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HAND AND HEMISPACE DIFFERENCES IN THE VISUAL CONTROL OF AIMING MOVEMENTS

by

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

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ABSTRACT

The purpose of this thesis was to examine left and right hand performance in three aiming movement experiments, designed to identify differences in movement kinematics when task demands were varied along dimensions thought to differ between the hemispheres. In Experiment 1, fourteen subjects were required to make aiming movements with the index finger to single light emitting diodes (LEDs) or to the midpoints of two simultaneously illuminated LEDs. Movements were recorded using a WATSMART system (Northern Digital, Inc.). Contrary to previous claims, no evidence was found for left hand advantages in accuracy in hand-invisible conditions. The large advantage in accuracy shown by the right hand in single target pointing was attenuated in bisecting. This attenuation may have been related to increased right hemispheric participation in the bisection task. In Experiment 2, the number of trials in which 11 subjects reached for in hand-invisible conditions was increased to over 800 trials. It was hypothesized that longer periods without the opportunity to recalibrate aiming movements with vision would result in a gradual increase in directional endpoint errors in both hands. Contrary to expectations, endpoint errors did not shift over the course of the sessions. Many of the changes in kinematic variables which occurred did so in the first 100-200 trials of the session and tended to remain stable for the remaining trials. Differences were found for movements made to the same vs. the opposite side of the reaching limb (i.e., hemispatial effects) in both hands, and tended to remain stable over the course of the sessions.

In the final experiment, the nature of these hemispatial effects in movement kinematics were examined by dissociating the side of stimulus presentation from the side of motor response. Twenty-six subjects were required to reach to the mirror symmetric position on the side opposite to the target. For movement duration, peak velocity and the percentage of the movement spent in deceleration, ipsilateral advantages were consistently seen for side of motor response, rather than side of stimulus presentation.

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My parents, Lawrence and Rita, and siblings Jim, Miriam and Anne (and the limited number of spousal-types who put up with the clan) have supported this work morally and finacially in more ways than are imaginable.

Finally, I am almost speechless when required to sum up all that I owe my supervisor, Mel Goodale. The interested reader is well-advised to consult the ackowledgments of the many (dare I say "other") successful theses which have come out of his laboratories. All of those comments are just as appropriate for describing my relationship with the boss over the past several years. But two characteristics in particular leap to mind when I think of my experiences at Western: PATIENCE and HUMOUR (capitalized for EMPHASIS). I doubt that either of us would have survived the experience otherwise. Its been swell, Mel! (sorry: couldn't resist).

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CHAPTER 1 - GENERAL INTRODUCTION

Most humans are right-handed. While it is true that there is pressure against adextrality (non-right handedness) in many cultures and, as a consequence, there is some variation in the incidence of right-handedness from culture to culture, the weight of the evidence suggests that approximately 90% of Homo sapiens use the right hand for skilled manual activities (Annett, 1967). Neuropsychologists have expressed a keen interest in this phenomenon for a number of reasons, not the least of which is the direct connection each hand has with the contralateral hemisphere. These connections suggest the possibility of understanding hemispheric specialization through differential hand performance. The purpose of the present series of investigations was to examine the necessary conditions for optimal right and left hand performance in the production of aiming movements to suddenly appearing targets. Producing such an aiming movement is not a simple act; it requires coordination of head and eye movements to foveate the target, precise timing of agonist and antagonist muscle pairs in the arm, as well as changes in trunk musculature to counteract the forces pushing back against the torso as a consequence of the limb movement. These complex interactions require translations across several different coordinate systems--retinal, oculocentric, craniocentric, and arm or shoulder-centric.

In this introduction, I will briefly review some of the general themes relevant to the control of visually-guided aiming movements (which will be supplemented in the introductions and discussions of the relevant experiments). In particular, I will argue for a left hemisphere motor control system, important for generation of movement sequences on both sides of the body. "Privileged access" to this system may account for the many observed right hand advantages in movement production and control (even if digit participation does not play a key role in the particular movement). Similarly, given the evidence for right hemisphere superiority in localizing targets and other visuospatial functions, the left hand should enjoy privileged access to those mechanisms and may show improved performance (relative to the appropriate control condition) on tasks which are visuospatially demanding. Thus, examination of performance asymmetries in aiming movements made by the two hands may reveal some of the organizational principles of each hemisphere's contribution to movement.

1.1 Hemispheric Lateralization

The concept of lateralization of function in the nervous system remains the dominant theme in experimental neuropsychology. Historically one of the earliest (and still most compelling) asymmetries is the lateralization of language function. Since Broca's original description of verbal dysfluency after lesions of the left frontal operculum (1861; 1863; cited in Joynt, 1982), numerous investigations have confirmed that aphasia in right handers is usually a consequence of left hemisphere damage. Subsequent discoveries of right ear-left hemisphere advantages in dichotic listening tasks in normal subjects (Kimura, 1961) and right visual field reading and naming in split-brain subjects (reviewed in Springer & Deutsch, 1993) are consistent with the notion of a left-hemisphere specialization for speech function.

Although lateralization of speech remains one of the more robust and reliable phenomena within neuropsychology, there is considerable debate over the exact nature of the left hemisphere processes which are interrupted in various aphasic syndromes. Many have argued that left hemispheric specialization is analytical, syntactic or semantic, and that the deficits in speech production and comprehension which follow left hemisphere are best described as linguistic (see Brown & Kosslyn, 1993 for a recent review). Similarly, a related left hemisphere syndrome, apraxia, is considered a disorder in the production of *meaningful* movements, i.e., failure in producing movements like saluting, pantomiming familiar acts like brushing teeth, combining hair, etc.

An alternative explanation of these syndromes has been advanced by Kimura (1982) and others (e.g., Goodale, 1988). Liepmann (1909, cited in Kimura, 1980, and Paillard, 1982a) and a number of contemporary neuropsychologists have postulated a left hemisphere system specialized for motor control for both sides of the body (Goodale, 1988; Kimura, 1982; Kimura & Archibald, 1974; Kimura & Humphrys, 1981; MacNeilage, et al., 1988; Peters, 1991; but see Haaland & Delany, 1981; Jones et al., 1989 for contrary views). This perspective suggests that many aphasic syndromes which occur after left-hemisphere damage are not a consequence of a linguistic system which has been disrupted, but instead result from deficits in motor programming and related subsystems. In the same way, apraxias may not be related to meaningful movements exclusively, but can result in poor production of many motor acts (which cannot be accounted for by muscle weakness or paresis).

Compelling evidence for this point of view has been reported by Kimura and her associates, who found that patients with left hemisphere damage are impaired in the production of single and multiple oral movements whether or not they were verbal (Kimura, 1982; Mateer & Kimura, 1977). Subsequent analyses of subgroups of patients with unilateral left hemisphere damage revealed that multiple oral movement production is most compromised by posterior lesions while single oral movements are most disrupted after anterior lesions (Kimura & Watson, 1989). Studies of oral movements in neurologically intact subjects have uncovered larger opening of the right side of the mouth during speech (Graves et al., 1982).

This postulated left hemisphere praxis system is not restricted to the control of oral movement. Kimura and Archibald (1974) examined the relationship between copying meaningless limb movements and the side of hemispheric damage. Kimura (1993) has collected additional data on movement copying and the production of "meaningful" movements (typically used in the standard neurological exam) and finds that impairments of movement copying of both types are highly correlated with one another (r=.78). Her data also suggests that there are orderly relationships between oral and manual movement copying deficits after left hemisphere damage, such that impairment in one type of movement is usually accompanied by impairment in the other (Kimura, 1993). Other studies have also demonstrated strong relationships between oral apraxia and limb apraxia (e.g., Basso et al., 1987).

