone (McCloskey, 1978). The subjects in the present study were told to relax their muscles, and because it is known that the fusimotor discharge to relaxed muscles is relatively slight (Vallbo, 1974), the muscle spindle discharge may have presented an unambiguous displacement and directional signal.

The aforementioned mechanisms may help to explain the increased sensitivity of subject JB. Although she was told to relax her muscles, there was no electromyographic recording of muscle tone, and so her spontaneous level may have been much greater than that of the other subjects. In addition, it is possible that she may have been making slight adjustments in finger position that produced small increments in muscular contraction. Several studies (Browne, Lee, & Ring, 1954; Goodwin, McCloskey, & Matthes, 1972a) have shown that kinesthetic sensitivity may be enhanced by contracting the appropriate muscles.

The possibility of cutaneous receptors contributing to displacement sensitivity in man has been described by Knibestol (1975). These slowly adapting units, heavily concentrated in the regions of the proximal and distal IP joints, responded over 80 of joint rotation, with a discharge linearly related to joint angle. Therefore it appears that each receptor type, either individually or in combination, may mediate displacement sensitivity.

The central response to kinesthetic stimulation is complicated by the fact that joint, muscle, and cutaneous afferents often course through the same nerve (Moberg, 1972), making it difficult to attribute to a specific type of kinesthetic afferent, the central response to joint rotation.

Two studies of the response properties of thalamic units responding to joint rotation (Mountcastle, Poggio, & Werner, 1963; Yin & Williams, 1976) yielded contradictory findings. While both found that most units were single ended, in one (Mountcastle et al., 1963) the majority were slowly adapting; in the other (Yin et al., 1976), rapidly adapting. Several hypotheses have sought to explain the contradictions, e.g., sampling biases, but as yet they are unresolved. These slowly adapting units were classified as joint afferents by Mountcastle because they had many of the properties of peripheral joint receptors. However, because their primary characteristic was a grade response to joint rotation, Matthews (1977) believed they could also have been classified as muscle afferents. Regardless of their classification, units with the same response proerties have also been identified in the cortex (Mountcastle & Powell, 1959). Additional evidence for cortical involvement in the mediation of displacement comes from two human investigations (Bergmark, 1909; Head & Holmes, 1911) in which damage to sensorimotor cortex resulted in elevated thresholds for both the detection of movement and the identification of direction. It was necessary to displace the joint by as much as 45° before a vague sensation of movement became an awareness of direction. Thus, as a consequence of the physiological response, one would expect psychophysical thresholds to vary as a function of angular displacement.

The lack of a significant directional effect in Experiment 1 can probably be attributed to the generally high range of velocities used. With four of the seven velocities (1.5, 3.0, 6.2, and 11.0°/ sec.) generating nearly 100% detection rates, it is likely that these stimuli produced high frequency dynamic discharges in the velocity sensitive kinesthetic receptors, and made movement in either direction equally easy to detect.

In contrast to the results of Experiment 1, Experiment 2 found a significant favoring of the detection of upward movements. The results amy reflect an interaction between the range of velocities presented and the resting position of the hand.

In the experiment, the velocity range was lowered to between .05°/ sec. and 1.5°/ sec. from the .15°/ sec. and 11.0°/ sec. of Experiment 1. These more slowly moving stimuli would be more difficult to detect because they would produce low frequency discharges in the velocity sensitive receptors, and generally smaller changes in the firing rates of the displacement sensitive receptors. In the latter case, the small angular displacements were the products of low velocity stimuli and short stimulus durations over which they were presented. The resting position of the hand was such that it was ventroflexed at both the wrist and metacarpophalangeal joints. As a consequence, the majority of movements around the IP joint occurred over the extension half of its movement range, and upward movements from the 25° starting position brought the joint close to full extension. It then follows that, if joint receptors discharge primarily at the extremes of movement, these upward movements would activate a population of extension sensitive joint receptors whose discharges, adding to those of the muscle and cutaneous receptors responding to the displacement, would account for the greater detectability of the upward movements.

The lack of a significant effect due to starting position may have been the result of too short an adaptation time spent at the given positions. Here, adaptation time was synonymous with foreperiod, and never exceeded ten seconds. However, the use of longer adaptation times, e.g., 30 or 60 seconds, would present a new problem. In this experiment, the joint was always returned to the same starting position prior to the onset of the next stimulus. However, the position from which the joint was returned varied in a random manner from trial to trial. While it was assumed that the discharge frequency recorded at a given position would be the same, regardless of the prior position, there is evidence that this is not true. What has been found is that when a joint has been rotated back into a position to which it had been adapted for up to ten minutes, there is a definite decrease in the firing rates of slowly adapting joint receptors (Grigg & Greenspan, 1977; McCall, Farias, Williams, & BeMent, 1974; Millar, 1975). Therefore, the firing rate at any given position was influenced by the joint's previous position. The hysteresis effect in the discharge rate was believed to be mediated by the viscoelastic properties of the joint capsule. Therefore, it appears that it would be necessary to monitor the discharges of the relevant receptors in order to determine that the firing rate at a specific starting position remained constant prior to the onset of each new stimulus.

