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The Spatial And Temporal Characteristics Of Visually Directed Limb Movements And Comparison Of Ocular And Manual Performance

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THE SPATIAL AND TEMPORAL CHARACTERISTICS OF VISUALLY DIRECTED LIMB MOVEMENTS AND COMPARISON OF OCULAR AND MANUAL PERFORMANCE

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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London, Ontario
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Abstract

The purpose of this thesis was to examine visually guided movements of the upper limbs which approximated normal reaching behaviour, and to describe the production of these movements on the basis of a number of interrelated measures. Most previous studies of visually directed or visually triggered limb movements had not provided complete descriptions of the behaviour. The series of studies included in this thesis required subjects to point quickly and accurately to small visual targets presented lateral to a visual fixation point, on an otherwise featureless screen. The most comprehensive description of the subjects' behaviour was performed in Study 1. The remaining two studies examined issues which were raised by the analysis of Study 1.

In studies 1 and 2 the kinematic characteristics of the limb movements were examined by a frame-by-frame analysis of video records of the subjects' performance. The use of visual feedback information in the guidance of the limb was evident from the modifications in trajectory during periods of low velocity at the end of the movements, and also from the increased accuracy and longer movement duration when the subjects pointed to persistent rather than briefly visible targets. Studies 1 and 2 also revealed that reaches of either limb which crossed the body axis were executed much less efficiently, in terms of movement velocity, than those performed within the extrapersonal space ipsilateral to the limb being used. As long as the subjects fixated a point directly in front of their body axis before the target was presented, these ipsilateral reaches were also initiated more quickly and were more accurate than reaches which crossed the body axis. Unlike movement velocity, the latency and accuracy of the limb movement were altered when the subjects fixated an eccentric point so that the visual field did not correspond to extrapersonal space relative to the body axis.

Studies 1 and 3 investigated the relationship between ocular and manual movements in the production of visually directed limb movements. In both studies a low but statistically significant correlation was found between the latency to initiate movement of the eyes and hand. The results of Study 3 suggested that this correlation may be reduced by previous trials in which only the eyes or the hand were directed to the target. In Study 1 the eye and limb movement latencies were lower for ipsilaterally presented targets and for blocks of trials in which the subjects reached with their right hand.

In summary the findings illustrated how the position of a visual target within extrapersonal space affects the programming and execution of a limb movement directed to that position. The results suggested that the programming of such visually directed limb movements involves a hemispherically organized network of cortical areas, and that this network may be involved in the integration of sensorimotor information for the ocular motor system as well as the manual motor system.

The following is dedicated to,

Susan Elizabeth Doble

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General Introduction

Fossil records suggest that the adoption of an upright stance was one of the earliest and most significant developments in hominid evolution. Man is distinct from other primates in his vertically upright stance and bipedal locomotion. The adoption of this posture requires extensive modifications of the skeletal-muscular system relative to quadrapedal primates such as monkeys or semi-erect apes such as the chimpanzee (Hooten, 1936). Since they lack these modifications, apes are able to walk only short distances when using just their lower limbs. Anyone who has chased after even a small animal such as a domestic cat or a rabbit will quickly realize that bipedalism is a very inefficient method of running (Lovejoy, 1980; as cited in Johanson and Edey, 1982). Therefore, the adoption of upright posture and two-legged locomotion by man's early ancestors must have yielded some other selective advantages to outweigh the disadvantage of inefficient running.

One clear advantage of upright walking is that it allows the upper limbs to be used for a variety of new adaptive behaviours. Although it has been suggested that tool use may have been such a behaviour, fossil records of fully bipedal hominids precede any evidence of tool manufacture by as much as one million years (Johanson and Edey, 1982). The increased ability to carry slowly developing infants and foodstuff over substantial distances may have provided a selective advantage sufficient to overcome the decrease in running ability (Lovejoy, 1980; as cited in Johanson and Edey, 1982), but the use and shaping of wooden tools which did not survive as archeological evidence, may have occurred very early. Although the exact temporal relationship is unknown, freedom of upper limb movement from locomotion undoubtedly preceded the eventual development of the manufacture of tools which could be carried from place to place. This transport of tools is a truly unique aspect of human behaviour (see Beck, 1980, page 220, for review).

The manufacture and use of tools by man requires precise visual guidance of upper limb movement, but such precision is evident in the behaviour of other primates as well. The use of the upper limbs for prey-catching, and for locomotion through the trees, also requires a well-developed system of visual motor control. This is perhaps best illustrated by the gibbon who uses his long arms to swing from branch to branch through the forest. Brachiation, as this form of locomotion is known, places a high demand on the accuracy of visually guided limb movements. It is unclear whether the ancestors of hominids used brachiation prior to bipedal locomotion. However, the skeletal-muscular system of the gibbon resembles that of modern man more than any other primate (Hooten, 1936), and like man, the gibbon is truly bipedal when walking, although this ability is poorly developed.

Sarnat and Netsky (1981) have discussed the probable evolutionary history of the visual control of motor behaviour which is evident in primates, and some of their thoughts are described below. The keen sense of vision and high degree of visual motor control probably developed at a very early stage in primate evolution. The forest environment in which prosimians lived placed a higher demand on the visual sense than olfaction, and required good coordination between movements of the eyes and limbs. Improved color vision may have resulted in the ability to extract more information from the visual environment. The shift of the eyes from a lateral to a forward position in the skull provided a large overlap in the visual fields of the two eyes, and allowed the use of stereoscopic cues for the perception of depth. Frontal eye placement is also found in a number of non-primate species, and may be related to a change from herbivorous to carnivorous diet since improved depth perception certainly aids in the capture of moving prey. The ability to use visual information to locate and seize prey with the forelimbs, that developed in prosimians, could have provided the basis for the fine visual control of limb movement possessed by later-evolving primates, and perhaps best developed in man.

The precise visual control of limb movement may, in turn, have provided a basis for the development of other complex human behaviours. It has been suggested that the development of human language may be based upon the skilled production of manual movements. This concept holds that human communication began in a gestural rather than a vocal form, and that it may have arisen from the precise manual control developed for tool use. A full historical review of this gestural theory of human language origin has been discussed by Hewes (1976). The close association between disruption of speech (aphasia) and manual movement (apraxia), following localized brain damage in humans, supports this theory (Kimura, 1979).

Human evolution is a complex subject with many unanswered questions and very little data from which to formulate answers. The environmental pressures responsible for the morphological and behavioural changes of hominids remain unclear. However, it appears that the development of precise visual control of limb movements occurred early in the evolution of all primates. The adoption of bipedal locomotion by hominids provided freedom of upper limb movement which allowed the development of tool use, manufacture and transport. The precision of manual movement associated with the use of tools may, in turn, have formed the basis for systems of communication. Thus from man's early beginnings visually-guided limb movements have been an important component of our behavioural repetoire, and they remain so today.

Human motor behaviour, in general, is determined to a large extent by our use of visual information. Although behavioural responses have provided the dependent measures for a variety of studies of human visual perception, there have been relatively few detailed studies of visual motor behaviour. For example, manual reaction time to the onset of a stimulus has often been used as a measure of the time required to process and perceive information, but experimenters have less frequently examined the manner in which movement appropriate to a particular stimulus is programmed and executed. In part, this lack of attention may reflect the difficulty in determining, categorizing, and measuring the relevant parameters of human motor behaviour. Many researchers have looked upon man as an organism that passively takes in and processes sensory information to form a perception of the external world. Since perceptual ability can be inferred only from a behavioural response, be it a verbal statement or some other form of movement, it is difficult to differentiate the information processing necessary for perceiving, from the sensory-motor processing of the movement. In fact such a differentiation may be meaningless. Some authors (Butter, 1979) have suggested that perception is a goal-directed activity, which depends upon the interaction of afferent sensory input with efferent motor output. Butter has argued that visual recognition results from the comparison of reafference of visual scanning movements to an internal reference signal, but the issue of whether perception and behaviour can, or should be considered as distinct processes remains unresolved.

Gibson (1957) first suggested that our perception of the orientation of objects and of ourselves within the external environment, depends upon dynamic processes associated with movement. This is an important concept in understanding the use of visual information in the control of movement. As he pointed out, convergence of the reflected rays of light from an illuminated environment, onto the eye of an animal constitutes an "optic array". For a behaving animal this optic array undergoes constant transformations. Gibson (1957) suggested that the pattern of transformation which accompanies locomotion "provides 'feedback' stimulation for the control and guidance of locomotor behaviour" (page 185), and proposed the term "visual kinesthesis" to describe this process. The information which is provided by visual kinaesthesis is displacement of the body relative to the visual world. For an animal moving through a textured visual environment this information is of vital importance. That visual kinaesthesis is important in controlling human behaviour is evident from the results of studies which have placed it in conflict with other sensory systems. Brandt, Dichgans and Koenig (1973) have described the manner in which rotation of the visual environment about seated human subjects leads to "apparent self-rotation...which is undistinguishable from an actual chair rotation" (page 476). By moving the visual environment Lishman and Lee (1973) reported visual dominance over the perception of motion for passively or actively moving subjects. The use of visual information was also demonstrated by a behavioural measure in which body sway was measured for normal human adults, during attempted maintenance of an upright stance (Lee and Lishman, 1975). Movements of the visual surroundings were found to affect body movements directly, during normal standing and during the maintenance of unusual postures which altered proprioceptive information.

The motor behaviours which depend upon the constant use of visual information, provided by changes in visual input for their control, need not be limited to locomotion or the maintenance of posture. Most human behaviour takes place with reference to objects or places within the space surrounding us. Attaining goal objects within the environment often involves foveation of the object by the production of an eye movement. Movements of the eyes also produce transformations of the optic array. When a limb movement is directed to a goal object there is a minimal transformation of the total optic array but the relative positions of the goal and the limb go through a transformation. This information of the change of the relative positions of important objects is undoubtedly as critical for the accurate guidance of an individual limb movement as transformations of the total optic array are for the control of whole-body movement. Certainly, it is true that the interaction of visual information and motor programming, during self-produced movement, is required for the development of proper visual control of limb movement in cats (Held and Hein, 1963), monkeys (Held and Bauer, 1967) and perhaps humans (White and Held, 1966). This interaction is also required for the maintenance of accurate visually guided motor control in the adult. The plasticity of visual motor control is elegantly demonstrated by the adaptation of subjects to prismatic distortions of the visual environment (Held and

Freedman, 1963; Gonshor and Melvill Jones, 1980). As with initial development, adaptation is dependent on the active production of movement by the subjects. These studies demonstrate the importance of the combination of visual input and motor output for our perception of, and behaviour in the world surrounding us.

Although the psychophysical approach to the study of human perception has provided a good basis for understanding how visual information is perceived, we have a relatively poor understanding of how this information directs human behaviour on a moment-to-moment basis. In other words, we have a better comprehension of how a particular pattern of wavelength and intensity of light reaching the visual system allows us to identify a coffee mug, than how this same information allows us to pick it up and drink from it.

Visually guided movements of the upper limbs, such as picking up a coffee mug, are a class of behaviour that occurs frequently, and for the most part, accurately thoughout the course of human daily activity. The ability to produce such movements is a particularly well-developed skill in humans and other primates, which allows us to contact and acquire objects of interest within the environment. The role of cortical brain areas in the control of this visually guided reaching has been investigated in some detail for the rhesus monkey (Myers, Sperry and McCurdy, 1962; Hamilton, 1967; Keating, 1973; Brinkman and Kuypers, 1973; Haaxma and Kuypers, 1975; Paillard and Beaubaton, 1975; Lawrence and Hopkins, 1976). The work of Kuypers and his colleagues (Lawrence and Kuypers, 1968a,b; Brinkman and Kuypers, 1973) has revealed that while one cerebral hemisphere can control visually-guided movement of the proximal musculature of both the ipsilateral and contralateral arms, it is able to control movements of the distal muscles only for the contralateral hand. These relatively independent finger movements, which are responsible for the proper grasping of objects such as food pellets, depend upon direct cortico-motorneuronal connections arising from the precentral gyrus and descending via the pyramidal tract (Lawrence and Kuypers, 1968a,b; Lawrence and Hopkins, 1976). Thus when visual information is restricted to one cerebral hemisphere an accurate movement of the ipsilateral limb including distal muscle activity requires the transfer of information to the opposite hemisphere (Brinkman and Kuypers, 1973; Haaxma and Kuypers, 1975). Haaxma and Kuypers (1975) also reported an impairment of visually guided independent finger movements for one limb following lesions of the contralateral cerebral hemisphere. These lesions were either unilateral occipital lobectomy, or unilateral leucotomy "restricted to the white matter of the parietal lobules and some of the white matter caudal to the insula" (page 257). The deficits in visual motor performance which arose from the interruption of cortico-cortical fibres suggested that both intrahemispheric (Haaxma and Kuypers, 1975) and interhemispheric (Brinkman and Kuypers, 1973) transfer of information are required for normal visually guided reaching. In fact, the neural organization of visualmotor behaviour undoubtedly involves the interaction of numerous sensorimotor channels.

The idea of multiple sensorimotor channels for visually-guided behaviour became popular with the "two-visual-systems" hypothesis introduced by Schneider (1968). Although clearly an oversimplification, this concept illustrated that subcortical structures play a large role in the analysis of visual spatial information. As a result of this subcortical processing, visual information may be available to both cerebral hemispheres in split-brain, as well as normal animals. Paillard and Beaubaton (1975) have proposed a distinction between two separate components of visually guided reaching behaviour. The first component constitutes the initiation of a motor program, which results in the "ballistic transport" of the limb toward the visual target. This component, which requires only visual spatial information of target location, and utilizes only the proximal limb muscles, is therefore preserved in the split-brain animal for all reaches. The second component which Paillard and Beaubaton (1975) propose is a final correction of limb trajectory, which may involve both proximal and distal muscle activity, but which requires visual feedback of the limb position for its execution. They suggest that the deficits in reaching that are observed in the split-brain monkey (Keating, 1973; Brinkman and Kuypers, 1973; Paillard and Beaubaton, 1975; Haaxma and Kuypers, 1976) result from the inability of one cerebral hemisphere to make use of visual feedback to adjust the trajectory of the ipsilateral limb. This distinction between various components of a visually guided limb movement and the various neural networks which may control these components is a very important step. Despite the insight which these primate studies have provided, a great deal remains to be learned about the programming and execution of visually directed limb movements. As noted by Georgopolous, Kalaska and Massey (1981) "It is unknown how the visuospatial information concerning target location is used by the brain for the generation of aimed movements, nor is it known how the trajectories of these movements are formed or what factors influence them." (page 726). Furthermore, we have relatively little information of how the manual motor system interacts with other distinct motor systems in the production of visually guided behaviour.

Objects in space are rarely acquired by isolated activity of the limb muscles. In addition to extension of the arm toward the target the eyes, head, and body may move in such a way that the image of the target falls on the fovea of the retinae. Thus the behaviour involves the coordinated interaction of a number of muscle groups. The ocular motor system and the manual motor system are usually both involved in the production of the integrated sequence of movements which result in visually guided reaching. In spite of this, the ocular motor and manual motor systems have rarely been studied together in the performance of one task, although visually guided movements of the individual systems have been studied extensively. The motor system that demonstrates the most direct relationship to the visual environment is the ocular motor system. For this reason, as well as others, saccadic and pursuit eye movements directed to visual targets have been studied in great detail and are undoubtedly the best understood example of visually guided movement (see Carpenter, 1977 for review). Because of the physical characteristics of the eye, and the rotational nature of its movements, the ocular motor system is unique and differs greatly from the manual motor system. The small mass of the eye means that the enertial forces opposing its movement are relatively small in comparison to the viscoelastic forces exerted by the ocular muscles. Since the eyes perform only rotational movements there is no need to account for changes in the gravitational force vector when calculating the pattern of muscular activity necessary to achieve a particular position. While postural adjustments are required to maintain the center of gravity during limb movements no such adjustments are required during eye movements. Furthermore, the muscles that can produce eye movements are limited in number and well defined, and no stretch reflexes exist to compensate for unexpected loads (see Carpenter, 1977 for review). Thus the eyes have provided a relatively simple motor system which can be monitored easily and accurately by a variety of methods that do not place extensive constraint on the movements. The application of systems analysis to the records of ocular motor performance has resulted in numerous models describing the neural circuitry which may underlie certain characteristics of ocular motor behaviour (Robinson, 1968; Weber and Daroff, 1972; Dell'Osso, Troost and Daroff, 1975; Schmid, Zambarbieri and Magenes, 1981). These elegant models provide a basis for understanding how the eyes move in response to changes in the visual environment, but we have little knowledge of how eye movements contribute to the complex interaction of motor systems, required for visually guided movements of the limbs.

Numerous motor physiologists have applied the same type of approach used in the study of ocular movements to the study of manual movements. Thus, researchers have investigated the performance of isolated limb movements in order to determine the parameters which characterize their execution and control. In contrast to movements of the eyes, limb movements are affected significantly by inertial and gravitational forces. Furthermore, limb movements often involve rotation about more than one joint and through three dimensional space. Along with an increased number of possible points of rotation there are more agonist/antagonist pairings of muscles that contribute to the behaviour. The increased complexity of such movements undoubtedly requires an increased complexity of the motor programs responsible for their production. In order to simplify the mechanics of the limbs a number of experimenters have restricted the movement to rotation about one joint (Desmedt and Godeaux, 1978; Bizzi, Dev, Morasso and Polit, 1978; Hallet and Marsden, 1979; Lestienne, 1979; Polit and Bizzi, 1979; Cooke, 1980; Brown and Cooke, 1981; Bizzi, Accornero, Chapple and Hogan, 1982; Hore, Vilis and Flament, in press). These investigations have provided valuable information concerning the timing of electromyographic activity associated with the velocity control of such movements. In addition, they have shown that the mechanical properties of the muscles themselves play a large role in determining the appropriate central motor control. Bizzi and his co-workers have suggested that a transition in the equilibrium point of the length-tension properties of agonist and antagonist muscles determines the extent of rotation about a single joint (Bizzi et al., 1978; Polit and Bizzi, 1979; Bizzi et al., 1982). Others, such as Cooke (1980) who described the limb as "a damped spring having mass" (page 203), have applied mathematical models to the mechanics of limb movements, much in the way that ocular motor behaviour has been modeled. While these studies have yielded a great deal of information about the motor control of relatively simple, single-joint movements, the contribution of such motor control to more complex behaviour is less clear. At the present time there have been few studies which have looked at whether the same, well documented, principles which have been found for rotations about a single joint, can be applied directly to more complex movements. As pointed out by Abend, Bizzi and Morasso (1982) "Although the physiology of one-degree-of-freedom movements has been explored extensively, there have been relatively few studies of the means by which the central nervous system (CNS) coordinates the large number of degrees of freedom of movement of the multijoint limb." (page 331).

It is only in the last few years that precise studies of multijoint limb movements have become more numerous (Morasso, 1981; Soechting and Lacquaniti, 1981; Georgopoulos et al., 1981; Abend et al., 1982; Lacquaniti and Soechting, 1982). By the use of a manipulandum, Morasso (1981) confined the arm movements of human subjects to flexion or extension at the elbow and shoulder. This limitation of the movement to one plane kept the effects of gravity constant. Morasso (1981) reported that when the subjects moved toward visual targets, notable invariances occurred in their performance. The paths which the subjects took between target positions were approximately straight lines. Furthermore, he reported that "the tangential hand velocity for the different movements has a single peaked curve that varies little between movements" (page 224), despite the fact that the joint angular velocities varied considerably. This led Morasso (1981) to propose that the control of the movement involves the formulation of space-related coordinates rather than specification of the angle of rotation about each joint. Using the same experimental paradigm Abend et al. (1982) required that subjects produce curved movement trajectories, and observed the resultant performance. They found that the behaviour of the subjects changed dramatically under these conditions such that "the path had a segmented appearance, as if the subjects were trying to approximate a curve with low curvature segments" (page 343). These results were discussed in terms of the possible use of the mechanical constraints of the skeletal-muscular system by a "biological controller" to determine the characteristics of the movement trajectory. Because sight of the arm was restricted in both paradigms it is difficult to interpret the results of these studies with regards to most everyday visually guided limb movements.

In a study of two-dimensional limb movement to visual targets by monkeys, Georgopoulos et al. (1982) found that the variability in the path of the movement decreased with practice, and increased with uncertainty about which of a number of spatially separate targets was to be used. These authors emphasized the degree to which the behaviour of the animals in the experimental paradigm, was similar to their normal visually directed behaviour, since they were allowed free viewing of their arms. However, the use of a manipulandum restricted these visually guided movements to only one plane. In what is perhaps the most elegant analysis of unrestricted human limb movements, Soechting and Lacquaniti (Soechting and Lacquaniti, 1981; Lacquaniti and Soechting, 1982) looked at the relation between angular acceleration of the shoulder, elbow and wrist during pointing and grasping movements. The targets were presented directly in front of the subjects so that movement in only two dimensions was required. They found that the trajectories of the movement were relatively constant and independent of velocity, but were "curvilinear with the degree of curvature depending on target location" (page 718). Angular rotation about the shoulder and elbow were found to be invariably related although no such relationship was evident for movement at the wrist. Despite this lack of a relationship, Lacquaniti and Soechting (1982) do not suggest independence of movement about these joints. Rather, they suggest that "provided that wrist pronation or supination is carried out within some temporal limits, the pattern of activity of bifunctional muscles (acting in wrist and elbow motions) will be regulated so as to satisfy the constraints of shoulder-elbow functional coupling" (page 408). Therefore, they support the concept that "it is the movement itself, and not the pattern of activity in individual muscles, which is invariant during compound motion of the arm" (page 408). These studies have advanced our knowledge of complex movements considerably, but there have been no analyses of limb movements through three-dimensional space, which more closely approximate most visually guided reaching movements. If we wish to extrapolate from the studies and models of simple systems to the motor control of behaviour in general, we must relate the performance under restricted, experimental conditions to the characteristic peformance of common behaviours.

All of these studies of the motor control of limb movements have indicated that, for the simple and complex movements which have been studied, there exist invariant aspects of their production. These invariances reflect the relationship between the mechanical constraints of the skeletal-muscular system and the neural organization controlling its movement. Although the movements have been directed to visual targets, the manner in which visual information contributes to the spatial control of limb movements has not been explored fully. Therefore, this approach to the study of visual behaviour, adopted by many motor physiologists, reflects the opposite end of the spectrum to the psychophysical approach. In each paradigm one aspect of the behaviour, either the visual information or the resultant motor output, has received relatively little attention.

The use of visual information in the control of limb movements has been studied in a variety of experimental paradigms, but most of these studies have not described the characteristics of the behaviour in much detail. Instead of analyzing the spatial and temporal characteristics of the movement trajectory they have generally concentrated on the accuracy of the final position of a directed limb movement, under varying conditions of visual information. Although such studies are deficient in their description of the behaviour, they have, nonetheless, contributed a great deal to our understanding of the visual control of limb movements. Both the manner in which visual information is used to initiate a motor response, and how this information is used throughout the behaviour for its control, have been addressed by these studies.

The work of Paillard and his co-workers (Paillard, 1982) perhaps demonstrates best the insight which has been gained through such approaches. He has looked at the accuracy of visually guided pointing of the limb in a situation which limited feedback of the relative positions of the arm and target to various portions of the trajectory. A significant improvement in accuracy was found when visual feedback was allowed and particularly when it was present "in the final phase of the movement" (Paillard, 1982, page 373). He has also used the accuracy of manual pointing to a visual target as a measure of the adaptation of subjects to prismatic distortion of visual space. By varying the amount and type of visual information available to the subject he has found evidence that peripheral visual processes make use of "movement cues...to control the direction of the trajectory" (page 381), while central vision uses "position cues" of the relative positions of the hand and target to control "the error-detecting mechanism involved in the late phase of adjustment of a reaching movement" (page 381). This differential use of information may relate to the differences in the hemispheric motor control of proximal and distal musculature, which has been discussed above with respect to studies of split-brain monkeys (Paillard and Beaubaton, 1975). The time required to process visual information, and modify the production of the movement, has also been the subject of investigation. Keele and Posner (1968) suggested, on the basis of pointing accuracy scores, that at least 200 ms is needed in order to modify the trajectory of movement on the basis of visual information. More recently Beaubaton and Hay (1982) have suggested that processing times of less than 100 ms may be possible. Despite these uncertainties of the time required to process information, for reaches to visual targets, visual information may contribute not only to the initial specification of the motor program but may also provide a basis for the modification of the program throughout its production.

In order to determine how this use of visual information affects the actual motor output during the production of visually guided pointing, Hay (1979) and Carlton (1981) analyzed video and film records of the limb movements. In a study of visual motor development, Hay (1979) observed the effects of wearing visual displacing prisms on the reaching of children of different ages. He reported that for the oldest children (9-11 years), changes in the trajectory of the movement which compensated for the prismatic displacement occurred primarily in the late stages of the movement. Carlton (1981) recorded subjects pointing to a visual target with a hand-held stylus under conditions which restricted the visual feedback of hand position to various portions of the movement. As with the study of Hay (1979), only movement in two dimensions was analyzed although movement in three dimensions was possible. He also suggested that corrections in the trajectory of the movement, based on visual information, were produced with a very brief processing time of less than 200 ms. These corrections were defined as changes in acceleration of the stylus movement, which occurred again in the later stages of the movement when the velocity was low. Carlton (1981) discussed at length the similarities between the visual control of the discrete limb movements which he had observed, and the control of saccadic eye movements. However, he did not require the subjects to look to the target to which they were pointing, and had no record of any eye movements produced by the subjects. The studies of Hay (1979) and Carlton (1981) illustrate the wealth of information which is provided by the analysis of video or film records of the movements, but many important questions, such as the roles of eye movements, and the position of the target in visual and extrapersonal space, must be addressed.

As I have discussed above, the production of eye movements is most often an integral part of visually guided limb movements. The importance of this interaction has been recognized and discussed by many researchers such as Carlton (1981) and Paillard (1982). Although there have been relatively few studies which have looked at movements of the eyes and limbs, directed to a common target, combined ocular and manual tracking has received some attention (Steinbach and Held, 1968; Steinbach, 1969; Mather and Lackner, 1980). These experiments have demonstrated that information about limb position can affect ocular tracking but the interaction of the two systems in the production of discrete movements remains unclear. Restriction of the arm movement to rotation about one joint simplifies the mechanics of the limb motor system and makes it more comparable to the ocular motor system, but the movements which are produced are quite different from the majority of movements in which the two systems interact. Manual tracking is clearly a well developed human skill and is used for some visual motor behaviours such as driving an automobile. However, the significance of manual pursuit movements for everyday human activity is much less clear than that of the discrete movements which comprise most human visually guided limb movements.

The only studies which have looked at the performance of the eyes and limbs in a task involving discrete movements, have been those of Prablanc, Eschallier, Jeannerod and Komilis (Prablanc, Eschallier, Komilis and Jeannerod, 1979a; Prablanc, Eschallier, Jeannerod and Komilis, 1979b). In these studies they compared the latency, duration and accuracy of both movements under a number of conditions of visual information. On the basis of a "loose correlation" (Prablanc et al., 1979a, page 123) between the latency to move the eyes and hand they suggested that the two motor systems "seem to be organized more in parallel than in series" (page 123). Further support for a parallel organization was gained by their failure to find a relationship between hand and eye errors. Visual information of the relative positions of the hand and target was found to improve pointing accuracy relative to open-loop reaching, even when the subjects were only allowed to view their hand either before movement was initiated, or while the limb was actually moving. As long as the target remained visible throughout the reach the production of eye movements significantly improved accuracy, when compared to reaches performed without accompanying eye movements.

When the target was extinguished at the start of the eye movement, pointing accuracy was no different than reaches to persistent targets without eye movements. Thus it was clear that foveation of the target, and not simply the production of an eye movement, was responsible for the increased accuracy of the movement. By measuring directly eye position Prablanc et al. (1979a,b) were able to understand better the nature of the visual information which could be used to guide the limb movement, and were also able to look at the relationship between the two systems. Such an approach can be strengthened greatly by the addition of kinematic measures of the limb movement to describe further the characteristics of its production.

The present series of studies was designed to begin with a more comprehensive description of the effects of varying amounts of visual information on the kinematics and accuracy of visually directed pointing movements. Unrestricted limb movements through three dimensions were employed, to approximate the normal reaching behaviour used to acquire objects in the environment. Video records of the subjects' reaching provided the data base for the description of the limb movement. In addition to an analysis of the kinematics and accuracy of pointing, the present studies were designed to compare the performance of the ocular and manual motor systems on the basis of their latency and accuracy, when both were directed to a common visual target. The first study incorporates these two approaches in one experimental paradigm. It includes analyses of the limb movement characteristics, and a comparison of the performance of the eye and limb motor systems. The second and third studies address specific questions raised by the analyses of the first study.

STUDY I

The Spatial and Temporal Characteristics of Visually Directed Limb Movements and Comparison of Ocular and Manual Performance

Summary

The present study attempted to describe the spatial and temporal characteristics of limb movements directed to small visual targets, presented at 10 or 20 degrees eccentric to a central fixation point. Eight young, right-handed adults with no known visual deficit participated in the study. They were asked to point quickly and accurately to the position on a screen at which the target light was presented. All reaches were recorded by two video cameras, and these records provided information of the position of the limb in three-dimensional space at a temporal resolution of 17 ms. The subjects' eye movements were monitored by infrared corneal reflection and were recorded on magnetic tape. The findings suggested that visual information was used to modify the programming of the limb movement during a deceleration phase, as the target was approached. If the target was visible throughout the movement this deceleration phase was prolonged and pointing accuracy was improved. Reaches to targets presented to the ipsilateral visual field and ipsilateral side of the body as the hand being used to reach were initiated more quickly, completed more rapidly and were more accurate than reaches to targets presented in the contralateral visual field which required that the subjects reach across their body axis. Although these results suggested the existence of a hemispherically organized network responsible for the programming of these visually directed limb movements, the confounding of the target position relative to the visual field and target position relative to the body axis made it difficult to determine how spatial information is integrated by such a network. The ocular and manual

motor systems were compared on the basis of movement latency and accuracy. A statistically significant correlation in movement latencies as well as similar magnitude effects of target laterality and the hand used for pointing on movement latency, suggested that the processing of sensorimotor information for the ocular and manual motor systems involves closely associated or common neural areas. A positive correlation of eye and limb movement accuracy for reaches to briefly presented targets suggested that, in the absence of feedback information of the target position, the point in space which the eyes fixate may be used as the target for a pointing movement by the limb.

Introduction

Visually guided movements of the limbs are a basic and important component of daily human activity. It is by such movements that we are able to reach to, and acquire objects of interest within the environment surrounding us. Despite the importance of these behaviours to man and other primates, the manner in which visual information is used in their motor programming is not well understood. Motor physiologists have examined the characteristics of relatively simple limb movements extensively (Desmedt and Godeaux, 1978; Bizzi, Dev, Morasso and Polit, 1978; Hallet and Marsden, 1979; Polit and Bizzi, 1979; Cooke, 1980; Brown and Cooke, 1981; Bizzi, Accornero, Chapple and Hogan, 1982; Hore, Vilis and Flament, in press) and have established well-defined principles and mathematical models to describe the performance of the skeletal-muscular system. Only recently has this approach been extended to more complex movements (Morasso, 1981; Soechting and Lacquaniti, 1981; Abend, Bizzi and Morasso, 1982; Lacquaniti and Soechting, 1982). While these studies have described the spatial and temporal characteristics of limb movements, they have not dealt with the manner in which visual information of the location of a goal object in space is used in the programming and production of the behaviour.

Researchers who have been interested in the use of visual information for the control of limb movements have generally approached the problem differently, by looking at the accuracy of the end point of the movement under various conditions of visual information (see for example, Paillard, 1982). Additional measures of the latency and duration of the movement (Keele and Posner, 1968; Beaubaton and Hay,

1982) have provided insight into the temporal limitations on the processing of visual information, but have not adequately described how the movements are performed. The present study was designed as a synthesis of these two approaches, in order to describe better the production of visually guided movements of the limbs and to investigate the factors which affect this performance. To accomplish this, video records were made of unrestricted limb movements directed to visual targets. From these records the latency and accuracy of movement were analyzed as were the form of the trajectory, and the velocity of movement throughout the trajectory.

The possible use of visual feedback during production of the movement was examined by comparing pointing to briefly illuminated targets with pointing to persistent targets. Beaubaton and Hay (1982) have shown that the accuracy of even very rapid movements is greater when visual feedback of the limb and target positions is available. Paillard (1982) has suggested that the type of visual feedback information which is used, differs for central and peripheral visual processes. In the present study subjects were restricted to the use of peripheral vision for half of the experimental trials by requiring them to maintain central fixation while pointing to a peripheral target. For the other trials they were allowed to make eye movements to the target positions and thus were able to make use of central visual processes in the guidance of the movements. Since hemispheric specialization for the control of human behaviour is such a prevalent finding, reaching into either visual hemifield with either hand was analyzed. Thus it was possible to look for differences in performance which could have reflected a lateralized or hemispheric organization of the neural systems responsible for these movements.

When studying the use of visual information in the production of visually guided limb movements, the characteristics of the accompanying eye movements must also be considered. Most directed reaching movements involve the coordinated interaction of these two motor systems and often include orienting movements of the head and body as well. Despite this fact, we have very little knowledge of how the stimulus characteristics and response requirements affect these two motor systems when they are both directed to a target. The most elegant study of this problem has been conducted by Prablanc and his co-workers (Prablanc, Eschallier, Jeannerod and Komilis, 1979a; Prablanc, Eschallier, Komilis and Jeannerod, 1979b), who compared the eyes and hands on the basis of latency, duration and accuracy of movement to visual targets. As a result of the failure to find a significant correlation between the errors of the two systems and on the basis of what was considered a "loose correlation" (Prablanc et al., 1979a, page 123) in the latency to initiate movement, they suggested that the two motor systems "seem to be organized more in parallel than in series" (page 123). The question of how the motor programming of the two systems is related under different conditions, and how the production of a visually directed movement is affected by these conditions, was examined further in the present study.

The various experimental conditions made it possible to compare the performance of each limb, for targets presented to each visual field. In addition, the role of eye movement production on the characteristics of the limb movement was examined. By varying the duration of the targets' presence it was also possible to examine the use of visual feedback information on the movements of the eyes and limb. All of these issues were studied within the context of a comprehensive description of visually guided reaching, in order to understand how the processing of visual information and the programming of motor output are integrated in the production of this behaviour.

Methods

Subjects

Subjects were 8 right-handed volunteers, 4 males and 4 females, ranging in age from 23 to 35 years. None of the subjects required visual correction.