In neurologically-intact subjects, Kawashima et al. (1993) have reported significant increases in blood flow (assessed by PET) in premotor and motor cortex of the left hemisphere when finger-thumb opposition movements were produced *with either hand.* There was no ipsilateral increase in the homologous right hemisphere regions when the movements were made by the right hand. This evidence is also supportive of a left-hemisphere system important for motor control on both sides of the body.

Specifying the exact nature of this praxis system has proven difficult. Some authors have suggested that sequencing a series of individual movements best describes what the left hemisphere does for both sides of the body. For example, Kimura and colleagues have suggested that selecting appropriate submovements and sequencing them is a crucial praxic function (cf. Goodale, 1988). Others have emphasized timing functions more explicitly: Calvin (1983) argues for the natural selection of throwing ability in hominids resulting in the development of redundant circuits for precise timing of motor events, like the release of projectiles thrown at intended prey. A similar emphasis on temporal aspects of motor control is put forward by Freund and Halsband and colleagues. On the basis of data from patients with unilateral frontal lesions, they (i.e., Halsband, et al., 1993) have suggested that the left hemisphere is crucial for temporal sequences like those required to reproduce rhythms. In their studies left hemisphere damage produced disruptions in timing in movements made with either left or right hands, while equivalent right hemisphere damage only produced impairments in the performance of the left hand on such tasks.

To summarize, the studies reviewed above strongly suggest that lesions of the left hemisphere may disrupt oral and manual movements whether or not they are related to speech or "meaningful" movement. Many additional lines of evidence strongly suggest that this left hemisphere system plays a special role in the control of hand and arm movements for both sides of the body, but the precise nature of that role (or roles) has yet to be specified.

1.2 Hand Preference

In neurologically-intact subjects, left hemisphere specialization for motor control is strongly suggested by the preponderance of right handedness in the general population (Annett, 1972; Bryden, 1982; for discussions of handedness in non-human primates, see Annett & Annett, 1991, Fagot & Vauclair, 1991; Hopkins & Morris, 1993; MacNeilage et al., 1988). The high incidence of right handedness in Western societies has never been questioned, but until recently, the theory that handedness could reflect biological rather than cultural origins was subject to considerable debate. Strong societal pressures against left handedness may have masked a much greater degree of adextrality than was suggested by early studies of hand preference. Nevertheless, more recent studies of the development of hand preference in infants (e.g., Humphrey & Humphrey, 1990) and of comparable levels of dextrality in cultures with differing biases against sinistrality strongly confirm the asymmetry in manual performance (e.g., Hoosain, 1990). Current estimates of hand preference consistently provide estimates of approximately 90% right hand preference in Homo sapiens. Further, heritability studies suggest a genetic component which plays a major role in handedness, although its exact mechanism is subject to considerable argument (Annett, 1985; McManus, 1985).

Investigators have pursued the asymmetry in human handedness in various ways, including factor analytic studies of hand preference questionnaires (e.g., Steenhuis & Bryden, 1989), relating handedness to anatomical (e.g., Annett, 1992; Witelson, 1989) or dichotic/tachistoscopically-measured asymmetries in normal subjects (e.g., Bryden, 1988), or describing subgroups of dextrals and adextrals based on performance on various perceptual and cognitive tests (e.g., Kimura & D'Amico, 1989). It has been noted repeatedly that simple dichotomous classification schemes (i.e., left-handed vs. right-handed) were ill-equipped to handle the variance in preferences uncovered in studied populations (i.e., Peters, 1992; Peters & Murphy, 1992; Provins & Magliaro, 1993). Similarly, the importance of the distinction between hand preference and hand performance has been emphasized by several recent analyses (Bryden, 1982; Fagot & Vauclair, 1990).

1.3 **Hand Performance**

A popular trend in handedness studies has been to examine asymmetries found in hand performance. In fact, investigators frequently attempt to make inferences about the contralateral hemisphere's control mechanisms by quantifying hand performance on circumscribed tasks. The assumption that hand performance is related to a single hemisphere is usually made because the sensorimotor control of the distal musculature of the upper limbs is largely crossed; each hand receives outputs from primary motor cortex of the contralateral hemisphere (for review see Hepp-Reymond, 1988) and sends tactile and proprioceptive information back to that same hemisphere (for review see Kaas & Pons, 1988). On the basis of the apparent exclusivity of these input-output relations, a number of investigators have made conclusions about hemispheric function based on performance differences between the two hands (cf. Carson et al., 1992; Elliot et al., 1993; Fisk & Goodale, 1985; Guiard et al., 1983; Todor & Doane, 1978; Watson & Kimura, 1989). The right hand advantages reported in these studies are usually elicited from right-handed subjects, a group who obviously have considerable practice making fine movements with their dominant hand. Yet few investigators examine the possibility that the movement advantages found for the right hand are the result of simple practice effects and not from left hemispheric specialization (but see Goodale 1988).

The right hand advantages typically obtained are often interpreted as a consequence of "privileged access" of the right hand motor output systems to the left hemisphere praxis system. Although this assumption has substantial explanatory power for right hand advantages in movements which rely critically on digit control, it is less clear whether or not whole arm movements (with less involvement of fingers and thumb) are similarly lateralized.

1.3.1. *Privileged Access and the Distal/Proximal Distinction*

The assumption that digit control is contralateral while more proximal muscle groups are bilaterally controlled originates in lesion studies in the monkey. Lawrence and Kuypers (1968) found that cutting the pyramidal tract caused a profound loss in the control of finger movements in the Rhesus monkey. Whole arm movements recovered, however, presumably due to remaining ipsilateral corticomotoneuronal connections which course through the ventromedial pons (Kuypers, 1967; Lawrence and Kuypers, 1968b). Some clinical evidence in humans is consistent with this position; in patients with upper motor neuron dysfunction, there is more sparing of the proximal muscles in hemiparesis (Colebatch & Gandevia, 1989; Freund, 1987). However, several lines of evidence suggest that the degree of contralateral control for whole arm and even axial motion may be greater than predicted by the Lawrence and Kuypers (1968a) experiments.

For example, in the monkey, microstimulation of small regions within primary motor cortex reveals that movements of discrete muscle groups can be elicited from multiple sites, and that this is not simply true for hand movements, but for facial, hindlimb and wrist movements as well (reviewed in Huntley and Jones, 1991). By combining microstimulation mapping with HRP (Horseradish peroxidase) tracing, Huntley and Jones uncovered connections within motor cortex which reciprocally connect digit representations with those which move small muscle groups about the wrist, the elbow and the shoulder (Huntley and Jones, 1991). These results strongly suggest that coordination of proximal and distal muscles of the upper extremities is present within contralateral primary motor cortex. Although in individual animals, the stimulation revealed that the largest extent of motor cortex was dedicated to digit motion, in other animals overall representation of other parts of the forelimb was almost as extensive (Huntley and Jones, 1991). Similarly, extensive overlap in the control of individual finger movements by single neurons in primary motor cortex of the Rhesus monkey has been reported (Schieber & Hibbard, 1993).

In humans, Colebatch et al. (1990) investigated the cortical control of two proximal muscles involved in arm movements, the deltoid and the pectoralis major (see Figure 1.1). They stimulated contralateral motor cortex (from the skull surface, with magnetic and anodal electrical stimulation) and recorded the evoked potentials in single motor units of six human volunteers. Their results suggest that the latencies and amplitudes of the evoked responses in these two proximal muscles are equivalent to those seen in an intrinsic hand muscle (the first dorsal interosseous, see Figure 1.2) stimulated in the same way, and suggest a strong monosynaptic projection from contralateral motor cortex to all three of these muscles. They conclude that this strong projection represents *a fundamental difference in the degree of contralateral control of proximal muscles in humans relative to monkeys* (italics mine). Although additional evidence for this position will not be discussed, the possibility of a further elaboration of corticomotoneuronal

Figure 1.1 The superficial musculature of the chest and upper arm.