In general, the findings of the present investigation are consistent with the known response properties of joint, muscle, and cutaneous afferents. While the contribution of each afferent type to kinesthetic sensitivity is supported both by their responses to joint rotation and by human kinesthetic deficits following their selective anesthesia, neither the nature of their inputs, e.g., direct or facilitatory, nor the mechanism by which their inputs are integrated, has been defined. Gross and unit recordings have helped to localize the subcortical structures and cortical regions mediating kinesthetic sensitivity, but contradictory findings as to the cellular response characteristics, e.g., rapidly adapting vs. slowly adapting, and even the specific afferent or afferents, e.g., joint vs. muscle, contributing to a given response, remain to be resolved. In brief, additional and well controlled psychophysical studies are needed to define the relevance or irrelevance of specific movement parameters, but in order that the findings of these studies have more meaning, it is equally important to obtain a clearer understanding of their underlying physiological mechanisms.

APPENDIX 1

TABLE AI - I

Summary of the Analysis of Variance for the Effects of Velocity, Direction, and Starting Position on Percent Correct Detection, Using Arc Sin Transformed Values.

Source	Error Term	Sum of Squares	df	Mean Square	F
Mean	S	700.9526	1	700.9526	639.4688
S		.8963889E - 01	2	.4481944E - 01	
D	SD	.3605839E - 01	1	.3605839E - 01	.9371
V	SV	72.31332	6	12.05222	213.8643***
P	SP	.1298749	2	.6493747E - 01	.3689
SD		.7696056E - 01	2	.3848028E - 01	
SV		.6762543	12	.5635452E - 01	
DV	SDV	.1009216	6	.1682027E - 01	1.0839
SP		.7041398	4	.1760349	
DP	SDP	.7190859E - 01	2	.3595430E - 01	1.6240
VP	SVP	.2908862	12	.2424051E - 01	.3350
SDV		.1862230	12	.1551858E - 01	
SDP		.8855873E - 01	4	.2213968E - 01	
SVP		1.736441	24	.7235169E - 01	
DVP	SDVP	.1701111	12	.1417592E - 01	.4050
SDVP		.8400599	24	.3500249E - 01	

S = subject
D = direction

V = velocity
SP = starting position

* = $P < .05$
** = $P < .01$
*** = $P < .001$

TABLE A1 - 2

Scheffe Test for the Significance of the Differences in Mean Percent Correct Detection Across Levels of Velocity, Using Arc Sin Transformed Values (N = 3).

	V1	V2	V3	V4	V5	V6	V7
Velocity (deg./ sec.)	.15	.30	.80	1.5	3.0	6.2	11.0
Mean Arc Sin Values	.99169	1.40761	2.45375	2.90489	2.91750	2.91750	2.91750

Comparisons

V1 vs. V2	V2 vs. V3	V3 vs. V4	V4 vs. V5	V5 vs. V6	V6 vs. V7
V3*	V4*	V5	V6	V7	
V4*	V5*	V6	V7		
V5*	V6*	V7			
V6*	V7*				
V7*					

* = $P < .05$

Fig. A1 - 1 Response time (sec.) as a function of log angular velocity (deg./ sec.) for both upward (solid line) and downward (broken line) movements at starting positions of 15 , 25 , and 35 , for subject ER. Each data point represents a mean for correct detections. The variability measure is ± 1 SD.