Apparatus for Data Collection

During testing the subject was seated facing a 1 m by 1 m back-projection screen with his head held in a chin and head rest. The distance between the subject's eyes and the screen was 50 cm. A start platform, which contained a microswitch, was situated immediately in front of the base of the chin rest. All reaches were initiated from this platform, although the actual position of the hand and fingers was allowed to vary slightly across trials. A fixation light was illuminated directly in front of the subject at approximately eye level on the screen and remained illuminated throughout the test session. One degree diameter target lights were presented at four positions, 10 degrees and 20 degrees of visual angle to either side of the fixation point, in the horizontal plane. They were illuminated for either 100 ms (brief target), or until the subject completed the reach (persistent target). The luminance of the screen was 60 cd/m^2 while the target luminance was 73 cd/m^2. The targets were therefore of 9.3 percent contrast (percent contrast = (Imax - Imin) / (Imax + Imin) X 100).

All reaches were videotaped using two rotary shutter cameras (Sony RSC 1020) which provided clear images at 60 frames per second. One camera viewed the subject from the right side, while a 1 m by 0.5 m mirror suspended at a 45 degree angle above the subject provided a top view for the second camera. The two camera signals were synchronized and fed to a split screen of a single video frame. Onset of the target was marked on the videotape by the illumination of a row of light-emitting diodes, located outside of the subject's line of sight.

Horizontal eye position was monitored by the use of infrared corneal reflection (Eye Trac Model 200, G&W Applied Science Laboratories), and was displayed on a video monitor, as well as stored on one channel of an FM magnetic tape recorder (Model A, A. R. Vetter Co.). The onset of the target light and the release of the start platform microswitch were recorded as a voltage change on separate channels of the same tape recorder.

Procedure

Test sessions consisted of four blocks of 32 trials. Each hand was tested separately in alternating blocks. The subject was asked to use his index finger to point quickly and accurately, immediately following illumination of the target. All trials began with the subject fixating the central light. After a variable interval following a "ready" command, the experimenter illuminated one of the targets. The position and duration of the target was varied randomly throughout each block of trials. Each target was therefore presented 8 times per block, 4 at the brief duration and 4 at the persistent duration. Practice trials were given at the start of each block to familiarize the subject with the test conditions.

For half of the blocks, the subject was instructed to look to the targets as well as point to them (Eye Movement Condition). For the other two blocks, he was instructed to maintain fixation on the central light while pointing (No Eye Movement Condition). During the No Eye Movement Condition the fixation of the subject was observed on a video monitor. Those trials in which the subject failed to maintain fixation were repeated at the end of the block. Horizontal eye position was calibrated at the start of both Eye Movement blocks and a calibration signal was recorded on magnetic tape by having the subject fixate each target for a 2 second period. The order of eye movement condition, and hand used was counterbalanced across subjects. The test session lasted for approximately 50 minutes, and the subject was given rest periods between blocks if fatigued.

Apparatus for Data Analysis

The videotape record was analyzed with the use of a Sony Video Motion Analyzer, which allowed stable single frame advancement of the video image. Each frame was projected onto the surface of a digitizing tablet interfaced with an Apple II Plus microcomputer. A whie card containing 0.5 mm black lines which bisected one another, was placed such that the intersection of these lines was situated at the tip of the index finger. Initiation of a reach was defined as the first visible movement of the index finger on the top view of the subject. The number of frames from the target onset to first finger movement served as a measure of response latency. The position of the index finger for each frame was then stored by the computer as X and Y coordinates, by touching the finger position with the tablet pen. This process was continued until the subject touched the screen. The forward and lateral movement of the reach was taken from the top view of the subject, while the vertical movement was taken from the side view. This three-dimensional information was stored as data files to be analyzed at a later time. Analysis of the data files produced a number of measures derived from the vector distance between positions on successive frames. These measures included the total distance of the reach; the mean velocity of the reach; the velocity at each frame; the maximum velocity; and the time at which maximum velocity was attained. The difference between the final finger position and the actual target position provided measures of error in the lateral and vertical dimensions as well as total vector sum of these two error scores. The final position of the finger was taken as the first point of contact of the finger with the screen and therefore did not include any corrections performed after the screen was touched.

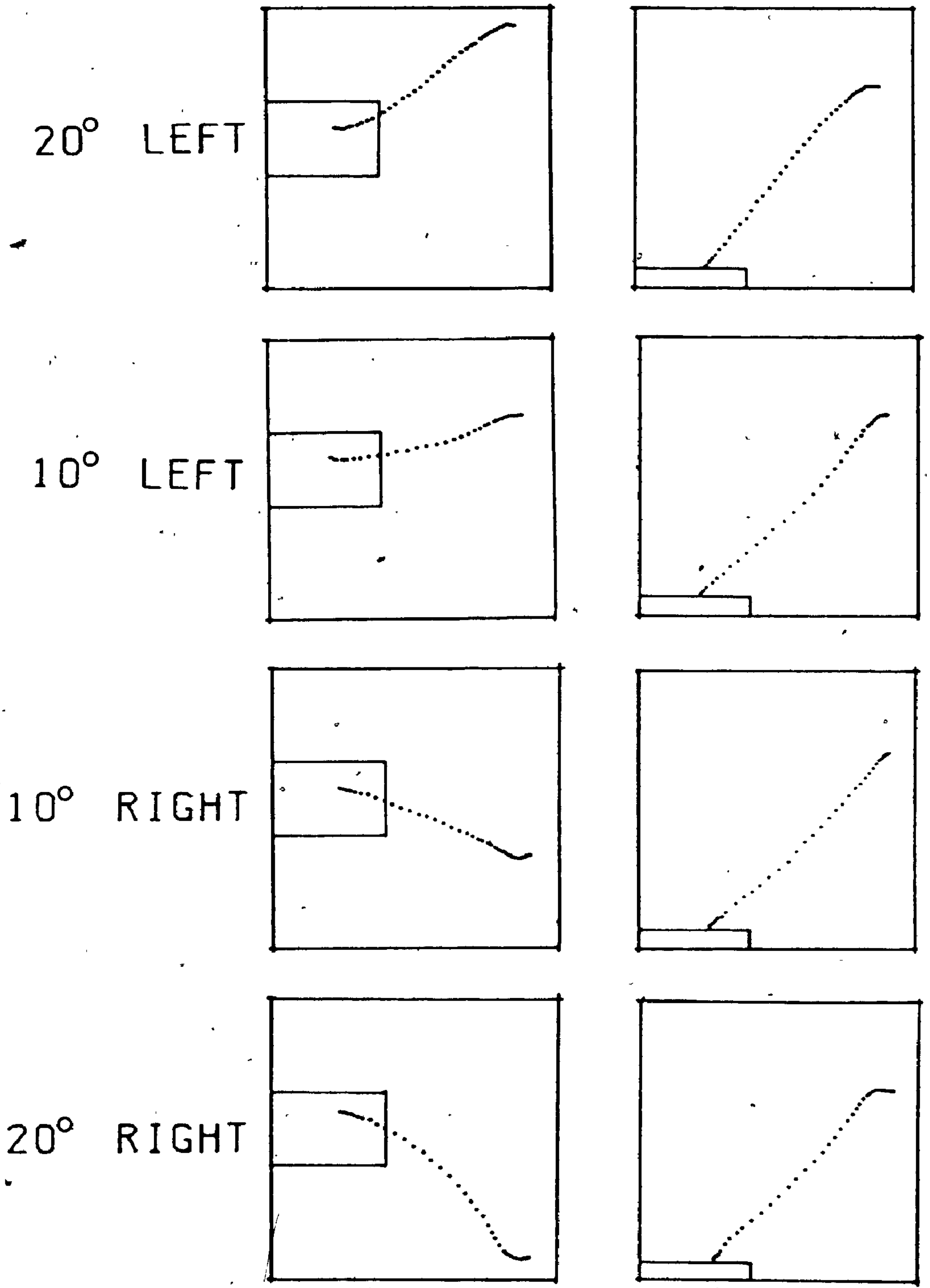
Analysis of the FM tape record was also undertaken. Hard copy of the FM record was produced by means of a polygraph (Grass Model 7, Grass Instrument Co., Quincy Massachusetts) with a paper speed of 30 mm/s which provided a temporal resolution of approximately 17 ms. The time from stimulus onset to the release of the start platform microswitch provided a second measure of hand latency. Analysis of horizontal eye position records yielded measures of eye movement latency and accuracy with a resolution for the eye position of .5 mm, which equaled .5 degrees.

Results

In the present study the instructions to the subjects were deliberately left open-ended and there were no specific requirements placed upon the speed and accuracy of the subjects' responses. This resulted in a great deal of between-subject variability on the response measures although there were consistent within-subject differences under the various experimental conditions. For the figures which follow, standard error bars have not been included since they serve only to illustrate the between-subject differences and do not add to the illustration of the important between-condition comparisons.

Despite the variability in the performance of this task, both between and within individual subjects, some general statements are possible. All subjects performed the task quickly and accurately. Figure 1 illustrates examples of a reach to each of the 4 targets by one subject with both the top and side view plotted for each movement. Within 500 ms following target illumination the subjects initiated a reach, which consisted of an acceleration to maximum velocity, followed by a deceleration until the screen was contacted. Since the points in Figure 1 illustrate the finger position on successive frames, the separation between points indicates the velocity of movement. On average the acceleration phase constituted the first third of the total duration of the movement. The relatively longer deceleration phase usually included a period of low velocity movement, just before the finger came into contact with the screen. Previous studies have reported both straight line, and slightly curved limb movement trajectories, so an attempt was made to quantify how close the trajectories fit to a

Figure 1. Examples of the trajectories of reaches to targets at all four positions, performed by one subject, with the right hand. The column of figures on the left represent the top view of the trajectory, while the figures on the right represent the side view of the same trajectory. Target positions are indicated at the left of each pair of trajectories. The position of the start platform is indicated by the rectangle on the left of each figure. The dots represent the position of the tip of the index finger, in successive frames, following the onset of movement. Note the slight curvature of the trajectories and the relatively low velocity of movement as the target was approached.


20° LEFT
10° LEFT
10° RIGHT
20° RIGHT

straight path. Although the trajectories of the subjects' reaches approximated a straight line there were consistent, measurable deviations from this. A ratio of the minimum necessary distance between the initial and final positions of the finger to the actual distance travelled, gave an indication of the efficiency of the movement. This ratio ranged from .86 to .96 between individuals but averaged to .94, and was not affected by the various experimental conditions. The trajectory, in many cases, showed a slight overshoot of the final position, in both the lateral and vertical dimensions, which was corrected at the end of the movement. These corrective movements contributed to the deviation of the trajectory from a straight line path. The amount of such overshoot varied considerably but a corrected undershoot in the trajectory was rarely encountered. The corrected overshoot of final position in the movement trajectory, did not correspond to an overshoot of the actual target position since the vast majority of reaching errors were underestimates of the actual target position. Although the shape of the trajectory was not analysed quantitatively, a number of measures were collected which described the spatial and temporal characteristics of the limb movement as well as the accompanying eye movements.

Two separate analyses were performed on this body of data. Analysis I investigated the kinematics and accuracy of the limb movement. Analysis II studied the relationship between the eye and limb movements, on the basis of latency and accuracy, for those blocks of trials in which the subject was asked to look as well as point to the targets.

Analysis I

A total of 8 measures were extracted from the videotape record of each reaching movement. These measures were divided into those that describe the temporal and spatial-temporal characteristics of the movement and those that describe the accuracy of the final position of the movement. The measures that describe the temporal and spatial-temporal characteristics of the movement are: 1) the latency to initiate the first visible finger movement following target illumination; 2) the maximum velocity attained during the movement; 3) the latency to attain maximum velocity following the initiation of the movement, or the duration of the acceleration phase of the movement; 4) the mean velocity of the movement; and 5) the duration of the movement. The accuracy of the final finger position was recorded as an error score, in degrees of visual angle, between the positions of the target and the index finger. Error in the lateral dimension, the vertical dimension, and the vector sum of these errors, was calculated for each reach.

Separate analyses of variance were carried out for each of these measures. The analyses compared performance under each of the experimental conditions, across all subjects. A completely balanced design was employed such that all interactions were possible. Each of the factors had two levels. They were: 1) the target duration--brief and persistent targets; 2) the target eccentricity--10 and 20 degrees; 3) the hand used for responding--left and right; 4) the visual field in which the target was presented--left and right; 5) the nature of the response--arm movements alone (NEM) or arm movements with accompanying eye movements (EM). There were 4 trial repetitions within each cell.

The mean of the 4 trials was calculated for each measure and all analyses were conducted on these cell means. Analysis of the cell means served to reduce variability in the scores which could have resulted from inaccuracies in the measurement technique.

Temporal and Spatial-temporal Measures. These analyses were conducted in order to relate the performance of this task, in terms of the velocity characteristics, to the performance of less complex limb movements which has been documented previously. Also, these analyses examined the relationship of these velocity measures to other characteristics of performance, such as the duration and accuracy of movement, which have been examined in previous studies of the use of visual information in directed limb movements. A consistent pattern of effects was evident which depended upon the interaction of three factors. These were: the hand used for responding; the visual field in which the target was presented; and the eccentricity of the target. For reaches to more eccentric targets, the latency to initiate the movement was greater, the acceleration phase of the reach was prolonged, a higher maximum velocity was attained, and the duration of the movement was increased. All of these effects were revealed as statistically significant main effects of target eccentricity and are summarized in Table I.

Another factor which affected the spatial-temporal characteristics was whether the reach was directed to a target presented to the visual field ipsilateral or contralateral to the hand used for reaching. This effect was demonstrated by a Hand x Field interaction which was statistically significant ($p < .05$) for all five characteristics (see

TABLE I

Effect of Stimulus Eccentricity on the Temporal and Spatial-temporal Measures of the Limb Movement

	Eccentricity of Targets		Significance Level		
	10°	20°			
Latency (ms)	390.8	410.7	F1,7	7.98	$p < .05$
Maximum Velocity (cm/s)	155.8	163.3	F1,7	34.26	$p < .001$
Maximum Velocity Latency (ms)	213.9	222.2	F1,7	18.87	$p < .01$
Mean Velocity (cm/s)	78.6	80.7	F1,7	3.26	$p > .10$
Duration (ms)	639.0	672.1	F1,7	10.01	$p < .05$

Appendices IIa, IIb). The ipsilateral and contralateral conditions are compared for each measure in Figures 2 through 6. Ipsilateral reaches were initiated with a lower Latency than contralateral reaches (Figure 2), the acceleration phase of ipsilateral movements was shorter (Figure 3), and a higher Maximum Velocity was attained (Figure 4). The Mean Velocity of ipsilateral reaches was also greater (Figure 5), and resulted in a shorter movement Duration (Figure 6). Comparison of the velocity/time functions of ipsilateral and contralateral reaches, in which the velocity for each frame following movement onset was averaged across all subjects and all trials, also demonstrates these findings (Figure 7).

In general the difference between ipsilateral and contralateral reaches was more pronounced for the left hand, which was the non-dominant hand in all subjects. This can be seen in Figures 3 through 6. While the performance of the two hands was quite comparable for contralaterally directed reaches, higher Maximum and Mean Velocities, and a shorter duration of acceleration were present for ipsilateral reaches performed by the left hand. As a result of these Hand x Field interactions, reaches into the left visual field differed from reaches into the right visual field on these measures, and significant main effects of Visual Field were present for the Maximum Velocity ($\underline{F}(1,7) = 52.66$, $\underline{p} < .001$), Latency to attain Maximum Velocity ($\underline{F}(1,7) = 9.11$, $\underline{p} < .05$), and Mean Velocity ($\underline{F}(1,7) = 52.42$, $\underline{p} < .01$) of the movement.

The effect of Target Eccentricity was found to depend upon whether the reach was directed ipsilaterally or contralaterally. This finding was revealed by a Hand x Field x Eccentricity interaction which was

Figure 2. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on latency to initiate limb movement. ◇ - Left hand; △ - Right hand. Contralateral reaches were initiated at a longer latency for both limbs.

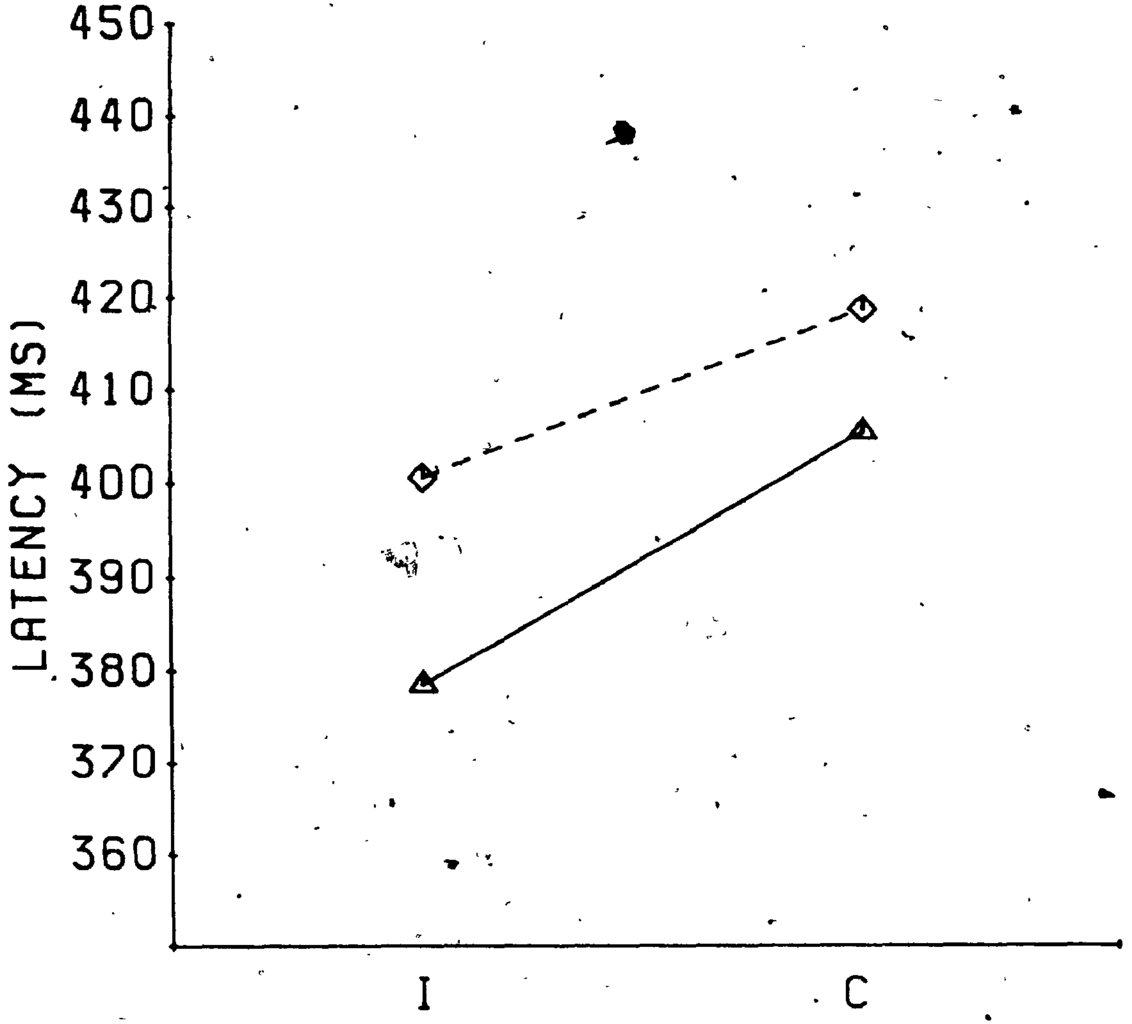

LATENCY (MS)
450
440
430
420
410
400
390
380
370
360
I
C

Figure 3. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on latency to attain maximum velocity. ◇ - Left hand; △ - Right hand. The duration of the acceleration phase of the movement was shorter for ipsilateral reaches by either limb.

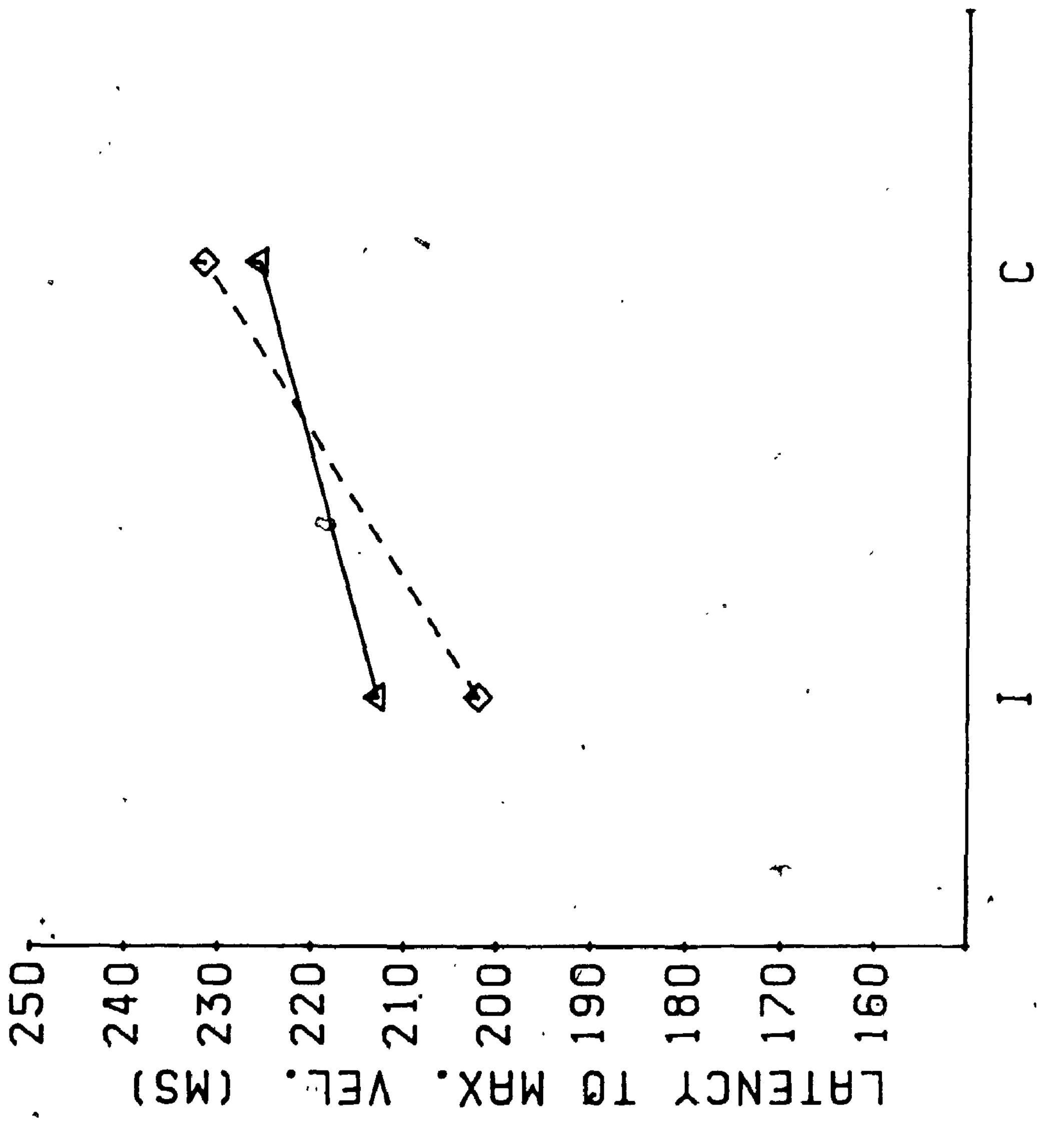

LATENCY TO MAX. VEL. (MS)
250
240
230
220
210
200
190
180
170
160
I
C

Figure 4. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on maximum velocity of limb movement. ◇ -Left hand; △ - Right hand. Reaches to ipsilateral targets attained a higher maximum velocity than reaches to contralateral targets. This effect was largest for reaches by the left hand.

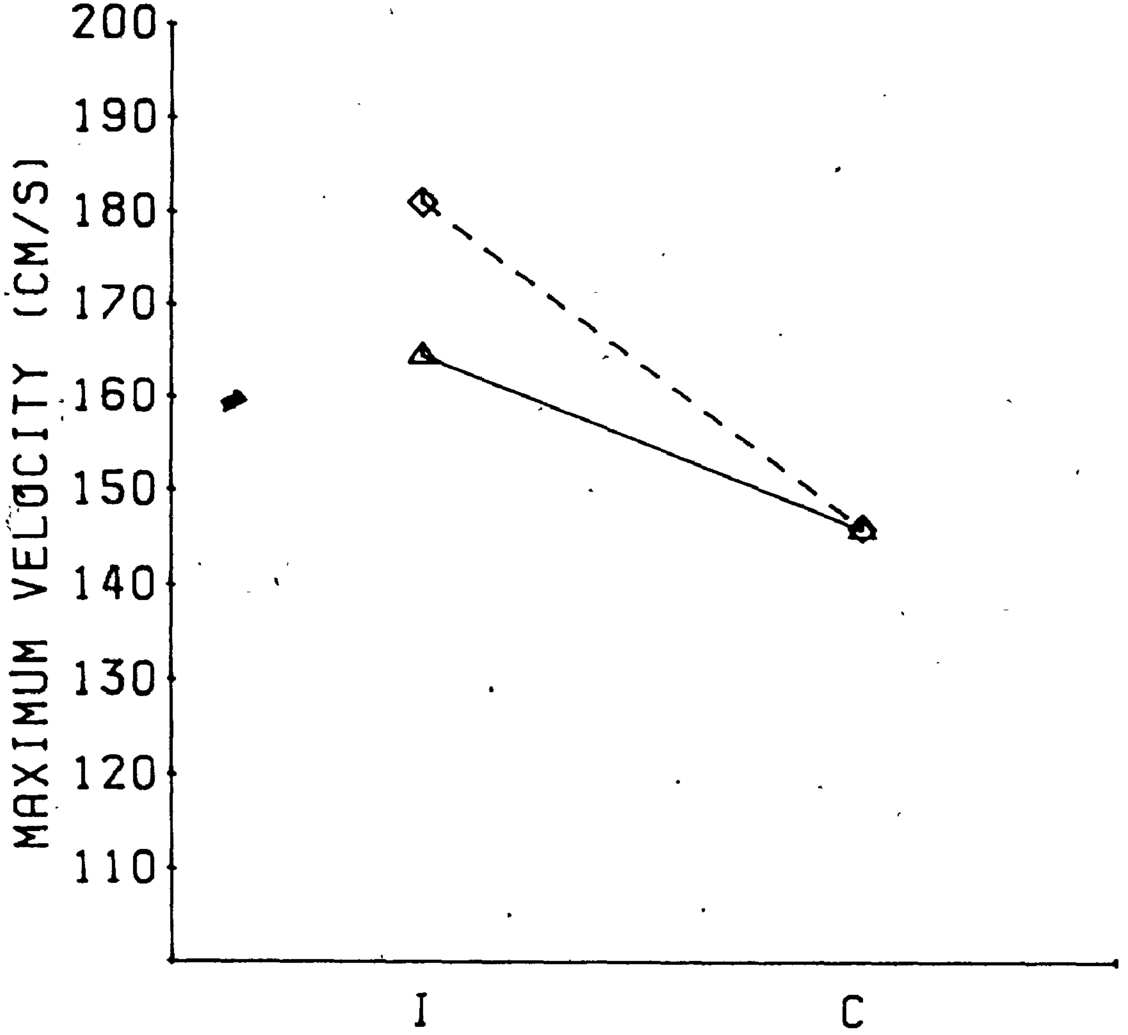

MAXIMUM VELOCITY (CM/S)
200
190
180
170
160
150
140
130
120
110
I
C

Figure 5. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on mean velocity of limb movement. ◇ - Left hand; △ - Right hand. The mean velocity of reaches to ipsilateral targets was higher than the mean velocity of reaches to contralateral targets.

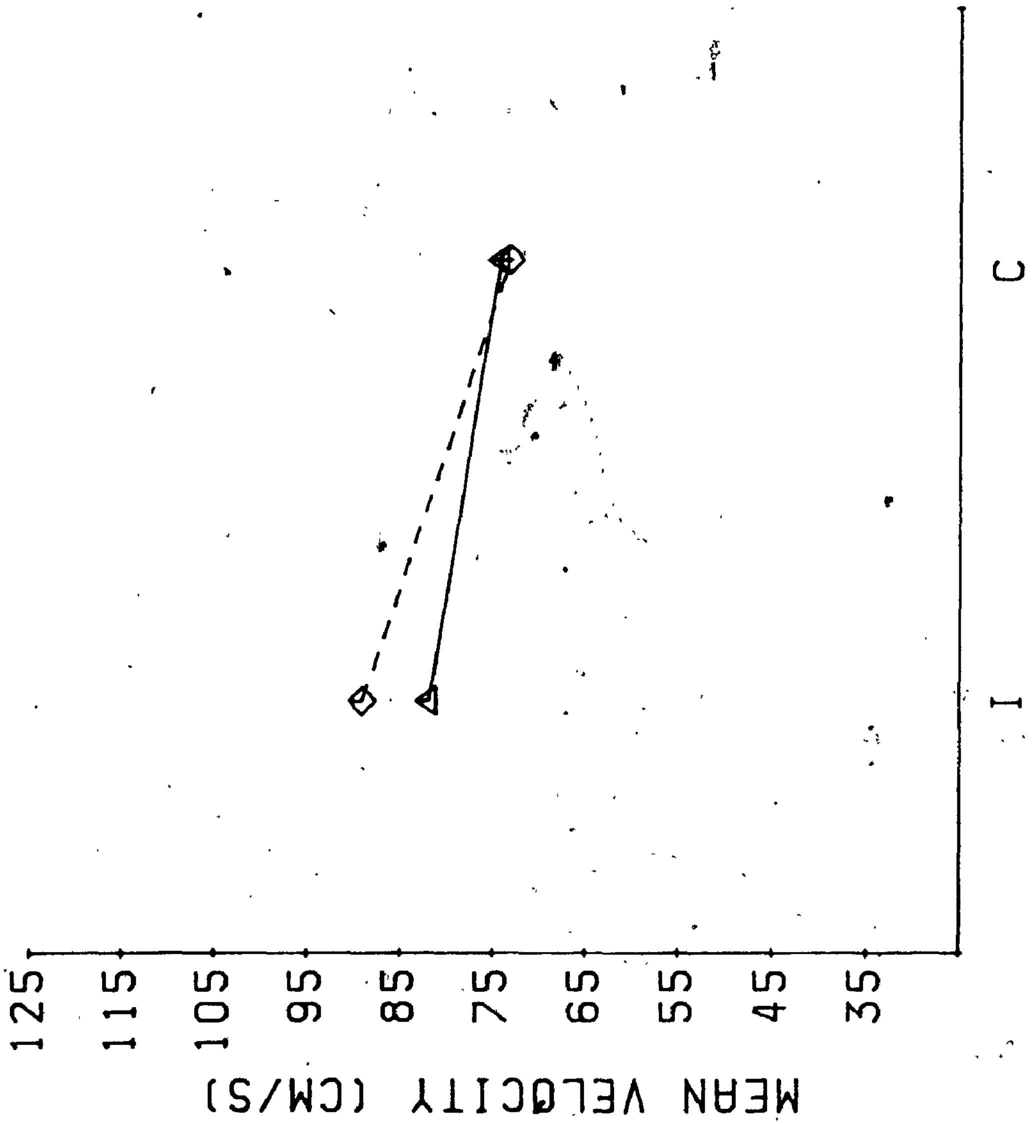

MEAN VELOCITY (CM/S)
125
115
105
95
85
75
65
55
45
35
I
C

Figure 6. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on duration of limb movement. ◇ - Left hand; △ - Right hand. Reaches to contralateral targets required a longer period of time to complete the movements than reaches to ipsilateral targets.