Modified from Johnston & Whillis (1954).

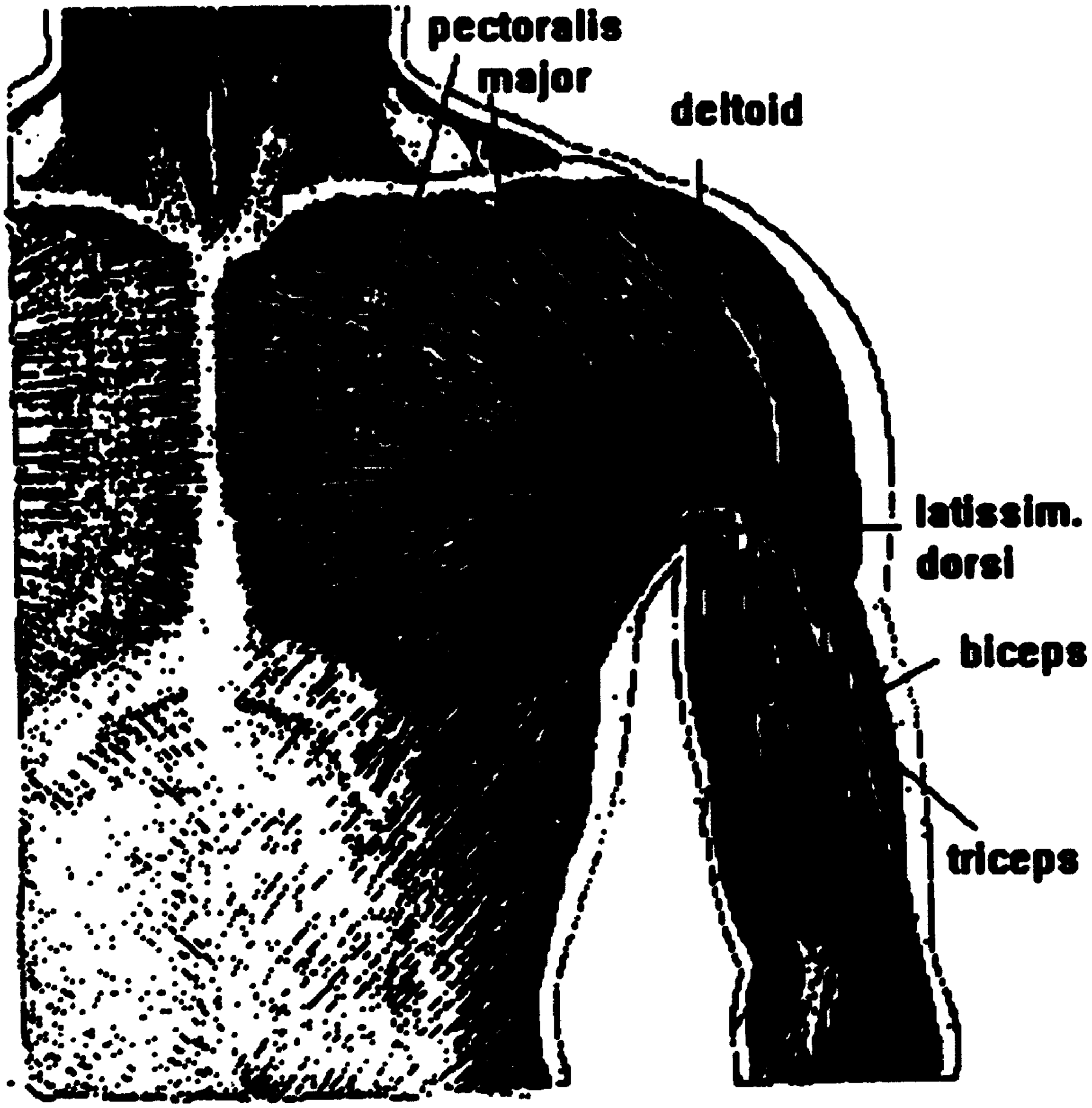
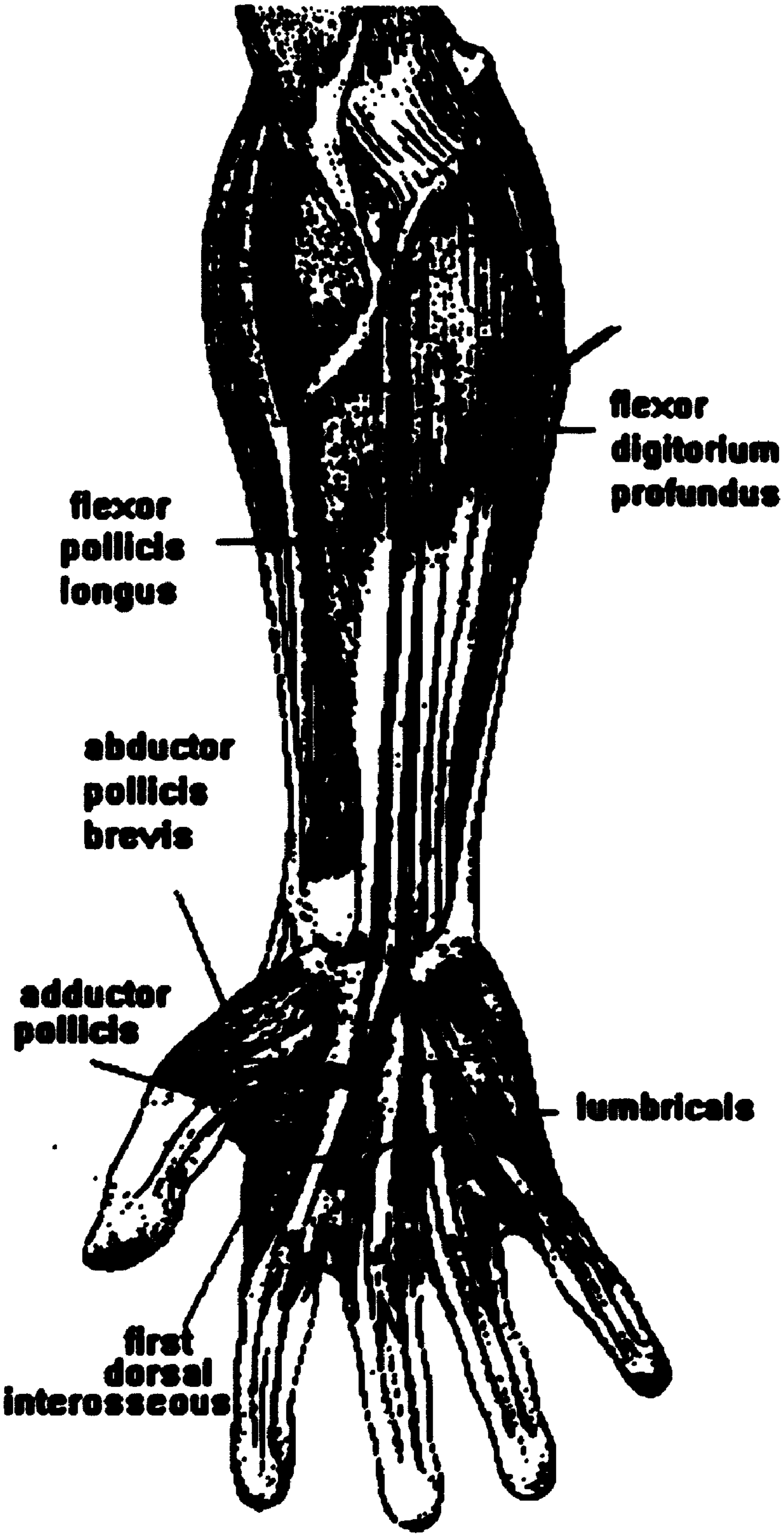

pectoralis
major
deltoid
latissim.
dorsi
biceps
triceps

Figure 1.2 The deep musculature of the lower arm and hand. Modified from Johnston & Whillis (1954).