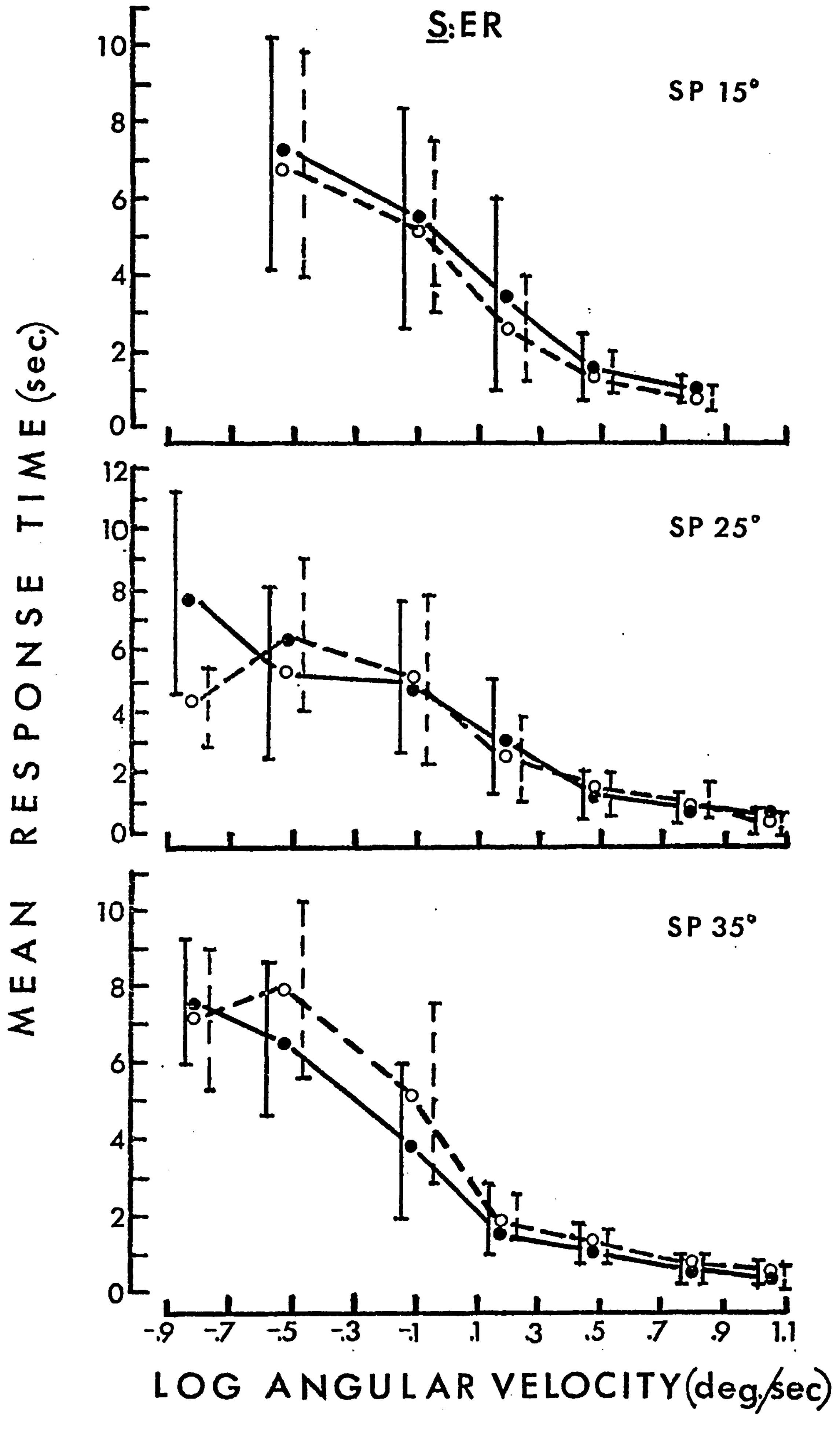

S:ER
SP 15°
SP 25°
SP 35°
MEAN RESPONSE TIME (sec.)
0
2
4
6
8
10
12
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg./sec)

Fig. A1-2 Response time (sec.) as a function of log angular velocity (deg./ sec.) for both upward (solid line) and downward (broken line) movements at starting positions of 15°, 25°, and 35° for subject MG. Each data point represents a mean for correct detections. The variability measure is ± 1 SD.