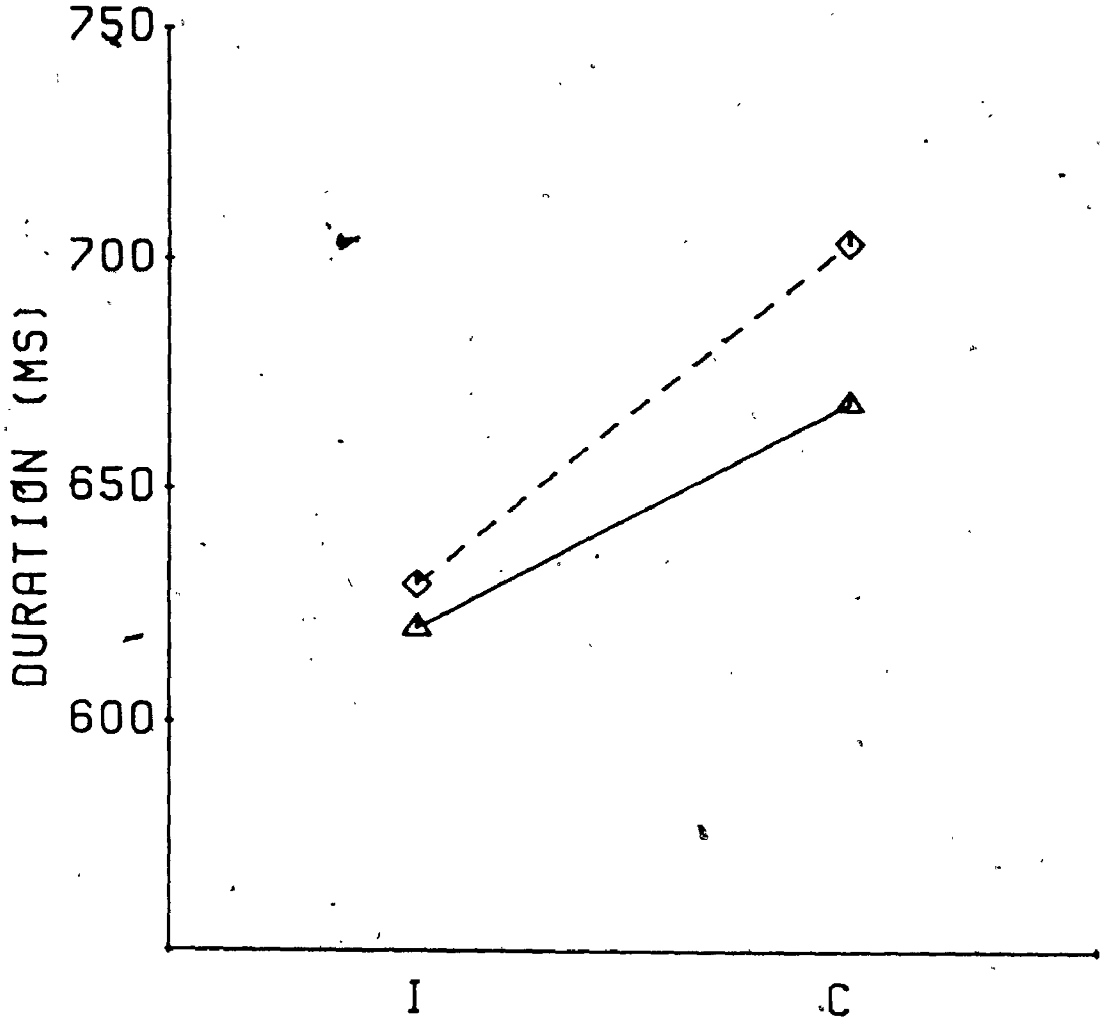
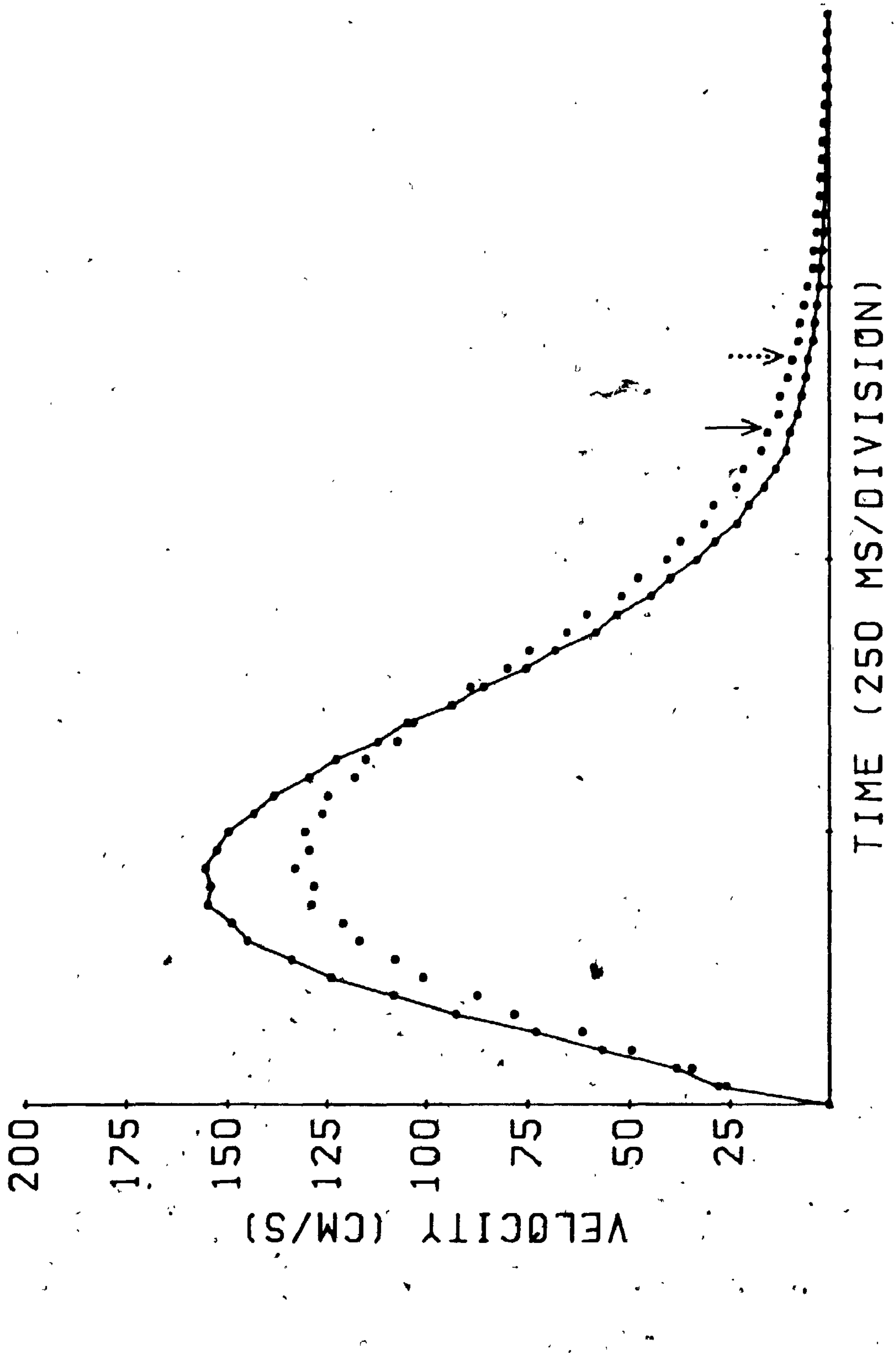

750
700
650
600
DURATION (MS)
I
C

Figure 7. Velocity of limb movement as a function of time following movement onset. Reaches to Ipsilaterally presented targets are indicated by ●-●-●; reaches to Contralaterally presented targets are presented by ● ● ●. The mean duration of ipsilateral reaches is indicated by ↓: the mean duration of contralateral reaches is indicated by ⇣. Each point represents an average velocity over all trials by all 8 subjects for a given time following initiation of a reach. The data indicate acceleration to a higher maximum velocity and a more rapid deceleration for reaches to ipsilateral as compared to contralateral targets. Note also that the general shape of the velocity profile of both reaches is skewed with an initial, rapid acceleration phase, followed by a more prolonged deceleration as the target was approached.


200
175
150
125
100
75
50
25
VELOCITY (CM/S)
TIME (250 MS/DIVISION)

significant for Latency ($F(1,7) = 5.61$, $p < .05$), Maximum Velocity ($F(1,7) = 32.16$, $p < .001$), Mean Velocity ($F(1,7) = 33.64$, $p < .001$), and Duration ($F(1,7) = 28.89$, $p < .01$) of movement. Pairwise comparisons were made between 10 and 20 degree eccentric targets, within the conditions of hand used and ipsilateral/contralateral reaching directions. These results are summarized in Figures 8 through 11. It is clear from these data, that the main effect of Target Eccentricity on the measures noted above may be accounted for, in large part, by an effect on either ipsilateral or contralateral reaches. The increase in Latency with increasing eccentricity averaged 30 ms for contralateral reaches, while this increase was only 12 ms for ipsilateral reaches (Figure 8). Both Maximum Velocity (Figure 9) and Mean Velocity (Figure 10) increased for more eccentric reaches, only when the targets were presented in the ipsilateral visual field (significant pairwise comparisons, $p < .05$, with Tukey's HSD statistic). Contralaterally directed reaches did not demonstrate these increases, and a decrease in Mean Velocity with increasing eccentricity was noted for the left hand (HSD, $p < .05$). This resulted in a long duration of reaches to more eccentric contralateral targets, particularly for the left hand (Figure 11).

Ipsilaterally directed reaches were performed quite differently from contralaterally directed reaches. In general, ipsilateral reaches were performed more efficiently. They were initiated more quickly and completed in a shorter period of time. In addition, ipsilateral reaches demonstrated an increase in Maximum and Mean Velocity when confronted with a more eccentric target but contralateral reaches did not.

Figure 8. Effect of target eccentricity (10 and 20 degrees of visual angle) on the latency to initiate movement of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. Note that latency increased with increased target eccentricity overall, but that this increase was larger for contralaterally presented targets. Note also that reaches by the right hand were initiated at a lower latency than those by the left hand. This difference approached, but did not attain statistical significance.

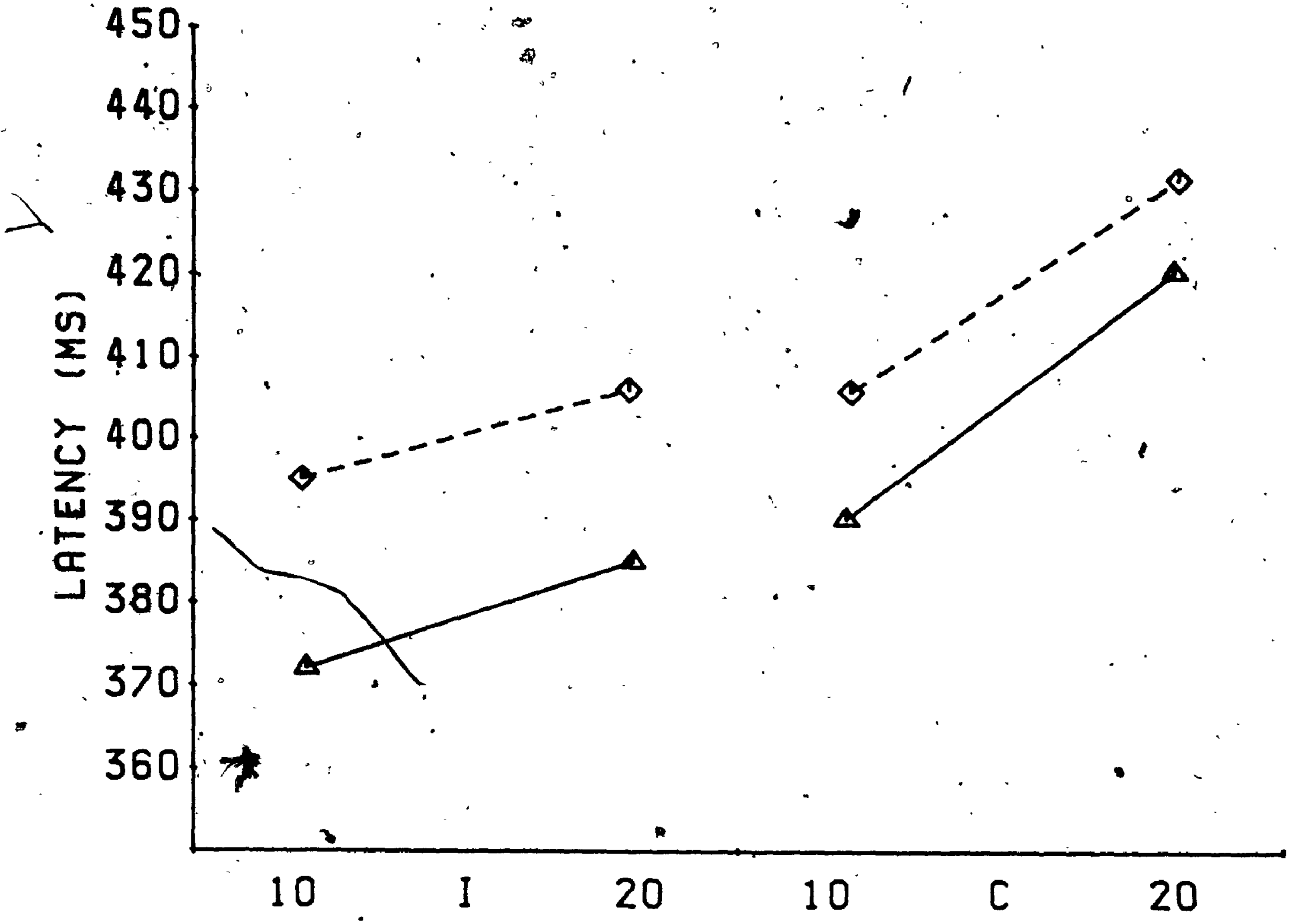

LATENCY (MS)
450
440
430
420
410
400
390
380
370
360
10
I
20
10
C
20

Figure 9. Effect of target eccentricity (10 and 20 degrees of visual angle) on the maximum velocity of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. The maximum velocity was higher for ipsilateral presented targets as compared to contralateral targets. For ipsilateral reaches the maximum velocity attained during the trajectory was greater for reaches to more eccentric targets, but for contralateral reaches no such changes in maximum velocity were evident.

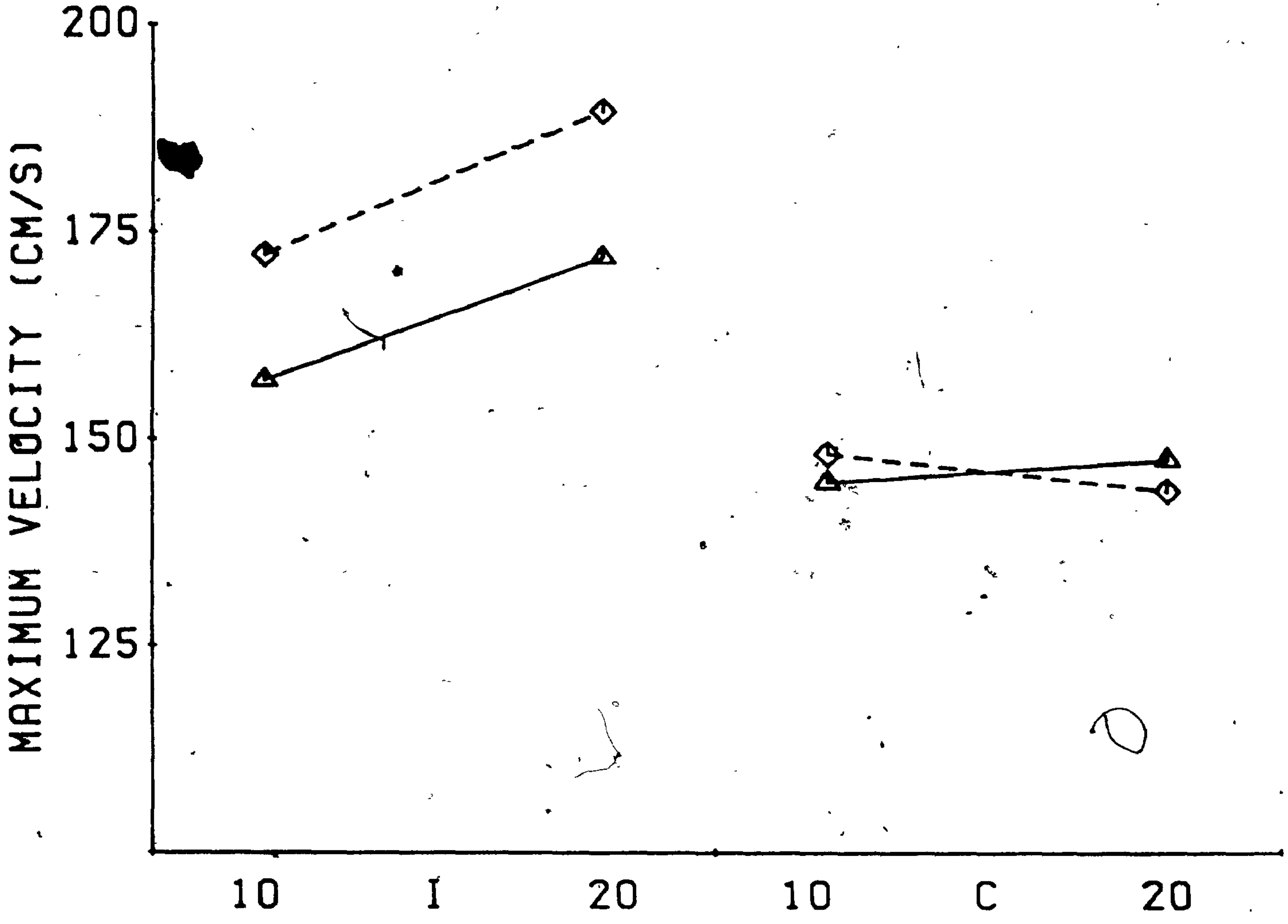

MAXIMUM VELOCITY (CM/S)
200
175
150
125
10
I
20
10
C
20

Figure 10. Effect of target eccentricity (10 and 20 degrees of visual angle) on the mean velocity of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. Mean velocity was higher for ipsilateral targets as compared to contralateral targets. For ipsilateral reaches the mean velocity of the movement was greater for reaches to more eccentric targets, but for contralateral reaches no such changes in mean velocity were evident.

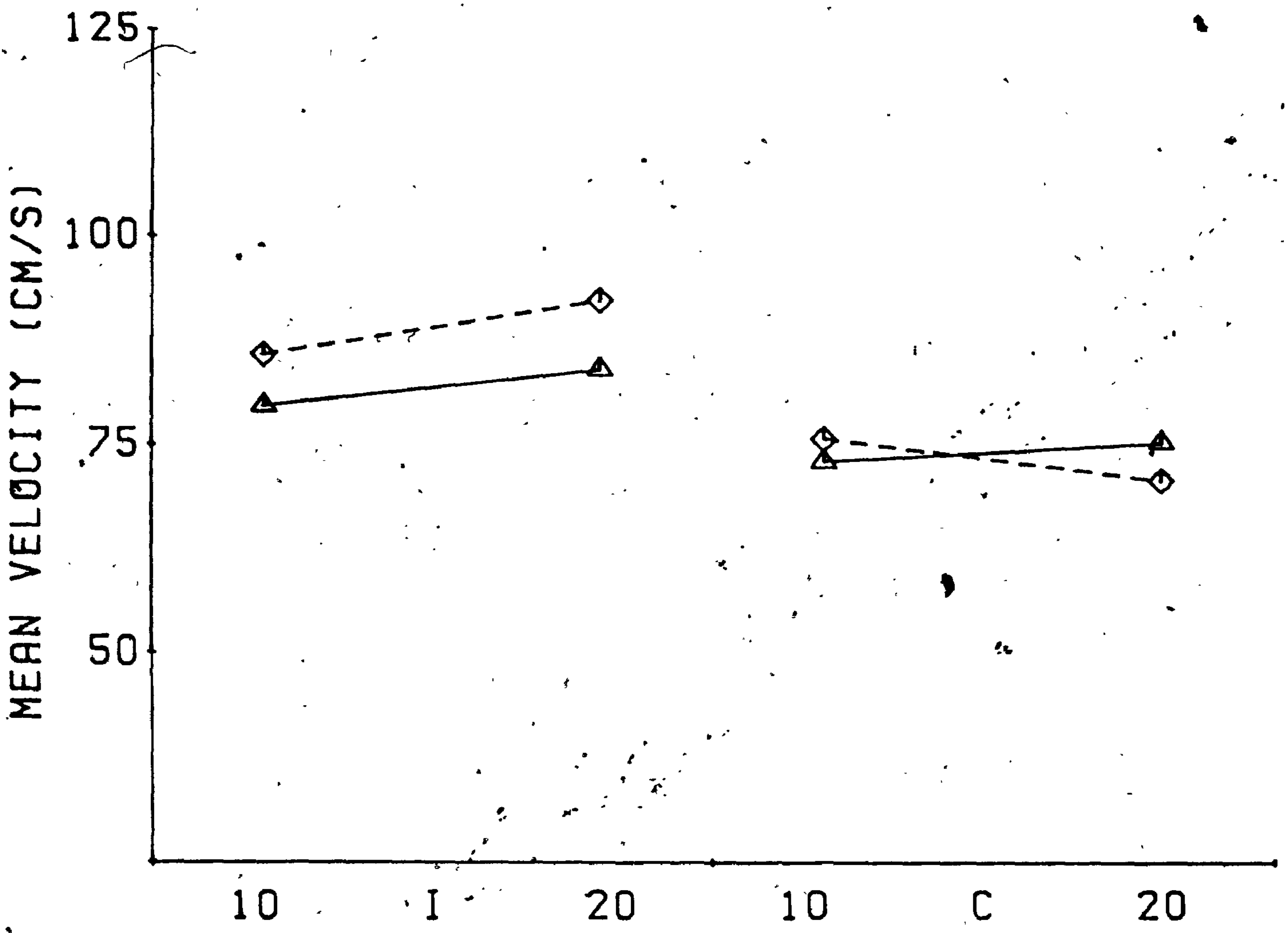
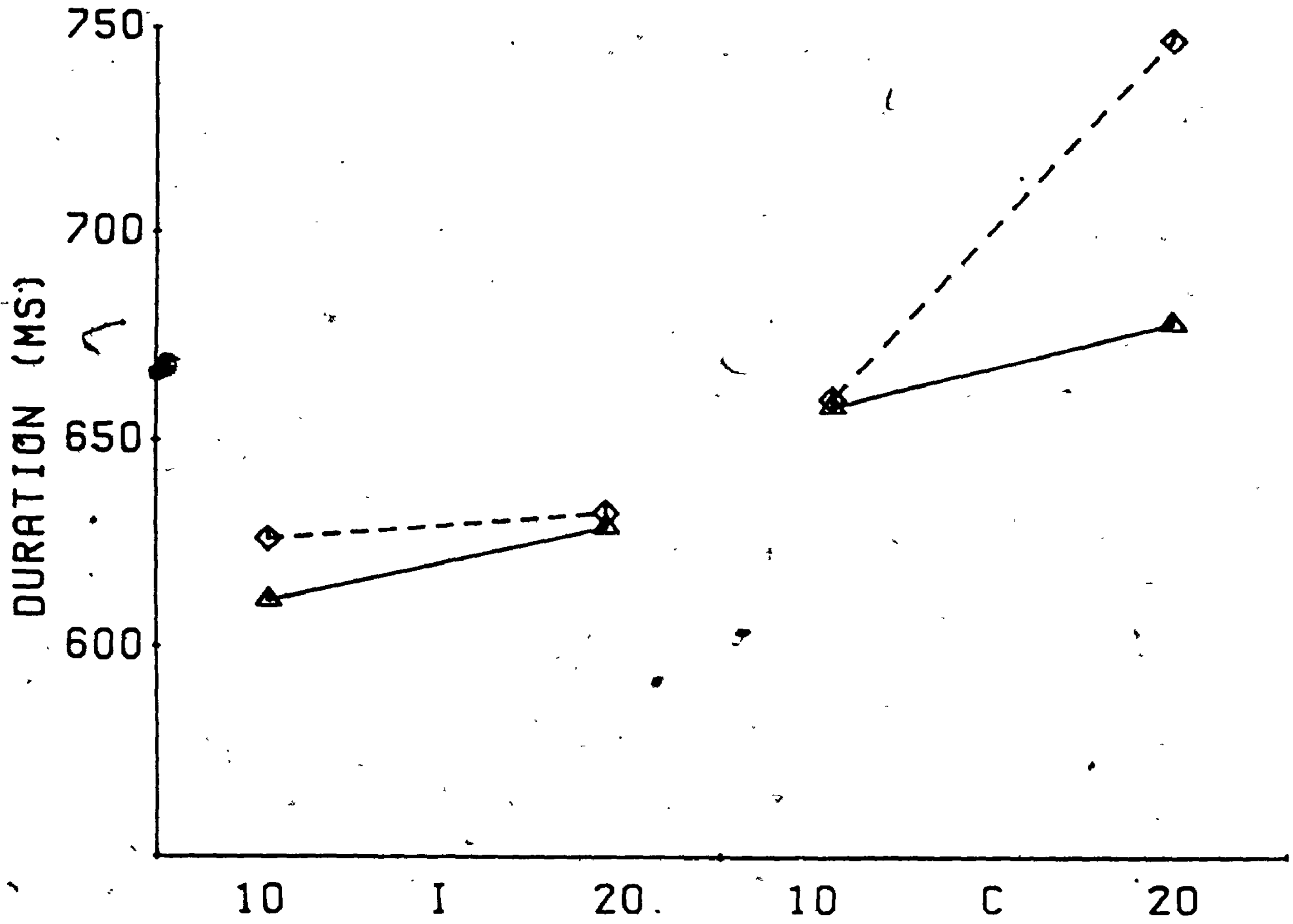

MEAN VELOCITY (CM/S)
125
100
75
50
10
I
20
10
C
20

Figure 11. Effect of target eccentricity (10 and 20 degrees of visual angle) on the duration of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. The duration of movement was greater for contralateral reaches and increased for more eccentric, contralateral targets. This increase was particularly marked for reaches by the left hand. Ipsilaterally directed reaches required approximately the same duration to complete movement to either eccentricity.


DURATION (MS)
750
700
650
600
10
I
20.
10
C
20

The production or absence of eye movements did not affect any of these laterality effects.

The only spatial-temporal measure of the limb movement affected by the Stimulus Duration was the Duration of the movement ($\underline{F}(1,7) = 5.83$, $\underline{p} < .05$). Reaches to persistent targets had a mean Duration of 664 ms (sd = 134) which was longer than the duration of 647 ms (sd = 112) for reaches to brief targets. This average difference of 17 ms corresponded to approximately one video frame.

Accuracy of Final Position. Since the target was only displaced in the horizontal plane it was necessary to examine errors in this plane separate from vertical errors and to determine the contribution of the errors in each plane to the total error of final position. Therefore, analyses of variance were carried out for the Lateral Error, Vertical Error, and the total Vector Error with the same 5 factors as the previous analyses. The errors were small and indicated a good level of accuracy in the performance of this task. The majority of errors were an undershoot of the target position, with undershoots constituting 75% of the lateral errors and 68% of the vertical errors. However, only the absolute error, independent of its direction was considered in the analyses of this section. Since the fixation point was always present at the same vertical position as the targets and since vertical position did not vary, it was expected that the Lateral Errors would be larger than the Vertical Errors and would account for a greater amount of variability in the Vector Errors. The mean Lateral Error was 1.39 degrees, while the mean Vertical Error was 0.80 degrees.

Analyses of variance revealed effects which were similar for both Lateral and Vector Errors. Target Eccentricity had a significant main effect for both errors. These findings are summarized in Table II. Errors were larger for 20 degree eccentric targets as compared to the 10 degree targets. As with the analyses reported above, Lateral and Vector Errors were affected by whether the reach was directed to a target presented in the visual field ipsilateral or contralateral to the hand being used. Significant Hand x Field interactions were present for both Lateral Error ($\underline{F}(1,7) = 13.62$, $\underline{p} < .01$) and Vector Error ($\underline{F}(1,7) = 12.48$, $\underline{p} < .01$) analyses. Figures 12 and 13 illustrate these data. In addition to being less accurate, contralateral reaches demonstrated an effect of Target Eccentricity which was more pronounced than that of ipsilateral reaches. This latter result was revealed by significant Hand x Field x Eccentricity interactions (Lateral Error, $\underline{F}(1,7) = 9.96$, $\underline{p} < .05$; Vector Error, $\underline{F}(1,7) = 11.64$, $\underline{p} < .05$) which are illustrated in Figures 14 and 15. Although both ipsilateral and contralateral reaches show an increase in Lateral and Vector Error with increasing target eccentricity the increase is most dramatic for contralaterally directed reaches performed by the left hand.

The possibility of using visual feedback to increase the accuracy of the movement was manipulated by varying the Stimulus Duration. With brief target presentations there were no cues as to the relative positions of the hand and target throughout the movement although other feedback cues were available. Stimulus Duration had a significant effect on the Lateral ($\underline{F}(1,7) = 35.85$, $\underline{p} < .001$) and Vector Errors ($\underline{F}(1,7) = 34.51$, $\underline{p} < .001$), which indicated a reduction in accuracy for the Brief Target condition (Table III). However Vertical Error was not

TABLE II

Effect of Target Eccentricity on Errors (degrees of visual angle) of Final Position of the Finger

	Eccentricity of Targets		Significance Level		
	10°	20°			
Lateral Error	1.07	1.72	F1,7	19.00	$p < .005$
Vector Error	1.29	1.79	F1,7	16.82	$p < .01$

Figure 12. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on lateral error of the final position of the hand (degrees of visual angle). ◇ - Left hand; △ - Right hand. Lateral error was larger for contralateral target presentations.

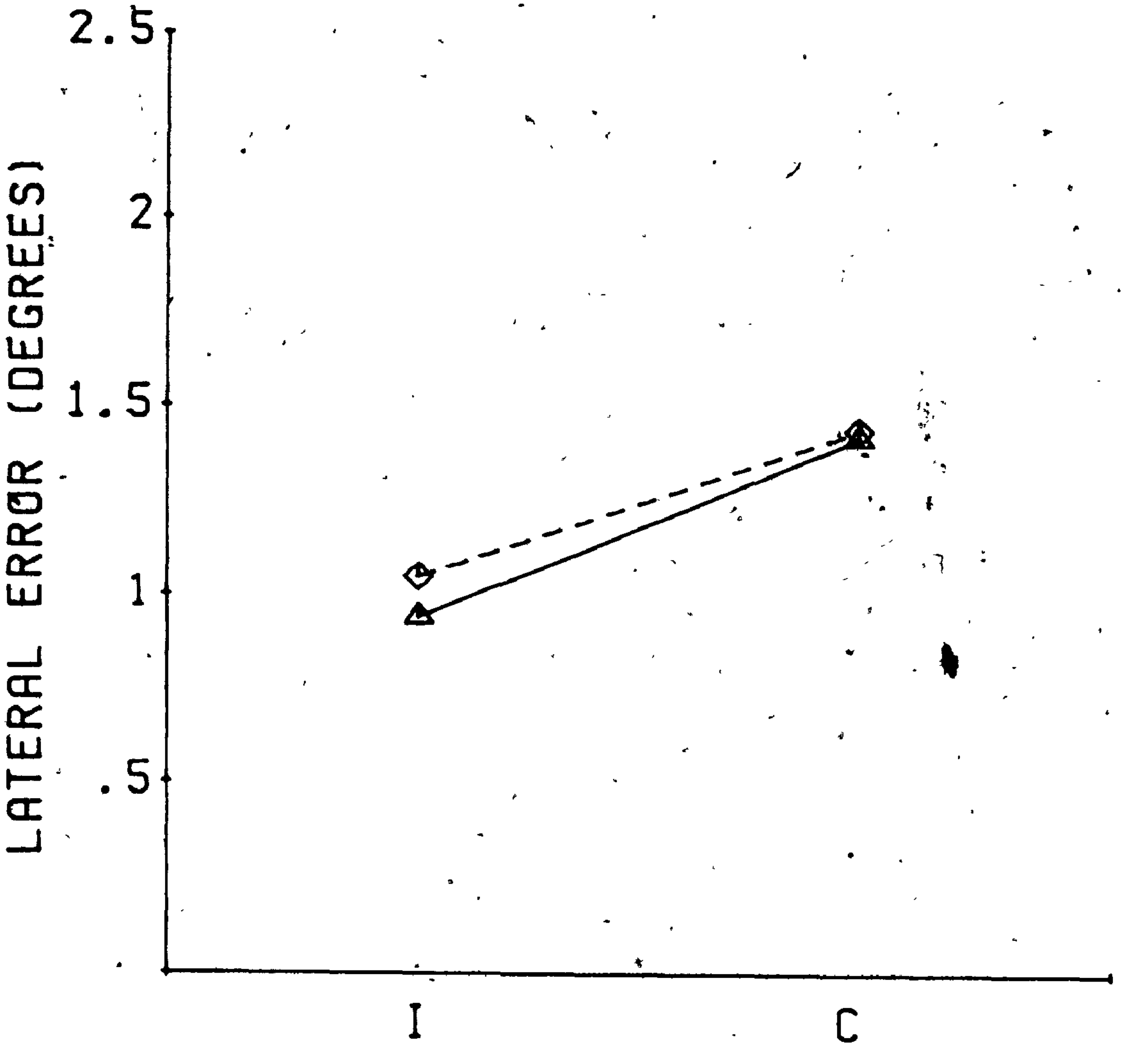

LATERAL ERRØR (DEGREES)
2.5
2
1.5
1
.5
I
C

Figure 13. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on vector error of the final position of the hand (degrees of visual angle). ◇ - Left hand; △ - Right hand. Vector error was larger for ipsilateral target presentations.

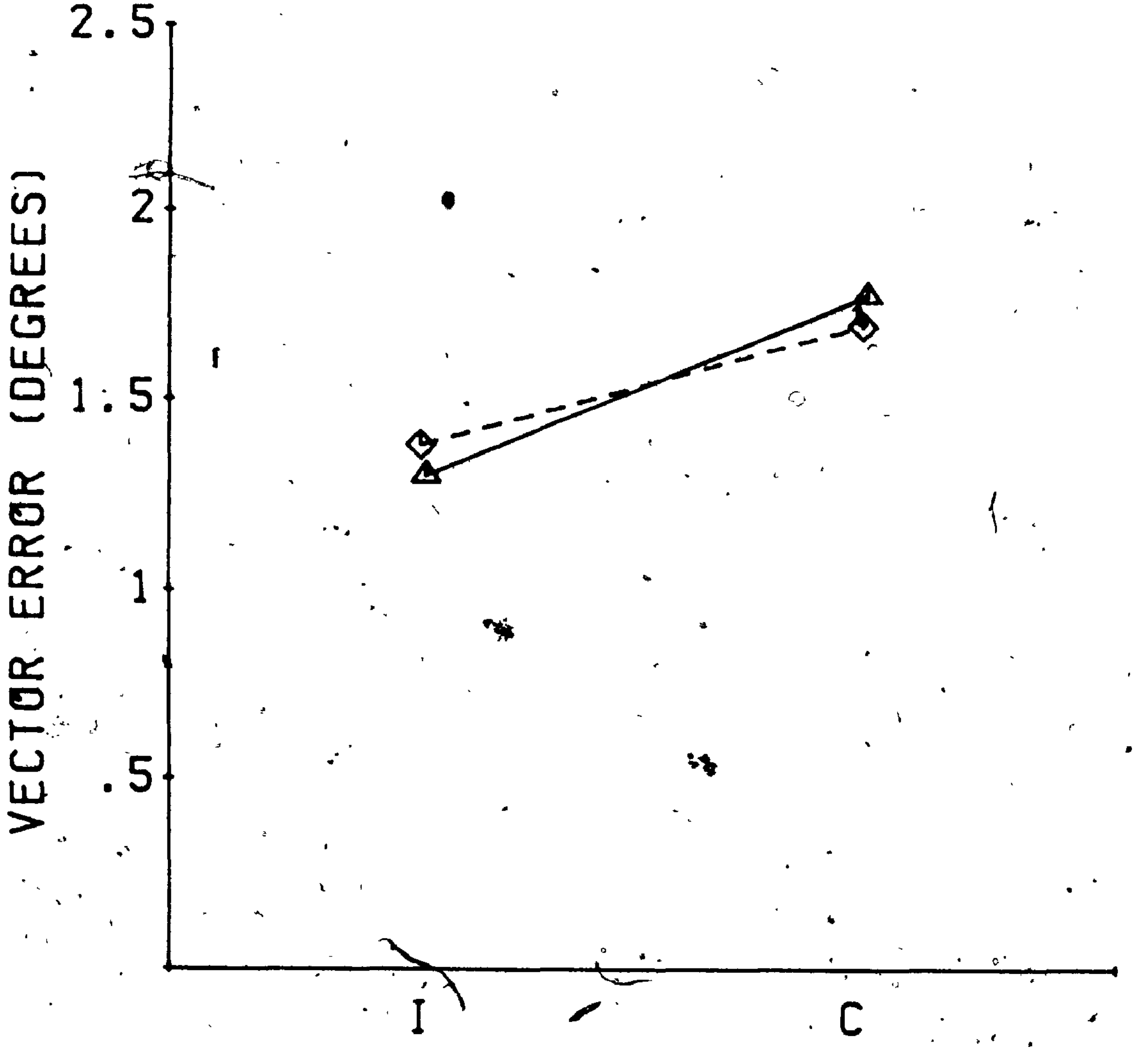

VECTOR ERROR (DEGREES)
2.5
2
1.5
1
.5
I
C

Figure 14. Effect of target eccentricity (10) and 20 degrees of visual angle) on the lateral error of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. Lateral error increased with increased target eccentricity, but this increase was greatest for contralateral target presentations.