flexor digitorium profundus
flexor pollicis longus
abductor pollicis brevis
adductor pollicis
lumbricals
first dorsal interosseous

systems in Homo could help explain why the nonhuman primate handedness data is not nearly as conclusive as that found in our species, e.g., Annett & Annett 1991; Byrne & Byrne, 1990. The results of the Colebatch et al. (1990) study are not quite that simple, however. An additional finding in the proximal muscles was a later burst in activity unaffected by the direction of magnetic current flow that typically differentiates left from right hemisphere stimulation. Colebatch et al. conclude that this medium latency excitation is at least suggestive of a later bilateral contribution to proximal motor unit activity (Colebatch et al., 1990). More recent work using magnetic stimulation has been supportive of Colebatch's position. Triggs et al. (1994) report lower thresholds for contralateral EMG activation in both the biceps (a 5% reduction) and the abductor pollicis brevis (a 4.5% reduction) in consistent right handers. These new techniques may contribute substantially to our understanding of the degree of contralateral and ipsilateral control for proximal and distal musculature.

Imaging techniques are also beginning to suggest that the story is more complicated than suggested by the Kuypers data. Colebatch et al. (1991) used PET (Positron Emission Tomography) to measure cerebral blood flow changes in normal volunteers who performed four different motor tasks; abduction of the index finger, making a fist, sequential thumb-digit opposition, and shoulder flexion. Surprisingly, although all of the movements produced substantial and significant increases in blood flow in the contralateral sensorimotor cortex (pre- and postcentral gyri could not be individually resolved), the greatest increase (31%) was seen when the shoulder flexions were being made. It should be noted that some degree of bilateral control of the shoulder was also suggested; shoulder flexion was the only movement studied which produced smaller but statistically significant changes in ipsilateral sensorimotor cortex. Shoulder movements also elevated blood flow in other brain areas to a greater degree than the three other movements tested, including the superior cerebellar vermis, and left hemisphere areas 5 and 40 (Colebatch, et al., 1991). Although the use of PET technology is still relatively new, it is compelling to note that Colebatch's group came up with nearly identical blood flow increases in contralateral sensorimotor cortex and the supplementary motor area to those observed by Fox et. al. (1985) for fist-making movements.

Rizzolatti and colleagues have used PET scans with six subjects comparing distal and proximal movement activation of the motor cortices. They found that whole arm movements produced additional increases in blood flow in ipsilateral premotor cortex beyond the contralateral increases seen for both shoulder and thumb or finger movements (Matelli et al., 1993). Nevertheless, they do not find any evidence for ipsilateral activation for shoulder movements when other arm and hand muscles are immobilized. This result could be interpreted as additional ipsilateral involvement when proximal and distal musculature are required in generating movements, not simply as a consequence of proximal movement per se.

In human subjects, other data support stronger contralateral control of the proximal musculature than suggested by the Kuypers data. For example, contralateral advantages for shoulder tapping in right-handed subjects are similar in magnitude to those seen in index finger tapping (Kimura & Davidson, 1975; Peters & Pang, 1992; Todor et al., 1982; see also DiStefano et al., 1980).

Of course, primary motor cortex is only one region of the cerebral cortex crucial for motor control. Other areas include several subregions of parietal cortex (e.g., Burbaud et al., 1991; Johnson et al., 1993; Sakata et al., 1992; Pause & Freund, 1989), the supplementary motor area and its subdivisions (Wiesendanger et al., 1991; Dum & Strick, 1991), and the various subregions of premotor cortex (Kurata, 1994; Rizzolatti et al., 1988). These systems make substantial contributions (directly and indirectly) to the corticospinal tract (see Hepp-Reymond, 1988; Nudo & Masterton, 1990a,b), and numerous lesion studies have established their importance in motor control (Humphrey, 1979). Some investigations suggest primarily contralateral consequences of premotor and supplementary motor lesions in humans. For example, Massion and colleagues have shown disrupted control of the contralateral biceps when weights were actively or passively removed from a flexed limb in patients with unilateral SMA lesions (Hugon et al., 1982, cited in Ghez, 1991). Similarly, unilateral premotor or SMA lesions produce contralateral impairments in reproduction of tapped rhythms which cannot be accounted for by tapping impairments or difficulties with perception of rhythm (Halsband et al., 1993).

In studies of clinically apraxic patients, the proximal/distal distinction is still subject to debate. Poeck and his colleagues have argued that there are often axial as well as distal deficits in apraxic patients (Poeck et al., 1982). Their conclusions are criticized on statistical grounds by Howes (1988), to which they reply (Poeck & Willmes, 1988).

Although this discussion might suggest that the proximal-distal differences in contralateral control are not as clear cut as once thought, it is still conceivable that higher levels of sensorimotor control do respect this distinction. For example, Kuypers and his colleagues argue that ipsilateral motor pathways in the monkey can maintain coordinated aiming movements as long as they do not require control of the distal musculature. Brinkman & Kuypers (1972) found that monkeys with no visual inputs to one hemisphere could still make accurate whole arm movements with the contralateral limb, while hand movements were impaired. An alternative interpretation is suggested by a recent metabolic mapping study (Savaki et al., 1993). Their data suggest that cross-cueing by proprioceptive and oculomotor control systems can maintain contralateral motor coordination in split brain monkeys denied visual inputs to the hemisphere controlling the moving hand. Such signals might be able to maintain relatively accurate localization, but seem unable to provide details about target shape, size and orientation necessary for accurate grasping behaviour. In other words, contralateral motor cortex may have controlled the relatively preserved whole arm movements in the monkeys, thanks to cross-cueing from other intact sensory and motor systems, and not because of remaining ipsilateral control of the proximal musculature.

A related suggestion of Kuypers and colleagues is that projection systems from parietal cortex to various frontal subdivisions are responsible for the visual control of the contralateral distal but not proximal musculature. Haaxma and Kuypers (1975) found that whole arm movements were relatively undisturbed after lesions in parietal cortex intended to deafferent premotor cortical structures in the monkey. When the monkeys were required to use a pincer grasp with index finger and thumb to retrieve food from a small well, they were grossly impaired. Again, observations of whole arm movements suggested little or no impairment, which was interpreted as ipsilateral control of proximal but not distal muscles.

A different explanation for this finding has been made by Mitchell Glickstein, however. He claims that the disordered contralateral finger control produced by the path cuts of Haaxma and Kuypers (1975) may have been a consequence of interruption of the corticoponto-cerebellar pathway (Glickstein, 1980; 1990), since lesions of the frontal targets of the parietal lobe produce only small impairments on the Haaxma & Kuypers (1975) task (Glickstein, 1980). In other words, the disrupted manual behaviours produced by the parietal lesions may have interrupted a subsidiary control system which cooperates with a lateralized praxis system; the praxis system itself may have been less affected in these animals. More recent anatomical evidence confirms that extrastriate cortical contributions to the pontocerebellar system are exclusively from parietal cortex and other areas of the so-called "dorsal stream" (Schmahmann & Pandya, 1993), implicated in the visual control of motion by Goodale and Milner (1992).