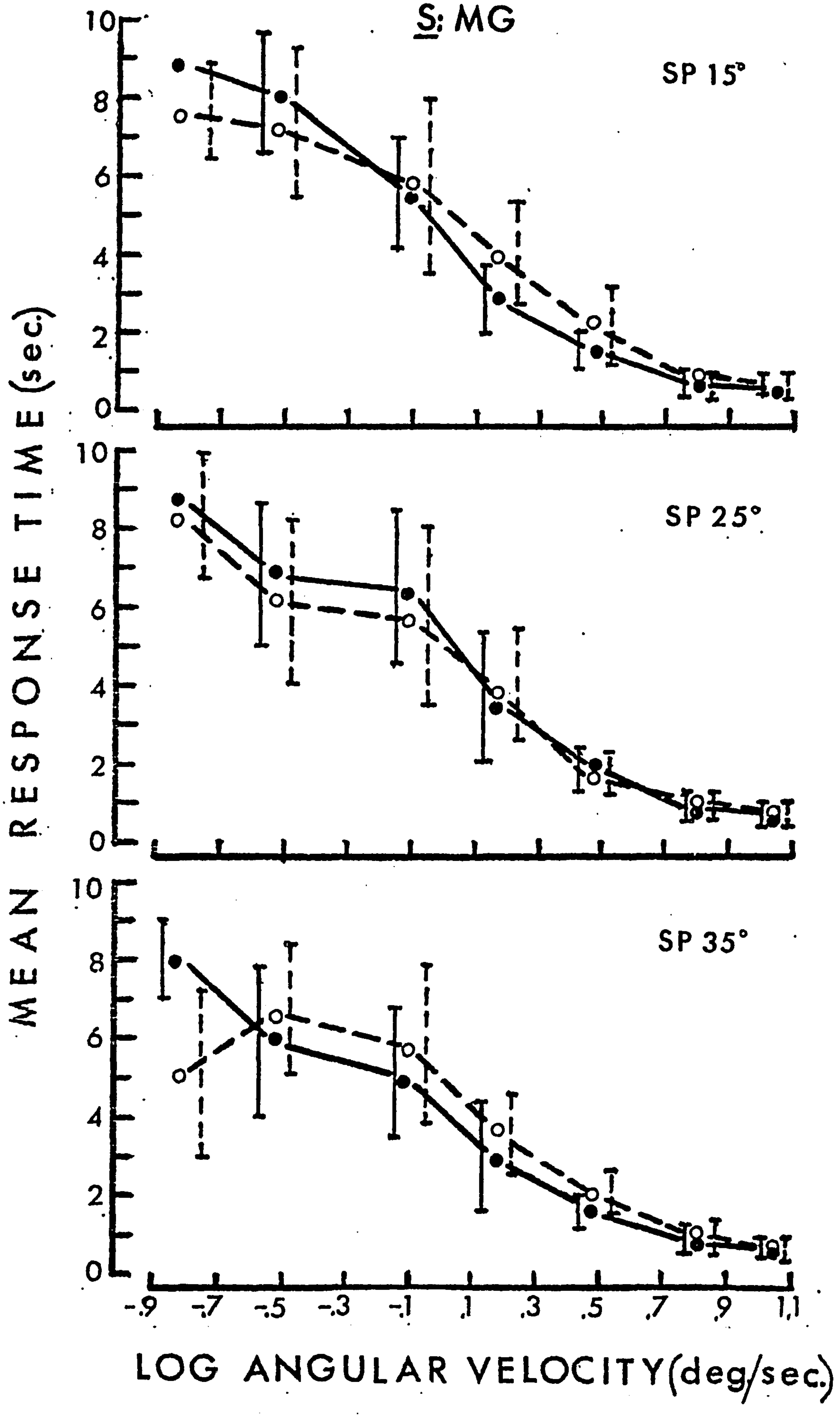

S: MG
SP 15°
SP 25°
SP 35°
MEAN RESPONSE TIME (sec)
0
2
4
6
8
10
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec)

TABLE A1 - 3

Summary of the Analysis of Variance for the Effects of Velocity, Direction, and Starting Position on Response Time.

Source	Error Term	Sum of Squares	df	Mean Square	F
Mean	S	1844.166	1	1844.166	362.7605
S		10.16740	2	5.083699	
D	SD	.6286204E - 01	1	.6286204E - 02	.0210
V	SV	888.3428	6	148.0571	297.9568***
P	SP	.8146715E - 01	2	.4073358E - 01	.0170
SD		.5988068	2	.2994034	
SV		5.962891	12	.4969075	
DV	SDV	6.829102	6	1.138184	2.9187
SP		9.578771	4	2.394692	
DP	SDP	1.254490	2	.6272449	3.4794
VP	SVP	2.286696	12	.1905580	.3296
SDV		4.679504	12	.3899587	
SDP		.7210894	4	.1802723	
SVP		13.87483	24	.5781180	
DVP	SDVP	2.378811	12	.1982342	.9138
SDVP		5.206134	24	.2169222	

S = subject
D = direction
V = velocity
P = starting position

* = P<.05
** = P<.01
*** = P<.001

TABLE A1 - 4

Scheffe Test for the Significance of the Differences in Mean Response Time Across Levels of Velocity (N = 3).

Velocity (deg./ sec.)	V1	V2	V3	V4	V5	V6	V7
	.15	.30	.80	1.5	3.0	6.2	11.0
Mean Response Time (sec.)	7.41555	7.04888	5.66111	3.29666	1.66333	.92722	.76778

Comparisons

V1 vs.	V2 vs.	V3 vs.	V4 vs.	V5 vs.	V6 vs.
V2	V3	V4	V5*	V6	V7
V3	V4	V5*	V6*	V7	
V4*	V5*	V6*	V7*		
V5*	V6*	V7*			
V6*	V7*				
V7*					

* = $P < .05$

TABLE A1 - 5

Summary of the Analysis of Variance for the Effects of Velocity, Duration, and Direction on Percent Correct Detection, Using Arc Sin Transformed Values.

Source	Error Term	Sum of Squares	df	Mean Square	F
Mean	S	489.8850	1	489.8850	282.4976
S		.2984831	2	.1492415	
D	SD	.6754572	1	.6754572	63.2264***
V	SV	82.27338	5	16.45467	93.6258***
T	ST	20.32983	5	4.065967	29.2606***
SD		.2136630E - 01	2	.1068315E - 01	
SV		1.757492	10	.1757492	
DV	SDV	.1004486	5	.2008972E - 01	.1009
ST		1.389572	10	.1389572	
DT	SDT	.5719147	5	.1143829	.8173
VT	SVT	7.325775	25	.2930310	4.4042***
SDV		1.991115	10	.1991115	
SDT		1.399592	10	.1399592	
SVT		3.326736	50	.6653470E - 01	
DVT	SDVT	6.217819	25	.2487127	1.2729
SDVT		9.769684	50	.1953936	

S = subject
D= direction
V = velocity
T = duration

* = P<.05
** = P<.01
*** = P<.001

TABLE A1 - 6

Scheffe Test for the Significance of the Differences in Mean Percent Correct Detection Across Levels of Velocity and Duration, Using Arc Sin Transformed Values (N = 3).

Velocity (deg./ sec.)

V1	V2	V3	V4	V5	V6
.05	.10	.15	.30	.80	1.5

Mean Arc Sin Values

V1	V2	V3	V4	V5	V6
.70079	.97849	1.24054	1.53426	2.12499	2.45695

Comparisons

V1 vs.	V2 vs.	V3 vs.	V4 vs.	V5 vs.
V2	V3	V4	V5	V6
V3	V4	V5	V6	
V4	V5	V6		
V5*	V6*			
V6*				

Duration (sec.)

D1	D2	D3	D4	D5	D6
1	2	4	6	8	10

Mean Arc Sin Values

D1	D2	D3	D4	D5	D6
1.03959	1.21923	1.49851	1.58804	1.72728	1.96337

Comparisons

D1 vs.	D2 vs.	D3 vs.	D4 vs.	D5 vs.
D2	D3	D4	D5	D6
D3	D4	D5	D6	
D4	D5	D6		
D5	D6			
D6				

$* = P < .05$

TABLE A1 - 7

Scheffe Test for Simple Main Effects on the Velocity by Duration Interaction for Percent Correct Detection, Using Arc Sin Transformed Values (N = 3).