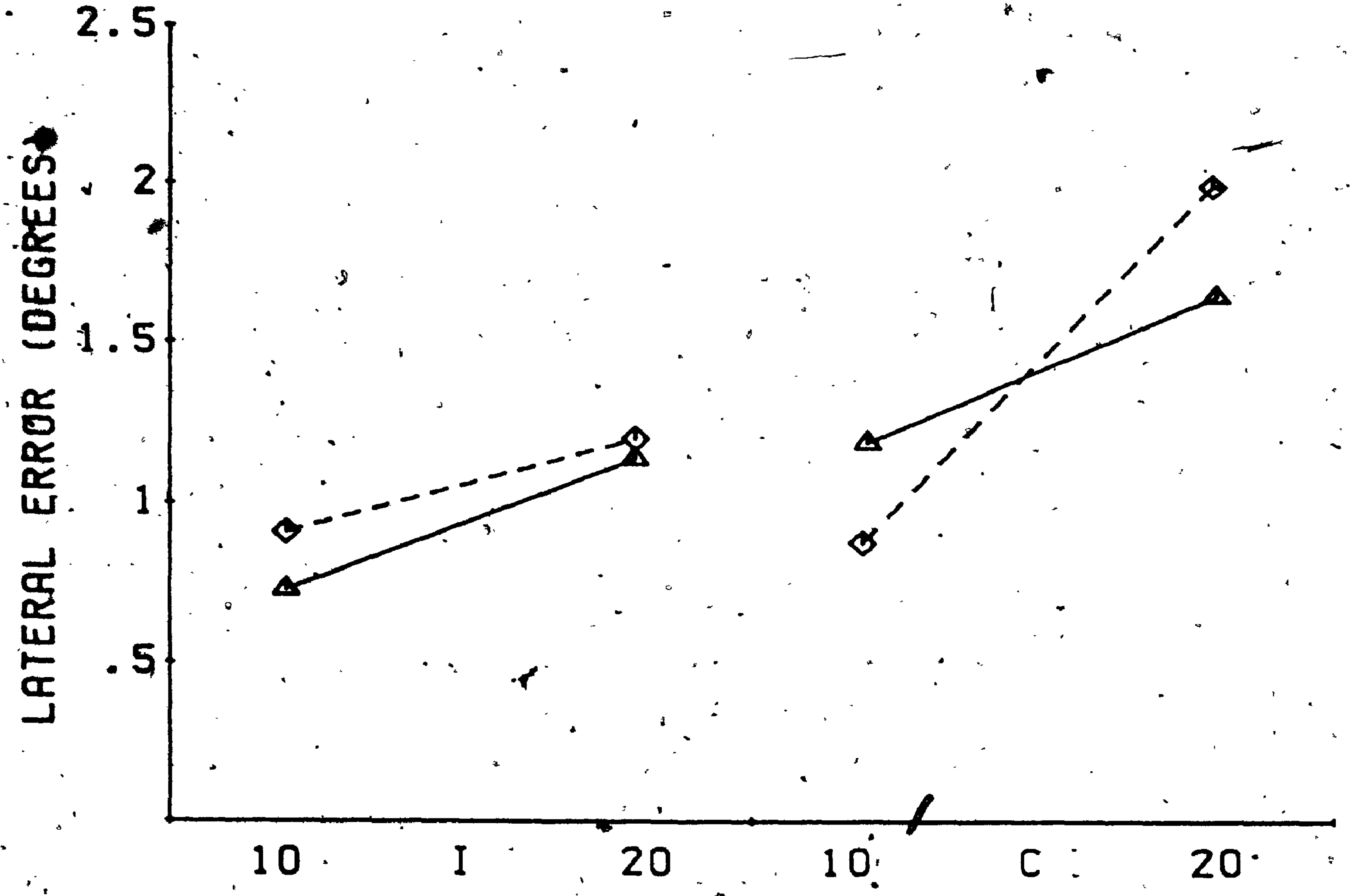

LATERAL ERROR (DEGREES)
2.5
2
1.5
1
.5
10
I
20
10
C
20

Figure 15. Effect of target eccentricity (10 and 20 degrees of visual angle) on the vector error of ipsilateral (I) and contralateral (C) reaches. ◇ - Left hand; △ - Right hand. Vector error increased with increased target eccentricity, but this increase was greatest for contralateral target presentations. Reaches by the left hand were most accurate for targets presented at the 10 degree contralateral position but were least accurate for targets at the 20 degree contralateral position.

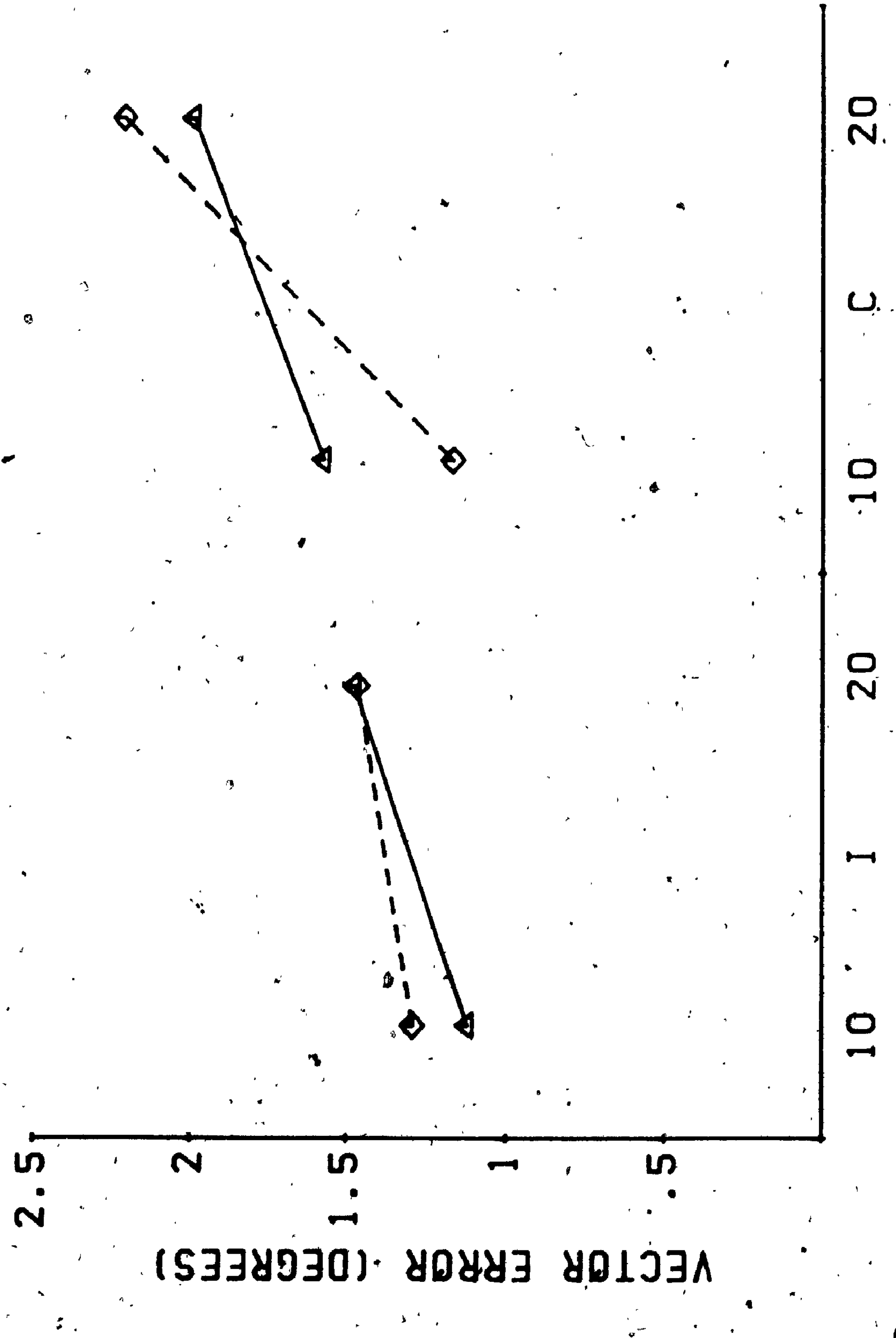

VECTOR ERROR (DEGREES)
2.5
2
1.5
1
.5
10
I
20
10
C
20

TABLE III

Effect of Stimulus Duration on Errors (degrees of visual angle) of Final Position of the Finger

	Stimulus Duration		Significance Level		
	Brief	Persistent			
Lateral Error	1.87	0.93	F1,7	35.85	$p < .001$
Vector Error	2.18	1.35	F1,7	34.51	$p < .001$

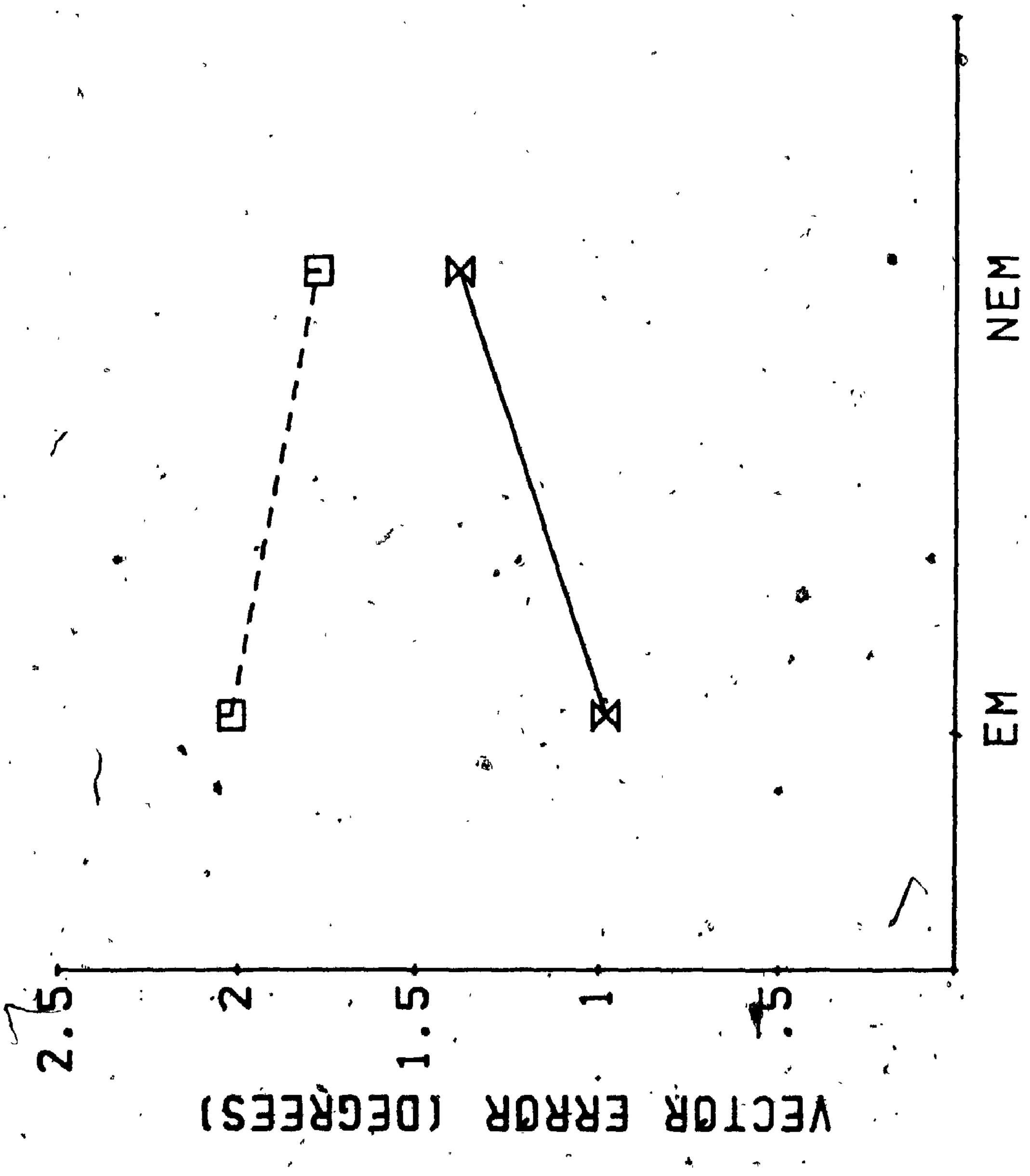
affected by either Stimulus Duration ($F(1,7) = 0.13$, $p > .70$), or by the direction of reaching relative to the hand used (Hand x Field, $F(1,7) = 0.15$, $p > .70$).

The factor which did affect Vertical Error was whether the subjects looked to the target while pointing to it ($F(1,7) = 9.66$, $p < .05$). Errors in the NEM condition (0.82 degrees, sd = 0.47) were larger than in the EM condition (0.58 degrees, sd = 0.35). Reduction of the Vertical Error in the EM condition contributed to a significant Stimulus Duration x Eye Movement interaction ($F(1,7) = 12.81$, $p < .01$) for the Vector Error. Figure 16 illustrates this interaction. The most accurate condition was the Persistent Target/EM condition in which the Vector Error was significantly smaller than either the Brief Target/EM or Brief Target/NEM condition errors (Tukey's HSD statistic, $p < .05$), and approached a significantly lower value than the Persistent Target/NEM error.

For NEM trials the errors to persistent targets approached a significantly lower value than the errors to brief targets. However, it is clear that the improvement in pointing accuracy for persistent versus brief targets was greatest when the subjects were allowed to move their eyes to the target.

To summarize, most of the factors which were found to affect the kinematics of the movement also affected its accuracy. Ipsilateral reaches were more accurate than contralateral reaches, and the non-dominant hand was most affected by the laterality of the reach. In addition, division of the total Vector Error into its Lateral and Vertical component vectors revealed that these components were affected differentially by the experimental conditions.

Figure 16. Effect of the production of eye movements (EM - eye movement condition; NEM - no-eye movement condition) on the vector error of reaches to Brief targets (□), and Persistent targets (⧗). Vector error of the final finger position was significantly smaller if the subjects were allowed to refixate a persistently illuminated target. No other conditions differed significantly from one another.


VECTOR ERROR (DEGREES)
2.5
2
1.5
1
.5
EM
NEM

Analysis II

This analysis investigated the relationship between the movements of the eyes and hand for those trials in which the subjects were asked to look as well as point to the targets. The two systems were compared on a trial-by-trial basis, for their latency to initiate movement, and the accuracy of their final positions relative to the target position. Since a portion of the eye movement data for one subject was lost, all further analyses were conducted on the data from 7 subjects. Although the video records of the limb movements provided a large number of measures of manual performance, the number of measures provided by the eye movement records was much more limited. One unique feature of the records of the eye movements was the production of more than one saccade before the final position was attained. Secondary saccades (Becker and Fuchs, 1969) were produced by all subjects, but occurred more often with persistent targets (40% of trials) than with brief targets (17% of trials). These proportions differed significantly, as revealed by a correlated T-test ($T = 3.99$, $df = 6$, $\underline{p} < .01$). Since eye movements in the vertical plane could not be recorded accurately only horizontal errors were analyzed. Velocity/time data was also not available for the eye movements. Therefore, the latency and accuracy of the eyes and hand were compared on a trial-by-trial basis, and were also compared under the various experimental conditions.

Latency. The latency to initiate both movements was measured from the FM tape records. This meant that the measure of hand latency used in this analysis differed from the measure used in the previous analysis. Hand latency in Analysis I represented the first visible movement of the fingertip on the videotape records, while the hand latency measure for Analysis II was the release of the start platform microswitch by the hand. Since most subjects produced a movement of the finger before the hand had been lifted sufficiently to release the microswitch, the hand movement latencies were higher for Analysis II. The mean latency for the videotape measure was 394 ms while the mean latency for the FM measure was 449 ms. The correlation between these two measures was .85 over all trials, and all subjects.

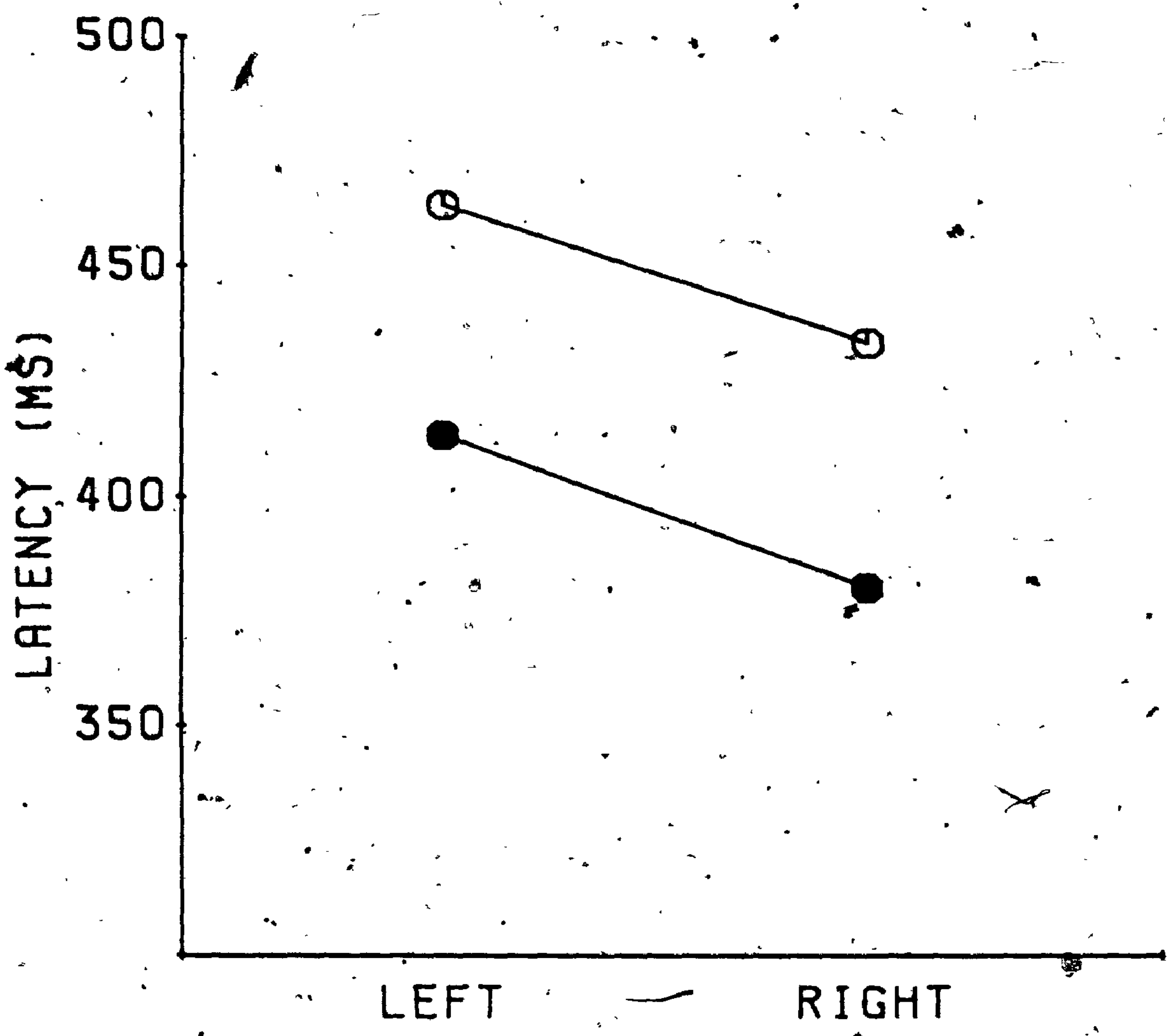
There were a total of 16 conditions (2 Stimulus Durations x 2 Hands x 2 Visual Fields x 2 Target Eccentricities) with 4 trials within each cell. The correlations between the latency for the eye and hand movements were calculated within each condition, for each subject. This yielded a total of 112 correlations, each based on 4 trials performed by a single subject, which were normalized by conversion to Z-scores. These transformed scores were tested against the null hypothesis of a correlation of zero, by means of a t-test. The overall mean correlation between the eye and hand latencies was .36 which was significantly greater than zero $\underline{t} = 7.1$, df = 111 ($\underline{p} < .01$).

In order to determine if this correlation was altered by the different experimental conditions the Z-scores were subjected to an analysis of variance. However, no significant main effects or 2-way interactions were found (Appendix IIc). Therefore, the overall correlation between eye and hand latency held across all of the experimental conditions. Unfortunately a large amount of variability was introduced into the data by having only a small number of pairs of scores make up the correlation in each cell.

Although changes in the experimental conditions did not affect the correlation between the two systems, this did not answer the question of whether changes in the experimental conditions affected each system in the same direction or to the same extent. Therefore, the similarity of the effects of the experimental conditions, on the eye and hand movement latency, was examined by another analysis. The mean response latency of the eye and hand was calculated for each experimental condition. An analysis of variance was then carried out on the latency to initiate movement with the System of Movement (eye versus hand) as an additional factor. The mean latency for the initiation of hand movements was 449 ms (sd = 49) while the eye movement latency was 396 ms (sd = 97). There was a large amount of variability between various conditions and subjects, including one subject who always initiated movement of the hand prior to movement of the eyes. As a result the main effect of System of Movement failed to attain statistical significance ($F(1,6) = 3.04$, $p > .10$). However, comparison of the eye and hand latencies by a correlated t-test yielded a statistically significant difference between them ($t = 5.91$, df = 111, $p < .001$).

An interesting finding was the presence of a main effect of the hand used for the response, on the latency to initiate movement ($F(1,6) = 9.74$, $p < .05$). Both eye and hand latency were reduced when reaches were made by the right hand as opposed to the left hand. This result is illustrated in Figure 17 with the eye and hand latencies presented separately. A right hand advantage for hand movement latency was also evident in Analysis I (see Figure 2) although the effect just failed to reach statistical significance ($F(1,7) = 4.75$, $p < .07$).

<u>Figure 17</u>. Effect of hand used for pointing on the latency to initiate movement of the eyes (●) and hands (○). Note the similar advantage in movement latency of the eyes and hand for blocks of trials performed with the right hand as compared to blocks performed with the left hand.

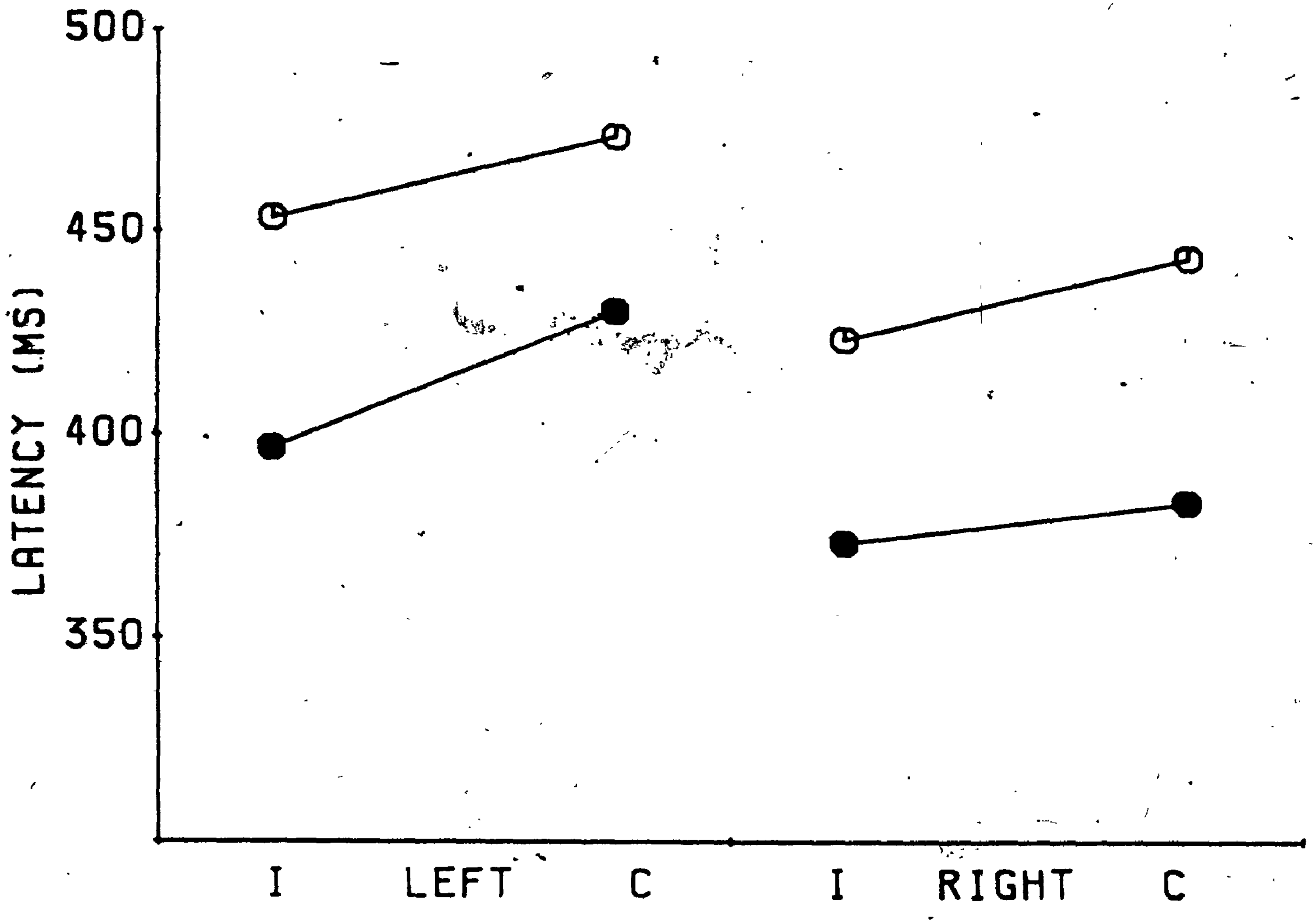

LATENCY (MS)
500
450
400
350
LEFT
RIGHT

An advantage for ipsilateral over contralateral reaches in hand response latency was noted previously, in Analysis I (see Figure 2). This same effect was found in Analysis II for movements of the eyes and hands. A significant Hand x Field interaction ($F(1,6) = 10.84$, $p < .05$) was present and is illustrated in Figure 18. In this figure the latencies for the eyes and hands are presented separately. These results demonstrate that although the two systems differed in their overall latency, changes in the hand responding and the laterality of the target affected both systems to a similar extent.

Accuracy. The same series of analyses was performed for the lateral error of the final eye and finger positions. Eye position was measured after all saccadic movements toward the target had been completed. Unlike Analysis I, for these analyses the direction of the error was considered, with an overshoot of the target position assigned a positive value and an undershoot assigned a negative value. Correlations of the 4 trials within each cell, for each subject, were again calculated. Although the mean correlation between the error scores was low ($r = .17$) a t-test of the Z-score transformations revealed that it was significantly greater than zero ($p < .01$). An analysi[illegible] variance of the Z-scores was also performed (Appendix IIc). No interactions were found to be significant, but Stimulus Duration had a main effect which approached statistical significance ($F(1,6) = 5.18$, $p < .07$). The reason for this effect was apparent when the mean correlation for the Brief and Persistent stimulus conditions were compared. The mean correlation for the Persistent target condition was only .03 but the mean correlation for the Brief target condition was

Flament, in press). Some of these studies used movements which were restricted to rotation about one joint (Lestienne, 1979; Hore et al., in press) or movement in only one plane (Morasso, 1981), rather than unrestricted, three-dimensional movement. Laquaniti and Soechting (1982) have reported symmetrical velocity profiles for shoulder and elbow angular velocity during an unrestricted arm movement but found more variable and less symmetrical profiles for wrist movement. Since velocity in the present study represented movement of the fingertip through three-dimensional space, and since a high degree of accuracy was required, the skewed velocity profiles may not be incompatible with previous findings. For more complex, multiple joint movements, such as those examined in the present study, the manner in which instantaneous angular velocity about individual joints relates to the velocity of the hand and fingers remains to be explored. In another study which demanded highly accurate, unrestricted limb movement Carlton (1981) recorded the velocity of a hand-held stylus, directed at a visual target. He also found a prolonged deceleration phase with a period of very low velocity in the final portion of the movement. Thus the constraints placed upon the movement, and the degree of accuracy required, may affect the resultant velocity profile. Most studies of limb movements have looked at highly practiced movements. Georgopoulos et al. (1982) found that the variability in the trajectories produced by his monkeys, was reduced with practice. It is possible that with increased practice there is less reliance upon terminal corrections in the movement trajectory to ensure an accurate movement. Elimination of the period of low velocity, in which such

Figure 18. Effect of laterality of stimulus presentation (I-ipsilateral; C-contralateral) on the latency to initiate movement of the eyes (●) and hands (○), when either the Left or Right hands were used for reaching. Note that both the eyes and hands initiated movement more quickly for ipsilateral target presentations than contralateral target presentations.

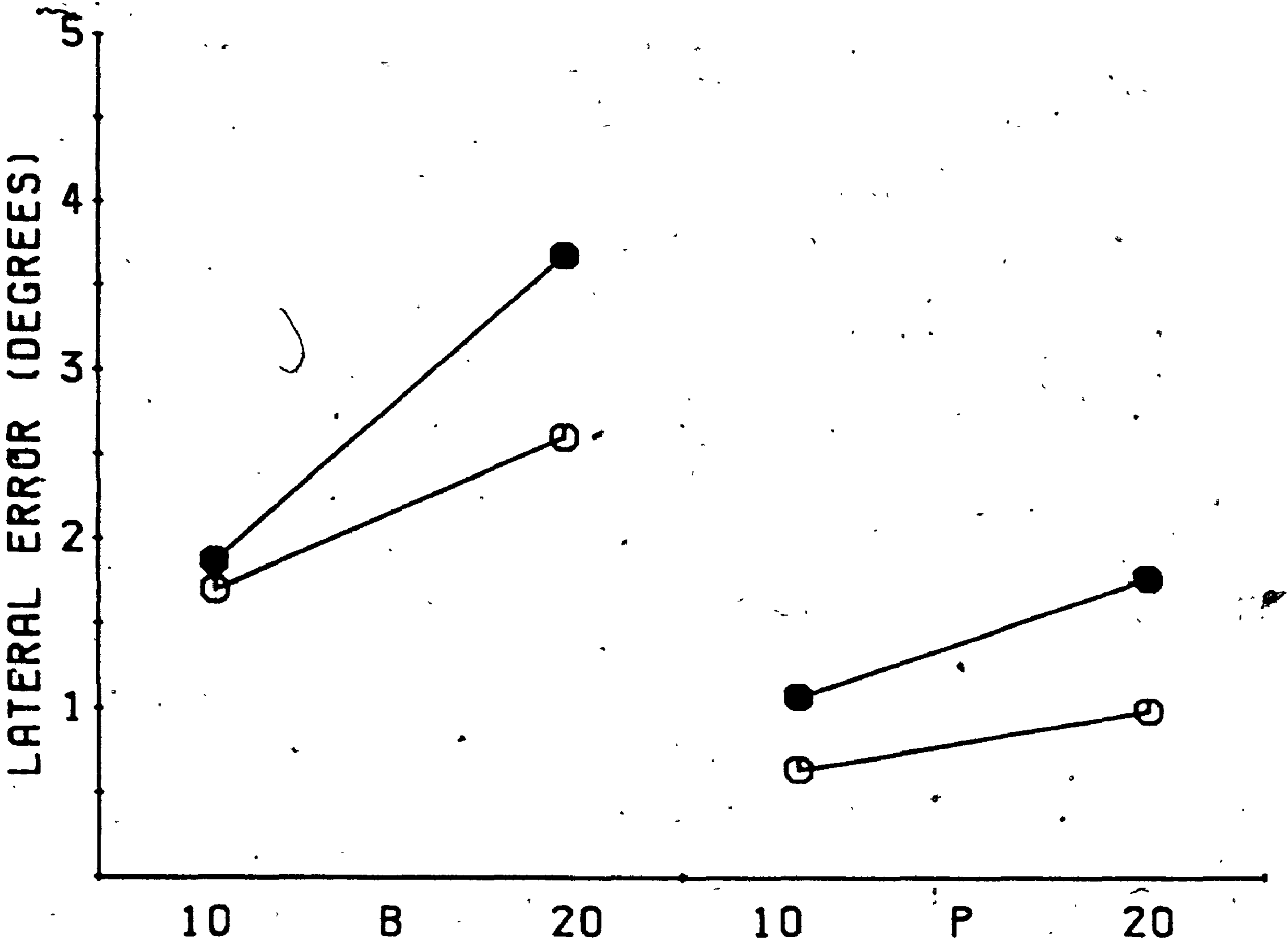

LATENCY (MS)
500
450
400
350
I
LEFT
C
I
RIGHT
C

.31. Indeed, when separate t-tests were performed for the Z-scores of these two conditions only the Brief target correlation was significantly greater than zero $t = 4.19$, $df = 55$, ($p < .001$). Thus, the lateral errors of the two systems were positively correlated only when the target was briefly presented.

The final investigation of the data was an analysis of variance of the mean lateral errors with the System of Movement (eye versus hand) as an additional factor. Eye position errors (2.10 degrees, sd = 2.03) were larger than the hand position errors (1.29 degrees, sd = 1.02) and this difference was statistically significant ($F(1,6) = 12.40$, $p < .05$), despite the large amount of variability. Main effects of Stimulus Duration ($F(1,6) = 91.46$, $p < .0001$) and Eccentricity ($F(1,6) = 39.93$, $p < .001$) were both present, and a Stimulus Duration x Eccentricity interaction was present ($F(1,6) = 8.91$, $p < .05$). The lack of interactions between the system of movement and any of the experimental conditions indicated that both the eye and hand movement errors were affected similarly by these experimental conditions. Figure 19 illustrates the Stimulus Duration x Eccentricity interaction for the eye and hand errors separately. Errors were larger for Brief targets overall, and for 20 degree targets overall. In addition, the increase in error with increasing target eccentricity was greatest for Brief target presentations. These effects are clearly evident for both the eye and limb movements.

The analyses performed in this section indicate that not only was the performance of the ocular and manual motor systems correlated for the latency to initiate movement and the accuracy of movements to Brief targets, but both systems were affected similarly by changes in the

Figure 19. Effect of target eccentricity (10 and 20 degrees of visual angle) on the lateral error of eye (●) and hand (○) movements to brief (B) and persistent (P) targets. Errors of both the eyes and hands were larger for brief target presentations and for more eccentrically presented targets.


LATERAL ERROR (DEGREES)
5
4
3
2
1
10
B
20
10
P
20

experimental conditions. The implications of these findings to the visual motor control of reaching are discussed below.

Discussion

The present study attempted to integrate a number of approaches in the study of visually guided reaching, so as to describe this important behaviour in greater detail. To accomplish this, the latency, accuracy and kinematics of an unrestricted limb movement through 3-dimensional space, were studied under varying conditions of visual information, and the relationship between eye and limb movements, under these same conditions, was also explored. The findings have implications for a number of specific issues but some general statements about performance of this task can be made.

The accuracy with which all subjects performed the task was excellent. Even when the target was presented very briefly the subjects were able to localize its position by a pointing movement, with errors of only a few degrees of visual angle. The fact that the subjects demonstrated such precision without the benefit of a great deal of practice in the paradigm, indicates that the production of such visually guided limb movements is a highly skilled human behaviour. Although the specific paradigm was unique, the required movement was similar to the common behaviour of reaching to, and acquiring objects in space.