To conclude, this brief review at least suggests that the degree of contralateral control for the proximal arm musculature may be much more equivalent to that of the distal musculature than previously suggested, at least in Homo and perhaps in infrahuman primates as well. Of course, the control systems at "higher" levels in motor cortex (and elsewhere) may be substantially lateralized while the subsystems they control are not (see Kimura, 1993, for a discussion). However, if only the highest levels of control are lateralized, then a simple "privileged access" description of right hand or limb motor control advantages would require substantial elaboration, since ipsilateral systems would require appropriate coordination across the corpus callosum. The evidence presented in this section is consistent with the "privileged access" account of even whole arm movement advantages for the right arm.

Less evidence is available for the complementary suggestion: Bilateral control of distal musculature. However, Trope et al. (1987) found that there was a substantial degree of ipsilateral control of finger movements in two patients with complete callosotomy. Interestingly, all of the fingers of the left hand showed this preserved ipsilateral control, while only the thumb and index finger movements of the right hand were spared (Trope et al., 1987). Although speculative, this finding is also consistent with the "privileged access" assumption (i.e., more contralateral control in the right hand).

1.3.2 *Asymmetries in Hand Performance and the Cerebral Hemispheres*

Even though the privileged access assumption has not been completely evaluated, the results of many studies of hand differences in performance have been organized to a large degree by appealing to the two theoretical accounts of left and right hemisphere function that have a long history in human neuropsychology. The first of these is that there is a left hemisphere specialization for some aspect(s) of motor control (discussed above); the second is a right hemisphere system specialized for some type of visuospatial/visuoperceptual analysis (De Renzi, 1982; Hamsher, Capruso, & Benton, 1992; Young & Ratcliff, 1983; although see Mehta et al., 1987).

When evaluating hand performance in light of hemispheric specialization, a coherent picture has yet to emerge for several reasons. Perhaps the most crucial difficulty is that the design and demands of the tasks used in hand difference experiments, even when only simple aiming movements were required, have varied enormously. Some experimenters have constrained the movements in different ways by using hand-held manipulanda (Bock, 1986; Carson et al. 1992; Carlton, 1981; 1993; Elliot & Allard, 1985; Elliot & Madalena, 1987; Elliot et al., 1993; Kerr & Langolf, 1977); by restricting the movement axes to one or two dimensions (e.g., Bock, et al., 1990; Flament et al., 1984; Heuer, 1981; Lestienne, 1979); and/or by requiring subjects to make movements of a particular duration (e.g., Eliot & Allard, 1985 [Experiment 3]; Proteau et al., 1987; Young and Zelaznik, 1992). Aiming has also been investigated where the subject has been required to point a laser or light source at a distant surface (Soechting & Flanders, 1989; Vanden Abeele et al., 1993). Other experiments have explored more 'natural' movements by requiring only simple pointing movements with the finger, and by allowing subjects to move at their own speed (Carson et al., 1992; Fisk & Goodale, 1985; Miller et al., 1992). The number of targets used by different experimenters has varied from as few as one (Roy & Elliot, 1986) to as many as eight (Biguer et al., 1984; Prablanc et al., 1979; Carson et al., 1990a). Instructions to subjects have also varied, emphasizing speed (e.g., Abrams & Pratt, 1993; Carson et al., 1993), or accuracy (Carson et al., 1993) or both concurrently (Carson et al., 1990a; Fisk & Goodale, 1985; 1990). Such manipulations alone can have dramatic effects on movement kinematics (Carson et al., 1993; Fisk & Goodale 1990; Wing et al., 1986).

It is no surprise, therefore, that claims regarding the roles of each hemisphere in aiming movement control are as varied as the methods used to examine them.

1.3.2.1 *Left Hemisphere and Motor Control*

Liepmann (1909, cited in Kimura, 1980; Paillard, 1982a) and a number of contemporary neuropsychologists have postulated a left hemisphere system specialized for a type of supraordinate motor control for both sides of the body (Goodale, 1988; Kimura, 1982; Kimura & Archibald, 1974; MacNeilage, et al., 1988; but cf. Haaland & Delany, 1981; and Jones et al., 1989 for contrary views). Consistent with this position, a number of studies of aiming movements have demonstrated right hand advantages on several measures of performance. Fisk and Goodale (1985), for example, found a shorter deceleration phase, quicker movement onset, and higher peak velocity for aiming movements made with the right hand relative to those made with the left in normal right handers. Furthermore, the mean absolute (independent of direction) and constant (directional) endpoint errors were smaller for the right-handed reaches. These authors did not find any significant differences in variable error (endpoint variability) between the two hands, although the right hand tended to be superior in this measure as well.

In addition to these significant right hand advantages, a hemispatial effect on movement kinematics was also uncovered. Hemispace refers to the side of space relative to the body and/or head midline. Fisk and Goodale found that the left-handed reaches into left space and the right-handed reaches into right space were initiated faster, had shorter durations, and were even more accurate (although in terms of variable, not constant error) than contralateral reaches (Fisk & Goodale, 1985). Many other investigators have also revealed hemispatial effects of stimulus and response on perceptual and manual asymmetries (Bradshaw et al., 1989; Carson et al., 1990a; Chokron & Imbert, 1993; Gras et al., 1993; Heilman et al., 1985; Schenkenberg et al., 1980; van Der Staak, 1975).

1.3.2.2 ***Right hemisphere and visuospatial analysis***

In sharp contrast to the literature on the left hemisphere and motor control, the examination of right hemisphere function has focused largely on more perceptual tasks; this hemisphere seems to be better able to process dot location and number (Kimura, 1966; 1969), use stereoscopic depth cues (Durnford & Kimura, 1971, but see Breitmeyer et al., 1975) to recognize musical tones (Kimura, 1964), and to identify faces and the emotions they portray (Ley & Bryden, 1979).

Beyond some indirect clinical evidence (i.e., some of the manifestations of contralateral neglect after right hemisphere lesions are related to movement, see Heilman et al. 1985), very few studies have suggested advantages in visuomotor control for the right hemisphere, in spite of the obvious visuospatial demands of some tasks requiring movements to (and around) targets in space (i.e., aiming and tracking movements, locomotion around targets, reaching and grasping, etc.).

An exception to this general rule is an often-cited paper by Guiard et al. (1983). These authors predicted that the left hand of right handers would show "an advantage for some aspect of motor activity" if a task has sufficient spatial demands. Guiard et. al examined the reaches of 8 right-handed males towards one of two LED targets made *without vision of the reaching limb.* These targets were either 3 cm to the right or 3 cm to the left of a central position in line with the subject's midline. Guiard et al. reported a significantly smaller constant error in the left-handed and the left-sided reaches, suggestive of a right-hemisphere advantage for reaching without vision of the moving limb. Guiard et al. conclude that the ballistic nature of the hand-invisible reaches led to a greater left-handed accuracy, an accuracy usually masked in hand visible conditions by the superiority of the left hemisphere/right hand system in movement execution (Guiard et al., 1983).

A related (but not synonymous) claim is that movements which require utilization of on-line visual feedback reveal right-hand/left hemisphere superiorities in performance relative to the left-hand/right hemisphere (Carson et al., 1990a; Todor & Doane, 1978; Todor & Cisneros, 1985). However, Lomas (1980) found that concurrent speaking (primarily engaging left hemispheric mechanisms) interferes with right hand performance (and not left) on sequential finger and arm tapping only when the manual task is being performed *without visual guidance*. This finding suggests that left-hemisphere systems for motor control may be especially vital in movements not guided by vision of the limb (Lomas & Kimura, 1976; Lomas, 1980; Watson & Kimura, 1989).

1.3.2.3 *Feedback and Hand Differences*

A difficulty with most of the claims of superior feedback utilization (or, less frequently, greater dependence on a type of feedback) has been a failure to distinguish in a rigorous way what kind of feedback the investigators were referring to. In the motor domain, kinesthesis and proprioception can be specified by a number of different physiological mechanisms, including golgi tendon organs, gamma motorneurons, and slowly and rapidly adapting mechanoreceptors in skin and connective tissue (Kaas & Pons, 1988). These somatosensory feedback mechanisms are often contrasted with outflow, or efference copy of the original motor command, as two opposing possibilities for specifying the position of the effector (for review, see Jeannerod 1988; and Jeannerod et al. 1979).