Mean Arc Sin Values

	Duration (sec.)					
	D1	D2	D3	D4	D5	D6
Velocity (deg./ sec.)	1	2	4	6	8	10
V1 (.05)	.83859	.96515	1.04136	1.15189	1.02041	1.20715
V2 (.10)	.85954	1.04136	1.19379	1.22810	1.28336	1.68132
V3 (.15)	1.04627	1.28336	1.49105	1.54631	1.70719	2.04989
V4 (.30)	1.25396	1.38052	1.75754	1.88410	1.98971	2.17999
V5 (.80)	1.41484	1.70227	2.38767	2.46389	2.74778	2.74778
V6 (1.5)	1.83729	2.51915	2.54010	2.59536	2.82400	2.82400

Comparisons

at 1 sec.	V1 vs.	V2 vs.	V3 vs.	V4 vs.	V5 vs.
	V2	V3	V4	V5	V6
	V3	V4	V5	V6*	
	V4	V5	V6		
	V5*	V6*			
	V6*				

at 2 sec.	V1 vs.	V2 vs.	V3 vs.	V4 vs.	V5 vs.
	V2	V3	V4	V5	V6*
	V3	V4	V5	V6*	
	V4	V5	V6*		
	V5*	V6*			
	V6*				

at 4 sec.	V1 vs.	V2 vs.	V3 vs.	V4 vs.	V5 vs.
	V2	V3	V4	V5*	V6
	V3	V4	V5*	V6	
	V4*	V5*	V6*		
	V5*	V6*			
	V6*				

* = P < .05

TABLE A1-7 (cont.)

Comparisons

at 6 sec.	V1 vs. V2	V2 vs. V3	V3 vs. V4	V4 vs. V5*	V5 vs. V6
	V3	V4*	V5*	V6*	
	V4*	V5*	V6*		
	V5*	V6*			
	V6*				
at 8 sec.	V1 vs. V2	V2 vs. V3	V3 vs. V4	V4 vs. V5*	V5 vs. V6
	V3*	V4*	V5*	V6*	
	V4*	V5*	V6*		
	V5*	V6*			
	V6*				
at 10 sec.	V1 vs. V2	V2 vs. V3	V3 vs. V4	V4 vs. V5	V5 vs. V6
	V3*	V4	V5*	V6*	
	V4*	V5*	V6*		
	V5*	V6*			
	V6*				

at .05% sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5	D5 vs. D6
	D3	D4	D5	D6	
	D4	D5	D6		
	D5	D6			
	D6				
at .10% sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5	D5 vs. D6
	D3	D4	D5	D6	
	D4	D5	D6		
	D5*	D6			
	D6*				
at .15% sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5	D5 vs. D6
	D3	D4	D5	D6	
	D4	D5	D6		
	D5*	D6			
	D6*				

* = $P < .05$

TABLE A1-7 (cont.)

at .30°/ sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5	D5 vs. D6
	D3	D4	D5	D6	
	D4	D5*	D6		
	D5*	D6*			
	D6*				
at .80°/ sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5*	D5 vs. D6
	D3	D4	D5*	D6*	
	D4	D5*	D6*		
	D5*	D6*			
	D6*				
at 1.5°/ sec.	D1 vs. D2	D2 vs. D3	D3 vs. D4	D4 vs. D5	D5 vs. D6*
	D3	D4	D5	D6*	
	D4	D5	D6*		
	D5	D6*			
	D6*				

* = $P < .05$

APPENDIX 2

Fig. A2 - 1 Response time (sec.) as a function of log angular velocity (deg./sec.) for both upward (solid line) and downward (broken line) movements at starting positions of 15°, 25°, and 35° for subject JB. Each data point represents a mean for correct detections. The variability measure is ± 1 SD.