The movements consisted of an initial rapid acceleration phase, followed by a more prolonged deceleration as the target was approached. The majority of studies of limb movement have reported more symmetrical velocity profiles than those found in the present study (Lestienne, 1979; Morasso, 1981; Laquaniti and Soechting, 1982; Hore, Vilis and

Flament, in press). Some of these studies used movements which were restricted to rotation about one joint (Lestienne, 1979; Hore et al., in press) or movement in only one plane (Morasso, 1981), rather than unrestricted, three-dimensional movement. Laquaniti and Soechting (1982) have reported symmetrical velocity profiles for shoulder and elbow angular velocity during an unrestricted arm movement but found more variable and less symmetrical profiles for wrist movement. Since velocity in the present study represented movement of the fingertip through three-dimensional space, and since a high degree of accuracy was required, the skewed velocity profiles may not be incompatible with previous findings. For more complex, multiple joint movements, such as those examined in the present study, the manner in which instantaneous angular velocity about individual joints relates to the velocity of the hand and fingers remains to be explored. In another study which demanded highly accurate, unrestricted limb movement Carlton (1981) recorded the velocity of a hand-held stylus, directed at a visual target. He also found a prolonged deceleration phase with a period of very low velocity in the final portion of the movement. Thus the constraints placed upon the movement, and the degree of accuracy required, may affect the resultant velocity profile. Most studies of limb movements have looked at highly practiced movements. Georgopoulos et al. (1982) found that the variability in the trajectories produced by his monkeys, was reduced with practice. It is possible that with increased practice there is less reliance upon terminal corrections in the movement trajectory to ensure an accurate movement. Elimination of the period of low velocity, in which such corrections take place could result in a more symmetric velocity profile of the movement.

The aspect of the required movement that most consistently affected the performance of the subjects was the difference between ipsilateral and contralateral reaches. This factor affected almost all of the measures that were analyzed, and in addition interacted with the effects of variations in target eccentricity. A number of possible hypotheses can be proposed to explain these differences. Although some are more plausible than others they are not mutually exclusive. One problem in interpreting the findings arises from the fact that contralateral reaches involved reaching into contralateral visual space, as well as contralateral extrapersonal space. Therefore reaches directed to a different visual field relative to the hand being used also involved reaching across the body axis, and thus required a different pattern of muscular activity. Both the position of the target in visual space, and the pattern of muscular activity required to reach to this position, could have affected the measures which were analyzed.

Studies of the cerebral motor control of limb movements in the rhesus monkey (Lawrence and Kuypers, 1968a,b; Brinkman and Kuypers, 1973) have revealed that while one hemisphere can control the proximal musculature of both ipsilateral and contralateral limbs, it can control the more distal musculature of only the contralateral limb. This control of the distal muscles is required for the relatively independent finger movements necessary for the proper grasping of objects such as food pellets, and is dependent upon direct corticomotoneuronal connections via the pyramidal tract. From the study of split-brain monkeys, Paillard and Beaubaton (1975) have suggested that the cerebral hemisphere ipsilateral to the limb that reaches, is unable to make use of visual feedback information to modify the trajectory of the movement. Thus, they found that the combination of the ipsilateral hemisphere and limb resulted in decreased accuracy of reaching. These primate studies suggest that normal visually guided reaching of human subjects may be initiated and controlled by the cerebral hemisphere contralateral to the limb being used. If the motor response to the target presentation relies on hemispherically organized mechanisms, the programming of a reach into the visual field ipsilateral to the hand used could take place within the same hemisphere that is initially stimulated by the target presentation. Contralateral reaches would require that either information of the location of the target in space or the motor program of the reaching movement, cross from the hemisphere initially stimulated to the opposite hemisphere. Indeed, the latency to initiate a movement was higher for contralateral reaches, which is suggestive of such a transfer of information.

Poffenberger (1912) was the first to suggest that estimates of the time required for transfer of information between the hemispheres could be made on the basis of differences in manual reaction time to lateralized visual stimuli. Since then a number of studies have been conducted on this topic, with various paradigms (see for review, Bashore, 1981). The estimates from such studies have ranged between 1 ms and 6 ms for simple reaction time paradigms and have been larger and more variable for complex paradigms. The difference between ipsilateral and contralateral reaching latency in the present study averaged to 23 ms. This corresponds closely to a difference of 27 ms in reaching latency reported by Prablanc et al (1979a), although they had an unequal probability of the laterality of target onset and used the responses of only one hand. Complex reaction time paradigms have also yielded estimates of interhemispheric transmission time in this range (Bashore, 1981). This increased complexity has generally referred to a requirement that the subject make a decision, either to respond or not, or to respond in one manner versus another, based on the characteristics of the stimulus. The present paradigm represented a different increase in complexity since movements were directed to the location of the target, and thus the response consisted of more than the release of a simple, preprogrammed motor behaviour such as a finger flexion. The difference between ipsilateral and contralateral latency may represent an estimate of the time required to transfer the complex information that codes either the location of the target in space or the motor program for a directed limb movement, between the two hemispheres by callosal or extracallosal routes.

Factors other than the transfer of information between the two hemispheres may also contribute to the difference between ipsilateral and contralateral latency. Heilman (Heilman and Valenstein, 1979) has suggested that the body axis is an important reference point for all human spatial behaviour. On the basis of studies of patients with unilateral brain damage, he has proposed that unilateral spatial neglect represents "an akinesia for any act which must be performed in the neglected (contralateral) hemispatial field" (page 290). If human behaviour is organized with such a spatial reference, it may be the case that a limb movement which crosses the body axis is programmed differently from a movement which takes place entirely within the ipsilateral hemispace. An increase in the complexity of the required motor programming or a change in the neural circuits involved in such programming could also account for differences in the latency to initiate movement. Another possible factor which could account for this finding is the differences in the muscles which are responsible for producing ipsilateral and contralateral reaches. Although the movement at the fingers, wrist and elbow were the same for both directions of reaching, the movement about the shoulder differed. While ipsilateral reaches primarily involved contraction of the deltiod and trapezius muscles, contralateral reaches involved contraction of the deltiod and pectoralis major. It is possible that an increased period of isometric contraction time for the muscles used in contralateral reaches was responsible for the increased latency to initiate movement. In fact, all of these explanations are possible and may have contributed to the differences in latency which were found.

Movement latency was also affected by the eccentricity of the targets with an increase in latency at greater eccentricity. Prablanc et al (1979) reported the same finding, and suggested that this difference may reflect "the increase in visual latency on the peripheral retina". It is unclear what was meant by "visual latency" but the magnitude of the differences make it unlikely that the increased distance travelled by peripheral retinal axons could account for this result. A reduction in the number of ganglion cells activated by a peripheral stimulus may have also resulted in less efficient transmission for more eccentric targets, but the increase in latency with increasing eccentricity was also found to be greater for contralateral as opposed to ipsilateral reaches. This result cannot be explained solely on the basis of differential transmission times for central versus peripheral retinal processes. In addition, the pattern of activated muscles would be the same for reaches to either eccentricity on the same side of the body, and thus the differing effects of target eccentricity for ipsilateral and contralateral reaches does not reflect differences in isometric contraction time. If an increased period of isometric contraction is required for movements which cover a greater distance, this effect should have been comparable for ipsilateral and contralateral reaches. Rather, an increase in the time required to transfer information between the hemispheres when a more eccentric target must be achieved, or an increase in the time required to program a movement which crosses the body axis to a greater extent may account for the differing effects of eccentricity for ipsilateral and contralateral reaches. Such explanations would not be expected to hold in simple reaction time paradigms such as that studied by Berlucchi, Heron, Hyman, Rizzolatti and Umilta (1971), which do not require a movement to the target location. Although it is apparent that contralateral reaches are initiated more slowly and are affected by the eccentricity of the target to a greater extent, the source of these differences remains unclear.

Differences between ipsilateral and contralateral reaches were also evident for all of the kinematic measures derived from the video records. Ipsilateral reaches were generally completed more quickly than contralateral reaches, and with a higher peak velocity. A number of interpretations of these findings exist. One possibility is that the mechanical constraints of the skeletal-muscular system differ between ipsilateral and contralateral reaches, such that antagonist activity opposing extension of the arm is greater for contralateral reaches.

This is difficult to assess without EMG records of agonist and antagonist activity, but such an assessment would be difficult since it would involve comparison of the activities of different groups of agonist and antagonist muscles for the two directions of movement. Since the maximum velocity of the movement occurs early in the reach and therefore close to the midline of the body, any additional "braking" by antagonist activity in contralateral as opposed to ipsilateral reaches may be minimal. A second possibility is that the different pattern of muscular activity required for contralateral reaches make it impossible to produce movement at the same velocity as ipsilateral reaches. This is again difficult to assess, but while these possibilities may hold for the comparison of ipsilateral and contralateral reaches in general, it is less likely that they can account for the differing effects of target eccentricity within ipsilateral and contralateral conditions.

An increase in the maximum velocity of reaches to 20 degree targets over 10 degree targets was evident for ipsilateral reaches but not for contralateral reaches. Scaling movement amplitude by changes in the magnitude of the maximum velocity has been reported for limb movements about a single joint (Cooke, 1980; Freund and Budingen, 1978; Hallett and Marsden, 1979), saccadic eye movements (for review, see Carpenter, 1977), and tongue dorsum movement during articulation (Ostry, Keller and Parush, personal communication). Therefore, although the findings of the present study demonstrate that similar scaling of movement amplitude may take place for unrestricted, three-dimensional limb movements, it is true of ipsilateral reaches only. Contralateral reaches demonstrated instead, a prolonged deceleration phase of the movement when required to move a greater distance. Since scaling of movement distance by changes in maximum velocity has been reported with a variety of muscle systems, it is unlikely that the difference in pattern of muscles required for contralateral reaches can account for the failure of scaling in this condition. If antagonistic activity of axial muscles was resulting in a "braking" effect for contralateral reaches one might expect a lower standard deviation of the maximum velocity for more eccentric reaches because of a ceiling effect, but no evidence of this was found in the data. Although the mechanical constraints and the different pattern of muscular activity may have contributed to the obtained results they cannot totally account for the differences between ipsilateral and contralateral reaches.

As with the latency findings, the possibility exists that the ipsilateral/contralateral differences in kinematic measures reflect differences in the programming of movements directed to different visual fields or to different sides of the body axis. Since position of the target relative to visual space and relative to the body are confounded in the present study, it is not possible to determine which of these two factors makes a contribution to the observed effects. By varying the position of the target in the visual field independent of its position in space relative to the body axis, one may be able to determine which of these factors is dominant for a particular measure, or how the two factors interact. It is clear that ipsilateral and contralateral reaches to visual targets differ in the time required to initiate them and in their spatial-temporal characteristics, but the factors which underlie these differences remain to be explored.

It is not surprising, given the previous discussion, that the accuracy of the final position of the movement was also affected by whether the reach was ipsilateral or contralateral. On average, contralateral reaches were less accurate than ipsilateral reaches. The left hand errors were roughly equivalent for ipsilateral and contralateral 10 degree targets, but there was a marked difference between ipsilateral and contralateral 20 degree targets, regardless of the hand used. Since this effect was independent of the target duration or the production of eye movements it cannot be attributed exclusively to an inadequate use of visual feedback or to the poor spatial resolution of the peripheral retina. One could speculate that a failure to anticipate the effect of an increased stretch of antagonist muscles might result in an increased undershoot of the lateral position of the target for the more eccentric, contralateral reaches. However, increased antagonist activity would also be expected to result in an undershoot of the vertical, as well as the lateral position of the target, and this did not occur. Thus, it is unlikely that increased antagonist activity alone could account for the obtained results. As I have discussed above, it is impossible to distinguish whether the ipsilateral/contralateral differences result from the position of the target relative to the body axis or the visual field. Because these differences are so pronounced for the majority of movement characteristics studied, it is important that a distinction be made between these two possibilities.

From the early part of this century, researchers have attempted to determine the neural areas involved in visual motor control through the study of patients suffering from brain damage (Balint, 1909; Holmes, 1918). Studies of this nature have examined the accuracy of movements directed to the visual field, or side of the body axis, ipsilateral or contralateral to the site of brain damage. Although deficits in the localization of objects in the contralateral visual space, following unilateral brain damage have been reported (Riddoch, 1935; Brain, 1941; Ratcliff and Davies-Jones, 1972; Rondot and de Recondo, 1974; Levine, Kaufman and Mohr, 1978) only Levine et al (1978), in a case study, have attempted to distinguish carefully, between effects related to the hand being used, versus the visual field in which the target is presented. It is unfortunate that this area of investigation has lacked quantitative measures and a good base of normative data with which to compare the patients' performance. The results of the present study demonstrate that a number of measures, in addition to accuracy, may be used to describe visually guided reaching, and that a number of complex factors may affect this behaviour in normal subjects. If we are to gain an understanding of the neural organization of visual motor behaviour, we must consider how the movements are related to the visual field and extrapersonal space in which they occur, for both normal human subjects and for patients suffering from neural dysfunction.

The present study also addressed the question of how visual information contributes to the guidance of movement of the limbs. Prablanc et al. (1979a) suggested that optimal visual guidance of the limb involves the triggered release of a central program; central processing of peripheral information which allows early modification of the motor program; and processing of peripheral information through an external comparator such as the retina in order to achieve an accurate final position. Paillard (1982) has suggested that the type of information used for the comparison of the hand and target positions varies with the portion of the retina on which their images fall. He proposed that "dynamic" information is used by peripheral visual processes while central vision makes use of "static" cues. In the present study the use of visual feedback of the relative positions of the hand and target, was only possible during persistent target presentations. The use of this information in the accurate completion of the movement was evident from the increased duration and accuracy of reaches to persistent targets, a finding consistent with that of Prablanc et al. (1979a). Since the kinematic measures of the initial acceleration phase of the movement were not affected by the target duration, the modifications of the motor program responsible for the improved accuracy most likely occurred during the deceleration phase of the movement.

An advantage for the use of central visual processes as opposed to only peripheral visual guidance of the movement was also apparent. When the subjects reached to persistent targets without looking to them, feedback of the relative positions of the target and hand was available only to the peripheral visual field. In contrast, foveation of the target allowed the subjects to use the central visual field for this comparison, and resulted in the greatest degree of overall accuracy. The vertical component of the overall vector error was also reduced by the production of eye movements, but this effect was independent of the target duration and therefore did not reflect a comparison of hand and target positions. Since the eyes were not required to move in the vertical plane, the point in space which the eyes fixated could have served as a reference point for the vertical position of the target. Therefore, movements of the eyes could have allowed for the comparison of the position of the hand relative to this point of fixation within the central visual field. The present findings support the concept that visual feedback of the relative positions of a target and limb can be used to optimize the accuracy of a rapid pointing movement, and that such information is processed more efficiently within the central visual field. The finding that eye movements did not improve pointing accuracy to briefly presented targets, also confirms the results of Prablanc et al. (1979a), who found that the production of eye movements do not increase pointing accuracy unless these eye movements allow the subsequent comparison of hand and target positions, by central visual processes.

Comparisons of the eye and hand as motor systems directed to a common target, revealed the interaction of the two systems. The significant correlation of eye and hand latencies within the experimental subconditions argues against totally parallel processing of information by these two motor systems, and argues instead for a common sensorimotor integration of the two movements. Some parallel processing of the two motor systems undoubtedly occurs as well, since the correlation between the two systems was not perfect. However, the positive correlation between movement latencies, as well as other findings, point to some common processing. Prablanc et al. (1979a) previously reported correlations between the latency of eye and hand movement of a similar magnitude to that found in the present study, but they did not analyze the statistical significance of these correlations and considered them to be too small to be indicative of common sensorimotor processing. The fact that the positive correlation between the latencies in the present study was not unique to a particular set of experimental conditions, suggests that the common integration of eye and limb motor programming may occur for many visually guided limb movements. Additional support for the concept of common sensorimotor integration comes from the parallel effects of the experimental conditions on the latency of both systems. These results are most easily explained by changes in the processing time of a neural network engaged in the programming of both eye and limb movements.

The latency to initiate movement was affected by the position of the target relative to the hand being used for both motor systems. Thus, eye movement as well as hand movement latency was lower for ipsilateral reaches than contralateral reaches. If the integrated motor programming of both movements takes place within one cerebral hemisphere, this difference may reflect the interhemispheric transfer of information in the contralateral condition. The possibility of such interhemispheric transmission has already been discussed with reference to the movements of the hand alone, and may hold equally well when both systems are involved in the movement. Since the pattern of muscular activation was the same for eye movements to either ipsilateral or contralateral targets, variation in biomechanical constraints or isometric contraction time cannot account for these latency differences.

The suggestion that there is a hemispheric organization of the systems responsible for programming these directed movements is supported by the presence of a right hand advantage in movement latency. This advantage averaged 27 ms for the hand movements and 30 ms for the eye movements. Since the distal limb musculature involved in the reaching movement is controlled by the opposite cerebral hemisphere (Lawrence and Kuypers, 1968a,b; Brinkman and Kuypers, 1973), the right hand advantage in movement latency suggests that the sensorimotor integration of the eye and limb movement, is carried out more efficiently by the left hemisphere. Based on the study of patients with unilateral brain damage, Kimura (1982) has suggested that the left hemisphere is specialized for the control of complex manual movements performed by either the left or right limbs. Such specialization may extend also to the control of visually guided movements of the limbs and eyes. Although it remains unclear at which point in the motor programming this common processing of sensorimotor information takes place, and which neuroanatomical areas subserve such a function, it is apparent that for directed eye and limb movements there is a significant amount of interaction between the ocular motor and manual motor systems.

The positive correlation between the eye and hand error scores for the brief target condition conflicts with the findings of Prablanc et al. (1979a) who examined the accuracy of the eyes and hand under open and closed loop conditions. The present study did not examine the accuracy of the two systems in a truly open loop situation, which would have eliminated any possible use of visual feedback to guide the movements. The brief target presentation in the present study only eliminated the possible use of feedback of finger and target positions, but allowed visual feedback of the position of the limb in space. This information may have been used to compare the position of the limb relative to the point in space which was fixated or relative to a particular retinal locus. Since eye movements were completed before the limb movements, the position in space that was fixated by the eyes may have served as the best indication of where a brief target had appeared. Therefore, the finger could have been directed to this point of fixation, under visual guidance. If this occurred, errors in eye position would necessarily result in correlated errors in hand position. Although Parablanc et al. (1979) failed to find a significant correlation in errors with brief target presentations, their "restricted vision" condition differed from the present study in that the target remained illuminated until the eyes began to move. The additional amount of time to localize the target which this procedure allowed may have eliminated the use of the refixated center of gaze as a target for the limb movement.

Although the errors of the two systems were correlated only for briefly presented targets, the experimental conditions had similar effects on the accuracy with which the two systems localized the target. Errors for the eyes and hands increased with increased target eccentricity, and also increased when the use of visual feedback was reduced by brief target presentations. Thus the interaction between the two systems that is evident for the initiation of movement is also evident for their ultimate localization of the target in space. Carlton (1981) drew an analogy between corrected changes in limb movement trajectory and secondary saccades, which he suggested were both controlled through the analysis of visual feedback information. Based on the results of the present study this analogy seems good. The presence of visual feedback information resulted in an increased period of low velocity as the target was approached by the hand and in an increase in the production of secondary saccades by the eyes, both of which probably reflect the comparison of retinal error information.

The present study has made a number of contributions to the study of human visual behaviour. Perhaps most important, has been the demonstration that the more complete description, made possible by the use of a combination of recording techniques, provides a much better understanding of the complexities of the behaviour. Through such analyses, we are able to see how certain stimulus characteristics affect the total performance of an integrated motor response. A major finding of the present study was the pervasive effect of the relationship between the spatial position of the target and the hand being used to reach to it. The significance of this finding, and the questions it raises about the spatial control of visually guided movement, arise directly from the large number of characteristics of the behaviour which were affected. The simultaneous recording of the eye and limb movements demonstrated the manner in which these two distinct motor systems interact in coordinated, visually guided behaviour. It also demonstrated that factors which affect movement of one system alone can affect both systems, when they are performing in an integrated manner. The complexities of human behaviour which are under visual control is overwhelming, but through more complete examination of behaviour under controlled conditions, we can begin to understand how we control the movements of our bodies through space.

STUDY II

The Roles of Body-relative and Visual Field-relative Target Position on the Control of Visually Directed Limb Movements

Summary

Previous studies have indicated that the latency to initiate a motor response to a visual stimulus may vary with the lateral position of the stimulus relative to the visual field or relative to the body axis. In the preceding study, visually directed pointing movements to ipsilateral and contralateral targets were found to vary in latency, velocity and accuracy but it was not possible to determine if the laterality differences could be attributed to the target position relative to the visual field or relative to the body axis, or whether an interaction of the effects of both spatial frames of reference accounted for the findings. In this study four subjects, three of whom participated in the previous study, were asked to point quickly and accurately to visual targets presented at eccentricities of 10 and 20 degrees to either side of the body midline. The duration of target illumination was 100 ms so that visual information of the target position was presented to only one visual hemifield. The spatial and temporal characteristics of the limb movements were analyzed from video records of movement through all three dimensions. Blocks of trials were run in which visual fixation corresponded to the midline of the body axis, and additional blocks were run in which the fixation point was 30 degrees eccentric to the body midline. For these latter trials, target laterality and eccentricity differed with regard to body-relative and visual field-relative space. Movement velocity was found to be independent of the point of visual fixation, and varied according to the position of the target relative to the body. Movement latency and accuracy were affected by eccentric visual fixation. Latencies were

shorter for targets on the ipsilateral side of the body midline only when the subjects fixated centrally. Similarly, the accuracy of the pointing movement was decreased for reaches across the body axis only if the target had also been presented to the contralateral visual field. Thus, although the velocity characteristics of the movement execution depended only upon target position relative to the body axis, the accuracy with which the target could be localized and the speed with which the motor output was processed depended upon the position of the target relative to the visual world as well as relative to the body axis.

Introduction

Movements of the upper limbs toward objects in space, are a class of skilled motor behaviour which is particularly well developed in primates and in man. It is with such movements that we are able to reach to, and acquire, objects of interest within the environment. In order to gain an understanding of how the central nervous system produces such fundamental human behaviour we must begin by describing those features of the behaviour which characterize its production. The previous study provided a comprehensive examination of the characteristics of unrestricted, multiple joint movements of the limbs, through three-dimensional space, toward visual targets. The most striking findings of that study were the differences between reaches directed across the body axis toward targets presented in the visual hemifield contralateral to the hand being used, and those directed to targets presented on the ipsilateral side of the body and the ipsilateral visual hemifield. These differences were apparent in most of the measures that described the movements. Contralateral reaches were initiated with a longer latency, required a longer duration for completion, and were less accurate than ipsilateral reaches. Similar findings had also been noted by Prablanc, Eschallier, Komilis and Jeannerod (1979a) although they did not discuss these results or the possible sources of these differences in detail.

The previous study also examined the velocity of limb movement throughout its trajectory and found that ipsilateral and contralateral reaches differed significantly. Most important was the finding that ipsilaterally directed movements of differing amplitude showed appropriate scaling of the maximum velocity attained during the movement. Thus, movements of a greater amplitude attained a higher maximum velocity. Similar scaling of maximum velocity had been noted as a feature of the motor programming of rotational movements about a single joint for the arm and finger (Freund and Budinger, 1978; Hallet and Marsden, 1979; Cooke, 1980), but for the multiple joint movements of the previous study this was only true for ipsilateral reaches. In contrast, for contralaterally directed reaches the duration of movement rather than the maximum velocity appeared to be the parameter which was scaled. For contralateral reaches the same maximum velocity was attained, regardless of the required distance, and larger movements took a longer period of time to complete.

The differences between ipsilateral and contralateral reaches for a number of aspects of performance raises important questions about their possible sources. Unfortunately, there have been very few comparisons of these two types of movement and as a result it is difficult to determine the neural organization which may be responsible for these differences. Studies of the time required to react to lateralized visual stimuli may provide the best insight to this question. If subjects are asked to respond to the onset of a visual stimulus by pressing or releasing a switch with the finger, the latency to react to stimuli presented in the visual hemifield contralateral to the hand being used is higher than the latency to respond to ipsilateral stimuli (see Bashore, 1981 for review). This effect has been attributed to the additional time required to transfer information about target onset between the cortical hemispheres when the hemisphere which initiates the response is not that which is first stimulated by the target onset

(Pfoffenberger, 1912). The processing of a motor response to the onset of a lateralized stimulus is thought to be more efficient when performed within one hemisphere than when information must be transferred between the cerebral hemispheres. Differences between the latency to initiate responses to ipsilateral and contralateral stimuli are therefore considered as estimates of the time required to transmit information between the two hemispheres. In the previous study this average difference in movement latency was 27 ms. Although this value exceeds most estimates of interhemispheric transmission time (see Bashore, 1981 for review), it is possible that a transfer of information between the hemispheres accounted for the difference in ipsilateral and contralateral latency, at least in part. Since an accurate directed movement of the limb was required, the task demanded a greater amount of processing of sensorimotor information than is required for the release of a simple preprogrammed response to stimulus onset. This processing of visual information and programming of the appropriate motor response may be more efficient if carried out within one hemisphere rather than involving transfer of information between hemispherically organized systems. A difference in the efficiency of intrahemispheric versus interhemispheric processing of complex information could have accounted for the difference in latency to initiate movement, and in addition, may have accounted for the differences between ipsilateral and contralateral reaches on measures of movement velocity and accuracy.

There are difficulties in interpreting the results of the previous study within the context of the reaction time literature. First, both proximal and distal musculature were involved in the pointing movements. As Kuypers and his co-workers (Lawrence and Kuypers, 1968a,b;

Brinkman and Kuypers, 1973) have found, while the control of the distal muscles of the arms of monkeys is restricted to the contralateral cerebral hemisphere, activity of the proximal muscles can be controlled by either the contralateral or ipsilateral hemispheres. This raises the possibility that some of the differences between the two directions of movement may reflect control of the proximal limb muscles by the hemisphere on the same side of the body, for contralateral targets, as compared to control by the opposite hemisphere for ipsilateral targets. Other differences may indeed reflect transfer of information between the two hemispheres for the control of distal muscles. A second problem in interpretation of the previous study, which is not completely distinct from the first, arises from the different pattern of muscular activity required for the two movements. While the majority of the muscles responsible for extension of the limb toward the target did not vary, the most proximal muscles, responsible for rotation about the shoulder, differed for movements away from, as opposed to across the body axis. It is again possible that some or all of the differences between ipsilateral and contralateral reaches could have arisen from the different pattern of proximal muscle activation required by the two movements.

Another difficulty in the interpretation of the ipsilateral/contralateral differences is the fact that the production of a precise directed movement is a significant departure from a simple response. In reaction time studies, more complex forms of responses have generally been a choice response. In these paradigms subjects are required either to respond with one hand versus the other, or to respond or not respond (go-no go), depending upon the characteristics of the stimulus. Studies of this type have found that the reaction times for lateralized visual stimuli may vary if the spatial positions of the responding hands are varied (Wallace, 1971; Brebner, Shepherd and Cairney, 1972; Anzola, Bertoloni, Buchtel and Rizzolatti, 1977; Berlucchi, Crea, DiStephano and Tassinari, 1977). If the hands are crossed, the fastest response time to a stimulus lateralized in the left visual hemifield is no longer performed by the left hand. Rather, the fastest response is performed by the right hand which is now on the same side of the body as the stimulus. It has been suggested that this result reflects stimulus-response compatibility and "the natural tendency to respond to lateralized stimuli with the hand that is in the appropriate spatial position" (Anzola et al., 1977, page 295). However, Bowers and Heilman (1980) have suggested an alternative explanation, which is that "each hemisphere is important for the mediation of perception and/or activities in the contralateral hemispatial field" (page 495-496). The concept of hemispatial field is distinct from the division of the visual field into left and right hemifields. As Bowers and Heilman (1980) explain "the hemispatial body field refers to the external space to the left or right of the body midline. ...Regardless of where the eyes are fixated, the hemispatial body field remains constant." (page 496). In order to investigate the importance of the visual hemifield and body hemispace for a reaction time response, Bowers, Heilman and Van Den Abell (1981) used a go-no go reaction time paradigm. They required the subjects to fixate an eccentric position without changing the position of their head or body axis. Thus Bowers et al. (1981) were able to present stimuli to either visual hemifield within one body hemispatial field. Using this method they found some evidence of a visual hemifield/body hemispace compatibility effect in addition to an advantage for ipsilateral hand/visual hemifield responses.

In the previous study the positions of the targets in the visual hemifields and the body hemispace were the same. This confounding raises the question of whether the visual field or the body space serves as the spatial frame of reference within which directed movements of the limbs are organized. Since ipsilateral and contralateral reaches differed on a number of measures of performance, it is also possible that some aspects of the movement are organized relative to one frame of reference while other aspects are organized relative to another. As a first step in determining the possible neural basis for the results of the previous study, an attempt was made to eliminate the confounding of the visual field and body space. By varying the initial fixation point from directly in front of the subject to eccentric lateral positions it was possible to present the targets in one visual hemifield and the opposite body hemispace. It was then possible to examine whether the measures of movement latency, velocity and accuracy varied with the target position relative to one frame of reference independent of the other.

Methods

Subjects

Subjects were 4 right-handed volunteers, 2 males and 2 females, ranging in age from 26 to 28 years. Three of the subjects, both males and one female, had participated in the previous study. None of the subjects required visual correction.

Apparatus for Data Collection

During testing the subject was seated facing a 31 cm high by 90 cm long screen which contained a horizontal array of target lights. The subject sat with head held in a chin and head rest, and with a distance of 50 cm between his eyes and the screen. The screen was centered with respect to the eye level of the subject and was covered with a black cloth which eliminated any view of the unilluminated target lights. Three one-degree diameter, white fixation points were presented at approximately eye level on the screen. One fixation point was situated directly in front of the subject, and is referred to as the central fixation point. Two eccentric fixation points were also used. They were situated 30 degrees of visual angle to the left and right of the central point. For a given block of trials either the central or the eccentric fixation points were visible. Target lights, 0.25 degrees in diameter, were presented at 10 degrees and 20 degrees of visual angle in the horizontal plane, to either side of the central fixation point. The duration of target illumination was 100 ms. The luminance of the screen was 2 cd/m^2 while the fixation point luminance was 69 cd/m^2 and the target luminance was 91 cd/m^2. The targets were therefore of 98 percent contrast (percent contrast = (Imax - Min)/(Imax + Imin) x 100). A start platform, which contained a microswitch, was situated immediately in front of the base of the chin rest. All reaches were initiated from this platform, although the actual position of the hand and fingers was allowed to vary slightly across trials.

All reaches were videotaped using two rotary shutter cameras (Sony RSC 1020) which provided clear images at 60 frames per second.

One camera viewed the subject from the right side at a distance of 140 cm, while the second camera, situated 110 cm above the hand position, provided a top view of the subject through a 45 degree angled mirror. The two camera signals were synchronized and fed to a split screen of a single video frame. Onset of the target was marked on the videotape by the illumination of a light, located outside of the subject's line of sight. A video counter timer (TEL Video Products) recorded the elapsed time of the test session on each video frame with a resolution of 10 ms.

Procedure

Test sessions consisted of eight blocks of 16 trials. Each hand was tested separately in alternating blocks. Within each block, two targets (10 and 20 degrees left of the central point or 10 and 20 degrees right of the central point) were presented eight times each, in a random order. The subject was asked to look and point using his index finger, quickly and accurately immediately following illumination of the target. All trials began with the subject fixating a specified fixation point. At a variable interval following a "ready" command, the experimenter illuminated one of the targets. Practice trials were given at the start of each block to familiarize the subject with the test conditions. Thus the subject knew which pair of targets were to be presented in each block of trials before the test trials began. In the first four blocks of trials the central fixation point was used. For the remaining four blocks the point of initial fixation alternated between the two eccentric positions. In these eccentric fixation trials, the targets which were presented were always to the same side of center as the fixation point. Thus for alternate blocks of trials, different pairs of targets were presented. The order of the hand and target pair used was counterbalanced between the four subjects. The test sessions lasted for approximately 45 minutes, and the subject was given rest periods between blocks if fatigued.

Apparatus for Data Analysis

The videotape records were analyzed with the use of a Sony Video Motion Analyzer, which allowed stable single frame advancement of the video image. Each frame was projected onto the surface of a digitizing tablet interfaced with an Apple II Plus microcomputer. Initiation of the reach was defined as the first visible movement of the index finger evident in the top view of the subject. The elapsed time from target onset to first finger movement, taken from the video counter timer, served as a measure of response latency. The position of the index finger for each frame was then calculated by the computer as X, Y and Z coordinates, by touching the finger position with the tablet pen, for both views of the subject. This process was continued until the subject first contacted the screen at which point the movement was considered to be complete. The forward and lateral movement of the reach was taken from the top view of the subject, while the vertical movement was taken from the side view. This three-dimensional information was stored by the computer as data files, to be analyzed at a later time. Analysis of the data files produced a number of measures derived from the vector distance between the positions of the fingertip on successive frames. These measures included the total distance of the reach; the mean velocity of the reach; the velocity at each frame; the maximum velocity;

and the time at which maximum velocity was attained. The difference between the final finger position and the actual target position, provided measures of error in the lateral and vertical dimensions as well as the total vector sum of these component errors.

Results

In general, the characteristics of the subjects' performance were similar to those in the previous study. Reaches were initiated within 500 ms following stimulus onset, and consisted of an acceleration to maximum velocity followed by a deceleration until the screen was contacted. The initial acceleration phase constituted approximately the first third of the movement duration. The longer deceleration phase often included a period of relatively low velocity just before the finger touched the screen. Trajectories of finger movement were again noted to vary slightly from a straight line path, with modifications in the direction of movement often present during the periods of low velocity. As with the previous study, corrected overshoots of the final position of the finger were commonly observed although corrected undershoots of the final position were rare. The performance of the subjects was generally quite rapid and accurate. On the average, movements were initiated 338 ms following target illumination, took 595 ms to complete, and had a vector error of 1.9 degrees. Thus, despite the differences in apparatus and procedure, the general level of performance in the present study was quite comparable to that of the brief target trials of the previous study.

The analysis of the subjects' performance was conducted on the basis of 8 measures which were extracted from the videotape records of each reaching movement. The measures that describe the temporal and spatial-temporal characteristics of the movement were: 1) the latency to initiate the first visible finger movement following target illumination; 2) the maximum velocity attained during the movement; 3) the latency to attain maximum velocity, or the duration of the acceleration phase of the movement; 4) the mean velocity of the movement; and 5) the duration of the movement. The accuracy of the final finger position was recorded as an error score, in degrees of visual angle, between the positions of the target and the index finger. Error in the lateral dimension, the vertical dimension, and the vector sum of these two errors were calculated for each reach.