The role of kinesthetic/proprioceptive feedback of the limb has rarely been investigated in the hand difference literature. Although studies have demonstrated that visual information frequently outweighs information from proprioceptive and vestibular systems in posture and locomotion (i.e., Lishman and Lee, 1973), Lackner and Levine (1978) showed how proprioceptive information about limb position could produce a powerful visual illusion about target direction. Other studies have revealed that tendon vibration at the neck and eye results in predictable errors in perceptual and/or manual localization and perceived direction of movement of visual targets (e.g., Roll, et al. 1991; Dizio, et al. 1993). Unfortunately, these studies have not addressed potential lateralization of these effects, since typically only one limb or eye was tested.

In the visual domain, several different sources of feedback provided by vision could be useful for motor control: (1) Vision of the moving effector in peripheral or in central vision (a distinction underscored by Paillard, 1982b, following Trevarthen, 1967); (2) View of the effector relative to target; (3) View of the effector relative to any source of visual texture in the environment; (3) Persistent view of the target; and, (4) View of the movement endpoint relative to target and/or a visual texture. As with efference copy and proprioception/kinesthesis, these classes of visual feedback are seldom differentiated, and more often than not, differentially affected by changes in experimental procedure. A small change in an experimental parameter from one study to another could have dramatic effects on the pattern of results obtained. For example, by varying target duration, targets may or may not be foveated by saccadic eye movements. Fisk and Goodale (1985) have suggested a "yoking" or coupling of hand and eye movement onset to ensure foveation when the hand has completed a particular portion of the reach (discussed below). Other manipulations of visual feedback are not so subtle: Several investigations of motor control have subjects view the visual consequence of movement as a cursor of some sort on a computer screen, spatially distant from the kinesthetic/proprioceptive feedback from the movement itself (i.e., Abrams & Pratt, 1993; Abrams, Meyer, & Kornblum, 1990; Ghez, Gordon & Ghilardi, 1993).

Other types of information are also referred to as "feedback" in the literature. In the motor learning domain, a number of studies characterise feedback as "knowledge of results" (cf., Proteau, 1992); i.e., the subject is informed verbally of the 'accuracy' of an open loop movement ("two centimetres too high" or "a little too fast"). Although it is possible that manipulations of this class can tell us something about the "cognitive penetrability" of visuomotor control processes, it is substantially less clear what they can say about normally important types of reafferent sensory stimulation for more naturally occurring movements.

1.3.2.4 *Spatial demands and Hand Differences*

Beyond the Guiard et al. (1983) claim about the right hemisphere and ballistic movement, the other principal attempt to relate right hemisphere processes to hand movements has been to vary the visuospatial demands of the task, in an attempt to attenuate the usual large right hand advantages or even produce a left hand advantage in right-handed subjects. Several examples of this approach have been published (Carson et al., 1990b; Elliot et al. 1993; Hampson and Kimura, 1984; Watson & Kimura, 1989).

Watson and Kimura (1989) compared the performance of several groups on two visually-guided manual behaviours: dart throwing and projectile intercepting, and found smaller right hand advantages for the interception task. Hampson and Kimura (1984) produced a similar shift away from right hand advantages in right handers by increasing the spatial demands of a block manipulation task. In contrast to these findings, Carson et al. (1992) recently reported that having subjects anticipate the final target position in complex geometric stimuli did not result in decreased right hand advantages in accuracy (a manipulation that they characterized as spatial). These authors also criticized the Watson and Kimura study for claiming that the attenuation of the right hand advantage in intercepting was due to spatial factors when different motor responses were required (Carson, et al. 1992).

These demonstrations suggest that task demands can affect accuracy in various motor tasks. They are complicated, however, by the lack of agreement on what tasks are "spatial" and what tasks are not. Further, almost none of these experiments has recorded the complete three-dimensional movement and have instead emphasized reaction time, movement time, or endpoint accuracy exclusively. Even the measurement of endpoint accuracy is subject to considerable debate and variation across different studies (Schutz & Roy, 1973).

1.4 Eye and Head Movement Contributions to Aiming

An additional problem with many studies in the literature is that there has not always been an appreciation of the roles of eye and head movement in visually-guided aiming. Consequently, some investigators control head position (i.e., Biguer et al., 1984) while others do not (i.e., Carson et al. 1992). Computationally, the relevance of these other effectors is obvious. Understanding the control systems which allow for generation of accurate aiming movements is a useful exercise in establishing the nature of hand differences in performance on such tasks. A considerable literature in motor control (both empirical and computational/theoretical) has examined the roles of eye and head movements in aiming movement production. Engineers and roboticists frequently consult this growing literature, looking for new constraints and procedures to guide their applied efforts.

Any attempt to design a robotic arm which uses visual feedback reveals a number of control system parameters which much be considered. If the system is using a movable optical sensing device and a multiple degree of freedom effector, many of the engineering problems which have to be solved are similar to those solved in primate eye-head-hand coordination. For mammalian systems, specifying the location of the target in egocentric (i.e., body-centred) coordinates requires specification of eye and head position as well as some sort of depth information in order to determine the real world position of a target from its retinal locus. In primates and carnivores in particular, this process is facilitated by binocular vision, which results in positional disparities of the target on the two retinae and aids in the computation of depth. For example, Servos et al. (1992; 1994) have demonstrated that binocular vision facilitates grasping performance in prehensile space.

Beyond these computational considerations, which make clear the requirements of computing retinal and effector positions in egocentric space, empirical work has demonstrated that oculomotor, head, and limb motor systems are functionally coupled in a number of different ways in primate oculo- and skeletomotor routines (for reviews of eye-head-hand control, see Berthoz & Grantyn, 1986; Carnahan, 1992; Chapter 2 in Jeannerod 1988).

For example, in the Fisk and Goodale (1985) study, a remarkable coupling between hand and eye movement latency was uncovered: Saccadic onset time was coupled to the hand doing the reaching, such that contralateral reaches resulted in both slower arm and eye movement onset times (even though eye movements invariably preceded arm movements). Yet, an eye movement to the same target was significantly quicker off the mark if the ipsilateral limb was used. Saccades made for right-handed reaches were initiated faster than for left-handed reaches, although the opposite effect is not found if the reaches of consistent left-handers to left-sided targets are examined

(Goodale 1988). These results suggest a link between saccadic control and the left hemisphere praxis system (at least in the case where the saccade is part of a visually-guided reaching movement).

The coupling of saccades to reaching is also demonstrated when target foveation is not a consequence of a saccade. Honda (1984) found that if a visual target is acquired with a smooth pursuit movement before the target is extinguished, accuracy of aiming movements is substantially lower than if the position was acquired by a saccade (even though target locations were foveated before the target was extinguished in both conditions). This result also suggests a functional linkage between the saccadic and manual control systems. Interestingly, this effect was more dramatic in the subjects' preferred right hand (Honda, 1984). Although Honda's paper (and other work) suggest the importance of corollary discharge (a feedforward signal about a subsequent movement) of the saccade command, other studies have suggested that eye proprioception plays a role in aiming movement control (Gauthier et al. 1990; Roll, Roll & Velay, 1991). Gauthier et al. (1990) have shown that deviating an occluded eye actually biases movement endpoints in a visually-guided reaching task.