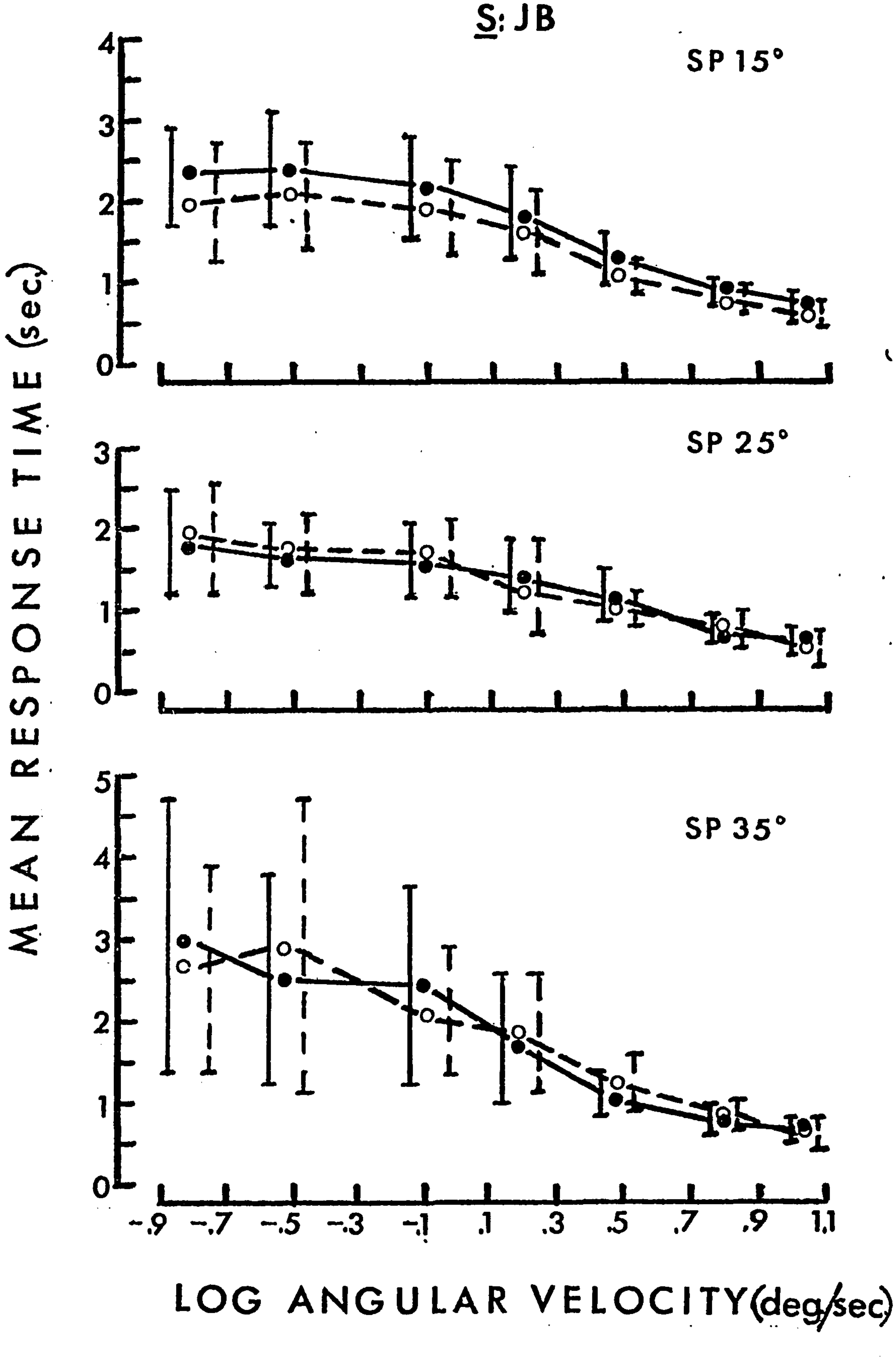

S: JB
SP 15°
SP 25°
SP 35°
MEAN RESPONSE TIME (sec)
0
1
2
3
4
5
-.9
-.7
-.5
-.3
-.1
.1
.3
.5
.7
.9
1.1
LOG ANGULAR VELOCITY (deg/sec)

Fig. A2 - 2 Percent correct detection as a function of log angular velocity (deg./ sec.) for movements of one second (open circle, dotted line), two seconds (open square, broken line), four seconds (open triangle, broken line), six seconds (filled circle, dotted line), eight seconds (filled square, broken line), and ten seconds (filled triangle, solid line) for subject JB.