Two separate series of analyses of variance were conducted on the body of data. The types of analyses corresponded to the two possible frames of reference within which the target position varied. For one series of analyses all target positions were coded according to the position in the visual field in which they appeared (Visual Field analysis). For the second series of analyses the target positions were coded in terms of their position in extrapersonal space, relative to the body axis (Body Space analysis). All analyses were balanced such that all interactions between factors were possible. The various experimental conditions provided a total of four factors, each of which had two levels. These factors were: 1) the hand used for reaching--left or right hands; 2) the position of the fixation point relative to the subjects' body axis--central or eccentric; 3) the target eccentricity--10 or 20 degrees of visual angle; 4) the laterality of the targets relative to the hand used for pointing--ipsilateral or contralateral. The level of the latter two factors for any given trial was a function of the position of the fixation point and the spatial frame of reference which was considered. For those blocks of trials in which the subjects fixated centrally, the eccentricity and laterality of the targets in the visual field and in the extrapersonal space corresponded. When the subjects fixated eccentrically a target presented to the contralateral side of the body space was in the ipsilateral visual field and a target presented 10 degrees from the body axis was 20 degrees from the point of visual fixation. Therefore when the subjects fixated eccentrically, the position of the target differed with respect to the two spatial frames of reference. By comparing the results of the two types of analyses it was possible to determine if the characteristics of performance noted in the previous study depended upon the position of the targets relative to one frame of reference only. It was also possible to examine how disruption of the correspondence be- tween body hemispace and visual hemifield affected these characteristics.

Most of the spatial-temporal measures, which reflect the kinematics of the movement, were unaffected by variations in the point of fixation. Therefore, the results of these measures were identical to the previous study, in which only a central fixation condition was employed. Significant main effects of target laterality and eccentricity were evident from the Body Space analyses of the maximum velocity, mean velocity and duration of movement. The effects of target laterality are summarized in Table I while the effects of target eccentricity are summarized in Table II. Reaches directed into the ipsilateral body hemispace attained a higher maximum velocity, had a higher mean velocity and were completed in a shorter period of time when compared to reaches directed into the contralateral body hemispace. Reaches to 20 degree

Table I

Effect of Target Laterality Relative to the Body Axis on Kinematic Measures of Pointing

	Target Laterality Relative to Body Space					
	Ipsilateral		Contralateral		F ratio (1,3)	Probability level
	Mean	(S.D.)	Mean	(S.D.)		
Maximum Velocity (cm/s)	198.9	(18.7)	173.1	(7.5)	25.05	$p < .05$
Mean Velocity (cm/s)	104.0	(13.5)	94.0	(11.0)	17.21	$p < .05$
Duration (ms)	570.4	(86.5)	618.4	(98.3)	11.71	$p < .05$

Table II

Effect of Target Eccentricity Relative to the Body Axis on Kinematic Measures of Pointing

	Target Eccentricity Relative to Body Space					
	10^{o}		20^{o}		F ratio (1,3)	Probability level
	Mean	(S.D.)	Mean	(S.D.)		
Maximum Velocity (cm/s)	180.5	(14.7)	191.4	(21.6)	70.68	$p < .05$
Mean Velocity (cm/s)	96.7	(10.7)	101.3	(15.0)	12.33	$p < .05$
Duration (ms)	580.9	(83.7)	607.9	(104.5)	19.35	$p < .05$

eccentric targets attained a higher maximum velocity, had a higher mean velocity and required a longer duration to complete the movement than reaches to 10 degree target positions.

The latency to attain maximum velocity was not affected significantly by the experimental conditions for either analysis (Appendices IIe, IIg).

As in the previous study, the main effects of target eccentricity relative to the body axis were found to depend upon whether the reach was directed to the body space ipsilateral or contralateral to the hand being used. These results were unaffected by variation of the point of visual fixation and were presented as significant Laterality by Eccentricity interactions for the Body Space analyses of maximum velocity ($F(1,3) = 74.45$, $p < .01$), mean velocity ($F(1,3) = 31.03$, $p < .05$) and duration ($F(1,3) = 21.06$, $p < .05$). Increased maximum velocity (Figure 1) and mean velocity (Figure 2) with increasing target eccentricity, were noted only for ipsilateral reaches, and as a consequence the duration of ipsilateral reaches to either 10 or 20 degree eccentric targets was roughly equivalent, while the duration of contralateral reaches increased dramatically with increased target eccentricity (Figure 3). These findings replicated those of the previous study, and indicated that the kinematic measures of the reach were not affected by the position in the visual field at which the target was presented.

The latency to initiate movement was quite different from the kinematic measures in that it was significantly affected by variation in the point of visual fixation. The average latency to initiate movement of the limb for eccentric fixation trials exceeded that of central

Figure 1. Effect of eccentricity of the target relative to the body axis (10 and 20 degrees of visual angle) on the maximum velocity of limb movements directed to the ipsilateral body space (◇) and to the contralateral body space (△). The maximum velocity of reaches across the body axis was lower than that of reaches performed within the ipsilateral body hemispace. An increase in the maximum velocity of reaches to more eccentric targets occurred only for those reaches performed within the ipsilateral body hemispace.

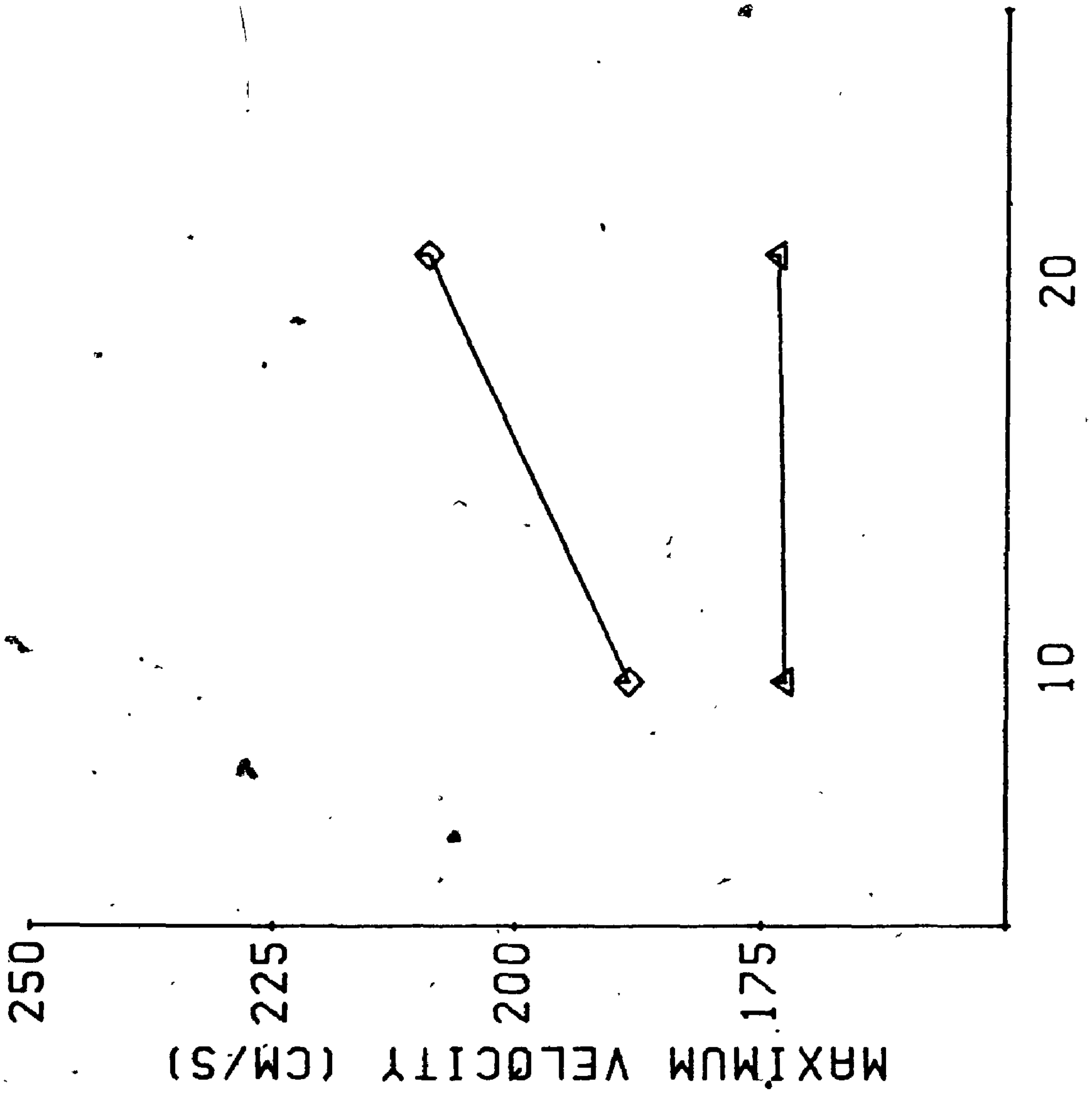

MAXIMUM VELOCITY (CM/S)
250
225
200
175
10
20

Figure 2. Effect of eccentricity of the target relative to the body axis (10 and 20 degrees of visual angle) on the mean velocity of limb movement to the ipsilateral body space (◇) and to the contralateral body space (△). The mean velocity of reaches performed within the ipsilateral body hemispace. An increase in the mean velocity of reaches to more eccentric targets occurred only for those reaches performed within the ipsilateral body hemispace.

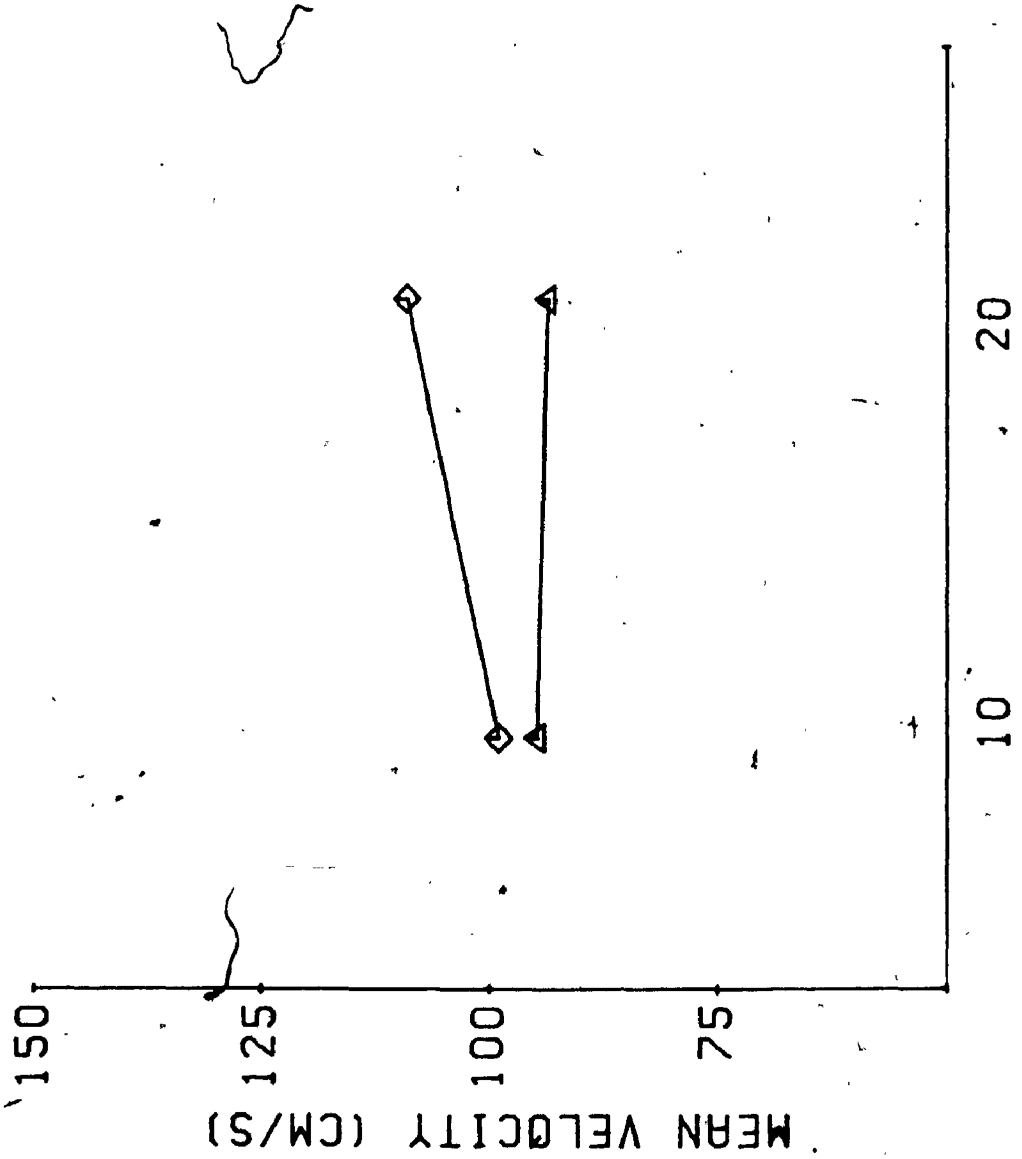
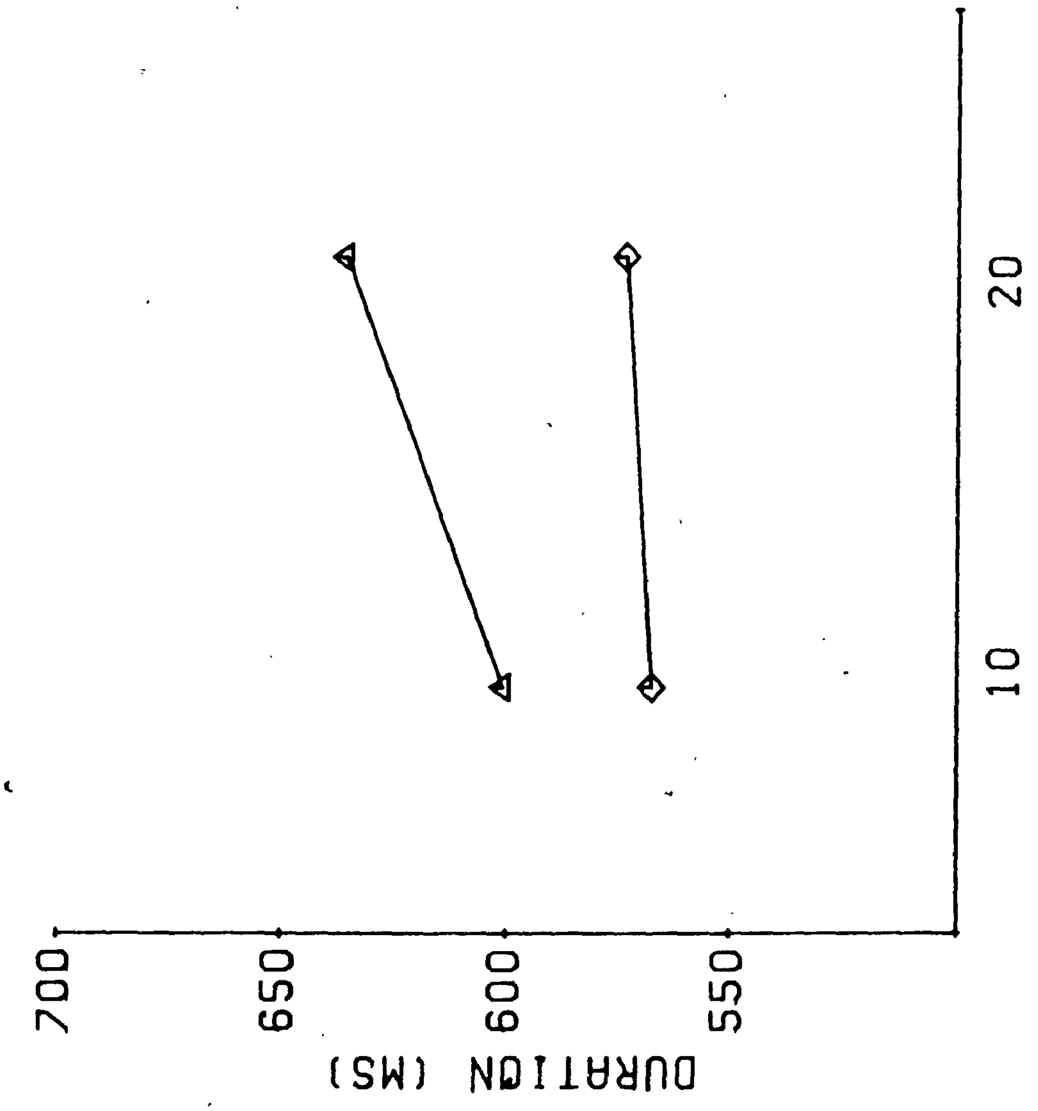

MEAN VELOCITY (CM/S)
150
125
100
75
10
20

Figure 3. Effect of the eccentricity of the target relative to the body axis (10 and 20 degrees of visual angle) on the duration of the limb movement to the ipsilateral body space (◇) and the contralateral body space (△). The duration of reaches which crossed the body axis was higher than the duration of reaches performed within the ipsilateral body hemispace. The duration of ipsilateral reaches was roughly equivalent for targets 10 and 20 degrees from the body axis, but reaches which crossed the body axis demonstrated an increase in duration of reaches to more eccentric targets.


DURATION (MS)
700
650
600
550
10
20

fixation trials by 16 ms, a difference which approached statistical significance ($F(1,3) = 7.84$, $p < .07$). Changes in the point of fixation also altered the effect of target laterality such that an advantage in response latency, for ipsilaterally presented targets, was only evident when the subjects fixated centrally. As in the previous study, for central fixation trials the two spatial frames of reference of Visual Field and Body Space coincided. Figure 4 illustrates the stimulus laterality by fixation point interaction for the analysis of target position relative to the body axis ($F(1,3) = 17.77$, $p < .05$). Pairwise comparisons revealed that the latency to initiate movement was significantly lower when the subjects reached toward ipsilaterally presented targets while they fixated centrally (Tukey's HSD statistic, $p < .05$). The latency to initiate movement did not differ significantly between any other conditions. This result indicated that eccentric fixation eliminated any advantage in movement latency for reaches directed to the ipsilateral side of the body axis.

Significant main effects of the laterality of the target relative to the body axis for the accuracy of final position confirmed the findings of the previous study. The lateral error of reaches to ipsilateral targets was significantly smaller than that of reaches to contralateral targets (Figure 5; $F(1,3) = 12.45$, $p < .05$). Although there was a similar trend for vector errors, this difference failed to attain statistical significance ($F(1,3) = 2.27$, $p > .20$). However, as with the measure of movement latency, the error of final position was affected by the point of visual fixation, with a target laterality effect present only for central fixation trials. This finding was evident from a significant interaction of target laterality by point of

Figure 4. Effect of the laterality of the target relative to the body axis (I-ipsilateral; C-contralateral) on the latency to initiate limb movements under conditions of central fixation (□) and eccentric fixation (⧗). With visual fixation on the central point responses to targets presented to the body hemispace and visual field ipsilateral to the hand being used were initiated at a lower latency than responses to contralateral targets. With eccentric visual fixation there was no advantage in response latency for targets presented to the body hemispace ipsilateral to the hand being used.

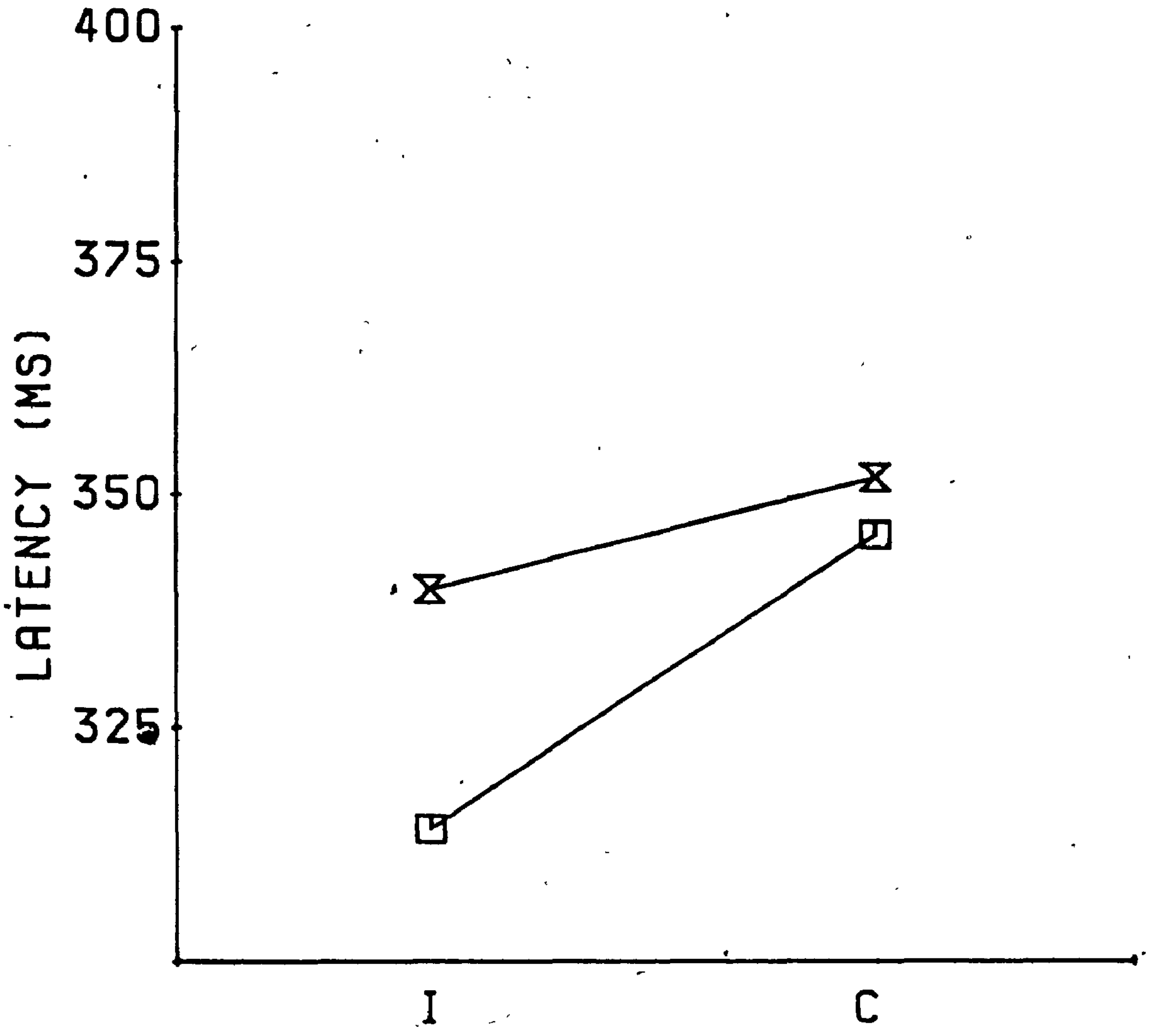
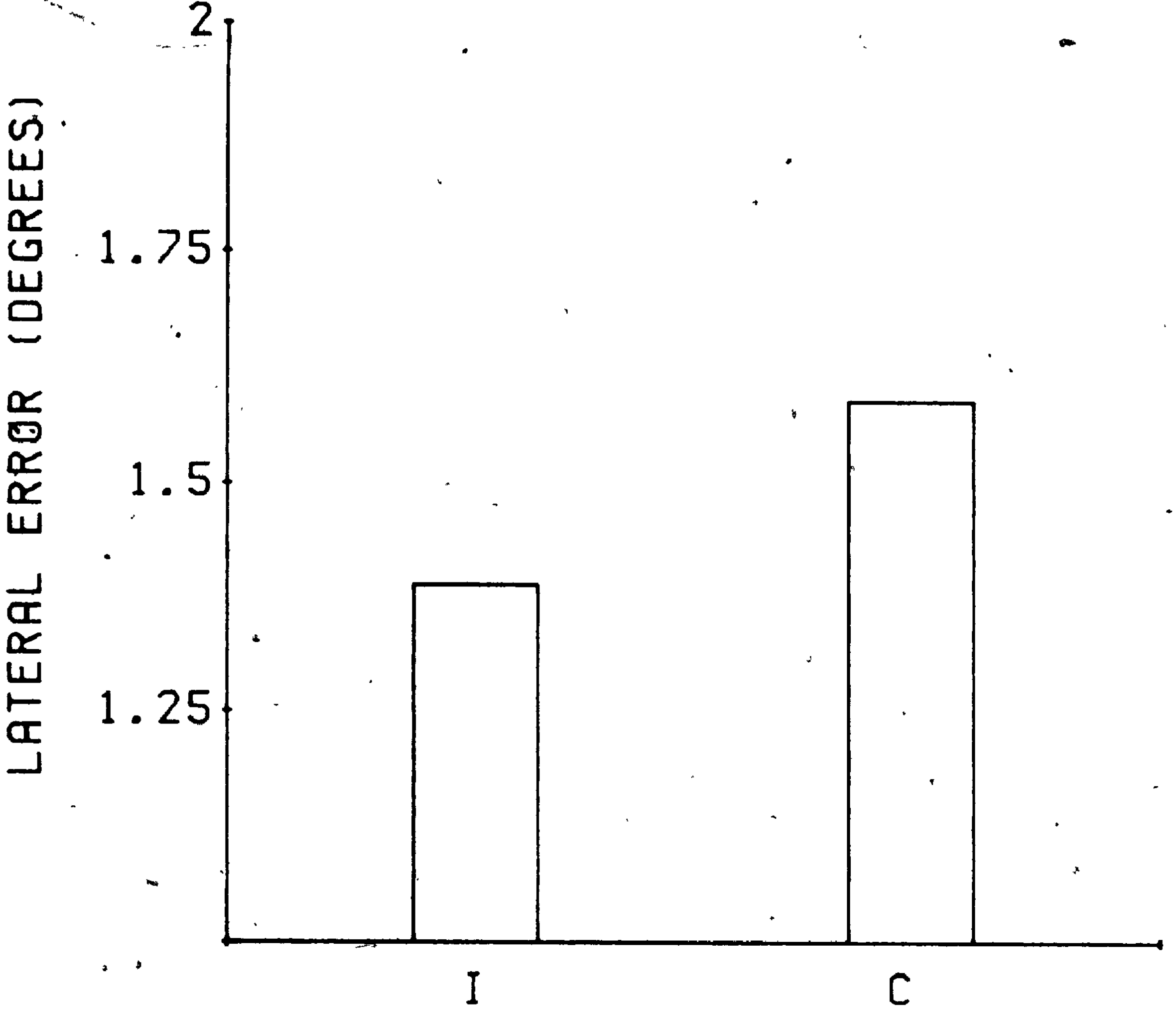

400
375
350
325
LATENCY (MS)
I
C

Figure 5. Effect of laterality of the target relative to the body axis (I-ipsilateral; C-contralateral) on lateral error of the final position of the finger. The mean lateral error of reaches to targets presented in the ipsilateral body hemispace were smaller than errors for contralateral targets.


LATERAL ERRØR (DEGREES)
2
1.75
1.5
1.25
I
C

fixation in the Visual Field analysis of lateral error (Figure 6; $F(1,3) = 12.45$, $p < .05$). It is apparent that an increased lateral error for reaches directed across the body axis occurred only when the subjects fixated centrally. Thus the accuracy of the movements was impaired when the subjects reached across the body axis, to a target which had been presented in the contralateral visual field, but reaches across the body axis were not inaccurate if the target was presented to the ipsilateral visual field. In addition, the errors of reaches to targets presented in the contralateral visual field were not larger if the movements were performed within the ipsilateral body space. A trend for a similar interaction was present for the vector errors although it failed to attain statistical significance ($F(1,3) = 2.27$, $p > .20$).

Although the two hands did not differ significantly in the latency to initiate movement ($F(1,3) = 2.33$, $p > .20$), there was a notable difference in their performance on the basis of the accuracy of final positions. Reaches performed with the right hand showed significantly smaller lateral errors ($F(1,3) = 16.45$, $p < .05$) and vector errors ($F(1,3) = 35.94$, $p < .01$). These results are summarized in Table III.

The vertical errors were not affected significantly by the experimental conditions for either analysis (Appendices IIf, IIh).

In summary, disruption of the correspondence between visual hemifield and body hemispace had significant effects on the pattern of results for the latency and accuracy of reaching but did not affect the kinematic measures of performance. The significance of the findings in terms of the programming and execution of visually directed limb movements is discussed below.

Figure 6. Effect of laterality of the target relative to the visual field (I-ipsilateral; C-contralateral) on the lateral error of the final position of the finger, under conditions of central fixation (□) and eccentric fixation (**X**). Note that the target laterality is presented relative to visual field rather than the body midline in this figure. With visual fixation of the central position the lateral error of reaches to targets presented to the contralateral visual field and the contralateral body hemispace were larger than the error of reaches to ipsilateral targets. With eccentric visual fixation trials lateral error did not differ from the central fixation, ipsilateral target presentations.

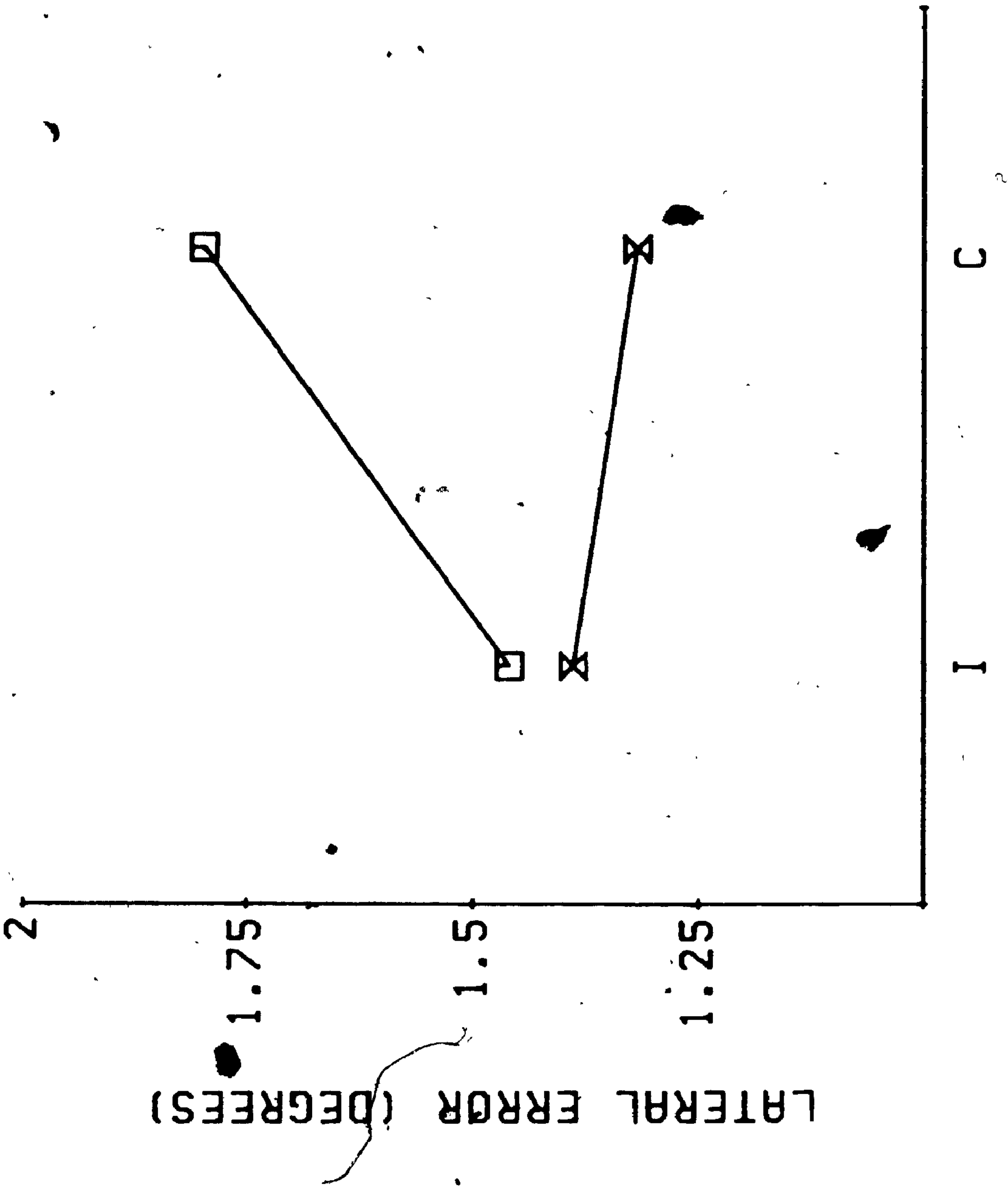

LATERAL ERROR (DEGREES)
2
1.75
1.5
1.25
I
C

Table III

Effect of Hand Used on Errors of Pointing

	Hand Used for Pointing					
	Left		Right		F ratio (1,3)	Probability level
	Mean	(S.D.)	Mean	(S.D.)		
Lateral Error (degrees)	1.57	(.74)	1.42	(.66)	16.45	$p < .05$
Vector Error (degrees)	1.96	(.74)	1.86	(.63)	35.94	$p < .01$

Discussion

The results of the present study make it clear that both the visual and spatial frames of reference are important determinants of the characteristics of the visually guided movements which were studied. Neither frame of reference, by itself, can account for all aspects of the subjects' performance. For most human daily activity the visual field and extrapersonal space relative to the body axis coincide. When they were separated, by requiring the subjects to fixate an eccentric position, it became apparent that both the time required to program and initiate the arm movement, and the accuracy of its final position, depended upon these two frames of reference, while the kinematic measures of the limb movement only depended upon the position of the target relative to the body axis and were independent of its position relative to the visual field.

The direct relationship between the hemispatial position of the target and the kinematic measures of the movement suggests that the manner in which a movement is executed is programmed with reference to the body axis rather than the visual field. The lack of any direct effect of varying the target position relative to the visual field on these measures, indicates that the programming of the velocity characteristics of the movement by either limb did not depend upon which cerebral hemisphere was initially stimulated by the target onset. Therefore, differences in the kinematic characteristics of reaches into ipsilateral versus contralateral hemispace cannot be attributed to an interhemispheric transfer of information. With eccentric fixation no transfer of information between the hemispheres would have been necessary for the production of reaches which crossed the body axis, since sensory and motor information could have been processed entirely within the hemisphere opposite to the hand being used. However, these reaches were performed differently than reaches on the same side of the body axis, with central fixation, a condition which also allowed intrahemispheric processing by the hemisphere opposite to the limb. As a result, the kinematic differences between reaches which crossed the body axis and those which did not, could not be attributed directly to an ipsilateral versus contralateral hemispheric control of the limb movements. The findings suggest instead, that the velocity of the limb movement was programmed with respect to the position of the target relative to the body axis, and that this hemispatial organization was independent of the position of the target in the visual field and independent of which cerebral hemisphere, ipsilateral or contralateral, was initially stimulated by the target onset. Although body hemispace determined the velocity characteristics of the movement, the relationship between this hemispatial programming and the neural systems which subserve it, remains unclear. These data did not provide any support for the suggestion by Bowers and Heilman (1980) that one cerebral hemisphere mediates the perceptual and motor activities in the contralateral hemispace.