Two final studies will be mentioned here which relate to another possible linkage between eye and hand movements. In a study of hand-invisible pointing, Foley and Held (1972) suggested a relationship between hand and "sighting eye" which resulted in dramatic constant errors in hand-invisible reaching. The sighting eye of a subject is revealed by forcing them to align a near pointer with a distant target, which requires them to do so with one eye and not the other in order to avoid a diplopic image. Money (1972) examined the effects of sighting dominance on a number of tasks performed monocularly. Interestingly, no differences between dominant and non-dominant eyes were found on tachistoscopic tasks which required no overt eye movements. However, when rapid scanning was required in two additional tasks, the subjects performed significantly better when using the dominant eye. Money concluded that sighting dominance was related to asymmetrical motor function.

A series of experiments performed by the York University Vision group (Canada) largely dismissed the notion of eye dominance from the neuropsychological literature. It is notable, however. that the majority of their tests utilized perceptual or static sighting tests which did not require rapid eye or limb movements (e.g., Barbeito, 1981; Ono & Barbeito, 1982).

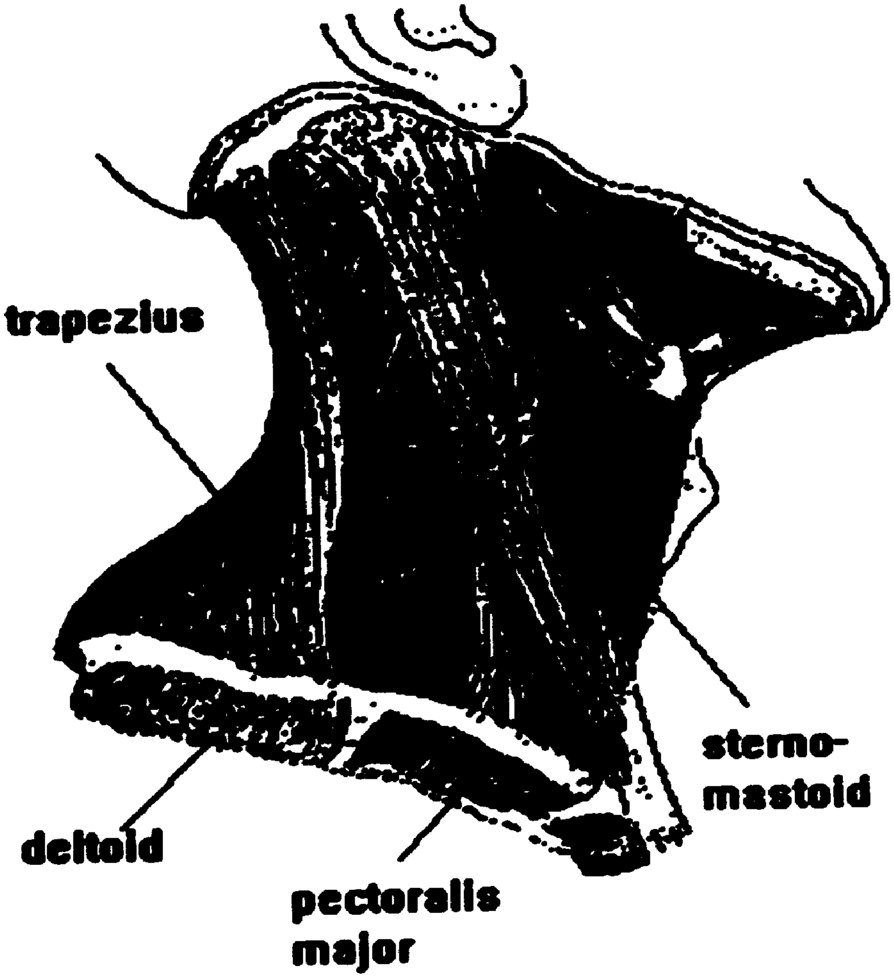
Of course, head movements play a substantial role in the direction of gaze and acquisition of targets in most animal species. For example, abolishing proprioceptive feedback from the neck musculature in the monkey produces inaccurate manual movements to visual targets, in spite of accurate fixation (Cohen, 1961). Tendon vibration of the neck, much like tendon vibration of the extraocular muscles discussed above, also results in errors of target localization (Roll, Roll & Velay, 1991). Like the arm/hand system, control of the neck musculature is also largely contralateral (especially the trapezius, which is exclusively contralateral, but the sternomastoid and the splenius show more contralateral control than ipsilateral control in humans; see Figure 1.3) and is likely to be mono- or perhaps disynaptic (Berardelli, et al. 1991; Gandevia & Applegate, 1988; but see Mazzini & Schieppati, 1992, for a different account).

1.5 Summary

In this introduction I have reviewed the suggestion of a left hemisphere praxis system, and have argued that "privileged access" to this system may account for many of the right hand advantages in movement production and control (even if digit participation does not plays a key role in the particular movement). Similarly, right hemisphere contributions to manual control may be elicited by varying spatial demands of aiming tasks while maintaining the same motor response requirement. The possible contributions of eye and head movement control were discussed, as were some consequences of movement and target hemispace. Thus, appropriate examination of performance asymmetries in aiming movements made by the two hands may reveal some of the organizational principles of each hemisphere's contribution to movement.

The purpose of the investigations in this thesis was to examine further the fundamental nature of left and right hand performance on a series of simple aiming movement tasks. The contribution of visual feedback to performance was examined by

Figure 1.3 The musculature of neck. Modified from Johnston & Whillis (1954).


trapezius
sterno-
mastoid
deltoid
pectoralis
major

having subjects reach in hand-visible (Experiments 1 and 3) and hand-invisible conditions (Experiments 1, 2, and 3). Visual feedback utilization has been suggested to play a role in the expression of manual asymmetries by a number of investigators (Elliot et al. 1994) but the exact nature of that role remains subject to considerable debate (Carson et al., 1990a; Guiard et al., 1983; Roy & Elliot, 1986).

In two experiments, an attempt was made to vary the visuospatial demands of the tasks while keeping the essential motor demands constant (Experiments 1 and 3). Possible hand differences in the visuomotor calibration process suggested by the results of Experiment 1 were examined by a series of extended dark reaching trials (Experiment 2). Hemispatial effects of side of target presentation were dissociated from those effects related to side of motor response (Experiment 3). Finally, the contributions of sighting dominance to motor asymmetries as suggested by Held and Foley (1972) and Money (1972) were investigated examining the hand performances of subjects who were either left or right eye dominant for sighting (Experiment 3).

CHAPTER 2 - EXPERIMENT 1: POINTING AND BISECTING.

Abstract

This experiment was designed for two purposes. The first was to examine the effects of removing visual feedback from the limb on the performance of the right and the left hand in a simple aiming movement task. The second purpose was to increase the spatial demands of the task to attenuate the advantages shown in the right hand by requiring the subjects to "bisect" an area formed by two light-emitting diodes. No evidence for left-hand advantages in movement accuracy were found, contrary to the results of Guiard et al. (1983). Removal of visual feedback increased movement onset time, but not the overall duration of the movements. Some evidence for attenuation of endpoint accuracy advantages for the right hand was found in the bisecting task, but this effect was only significant in the constant error data.

2.1 Introduction

The main aim of Experiment 1 was to examine the effects of removing visual feedback of the reaching limb in a visually-guided aiming task, with the only constraint on the subject being that he was to reach as quickly and accurately as possible. Because the right hand enjoys "privileged access" to the left hemisphere, and given the data from the concurrent interference literature (Lomas, 1980; Lomas & Kimura, 1976), I expected to see right hand advantages in measures of terminal accuracy even when visual feedback about limb position was removed (Roy & Elliot, 1986). In hand-visible conditions, I also expected to see right hand advantages, given the many instances of similar findings throughout the neuropsychological literature (Fisk & Goodale, 1985; Todor & Doane 1978). Additionally, because the entire reach was recorded, any relationships between other kinematic variables and the hand used would be revealed.