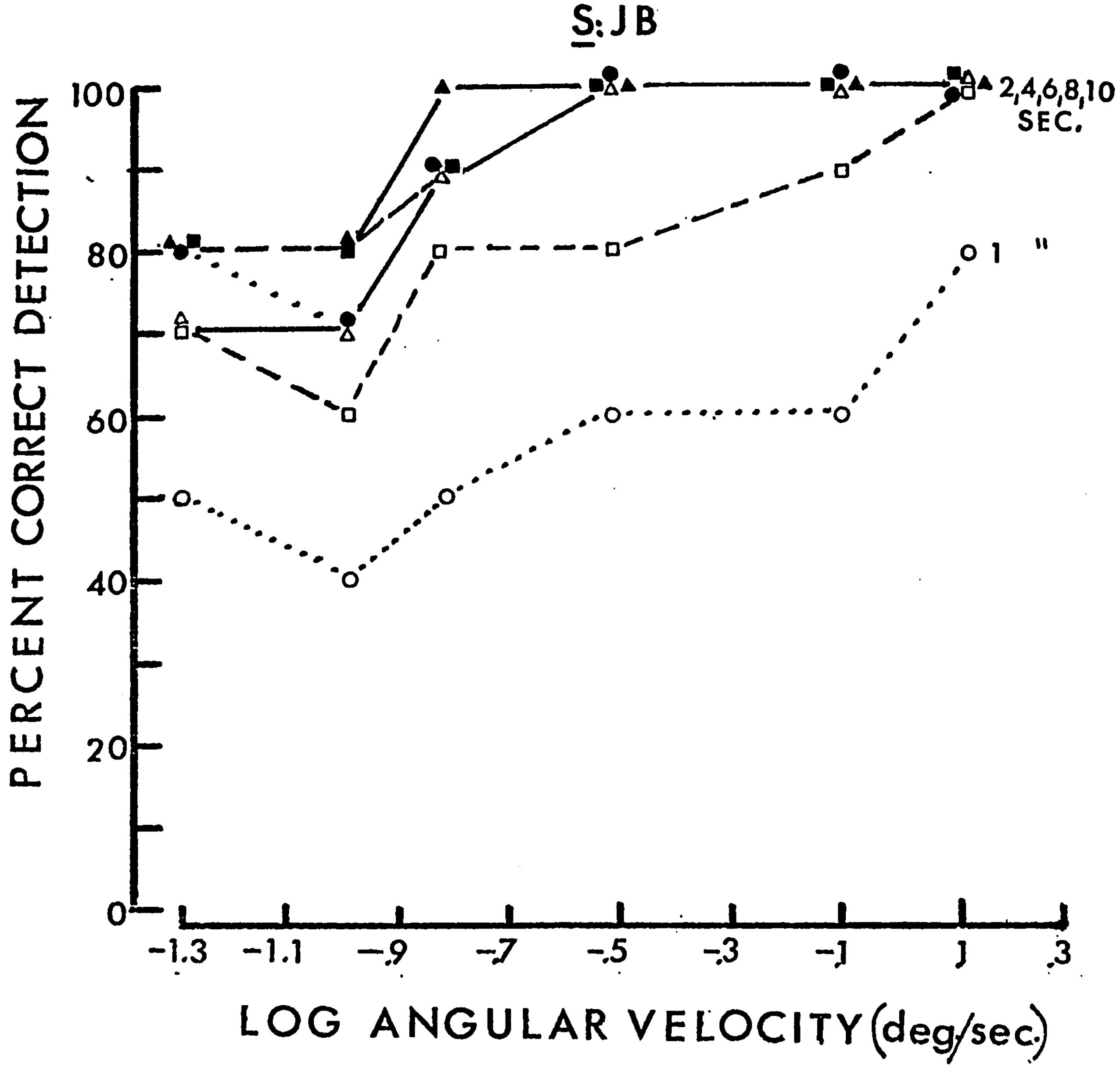

S: JB
PERCENT CORRECT DETECTION
100
80
60
40
20
0
-1.3
-1.1
-.9
-.7
-.5
-.3
-.1
.1
.3
LOG ANGULAR VELOCITY (deg/sec)
2,4,6,8,10 SEC.
1 "

Fig. A2-3 Percent correct detection as a function of stimulus duration (sec.) for movements at .05°/ sec. (open circle, dotted line), .10°/ sec. (open square, broken line), .15°/ sec. (open triangle, solid line), .30°/ sec. (filled circle, dotted line), .80°/ sec. (filled square, broken line), and 1.5°/ sec. (filled triangle, solid line) for subject JB.