The measures of the latency to initiate movement and the accuracy of final position differed from the kinematic measures in that the effects of changes in target position could not be related to one frame of reference directly. When the subjects fixated straight ahead and the position of the target relative to the visual field and body space coincided, the latency to initiate contralateral reaches was approximately 30 ms higher than that for ipsilateral reaches. This finding conformed to the results of the previous study. Simple reaction time studies which have investigated the effects of the laterality of target presentation have generally reported differences of less than 10 ms, which corresponds to the hypothesized interhemispheric transmission time (IHTT) of the large diameter fibres of the corpus callosum (see for review Bashore, 1981). Studies that have used more complex paradigms which require the subject to choose between two possible responses on the basis of the stimulus characteristics, have reported estimates of IHTT which approach the values found in the present study (Bradshaw and Perryman, 1970; Harvey, 1978; as cited in Bashore, 1981). To account for these increased estimates of IHTT with choice reaction time paradigms, Bashore (1981) has suggested that "systematically longer IHTTs are produced by the transmission of increasingly complex bits of information over smaller, more slowly conducting fibers" (page 366). Since pointing to the visual stimulus is a relatively complex response, such an explanation may hold for the present findings. Berlucchi et al. (1977) have suggested another possible explanation of the increased estimates of IHTT obtained by choice reaction time paradigms which again implies a decreased efficiency of transmission of complex information. They propose that these estimates can be "related both to interhemispheric transfer and to the deterioration of information taking place during such a transfer" (Berlucchi et al., 1977, page 511). An additional explanation is that the transfer of information is mediated by more slowly conducting, non-callosal routes. Simple reaction time studies of subjects who congenitally lack a corpus callosum and therefore must make use of non-callosal pathways, have revealed estimates of IHTT which are notably higher than those of normal subjects (see Reynolds and Jeeves, 1974 for review). The nature of the information required to produce a directed limb movement may require the use of similar, non-callosal routes. Although all of the above possibilities are viable explanations of the results for those trials in which the subjects fixated centrally, performance in the eccentric fixation condition did not fit with models of interhemispheric transmission.

When an eccentric fixation point was used, and the visual hemifield did not correspond to the body hemispace, there was no longer an advantage for reaches to the ipsilateral side of the body axis. Similarly, there was no difference in movement latency between the two visual hemifields and therefore no latency difference which could have been attributed to IHTT. Overall, the latency to initiate movements in the eccentric fixation condition was higher than that for central fixation. These findings can be compared to those of Anzola et al. (1977), who investigated the effects of stimulus-response (SR) compatibility on simple reaction time. They found that reaction times were lowest, and estimates of IHTT highest, when the responding hand was placed within the ipsilateral hemispace, and that reaction times were increased and IHTTs decreased if the responding hand was placed across the body axis in the contralateral hemispace. In order to account for these findings Bashore (1981) suggested that:

> "when both the (visual field) and spatial relations are compatible and a unimanual response is required, unilateral cerebral activation may be facilitated, the result being faster (reaction times) and slower transcommisural

> communication. In contrast, when there is anatomical incompatibility...bilateral cerebral activation may result to compensate for this difference and to relocate the hand in visual and kinaesthetic space; the effect is to slow (reaction times) but speed IHTT." (page 362).

In the present study, the starting position of the hands was always directly in front of the body axis, but eccentric fixation made the position of the target in the visual field different from its position relative to body space and this resulted in an increase in latency, and an elimination of any significant latency difference between reaches in either direction. In light of the differences between the present paradigm and that of Anzola et al. (1977) it would be premature to propose that the data support Bashore's (1981) suggestion of unilateral hemispheric activation when the frames of reference are compatible, versus bilateral hemispheric activation when the frames of reference are incompatible. However, it is clear that the pattern of latencies associated with IHTT can be eliminated when the two frames of reference are not compatible. The study of Bowers et al. (1981) represents a paradigm more similar to the present study in that eccentric fixation rather than changes in hand position was used to alter the compatibility of the visual hemifield and body hemispace although they required only a simple response rather than a directed pointing response. The physical limitations of pointing to the targets made it impossible to present targets in both visual hemifields and within one body hemispace in the present study. Bowers et al. (1981) also reported that reaction time was increased with eccentric fixation as compared to the central fixation, but it is unclear how estimates of IHTT were affected by their use of eccentric fixation points.

Although the present study confirmed the advantage in movement latency for ipsilateral reaches over contralateral reaches that was found in the previous study, there was no advantage in latency for one limb versus the other, and therefore no evidence of a hemispheric advantage in the efficiency of programming. The failure to confirm the presence of a right hand advantage for movement latency may have been due, in part, to the smaller number of subjects tested and to the limited number of central fixation trials for each subject. An additional methodological difference which may have also eliminated a right hand advantage was the use of only two brief targets for each block of trials as opposed to four targets which were presented randomly at brief and persistent durations.

Unlike the previous study, a right hand advantage was evident for the accuracy of final position. Thus pointing errors were significantly smaller when the right hand was used. Two possibilities, that are not mutually exclusive, may explain this finding. One is that the right hand advantage reflects an increased amount of practice in the use of the dominant hand for skilled, visually guided, behaviours. Another, related possibility refers more directly to the hemispheric control of the movement. The left hemisphere clearly dominates the control of "praxic" movements in man (Kimura, 1982). It may be that the visually guided reaching movements examined in the present study are closely related to such praxic limb movements in terms of their motor control. If this were true, an advantage in precision of movement would be expected for the limb contralateral to the dominant hemisphere since direct motorneuronal connections to the limb from this hemisphere would be possible.

The results of movement accuracy were somewhat similar to those of movement latency in that they could not be related directly to one frame of reference. For the central fixation trials, the accuracy results conformed to those of the previous study. Thus, when the visual and spatial frames of reference coincided, the accuracy of ipsilateral reaches was significantly better than that of contralateral reaches. The eccentric fixation trials revealed that both the visual and spatial frames of reference contributed to this laterality effect on pointing accuracy. Presentation of the targets to the ipsilateral side of either frame of reference was sufficient to ensure good accuracy. The errors increased only when the subjects were required to reach to targets presented to both the contralateral visual hemifield and the contralateral body hemispace. This result illustrates the interactive influence of these two frames of reference on the production of visually guided limb movements. As with the latency measure, there were no simple, additive laterality effects for each frame of reference. The position of the target, both relative to the visual field and relative to the body space, influenced the accuracy of the movement.

The present study examined the importance of the visual field and extrapersonal body space, as frames of reference within which visually guided movements of the limbs are executed. Since the performance of a movement can be characterized by a number of aspects of its performance, an attempt was made to explore the influence of these frames of reference on a number of measures of visually guided pointing. The velocity measures which characterized the production of the limb movements depended on target position relative to the body axis, and were not influenced by the position in the visual field in which the target first appeared. Further studies may help to determine if these hemispatial differences in the velocity of the movement reflect differences in the central programming of muscle activity, or differences in the biomechanical constraints of the skeletal-muscular system involved in the production of these movements. Regardless of the underlying neural organization responsible for the programming of the movement, the data indicate that the velocity of its execution is determined by the hemispatial positions of the limb and target.

Separation of the visual and spatial frames of reference had a significant effect on the latency and accuracy of the movements. Unlike the velocity measures, the latehcy and accuracy measures demonstrated an interactive influence of both frames of reference on the organization and execution of the movements. No simple additive model of effects can account for these results. Although the performance with central fixation is suggestive of a lateralized hemispheric organization of all aspects of the movement, it is clear that such an organization is altered extensively when the visual and spatial frames of reference do not coincide. With eccentric fixation there were no differences in movement latency which could be attributed to an interhemispheric transfer of information. The results of the eccentric fixation trials in the present study do not eliminate the possibility that a hemispheric organization is responsible for the sensory-motor integration of visually guided pointing movements but they indicate that such an organization must integrate both the visual and spatial frames of reference in the programming of these behaviours.

STUDY III

The Relationship Between the Latency of Ocular and Manual Movements to Eccentric Visual Targets

Summary

Movements of the eyes and limbs are coordinated in a number of motor activities but the degree to which the programming of ocular and manual movements involves common systems has not been explored extensively. In this study the latency to initiate orienting movements of the eyes and hands to lateralized visual targets was examined. Six right-handed subjects with no known visual problems were asked to fixate a central target and to look and/or point, quickly and accurately to visual targets, presented for 100 ms, at eccentricities of 10 and 20 degrees. Eye movements were monitored by infrared corneal reflection, and hand movement onset was taken from the release of microswitch. Both signals were recorded on FM tape and latency measures were calculated from polygraph records. A statistically significant positive correlation between movement latency of the eyes and hands, when both were used to orient to the target, was found over all of the subjects but this correlation was reduced in those subjects who experienced trials in which they were asked to look to the target without pointing prior to performing looking and pointing trials. Therefore, the findings of this study provided evidence for some processing of sensorimotor information by systems common to both ocular and manual movements, but suggested that this organization of information processing is flexible and may be influenced by factors such as experience with different task demands.

Introduction

The activity of orienting to a stimulus in the external visual world often involves the coordinated movement of the eyes, head and limbs. By the use of such different motor systems we are able to reach toward, and acquire accurately, objects of interest within the environment surrounding us. When the eyes, head and limbs are directed toward a common peripheral target there is a sequential ordering of movement onset. It has long been recognized that eye movements precede head movements to a visual target (Woodworth and Schlosberg, 1954, as cited in Bizzi, Kalil and Tagliasco, 1971). However, Bizzi et al. (1971) found that in monkeys, the onset of electromyographic (EMG) activity of the neck muscle agonists actually preceded that of the eye muscle agonists by about 20 ms, even though movement of the eyes preceded head movement by 20 to 40 ms. On the basis of these findings they suggested that "peripheral factors such as the longer contraction time of the neck muscles, as well as the inertial properties of the head" (Bizzi et al., 1971; page 453) determine the sequential ordering of the movement latencies of the different motor systems. Similar sequencing of movement latencies has also been reported for eye and limb movements when human subjects were asked to look and point to visual targets (Angel, Alston and Garland, 1970; Prablanc, Eschallier, Komilis and Jeannerod, 1979). Biguer, Jeannerod and Prablanc (1982) required subjects to track a step movement of a visual target by movements of their eyes, head and arm. Like Bizzi et al. (1971) they found that although the eyes moved before the head and arm, the onset of EMG activity in the arm and neck agonists occurred very close in time to the onset of the eye movement. Furthermore, they found significant correlations, ranging from .34 to .41 between the onset of the eye movement and the onset of EMG activity in the agonist muscles of the other motor systems.

The question which is raised by such correlations is what do they tell us about the sensorimotor processing involved in orienting to the target stimulus? One interpretation of a positive correlation in the latency to initiate movement by two motor systems is that it reflects the processing of information by some neural organization common to both systems. When the eyes and limbs are used to orient to a common visual target it is likely that the sensory input, at least to the level of the primary visual cortex or superior colliculus, is common to both movements. In contrast, the motor output undoubtedly involves distinct and separate neural pathways, at least below the level of the brainstem. The contribution of intermediate neural areas in the organization of the output of the two motor systems is much less clear. It remains to be established whether a correlation between the latency to move or the onset of muscle activity in two motor systems reflects more than the input of sensory information along channels common to both systems.

In Study 1, significant correlations were found between eye and arm movement latencies, and additional findings suggested that there was common sensorimotor processing of both movements which involved hemispherically organized neural systems. Unfortunately, the small number of trial repetitions (4) on which these within-cell correlations were based made interpretation of the correlation data difficult. It was not possible to examine the statistical significance of individual cell correlations and the large amount of variability introduced by having so few trials per cell also made valid comparisons of the strength of the correlations between subjects or between conditions difficult. Since an eye-movement-only condition was not included in Study 1 it was also impossible to determine if the latency to initiate movement of each system was altered if only one system was used to orient to the target. Therefore the present study recorded the latency of the eyes and arms to orient to visual targets when only the ocular motor or manual motor systems were employed, and when movement of both the eyes and arm was required.

Methods

Subjects

Subjects were 6 right-handed volunteers, 3 males and 3 females, ranging in age from 22 to 32 years. One of the female subjects had participated in Study 2. None of the subjects required visual correction.

Apparatus for Data Collection

During testing the subject was seated facing a 31 cm high by 90 cm long board, which contained a horizontal array of target lights. The subject sat with his head held in a chin and head rest, and with a distance of 50 cm between his eyes and the screen. The screen was centered with respect to the eye level of the subject and was covered with a black cloth which eliminated any view of the unilluminated target lights. A 1 degree diameter, white fixation point was used. The fixation point and all target lights were presented in the horizontal plane at approximately eye level on the screen. Target lights, 0.25 degrees in diameter, were presented at 10 degrees and 20 degrees of visual angle, to either side of the fixation point. The duration of target illumination was 100 ms. The luminance of the screen was 2 cd/m^2 while the fixation point luminance was 69 cd/m^2 and the target luminance was 91 cd/m^2. The targets were therefore of 98 percent contrast as defined in the previous studies. A start platform, which contained a microswitch, was situated immediately in front of the base of the chin rest. All reaches were initiated from this platform, although the actual position of the hand and fingers was allowed to vary slightly across trials. The eye position of the subjects was monitored by infrared corneal reflection (Eye-Trac Model 200, Gulf Western Ltd.) and was recorded on one channel of an FM magnetic tape recorder (Model A, A. R. Vetter Co.). The onset of the target light and the release of the start platform microswitch were recorded as voltage changes, on additional channels of the same tape record.

Procedure

Test sessions consisted of six blocks of 40 trials. Each hand was tested separately in alternating blocks. Within each block, all four targets were presented ten times each, in a random order. For two of the blocks the subjects were asked to look and point using their index finger, quickly and accurately to the target position, immediately following illumination of the target. For another two blocks of trials the subjects were asked to point to the target position while maintaining fixation on the central point. In the remaining two blocks the subjects were asked to look to the target positions but to keep their hands in the start position. During each of these three conditions the hand used either to respond or just placed on the start platform, was alternated between blocks. All trials began with the subjects fixating the central fixation point. At a variable interval following a "ready" command, the experimenter illuminated one of the targets. Practice trials were given at the start of each block to familiarize the subject with the test conditions. During the test session the eye position of the subject was monitored by the experimenter in order to ensure that the subject complied with the task requirements. The order of the hand which was first used and the order of presentation of the test conditions was balanced across the six subjects. The test session lasted for approximately 45 minutes, and the subjects were given rest periods between blocks if fatigued.

Apparatus for Data Analysis

Hard copy of the FM tape records was run off on a polygraph (Model 7, Grass Instrument Co.) at a paper speed of 60 mm/s. This provided a temporal resolution of approximately 9 ms. The time between the onset of the light stimulus and the beginning of movement were recorded for both the eyes and hands on all trials in which there was movement. Onset of movement of the hand was defined as the voltage change resulting from the release of the start platform microswitch. Onset of eye movement was defined as the first measurable change of the eye position from fixation (resolution of .5 mm, equal to .5 degrees) in the direction of the target, following stimulus onset.

Results

Analysis of Latency of Eye and Hand Movement

The mean latencies of the eyes and hands were calculated for each of the experimental conditions for each subject and an analysis of variance was conducted on these two sets of scores. The analysis was balanced such that all interactions between factors were possible. The factors were: 1) the eccentricity of the target--10 or 20 degrees; 2) the visual field of target presentation--left or right; 3) whether the response was movement of one system alone (eyes-only or hand-only) or movement of the eyes and hand together; 4) the hand used for pointing (hand-only and both together conditions) or the hand placed in the start position (eyes-only condition)--left or right. For the analysis of eye movement latency no statistically significant main effects or interactions were found and the overall mean latency was 283 ms. Analysis of the hand movement latency revealed an overall mean of 351 ms with one main effect and one 2-way interaction which attained statistical significance. For those trials in which the subjects looked and pointed to the targets the onset of the eye movements (mean latency = 286 ms) consistently preceded the onset of arm movements (mean latency = 356 ms).

A main effect of target eccentricity was found to be significant for the latency to initiate hand movement ($F(1,5) = 15.4$, $p < .05$), with a longer latency for 20 degree targets (357 ms) than 10 degree targets (345 ms). The latency to initiate eye movements was also higher for 20 degree targets (287 ms) than 10 degree targets (279 ms) but this difference was not statistically significant ($F(1,5) = 1.74$, $p < .25$).

An interaction of hand used for pointing by visual field of target presentation was found to be significant for the hand movement latency ($F(1,5) = 9.3$, $p < .05$). Figure 1 illustrates this advantage for ipsilateral (343 ms) over contralateral (360 ms) reaches.

Analysis of Correlation of Eye/Hand Latencies

A total of 80 trials were performed by each subject in which he was asked to look and point to the stimuli (40 trials with left hand and 40 trials with right hand). For each block of 40 trials there were 10 repetitions of each target. The latency to initiate movement of the eyes and hands were correlated for these 10 trials thus yielding a total of 8 correlations per subject. These correlations are summarized in Table I. A correlation based on 10 pairs of scores must exceed .63 in order to be stastistically different from 0.0 at the .05 probability level. It is apparent from Table I that all subjects demonstrated at least one positive correlation, which exceeded this value and for each experimental condition at least one subject demonstrated a positive correlation greater than .63. These correlations were converted to z-scores in order to normalize the data and these were subjected to an analysis of variance with [illegible] hand used for pointing (left or right); the visual field of target presentation (left or right); and the target eccentricity (10 or 20 degrees) as factors. However, no significant main effects or interactions were found (Appendix IIj).

The converted z-scores for all of the subjects were also tested against the null hypothesis of a zero correlation between eye and hand response latencies, by means of a t-test. The overall mean correlation for all subjects and all conditions was .36 which was statistically

Figure 1. Effect of laterality of the stimulus presentation (I-ipsilateral; C-contralateral) on latency to initiate limb movement. ◇ - Left hand; △ - Right hand. Reaches to contralaterally presented targets were initiated at a longer latency for both limbs.

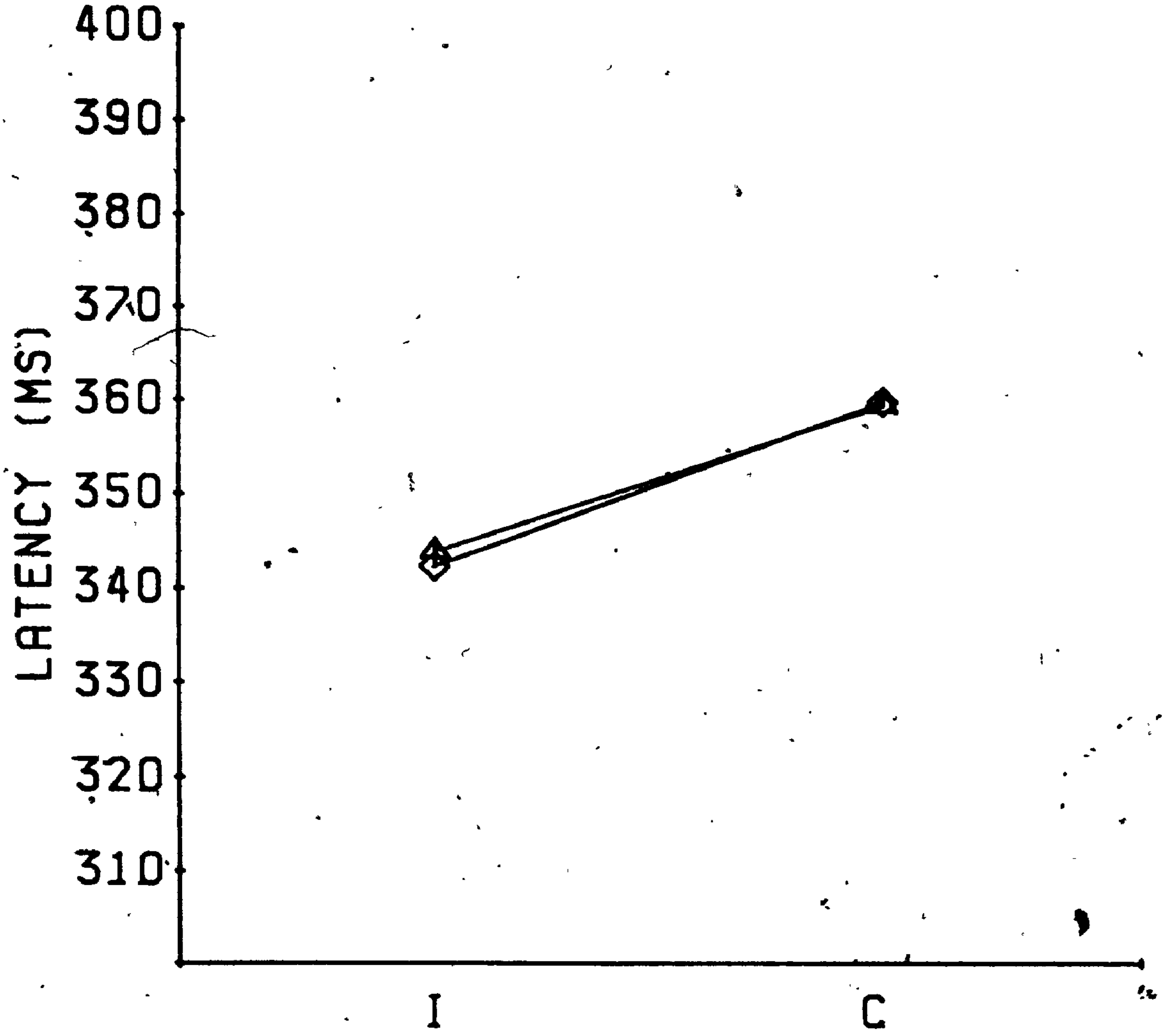

LATENCY (MS)
400
390
380
370
360
350
340
330
320
310
I
C

Table 1

Correlations of Eye and Hand Movement Latency for All Subjects Under All Experimental Conditions

Hand	Visual Field	Eccentricity	Subject #					
			1	2	3	4	5	6
L	L	10°	.53	.65*	.58	.41	.22	.46
L	L	20°	.03	.70*	.28	.76*	-.50	.72*
L	R	10°	.76*	.79*	-.30	-.60	.02	-.22
L	R	20°	-.12	.71*	-.12	.45	.37	.49
R	L	10°	.64*	.26	.91*	-.35	.60	.42
R	L	20°	.38	.46	-.16	-.42	.87*	.49
R	R	10°	.76*	.58	-.22	.10	-.21	.30
R	R	20°	.25	.32	.67*	.55	-.10	.37

* indicates a correlation greater than the value required for a statistically significant difference from zero, at the .05 probability level, for a comparison based on 10 pairs of scores.

greater than zero (t = 5.27, df = 47, p < .001). In a similar manner the correlations for each subject were tested against the null hypothesis of a zero correlation. These data are summarized in Table II. Three of the six subjects demonstrated significant positive correlations, but there was considerable intersubject variability in the strength of the correlation. Although the total number of subjects is small there is an indication that a difference in the order of presentation of the experimental conditions may be related to this intersubject variability. Subjects 1 and 2, who began the experimental session by responding with eye and hand movements, had the largest and statistically significant positive correlations for response latencies (r = .40, .56). Subjects 3 and 4, who had 80 trials of eyes-only and 80 trials of hand-only responses before responding with both systems together, had low and statistically non-significant positive correlations for eye and hand response latencies (r = .21, .11). Of the remaining two subjects, Subject 5 who had 80 eyes-only responses before responding with both systems, also had a non-significant positive correlation (r = .16). However, Subject 6 who had 80 hand-only responses before responding with both systems had a statistically significant positive correlation (r = .38). Thus all 3 subjects who were presented with the eyes-only condition before responding with both systems (Subjects 3, 4, 5) did not show a significant correlation of eye and hand response latencies. The subjects who responded with both systems as the first experimental condition (Subjects 1 and 2) and the subject who responded with both systems after the hand-only conditions (Subject 6) all demonstrated statistically significant, positive correlations of the latency to look and point to the visual target.

Table II

Mean Correlation of Eye and Hand Latency for All 6 Subjects,

Indicating the Order of Experimental Subconditions

Subject #	Mean Correlation	t(df=7)	Probability level	Sex	Order of Conditions*	Mean of Within-cell Standard Deviations (ms)	
						Eyes	Hands
1	.40	3.55	$p < .01$	F	B - E - H	28.8	32.3
2	.56	7.18	$p < .001$	M	B - H - E	53.6	31.1
3	.21	1.46	$p < .2$	F	H - E - B	53.8	36.0
4	.11	0.72	$p < .5$	F	E - H - B	67.4	60.6
5	.16	1.18	$p < .3$	M	E - B - H	52.5	29.0
6	.38	3.96	$p < .01$	M	H - B - E	48.6	38.4

* B = Both eyes and hand respond together

E = Eyes-only response

H = Hand-only response

Discussion

The most interesting data obtained from this investigation were those derived from the correlation of the latency to initiate movement of the two systems. By the inclusion of more trials to make up each correlation, it was possible to make a more detailed examination of these correlations than in Study 1. Within individual subjects the strength of the correlation was found to vary with the hand used for pointing or the position of the target, but none of these effects were significant for the population of subjects in the present study or in Study 1. The overall mean correlation of .36 was statistically significant and identical to the mean value of .36 obtained in Study 1. These values are also within the range of values reported by Prablanc et al. (1979) and close to the value reported by Biguer et al. (1982) for eye movement and biceps EMG (r = .41). Megaw and Armstrong (1973), after fitting their data of eye and arm movement latencies to a linear model, found a higher correlation between the residual error terms of the equations for each system (r = .6725). Thus, despite variations in the method of presentation of the visual stimuli, the type of limb movement required, and the methods of recording movement onset, these low but significant correlations seem to be robust and reproducible.

Although the correlations between eye and limb movement latencies are statistically significant they are far from a perfect correlation of 1.0. Serial processing of information for both motor systems along a single sensorimotor channel would be expected to result in a very high, if not perfect correlation between the latencies to initiate movement.

As Megaw and Armstrong (1973) point out "the single-channel model is denied in so far that certain features of information processing, most probably on the response side, can occur in parallel." (page 27). In fact Prablanc et al. (1979) use the lack of a strong correlation to argue "in favour of a parallel processing of the eye and hand motor systems." (page 120). The term "parallel processing" implies the use of completely separate sensorimotor chanels for the two systems although both channels operate at the same time. Such a system would allow factors to affect the processing time of one channel independent of the other and reduce the correlation between their response latencies. Given our knowledge of the distinct neuroanatomical differences in the ocular motor and manual motor systems, the presence of parallel processing is most likely, at least for the later stages of motor programming. Therefore, it is perhaps surprising that a significant correlation exists between the response latencies of the two systems.

Megaw and Armstrong (1973) suggested that "the question of serial or parallel processing on the input side is unlikely to arise if both the visual and motor systems employ the same stimulus analysis" (page 27). However, an analysis of sensory information by some common process before referral of this information to the two motor systems for parallel output, is by no means an established fact. The assumption which appears to be very prevalent is that at least up to the level of primary visual cortex or superior colliculus the visual information necessary for both movements will be carried over the same neuroanatomical pathways, but the strength of this assumption is questionable. Even at the level of the retinal ganglion cell there is evidence of distinct sensory channels. X- and Y-cells can be distinguished on the basis of their response characteristics, distribution across the retina, axonal conduction velocities, and the termination sites for their axonal projections (see Lennie, 1980, for review). Since distinct sensory channels are present there is also the possibility that parallel sensorimotor channels for distinct motor systems exist as well. If the same neural pathways are involved in sensory processing of ocular and manual movements up to some primary sensory level, it is still important to establish how much additional processing is carried out by systems common to both movements.

The sequential ordering of movement onset is clearly important for the normal production of combined eye and limb movements. The study of Prablanc et al. (1979) and Study 1 both demonstrated that accuracy of a pointing movement was increased when the subjects were allowed to refixate the target with their eyes. Thus, it is important that the eyes attain the target position before the hand so that visual information can be used to adjust the manual motor activity and ensure an accurate completion of the movement (Conti and Beaubaton, 1976; Carleton, 1980). The same argument probably holds for combined eye and head movements as well, since the timing of EMG activity and movement onset of the neck is so similar to that of limb movements (Biguer et al., 1982). The maintenance of such a sequential organization probably requires that there be sensorimotor processing, above the primary sensory level, which involves structures or systems common to the ocular and manual and perhaps cephalic motor systems.

Common processing for the ocular and manual motor systems has been implied from the similar effects of different experimental conditions on certain aspects of the performance of the two systems. Mather and

Putchat (1983) have reported similar effects of predictability of target movement on continuous tracking by the eyes and arm. Fisk and Mather (in preparation) found that the effects of changing the sensory modality of targets from visual to auditory were similar for directed ocular and manual movements. Shibasaki, Sadatoshi and Kuroiwa (1979), in a study of patients suffering from Parkinson's disease, suggested that this disease process results in a bradykinesia of the ocular motor system which is similar to the bradykinesia evident in other body movements. Findings such as these support the concept of a certain amount of common sensorimotor processing of ocular and manual movements.

In addition to the overall significance of the latency correlations there was a certain amount of variability in the strength of the correlations between the individual subjects. These differences also provided some insight into the possible organization of the ocular and manual responses. Although the total number of subjects was small, there was an indication that prior exposure to different experimental conditions affected the strength of the correlation between eye and arm movement latency. Those subjects who were asked to de-couple the two systems, moving only the eyes or only the arm, before moving both together had lower correlations than those subjects who began the session by looking and pointing to the stimuli. It is unlikely that this finding simply represents an effect of practice in the experimental situation since Megaw and Armstrong (1973) used well practiced subjects, and it is probable that Prablanc et al. (1979) did so as well, given the complexity and large number of different conditions which they employed. Thus, the finding that prior experience may alter the relationship between the two motor systems points to a very flexible organization of both. This flexibility as a result of experience, suggests an influence of relatively high level processing.

The failure to find a right-hand advantage for the hand and eye movements in the present study may have resulted from the use of only brief targets as opposed to the random series of brief and persistent targets that had been employed in Study 1. Study 2, which also employed brief targets only, also failed to reveal a right hand advantage for limb movement latency. In a recent investigation of eye and limb movements to visual and auditory targets it was found that when the subject were presented with blocks of either brief (200 ms) or long (5 s) targets, the latency of the eye and limb movements were lower for brief targets (Fisk and Mather, in preparation). This implies that the subjects may have bypassed the activation of neural systems which make use of target position information throughout the movement, when they were aware that no such information will be available. A reduction in the number of neural systems involved could conceivably have reduced the necessary processing time, and may have eliminated a hemispheric advantage for information processing as well. It is difficult to make comparisons between Study 1 and the present study since the subjects differed between them but the overall mean latencies of the eye and limb movements were indeed lower in the present study than in Study 1. Mean latencies were 286 ms for eye movement and 356 ms for arm movement in the present study, while the values for Study 1 were 397 ms and 450 ms for the eyes and arms respectively.

The use of brief targets only in the present study may have also reduced the importance of maintaining a common processing of the eye and limb movements. The 100 ms duration of the target did not allow the eyes to fixate it, and the amount of visual information which could be provided to guide the limb movement during its production was limited. The use of information based on fixation of the target in the completion of the limb movement, and the activation of the neural systems which subserve this analysis may be an important factor in the involvement of lateralized, hemispheric systems for the sensorimotor processing of both the eye and arm movements. However, the use of only brief duration targets did not eliminate the correlation between the latencies of the two systems. In future studies it would be wise to employ blocks of brief and long target durations and to allow for an examination of the effects of practice and prior experience on the relationship between the production of eye and limb movements. Clearly there is a common organization of the two systems which is flexible and dependent upon sensory information, experimental demands, and previous experience, and yet this common organization is important for the normal execution of visually guided behaviours. Further study of this interaction will be required if we are to understand better its underlying neural control.

General Discussion

The present series of studies was designed to examine behaviour which approximated reaching toward an object in the environment under visual control. An attempt was made to use a comprehensive description of the spatial and temporal characteristics of such movement through the collection of a number of interrelated measures of performance. These measures were examined under a variety of conditions including different amounts of visual information and variations in the position of the target in extrapersonal space and/or in the visual field. Movements of the eyes allow the subject to change the position of the target in the visual field and increase the available visual information. Since most visually guided behaviours involve the coordinated activity of the ocular motor system as well as other motor systems the relationship between ocular and manual performance was also explored in the present studies. Subjects were not practiced so that the variability within and between subjects would be similar to that found in natural situations. For a similar reason, the instructions to the subjects were deliberately open-ended. It was hoped that by allowing the subjects to choose the manner in which they approached the task, responses which approximated normal, everyday reaching would be performed. A result of this approach was the considerable variability in performance both within and between subjects, but despite this variability a number of consistent aspects of performance were evident.

All of the subjects' demonstrated slight but consistent and measurable deviations from a straight line path in their trajectories. The high efficiency most likely reflects the well-practiced nature of this type of behaviour in normal everyday activity. Some of the deviation from straight line trajectories was evident as changes in direction of movement which occurred during the periods of low velocity movement at the end of the reaches. The evidence suggests that during these periods, visual information was used to update and modify the motor program responsible for the production of the limb movement. This use of visual information was evident from the increased accuracy and prolonged deceleration phase of reaches to persistent versus brief targets.

The importance of accurate foveation of the visual target in the guidance of the limb movement was also evident since accuracy of pointing was greatest for persistent targets which could be fixated. Processing of information in the central visual field was also evident with manual movements directed to brief targets. Two findings suggest that the point of fixation was used as a target for the hand movement in the absence of other information about the target position. First, vertical errors were reduced when the subjects were allowed to move their eyes regardless of the target duration, and second, the eye and hand position errors for brief target trials were positively correlated. It is apparent that a variety of visual information can be used to guide the production of a directed limb movement and that the subjects adapted their behaviour to maximize the use of whatever information was available.

The present series of studies also revealed consistent characteristics of the motor control which were reflected in measures other than the accuracy of movement. The most consistent finding was the dependence of the movement velocity on the relationship between the position of the target in body hemispace and the limb used for reaching. Reaches into contralateral hemispace were slower, less accurate and did not demonstrate scaling of movement amplitude by changes in maximum velocity. Whether these results reflect central programming differences or peripheral factors such as the mechanical constraints of the skeletal muscular system could not be evaluated easily in the present paradigm. Although the measures of manual latency and accuracy were also affected by the hemispatial position of the target these effects were not simple. Both measures were also affected by the position of the target in the visual field. These results were revealed in Study 2 which removed the confounding of these two spatial frames of reference. The complexities of the relationships of the different measures of performance to these spatial frames of reference indicate the complex integration of visual spatial information which must take place in order to localize an object in space by means of a directed movement. In the present studies the orienting response was simplified by restriction of the head movements. Clearly, coordination of head movements with other motor behaviour can be involved in orientation to a visual stimulus (Bizzi, et al., 1971) and this may require the integration of head-relative, as well as body-relative and visual field-relative, spatial coordinates.

A suggestion of a lateralized organization of the neural systems responsible for the programming of visually guided limb movements arises from a number of findings. As long as central fixation was used, so that the visual hemifield and hemispatial field corresponded, there was an advantage in hand movement latency for ipsilateral as opposed to contralateral reaches. This finding was present in each of the three studies, and is consistent with other reaction time studies which have attributed these differences to the transfer of information between the hemispheres (see for review Bashore, 1981). Manual accuracy was also greater for ipsilateral versus contralateral reaches. The present findings may also represent an advantage for intrahemispheric processing of visual motor information, but since few other studies have examined localization of a visual target, it is difficult to draw comparisons. A hemispheric organization was also suggested by the right hand advantage for manual latency in Study 1 and for manual accuracy in Study 2.

The measures of ocular motor performance also provided an unexpected source of support for the suggestion of a hemispheric organization for sensorimotor integration. The same advantages in manual latency for ipsilateral reaches and for reaches by the right hand in Study 1 were found for the ocular latency as well. These findings, as well as the significant correlation of ocular and manual latency, suggest that there is a common sensorimotor integration of information for both ocular and manual motor systems by a hemispherically organized system. The failure to find a laterality effect for ocular latency or a right hand advantage for either ocular or manual latency in Study 3 may have been due to the differences in the procedure from Study 1, in particular the use of brief targets only. However, the correlation between the latencies to initiate movement of the two systems was confirmed. In addition, Study 3 indicated that prior exposure to different experimental conditions could affect the strength of these correlations. This supports the concept that the relationship between ocular and manual performance is the result of common processing by higher level systems.

The present series of studies provides behavioural evidence for a flexible system of motor programming of ocular and manual movements, which involves cortical structures. The question which must be addressed is how such a system is achieved. Humphrey (1969) has provided an elegant and detailed description of the interconnections of the cortical association areas which have been implicated in the control of visually guided limb movements. The following discussion will attempt to integrate the findings of the present studies with this body of information, which has been gathered from studies of nonhuman primates. It is evident that the association areas of the cerebral cortex provide an interconnected network which is well suited to the integration of visual spatial information and the programming of a coordinated output of the ocular and manual motor systems. These areas include the parietal areas 5 and 7, and the anterior areas 8 and 6 and the supplimentary motor cortex (SMA). As Humphrey (1979) points out, these areas all receive afferents from cortical and/or subcortical areas which are related to visual processing and all send efferent projections to other cortical association areas as well as to subcortical structures implicated in motor output. Thus, the potential exists for a number of parallel but interactive systems of motor output from cortical association areas.

The question of how such systems account for the findings of the present studies cannot be answered easily, but some speculation is possible. The present studies illustrated both parallel and common processing of visual information by the ocular and manual motor systems. The most probable source of this flexible interaction lies within the parietal association cortex. It is well known that ablation of this area results in disruption of visual spatial behaviours in man and other nonhuman species. In primates, areas 5 and 7 of the parietal cortex are ideally suited, in terms of their efferent and afferent connections to subserve the analysis of visual spatial information for the ocular and manual motor systems. Both areas 5 and 7 receive substantial subcortical afferents from the lateral posterior-pulvinar complex of the thalamus which receives input from somatosensory and visual pathways. The remaining input and output connections of these areas reflect their relative specialization. A major source of input to area 5 arises from somatosensory cortical areas 1 and 2, while its efferent projections are to subcortical areas including the pons and putamen and to area 6, SMA and area 4 of the cortex. Thus area 5 seems ideally situated to exert direct and indirect influences on cortical and subcortical structures involved in the motor control of limb movements. In contrast, area 7 seems more suited to a role in ocular motor programming. The subcortical and transcortical input to area 7 is much more diverse and its output to the precentral arm area of motor cortex is not direct. However, the direct efferent projections to the pretectum and superior colliculus suggest that area 7 has a role in the programming of eye movements.

Ocular and manual latencies were found to be positively correlated in both studies 1 and 3. This result would be expected if the programming of both movements involved the integration of information within the parietal cortex. In Study 3 the correlation in movement latency appeared to be altered by prior exposure to conditions that required movement of either the eyes or hand alone. Under such conditions the two systems may operate in parallel with less involvement of cortical areas and more direct output to the superior colliculus from area 7, and to the precentral motor cortex (area 4) from area 5. Another result of a de-coupling of the two systems would be a reduction in the total amount of processing time which could account for the overall lower movement latencies noted in Study 3 as compared to Study 1. One would also expect a greater degree of interaction between ocular and manual motor programming if movements of the eyes could provide relevant information for the guidance of the limb movement. In Study 1 such information was occasionally available since the persistent target presentations provided feedback of the relative positions of the hand and the target. In this study both the manual and ocular latency measures demonstrated comparable advantages for responses by the right hand or responses to ipsilateral targets, a finding which is consistent with the processing of information by a common, hemispherically organized system for both the eyes and limb.

The most striking and consistent findings of the present study were the differences in kinematic characteristics of limb movements to targets in the ipsilateral body hemispace as opposed to targets across the body axis, in the contralateral hemispace. These differences in the execution of the movement were independent of the position of the target in the visual field when the visual and body-relative space were disembedded in Study 2. Some recent electrophysiological findings of Georgopoulos, Kalaska, Caminiti, and Massey (1982) may be related to this behavioural difference. They examined the discharge characteristics of single units of the motor cortex of four rhesus monkeys in relation to movement of a hand-held manipulandum, over a plane surface, to visual targets. Most cells fired at a higher rate for movement in one of the eight possible directions of movement. This resulted in bell-shaped tuning curves of directional specificity with movement in a "preferred" direction accompanied by the greatest level of activity. Of these directionally specific cells, the greatest proportion had preferred directions of movement to the ipsilateral side of the body axis, with the most highly preferred direction representing extension of the arm forward and lateral from the body axis. This type of movement approximates the ipsilateral reaches of subjects in the present Study. Thus, the laterality differences in limb movement execution which were found in studies 1 and 2 may represent differences in motor programming at the level of the primary motor cortex.

The results of the present series of studies may raise more questions than they answer, but this should be expected. Visually guided behaviour is very complex in terms of the number of muscle groups involved, the type of information processed, the characteristics of its performance, and the neural systems involved. Because of these facts it is a topic which cannot be investigated in a simple manner. Yet it is an important topic to investigate since visually guided limb movements are such a basic component of everyday human activity, and since the ability to produce such movements accurately has undoubtably played a large role in human development. By attempting to use a more comprehensive approach to describing and characterizing the performance of a movement which begins to approximate normal behaviour, we are able to gain insight into how such behaviours may be organized within the nervous system. More specific questions, raised by an initial general approach, may then be formulated and investigated more fully. Although this work represents only a beginning, it is an essential step in the development of an understanding of how we are able to guide the movement of our bodies through space.

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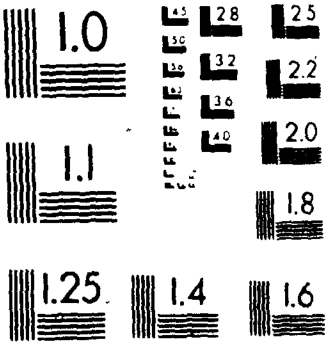

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Appendices

Appendix Ia

Table of the means and standard deviations of the values presented in the figures of Study 1. Values for all figures except Figure 7 are included.

Appendix Ia

Figure #	Measure	Condition	Mean	Standard Deviation
2	Latency (ms)	Left hand-Ipsilateral Target	400.5	52.3
		Left hand-Contralateral Target	418.7	56.7
		Right hand-Ipsilateral Target	378.5	47.0
		Right hand-Contralateral Target	401.0	64.9
3	Latency to Attain Maximum Velocity (ms)	Left hand-Ipsilateral Target	202.0	31.0
		Left hand-Contralateral Target	231.7	34.7
		Right hand-Ipsilateral Target	212.8	44.0
		Right hand-Contralateral Target	225.8	44.8
4	Maximum Velocity (cm/s)	Left hand-Ipsilateral Target	181.2	23.2
		Left hand-Contralateral Target	146.1	15.9
		Right hand-Ipsilateral Target	164.6	24.1
		Right hand-Contralateral Target	146.3	15.9
5	Mean Velocity (cm/s)	Left hand-Ipsilateral Target	89.1	15.7
		Left hand-Contralateral Target	73.3	13.4
		Right hand-Ipsilateral Target	81.9	12.0
		Right hand-Contralateral Target	74.3	10.8
6	Duration (ms)	Left hand-Ipsilateral Target	629.4	119.5
		Left hand-Contralateral Target	703.8	143.2
		Right hand-Ipsilateral Target	620.2	101.9
		Right hand-Contralateral Target	660.5	131.6

Continued...

Appendix Ia (Continued)

Figure #	Measure	Condition	Mean	Standard Deviation
8	Latency (ms)	Left hand-Ipsilateral-10° Target	395.0	46.6
		Left hand-Ipsilateral-20° Target	406.0	57.0
		Left hand-Contralateral-10° Target	405.9	55.3
		Left hand-Contralateral-20° Target	431.6	55.1
		Right hand-Ipsilateral-10° Target	372.1	45.1
		Right hand-Ipsilateral-20° Target	385.0	47.9
		Right hand-Contralateral-10° Target	390.3	37.4
		Right hand-Contralateral-20° Target	420.4	50.2
9	Maximum Velocity (cm/s)	Left hand-Ipsilateral-10° Target	172.8	22.2
		Left hand-Ipsilateral-20° Target	189.6	21.0
		Left hand-Contralateral-10° Target	148.3	15.5
		Left hand-Contralateral-20° Target	143.9	16.1
		Right hand-Ipsilateral-10° Target	157.1	20.9
		Right hand-Ipsilateral-20° Target	172.0	24.7
		Right hand-Contralateral-10° Target	144.9	15.8
		Right hand-Contralateral-20° Target	147.7	15.9
10	Mean Velocity (cm/s)	Left hand-Ipsilateral-10° Target	85.9	15.2
		Left hand-Ipsilateral-20° Target	92.4	15.6
		Left hand-Contralateral-10° Target	75.8	12.1
		Left hand-Contralateral-20° Target	70.8	14.2
		Right hand-Ipsilateral-10° Target	79.7	10.3
		Right hand-Ipsilateral-20° Target	84.2	13.0
		Right hand-Contralateral-10° Target	73.1	10.9
		Right hand-Contralateral-20° Target	75.5	10.5

Continued...

Appendix Ia (Continued)

Figure #	Measure	Condition	Mean	Standard Deviation
11	Duration (ms)	Left hand-Ipsilateral-10° Target	626.2	115.1
		Left hand-Ipsilateral-20° Target	632.6	123.5
		Left hand-Contralateral-10° Target	660.1	106.1
		Left hand-Contralateral-20° Target	747.6	161.1
		Right hand-Ipsilateral-10° Target	611.1	87.6
		Right hand-Ipsilateral-20° Target	629.2	113.7
		Right hand-Contralateral-10° Target	658.3	107.9
		Right hand-Contralateral-20° Target	678.9	106.3
12	Lateral Error (degrees)	Left hand-Ipsilateral Target	1.05	0.82
		Left hand-Contralateral Target	1.44	0.96
		Right hand-Ipsilateral Target	0.94	0.76
		Right hand-Contralateral Target	1.42	0.89
13	Vector Error (degrees)	Left hand-Ipsilateral Target	1.38	0.77
		Left hand-Contralateral Target	1.70	0.92
		Right hand-Ipsilateral Target	1.30	0.72
		Right hand-Contralateral Target	1.78	0.87
14	Lateral Error (degrees)	Left hand-Ipsilateral-10° Target	0.91	0.63
		Left hand-Ipsilateral-20° Target	1.20	0.95
		Left hand-Contralateral-10° Target	0.88	0.58
		Left hand-Contralateral-20° Target	2.00	0.94
		Right hand-Ipsilateral-10° Target	0.73	0.46
		Right hand-Ipsilateral-20° Target	1.14	0.92
		Right hand-Contralateral-10° Target	1.19	0.71
		Right hand-Contralateral-20° Target	1.65	1.00

Appendix Ia (Continued)

Figure #	Measure	Condition	Mean	Standard Deviation
15	Vector Error (degrees)	Left hand-Ipsilateral-10° Target	1.26	0.63
		Left hand-Ipsilateral-20° Target	1.[illegible]7	0.89
		Left hand-Contralateral-10° Target	1.17	0.54
		Left hand-Contralateral-20° Target	2.22	0.91
		Right hand-Ipsilateral-10° Target	1.12	0.43
		Right hand-Ipsilateral-20° Target	1.48	0.89
		Right hand-Contralateral-10° Target	1.58	0.71
		Right hand-Contralateral-20° Target	1.98	0.96
16	Vector Error (degrees)	Brief Targets-Eye Movement	2.02	0.98
		Brief Targets-No Eye Movement	1.78	0.76
		Persistent Targets-Eye Movements	0.98	0.50
		Persistent Targets-No Eye Movements	1.38	0.67
17	Latency (ms)	Left hand-Eye Movement	414.2	115.2
		Right hand-Eye Movement	379.0	71.9
		Left hand-Finger Movement	464.7	44.3
		Right hand-Finger Movement	433.3	48.7
18	Latency (ms)	Ipsilateral Targets-Left hand-Eye Movements	398.3	111.3
		Contralateral Targets-Left hand-Finger Movements	430.0	116.7
		Ipsilateral Targets-Left hand-Finger Movements	454.3	38.3
		Contralateral Targets-Left hand-Finger Movements	474.7	47.3
		Ipsilateral Targets-Right hand-Eye Movements	373.3	73.3
		Contralateral Targets-Right hand-Eye Movements	383.7	71.3
		Ipsilateral Targets-Right hand-Finger Movements	422.3	46.7
		Contralateral Targets-Right hand-Finger Movements	444.7	48.0

Appendix Ia (Continued)

Figure #	Measure	Condition	Mean	Standard Deviation
19	Lateral Error (degrees)	10°-Brief Targets-Eyes	1.87	1.09
		20°-Brief Targets-Eyes	3.68	2.91
		10°-Brief Targets-Finger	1.49	0.74
		20°-Brief Targets-Finger	2.27	1.21
		10°-Persistent Targets-Eyes	1.07	1.01
		20°-Persistent Targets-Eyes	1.77	1.48
		10°-Persistent Targets-Finger	0.55	0.37
		20°-Persistent Targets-Finger	0.86	0.58

Appendix Ib

Table of the means and standard deviations of the values presented in the figures of Study 2. Note that the laterality of the target position is coded relative to the body midline for figures 1 to 5 and is coded relative to the point of visual fixation for figure 6.

Appendix Ib

Figure #	Measure	Condition	Mean	Standard Deviation
1	Maximum Velocity	Ipsilateral-10° Targets	188.5	14.9
		Ipsilateral-20° Targets	209.2	16.2
		Contralateral-10° Targets	172.6	9.0
		Contralateral-20° Targets	173.6	5.6
2	Mean Velocity (cm/s)	Ipsilateral-10° Targets	98.9	10.9
		Ipsilateral-20° Targets	109.0	13.9
		Contralateral-10° Targets	89.3	23.0
		Contralateral-20° Targets	93.5	11.8
3	Duration (ms)	Ipsilateral-10° Targets	542.3	146.5
		Ipsilateral-20° Targets	567.2	89.2
		Contralateral-10° Targets	588.2	83.1
		Contralateral-20° Targets	648.6	102.8
4	Latency (ms)	Ipsilateral Targets-Central Fixation	314.3	20.7
		Contralateral Targets-Central Fixation	345.7	32.8
		Ipsilateral Targets-Eccentric Fixation	339.8	33.1
		Contralateral Targets-Eccentric Fixation	352.2	33.1
5	Lateral Error (degrees)	Ipsilateral Targets	1.21	0.61
		Contralateral Targets	1.39	0.62
6	Lateral Error (degrees)	Ipsilateral* Targets-Central Fixation	1.27	0.69
		Contralateral* Targets-Central Fixation	1.57	0.72
		Ipsilateral* Targets-Eccentric Fixation	1.21	0.44
		Contralateral* Targets-Eccentric Fixation	1.15	0.52

* Laterality coded relative to the visual field rather than relative to the body midline.

Appendix Ic

Table of the means and standard deviations of the values presented in the figure of Study 3.

Appendix Ic

Figure #	Measure	Condition	Mean	Standard Deviation
1	Latency (ms)	Left hand-Ipsilateral Targets	342.3	34.9
		Left hand-Contralateral Targets	359.9	37.1
		Right hand-Ipsilateral Targets	343.9	36.6
		Right hand-Contralateral Targets	359.5	36.8

Appendix IIa

Table of F ratios and Probability levels for analysis of variance (SPSS, Balanova program) of Maximum Velocity, Latency to Attain Maximum Velocity, Mean Velocity and Duration in Study 1. Probability levels are based on 1,7 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are target eccentricity (X); visual field/body hemispace (F); eye movements versus maintained fixation (E); target duration (D); and hand used to respond (H).

Appendix IIa

Source	Maximum Velocity		Latency to Attain Maximum Velocity		Mean Velocity		Duration	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
X	34.3	.00063*	18.9	.00338*	3.26	.11386	10.0	.01585*
F	25.6	.00147*	7.28	.03075*	26.5	.00133*	4.35	.07543
E	.019	.89474	.580	.47118	.083	.78152	.448	.52472
D	2.22	.18003	.268	.62038	4.41	.07392	5.83	.04646*
H	3.18	.11852	.084	.78033	1.74	.22878	1.74	.22830
X by F	6.72	.03579*	.191	.67521	10.6	.01394*	5.25	.05565
X by E	.001	.97709	4.69	.06691	9.25	.01882*	8.58	.02206*
X by D	.041	.84595	.602	.46321	.809	.39825	2.31	.17248
X by H	2.96	.12930	.034	.85904	7.65	.02787*	9.89	.01628*
F by E	.446	.51555	.226	.64876	1.22	.30584	.698	.43086
F by D	1.66	.23916	.017	.90045	.045	.83780	1.33	.28684
F by H	52.6	.00017*	9.11	.01945*	57.4	.00013*	45.3	.00027*
E by D	.027	.87435	5.60	.04989*	.561	.47830	.032	.86331
X by F by E	7.39	.02984*	.000	.99764	.222	.65180	.074	.79367
X by F by D	4.90	.06243	1.89	.21165	.040	.84779	.911	.37155
X by F by H	32.2	.00076*	2.77	.13992	33.6	.00066*	28.9	.00104*
X by E by D	.255	.62901	1.01	.34885	1.38	.27930	.936	.36564
F by E by D	.027	.87306	.169	.69294	.598	.46448	1.10	.32838
E by H	.000	.98610	.091	.77151	.219	.65396	.297	.60292
X by E by H	.079	.78614	.531	.48983	.591	.46717	.829	.39284
X by F by E by D	.055	.82152	.018	.89847	3.86	.09023	1.74	.22826
F by E by H	1.74	.22810	2.51	.15702	11.6	.01136*	15.2	.00588*
X by F by E by H	.051	.82803	2.48	.15914	.382	.55629	.074	.79349

Continued...

Appendix IIa (Continued)

Source	Maximum Velocity		Latency to Attain Maximum Velocity		Mean Velocity		Duration	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
D by H	1.02	.34564	.288	.60831	1.44	.26887	.792	.40303
X by D by H	.606	.46190	.073	.79534	.519	.49457	.565	.47665
F by D by H	1.07	.33621	5.67	.04885*	.843	.38901	.012	.91439
X by F by D by H	.573	.47373	1.29	.29268	.000	.98509	.033	.86038
E by D by H	1.68	.23614	1.69	.23477	.144	.71546	.737	.41903
X by E by D by H	.113	.74700	.599	.46442	.455	.52174	.539	.48673
F by E by D by H	1.45	.26694	2.36	.16850	.016	.90392	.028	.87076
X by F by E by D by H	.151	.70941	.088	.77553	2.87	.13384	1.35	.28261

Appendix IIb

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of Latency, Lateral Error, Vertical Error and Vector Error in Study 1. Probability levels are based on 1,7 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are target eccentricity (X); visual field/body hemispace (F); eye movements versus maintained fixation (E); target duration (D); and hand used to respond (H).

Appendix IIb

Source	Latency		Lateral Error		Vertical Error		Vector Error	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
X	7.98	.02560*	19.0	.00332*	.008	.93015	16.8	.00457*
F	.436	.52998	.330	.58358	.075	.79157	.545	.48440
E	.002	.96586	.360	.56757	9.66	.01713*	.517	.49525
D	.019	.89387	35.8	.00055*	.133	.72628	34.5	.00062*
H	4.75	.06568	.309	.59549	2.23	.17895	.000	.99138
X by F	.032	.86313	20.2	.00282*	6.85	.03456*	17.9	.00390*
X by E	5.54	.05076	.014	.90909	1.21	.30743	.024	.88099
X by D	.039	.84968	.767	.40995	.353	.57092	.829	.39296
X by H	.197	.67079	4.38	.07468	1.32	.28897	3.29	.11280
F by E	2.87	.13394	8.06	.02509*	.397	.54847	10.6	.01388*
F by D	1.20	.30982	.577	.47217	.202	.66669	1.55	.25260
F by H	13.0	.00865*	13.6	.00774*	.154	.70655	12.5	.00956*
E by D	1.70	.23332	8.76	.02112*	7.26	.03092*	12.8	.00899*
X by F by E	.440	.52841	.284	.61076	3.22	.11597	.408	.54348
X by F by D	.325	.52841	1.45	.26827	1.34	.28497	.529	.49051
X by F by H	5.61	.04973*	9.96	.01602*	.914	.37095	11.6	.01126*
X by E by D	.003	.95756	3.29	.11260	7.72	.02735*	3.52	.10278
F by E by D	.792	.40303	.158	.70264	1.16	.31725	1.41	.27353
E by H	.003	.95508	.042	.84318	.190	.67607	.000	.99999
X by E by H	7.90	.02610	.308	.59622	.052	.82551	.307	.59658
X by F by E by D	1.62	.24330	1.35	.28269	.001	.97531	1.62	.24397
F by E by H	4.99	.06046	1.41	.27417	.572	.47418	1.20	.31000
X by F by E by H	.929	.36724	12.3	.00987*	3.84	.09083	6.57	.03742*

Continued...

Appendix IIb (Continued)

Source	Latency		Lateral Error		Vertical Error		Vector Error	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
D by H	.191	.67491	1.25	.29996	2.26	.17609	.002	.96734
X by D by H	.958	.36031	1.36	.28161	1.20	.30873	.960	.35981
F by D by H	.142	.71707	.672	.43945	.770	.40922	1.29	.29345
X by F by D by H	.143	.71628	1.26	.29930	4.38	.07453	.859	.38476
E by D by H	.002	.98799	7.82	.02665*	.010	.92410	5.23	.05610
X by E by D by H	2.91	.13199	3.96	.08675	5.18	.05694	1.24	.30176
F by E by D by H	1.92	.20811	.414	.54028	.032	.86319	.508	.49927
X by F by E by D by H	2.30	.17302	.448	.52454	1.24	.30228	.287	.60882

Appendix IIc

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of the z-score transformations of the correlations of ocular and manual performance for the eye-movement trials in Study 1. These correlations were of response Latency and Lateral Error. Probability levels are based on 1,6 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are target duration (D); hand used for response (H); target eccentricity (E); and visual field/body hemispace (F).

Appendix IIc

Source	Latency F ratio	Latency Probability level	Error F ratio	Error Probability level
D	.104	.75820	5.18	.06322
H	.001	.97191	1.25	.30654
X	.076	.79252	1.33	.29193
F	.948	.36783	.120	.74096
D by H	.656	.44900	.459	.52354
D by X	.806	.40394	.076	.79218
D by F	.486	.51161	2.28	.18241
H by X	.157	.70606	.292	.60829
H by F	2.46	.16796	.086	.77882
X by F	.254	.63245	.162	.25073
D by H by X	.026	.87568	.050	.82972
D by H by F	6.09	.04855*	2.47	.16729
D by X by F	5.03	.06608	.038	.85119
H by X by F	5.39	.05931	1.44	.27581
D by H by X by F	.000	.98486	.308	.59903

Appendix IId

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of the Latency and Lateral Error of the eye-movement trials in Study 1. Probability levels less than .05 are indicated by "*". The factors are target duration (D); hand used for response (H); target eccentricity (X); visual field/body hemispace; and ocular versus manual response modality (M).

Appendix IId

	Latency		Lateral Error	
Source	F ratio	Probability level	F ratio	Probability level
D	1.47	.27109	91.5	.00007*
H	9.74	.02055*	11.0	.01604*
X	3.80	.09903	39.9	.00073*
F	.638	.45485	.396	.55257
M	3.04	.13194	12.4	.01250*
D by H	1.93	.21373	1.54	.26123
D by X	10.2	.01858*	8.91	.02446*
D by F	.117	.74374	1.40	.28176
D by M	2.29	.18124	.002	.96192
H by X	.208	.66441	2.87	.14094
H by F	10.8	.01657*	.420	.54075
H by M	.105	.75643	3.17	.12508
X by F	2.70	.15130	.004	.95148
D by X by X	3.29	.11968	.868	.38726
D by H by F	5.64	.05511	.368	.51962
D by H by M	.484	.51270	3.98	.09322
D by X by F	2.09	.19870	.319	.59252
H by X by F	.431	.53588	.063	.81003
X by M	.003	.96028	1.54	.26138
D by X by M	3.78	.09978	1.62	.25055
D by H by X by F	7.08	.03749*	.545	.48823
H by X by M	.401	.54975	7.74	.03193*
D by H by X by M	1.46	.27226	4.45	.07939
F by M	1.94	.21329	.322	.59099
D by F by M	1.14	.32672	.404	.54870
H by F by M	.001	.97354	.526	.49552
D by H by F by M	.225	.65215	1.95	.21177
X by F by M	2.67	.15337	.559	.48271
D by X by F by M	.937	.37043	2.45	.16890
H by X by F by M	.575	.47696	.142	.71920
D by H by X by F by M	0.00	1.0000	.168	.69584

Appendix IIe

Table of F ratios and Probability levels for analysis of variance (SPSS, Balanova program) of the Maximum Velocity, Latency to Attain Maximum Velocity, Mean Velocity and Duration in the Body Space analyses of Study 2. Target position was coded relative to the midline of the body axis for these analyses. Probability levels are based on 1,4 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand used for response (H); body hemispace (BS); central versus peripheral visual fixation (Fix); and target eccentricity (X).

Appendix IIe

Source	Maximum Velocity		Latency to Attain Maximum Velocity		Mean Velocity		Duration	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
H	.619	.48900	2.32	.22487	.137	.73553	.027	.87907
BS	25.1	.01535*	1.49	.30955	17.2	.02545*	11.7	.04177*
Fix	.618	.48922	4.69	.11905	1.06	.37799	2.17	.23683
X	70.7	.00353*	1.36	.32779	12.3	.03916*	19.4	.02177*
H by BS	.445	.55246	1.04	.38252	4.90	.11372	.009	.93228
H by Fix	1.50	.30840	.978	.39553	5.77	.09575	3.96	.14063
H by X	14.5	.03190*	.042	.85105	.026	.88231	.043	.84930
BS by Fix	.028	.87765	.741	.45251	.342	.59963	2.20	.23491
BS by X	74.4	.00327*	.397	.57317	31.0	.01142*	21.1	.01944*
Fix by X	2.79	.19343	1.10	.37043	.553	.51093	1.37	.32665
H by BS by Fix	1.03	.38513	.253	.64964	6.49	.08415	8.57	.06166
H by BS by X	.333	.60430	2.84	.19069	3.70	.15030	.542	.51507
H by Fix by X	.423	.56185	.076	.80076	1.08	.37466	.194	.68916
BS by Fix by X	5.75	.09604	.713	.46004	.888	.41563	.865	.42106
H by BS by Fix by X	.000	.98809	4.59	.12170	.328	.60716	.003	.96224

Appendix IIf

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of Latency, Lateral Error, Vertical Error, and Vector Error in the Body Space analyses of Study 2. Target position was coded relative to the midline of the body axis for these analyses. Probability levels are based on 1,4 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand used for response (H); body hemispace (BS); central versus peripheral visual fixation (Fix); and target eccentricity (X).

Appendix IIf

Source	Latency		Lateral Error		Vertical Error		Vector Error	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
H	2.32	.22479	16.5	.02700*	.706	.46246	35.9	.00929*
BS	7.24	.07440	12.4	.03870*	.761	.44192	2.27	.22872
Fix	7.84	.06787	5.76	.09589	1.60	.29516	5.94	.09275
X	4.35	.12818	1.24	.34748	1.87	.26495	.930	.40593
H by BS	1.34	.33141	5.18	.10732	1.94	.25810	8.61	.06079
H by Fix	1.81	.27151	10.4	.04815*	.435	.55669	2.64	.20284
H by X	.975	.39631	.382	.58035	.045	.84513	2.29	.22722
BS by Fix	17.8	.02440*	.873	.41906	.299	.62253	3.11	.17608
BS by X	1.78	.27446	3.52	.15716	1.74	.27853	6.19	.08858
Fix by X	3.80	.14622	1.25	.34579	.539	.51590	2.15	.23878
H by BS by Fix	12.1	.04005*	.019	.89865	.105	.76673	.166	.71064
H by BS by X	.644	.48105	.062	.81964	.005	.94941	.240	.65769
H by Fix by X	3.89	.14302	1.09	.37298	.328	.60680	4.71	.11851
BS by Fix by X	8.86	.05874	.030	.87381	1.55	.30170	.017	.90469
H by BS by Fix by X	9.73	.05251	1.22	.34996	.360	.59076	10.4	.04842*

Appendix IIg

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of the Maximum Velocity, Latency to Attain Maximum Velocity, Mean Velocity and Duration in the Visual Field analyses of Study 2. Target position was coded relative to the point of visual fixation. Probability levels are based on 1,4 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand used for response (H); visual field (VF); central versus peripheral visual fixation (Fix); and target eccentricity (X).

Appendix IIg

	Maximum Velocity		Latency to Attain Maximum Velocity		Mean Velocity		Duration	
Source	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
H	.619	.48900	2.32	.22487	.137	.73553	.027	.87907
VF	.028	.87765	.741	.45251	.342	.59963	2.20	.23491
Fix	.618	.48922	4.69	.11905	1.06	.37799	2.17	.23683
X	2.79	.19343	1.10	.37043	.553	.51093	1.37	.32665
H by VF	1.03	.38513	.253	.64963	6.49	.08415	8.57	.06116
H by Fix	1.50	.30840	.978	.39553	5.77	.09575	3.96	.14063
H by X	.423	.56185	.076	.80076	1.08	.37466	.194	.68916
VF by Fix	25.1	.01535*	1.49	.30955	17.2	.02545*	11.7	.04177*
VF by X	74.4	.00327*	.397	.57317	31.0	.01142*	21.1	.01944*
Fix by X	70.7	.00353*	1.36	.32779	12.3	.03916*	19.4	.02177*
H by VF by Fix	.445	.55246	1.04	.38252	4.90	.11372	.009	.93228
H by VF by X	.333	.60430	2.84	.19069	3.70	.15030	.512	.51507
H by Fix by X	14.5	.03190*	.042	.85105	.026	.88231	.043	.84930
VF by Fix by X	5.75	.09604	.713	.46044	.888	.41563	.865	.42106
H by VF by Fix by X	.000	.98809	4.59	.12170	.328	.60716	.003	.96224

Appendix IIh

Table of F ratios and Probability levels for analysis of variance (SPSS, Balanova program) of the Latency, Lateral Error, Vertical Error and Vector Error in the Visual Field analyses of Study 2. Target position was coded relative to the point of visual fixation. Probability levels are based on 1,4 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand used for response (H); visual field (VF); central versus peripheral visual fixation (Fix); and target eccentricity (X).

Appendix IIh

Source	Latency		Lateral Error		Vertical Error		Vector Error	
	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level	F ratio	Probability level
H	2.32	.22479	16.5	.02700*	.706	.46246	35.9	.00292*
VF	17.8	.02440*	.873	.41906	.299	.62253	3.11	.17608
Fix	7.84	.06787	5.76	.09589	1.60	.29516	5.94	.09275
X	3.80	.14622	1.25	.34579	.539	.51590	2.15	.23878
H by VF	12.1	.04005*	.019	.89865	.105	.76673	.166	.71064
H by Fix	1.81	.27151	10.4	.04815*	.435	.55669	2.64	.20284
H by X	3.89	.14302	1.09	.37298	.328	.60680	4.71	.11851
VF by Fix	7.24	.07440	12.4	.03870*	.761	.44719	2.27	.22872
VF by X	1.78	.27446	3.52	.15716	1.74	.27853	6.19	.08858
Fix by X	4.35	.12818	1.24	.34748	1.87	.26495	.930	.40593
H by VF by Fix	1.34	.33141	5.18	.10732	1.94	.25810	8.61	.06079
H by VF by X	.644	.48105	.062	.81964	.005	.94941	.240	.65769
H by Fix by X	.975	.39631	.382	.58035	.045	.84513	2.29	.22722
VF by Fix by X	8.86	.05874	.030	.87381	1.55	.30170	.017	.90469
H by VF by Fix by X	9.73	.05251	1.22	.34996	.360	.59076	10.4	.04842*

Appendix IIi

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of the Latency of movement by the eyes and hands in Study 3. Probability levels are based on 1,5 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand placed on the start platform (H); visual field/ body hemispace of target (F); target eccentricity (X); and response by either eyes or hand alone versus response by both together (R).

Appendix IIi

	Latency			
	Eyes		Hands	
Source	F ratio	Probability level	F ratio	Probability level
H	.097	.76835	.031	.86712
F	.179	.69012	.210	.66611
X	1.74	.24413	15.4	.01113*
R	2.11	.20629	3.23	.13246
H by F	.015	.90611	9.25	.02872*
H by X	.764	.42207	1.92	.22427
H by R	.051	.83058	1.45	.28251
F by X	.199	.67417	4.58	.08531
F by R	1.79	.23844	3.36	.12633
X by R	.015	.90820	.238	.64631
H by F by X	.370	.56957	.183	.68637
H by F by R	.000	.99593	.067	.80658
H by X by R	.002	.96208	.480	.51928
F by X by R	6.30	.05385	.118	.74559
H by F by X by R	.133	.72989	.000	.98429

Appendix IIj

Table of F ratios and Probability levels for analyses of variance (SPSS, Balanova program) of the z-score transformations of the correlations of eye and hand movement latencies for trials in which both systems responded in Study 3. Probability levels are based on 1,5 degrees of freedom. Probability levels less than .05 are indicated by "*". The factors are hand used for response (H); visual field/body hemispace of the target (F); and target eccentricity (X).

Appendix IIj

	Z-scores	
Source	F ratio	Probability level
H	.046	.83801
F	2.52	.17304
X	.000	.99099
H by F	.064	.80998
H by X	.192	.67967
F by X	.912	.38347
H by F by X	.000	.99246

END

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FIN