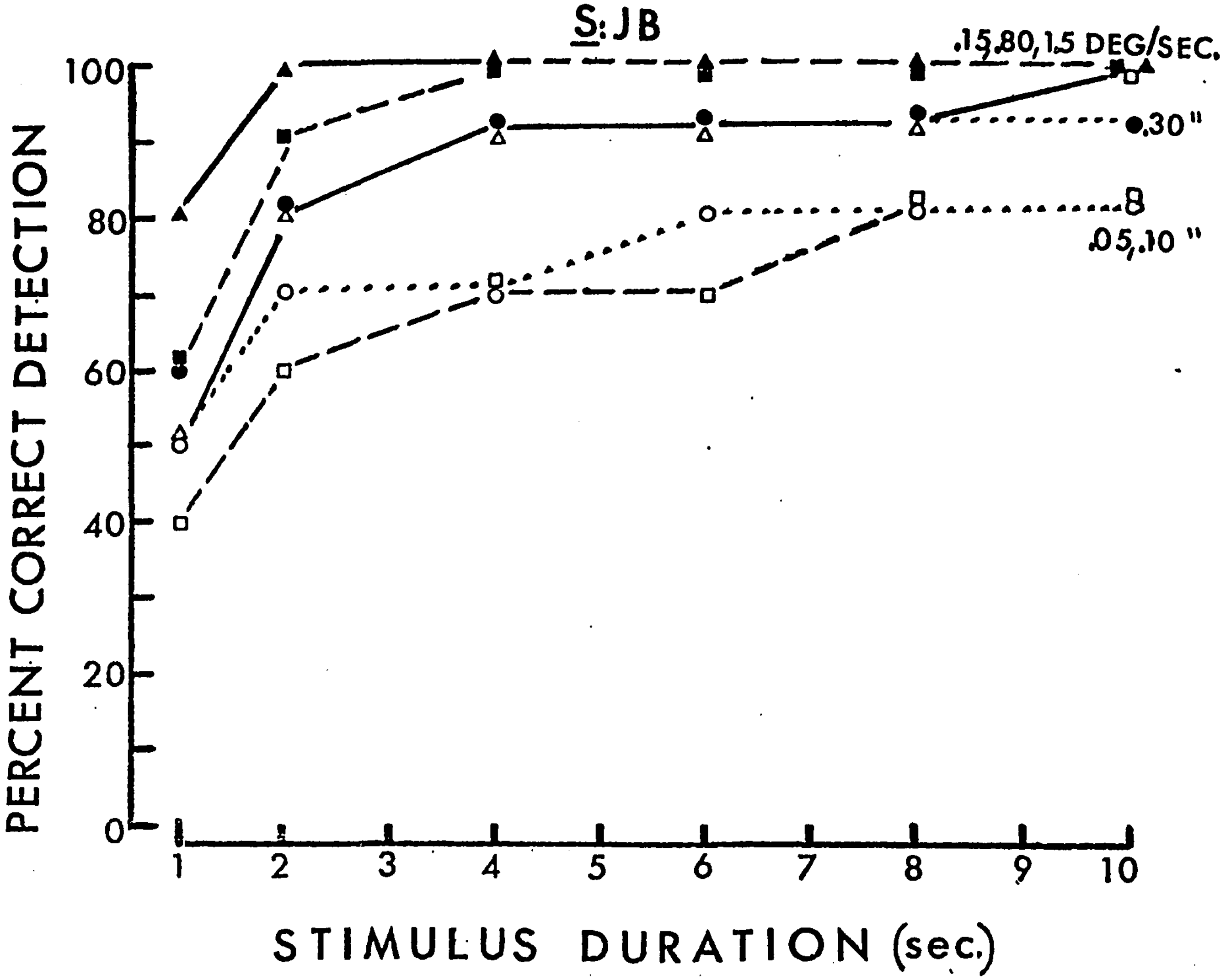
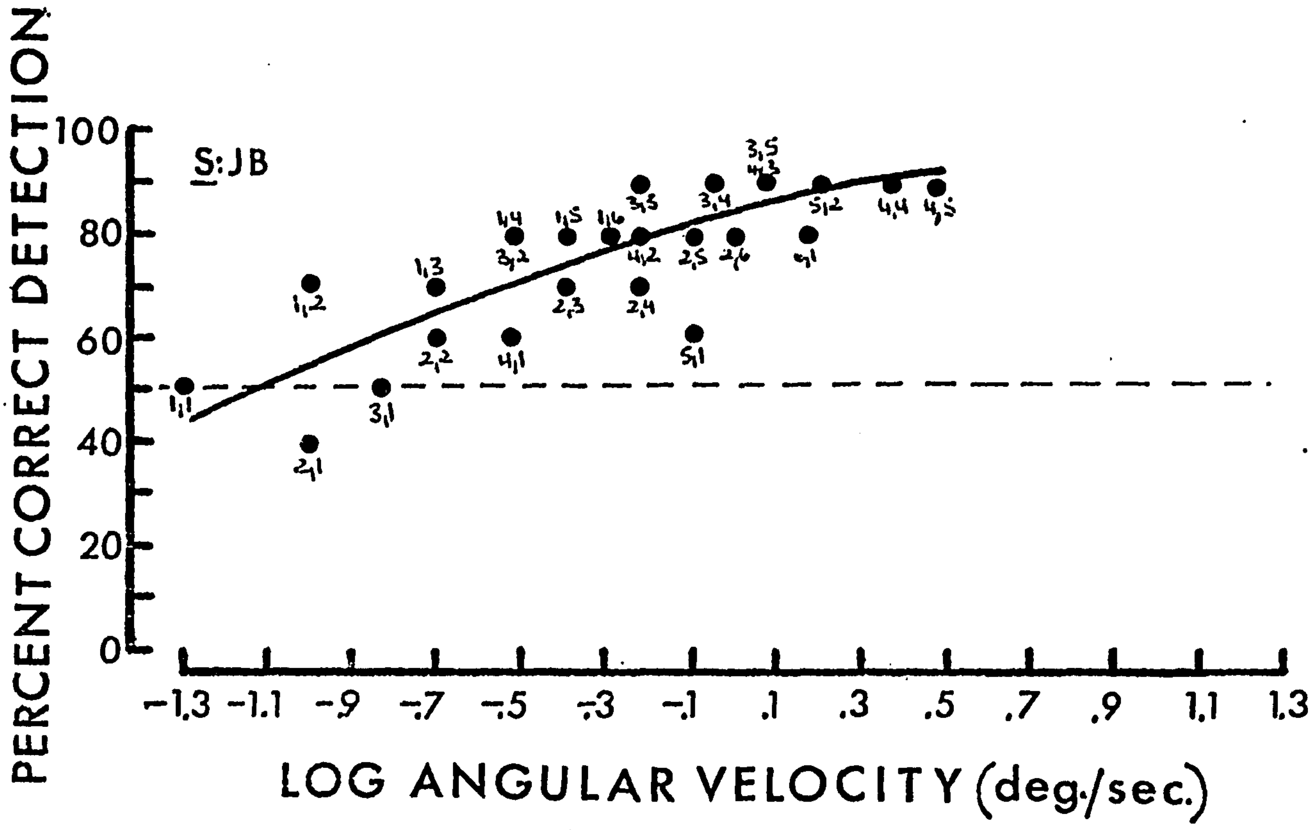

S: JB
.15,.80,1.5 DEG/SEC.
.30"
.05,.10"
PERCENT CORRECT DETECTION
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
STIMULUS DURATION (sec.)

Fig. A2-4 Percent correct detection as a function of log angular displacement (deg.) for subject JB. The subscripts for each data point represent the velocity - duration products indicated in Table 7. Multiple data points at a given displacement indicate that two or more velocity - duration combinations yielded the same product.


PERCENT CORRECT DETECTION
100
80
60
40
20
0
S:JB
1,1
1,2
2,1
3,1
1,3
2,2
4,4
3,2
4,1
1,5
2,3
1,6
3,3
4,2
2,4
2,5
5,1
3,4
2,6
3,5
4,3
6,1
5,2
4,4
4,5
−1.3
−1.1
−.9
−.7
−.5
−.3
−.1
.1
.3
.5
.7
.9
1.1
1.3
LOG ANGULAR VELOCITY (deg./sec.)

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