A second aim of this Experiment was to attempt to attenuate the magnitude of any right-hand advantages found in pointing by varying the visuo-spatial demands of the task while requiring the same motor response (as suggested by Carson et al. 1992). In order to do this, we asked the same subjects to participate in a bisecting task, where the correct endpoints were co-incident with the target locations in the pointing task. Previous investigations in our laboratory found that the endpoint errors in a bisecting task differentiated the performance of right-brain damaged (RBD) subjects from controls, whereas endpoint errors in a pointing task did not (Goodale, et al. 1990).

Paper-and-pencil line bisection frequently reveals neglect of left space in subjects with right-brain damage (Milner, Harvey, Roberts & Forster, 1993; Schenkenberg, Bradford, & Ajax, 1980). The patients in Goodale et al (1990) were recovered from neglect as assessed by line bisection, but produced rightward errors when required to bisect two targets with an aiming movement. If accurate performance in bisection is more reliant on the right hemisphere than performance in single-target pointing is, then the discrepancies between the two hands in pointing should be attenuated in bisection.

2.2 Methods

Subjects

Fourteen right-handed males were tested. These volunteers were research assistants, graduate students and senior undergraduates from the University of Western Ontario. Subjects completed a 9-item Handedness Questionnaire (based on Kimura, 1983) and were included in the study only if they performed all nine actions with their right hand. Subjects ranged in age from 19 to 30 years (mean=24.5).

Procedure

Subjects were required to reach quickly and accurately towards targets under two different conditions, run on separate days; one in which the reaching limb was visible and the other in which the limb was not visible. Both hands were tested on each day, and order of hands tested was counterbalanced across subjects. Subjects pointed to single targets or "bisected" two targets in 30-trial blocks. During a session, subjects wore a black glove on the reaching limb (in order to further eliminate visual cues from the limb during hand-invisible reaching). The order of bisecting and pointing was counterbalanced across subjects. Small, infrared-emitting diodes (IREDs) were attached with velcro to the tip and the base of the index finger on a black glove worn by the subject. The three-dimensional locations of these diodes during calibration and test trials were recorded at 100 Hz using an opto-electronic recording system (WATSMART, Northern Digital, Inc.). A ten-trial sample of a stationary IRED in the workspace in which these data were collected revealed largest differences across trials of 0.41, 0.86 and 1.03 mm in the x, y, and z dimensions respectively. Within each sample of 10 frames, the average standard deviations were 0.10 mm in X, 0.24 mm in y and 0.32 mm in z (Jakobson & Goodale, 1989). For further details on the 3-dimensional accuracy of this system in general and our particular setup see Jakobson and Goodale (1989) and Haggard and Wing (1990).

Subjects performed all calibration and test trials with their head in a chinrest, (angled to provide optimal viewing of the targets in the wedge), in order to examine potential hemispatial effects on reach kinematics. If differences in movements to left or right-sided targets were observed, they could be interpreted with reference to the body midline, since no fixation light was used and target illumination was continuous (and thus with free eye movements stimuli were not restricted to one visual field) during test trials. To further minimize potential visual feedback about hand position, subjects worn ski goggles with a green filter which allowed for view of the green LEDs only.

Calibration

At the beginning of each session, five calibration trials were collected for later calculation of terminal accuracy. For these trials, five different light-emitting diodes (LEDs, 0.25 deg) were independently illuminated. The LEDs were concealed from view by black speaker cloth within a target wedge, positioned 2 cm above the table surface. The wedge was located 32 cm in front of a starting position (defined by a thumbtack embedded in the table surface). The start position was located 10 cm from the near edge of the table surface, placed at the subject's midline and on the same axis as the central LED target. The LEDs were independently illuminated by the experimenter using an Apple IIe microcomputer located in the adjacent room. For calibration purposes, subjects were required to make a natural reach from the start position to the LED target as accurately as possible. They were informed that for these trials only, they could adjust their final landing position so that they occluded the target perfectly. After the subject indicated that he was satisfied with his final position, a 2.00 second, 100-Hz sample of the static position of the IREDs was collected.

Testing

After collection of the calibration trials, subjects were required to reach quickly and accurately to each presented LED target and to remain in their initial landing position until instructed to return to the start position and await the next trial. Subjects were told that targets could appear anywhere on the target wedge in front of them, but were not told how many different targets would appear. Five different target positions were used (far left, near left, centre, near right and far right, each 6 cm away from the adjacent target). The central target was located 32 cm in front of the start position, and the two most peripheral targets were 34 cm away from the start position (a 6% increase in distance, therefore trial durations, peak velocities and associated measures were normalized in the analysis). "Near" targets were 10.7 degrees peripheral to the central target while the two "far" targets were 21.5 degrees into the periphery. Each target appeared 6 times, in a pre-determined, pseudorandom sequence. Subjects also completed the bisecting task within the same half of a session. For bisecting, subjects were instructed to reach quickly and accurately to the midpoint between two simultaneously illuminated targets. The two LEDs for any particular bisecting trial were positioned 12 centimeters apart, and their true midpoints were located at the same positions as the five pointing targets.

After one hand was tested, calibration and test trials from the other hand were then collected. Session (i.e., Hand visibility condition), the order of hands tested within the session, and task (pointing or bisecting) were counterbalanced as much as possible for the 14 subjects.

After data collection, raw WATSMART files were converted to three-dimensional coordinates and filtered at 7-Hz with a second-order, low pass Butterworth filter. This type of filter removes high-frequency noise from the data in a two-pass procedure, which preserves the position of the signal in the time domain and has a sharp cut-off at 7 Hz (Lam, 1979).

Filtered files were used to compute peak velocity (cm/sec), movement onset time and movement duration (both in msec), and the percentage of the total reach spent decelerating (duration minus time to peak velocity/duration x 100). Recent investigations have suggested that movement onset times, durations, and peak velocities differentiate the performance of the right and the left hands. Typically, durations and peak velocities tend to favour the right hand (Fisk & Goodale, 1985) whereas movement onset times tend to favour the left hand or show no difference between hands (Chua et al., 1991; Elliot et al., 1993). Time to peak velocity and time to peak acceleration (measured in the next experiments) are gradually becoming acceptable markers of the transport component of a movement (i.e., Castiello et al. 1993). Deceleration duration is widely considered as a reliable index of movement precision (Marteniuk et al. 1987; Roy et al., 1994). Preliminary evidence suggests that deceleration durations may be shorter in the right hand than in the left (Roy et al., 1994).

Three measures of endpoint accuracy (relative to the position of the fingertip LED specified by the calibration trial for that particular target) were computed. Absolute error refers to the total unsigned distance, in X, Y, and Z axes, of the reach endpoint from the endpoint the subject produced in the calibration trial (this measure is similar to "constant error" as defined by Guiard et al., 1983, p. 112). Constant error in the horizontal plane is the signed horizontal distance between the reach endpoint and the calibration file-specified endpoint. Rightward constant errors are positive values, leftward errors are negative values. The final measure of endpoint accuracy calculated was variable error, defined as the standard deviation of the constant errors in the horizontal plane. All endpoint-based measures are provided in cm. The claims regarding which error measure provides the most consistent evidence for hand advantages varies from study to study.

Each dependent measure was analyzed using a BMDP-4v repeated measures analysis of variance, using the Geiser-Greenhouse adjustment of the degrees of freedom (for violations of homogeneity of covariance in repeated measures designs) when appropriate (Kirk, 1982; Tabachnick & Fidell, 1989). For comparison with Guiard et al.

(1983), the pointing data alone were subjected to a repeated-measures analysis, with Hand (right vs. left) Hand visibility (hand-visible vs. hand-invisible) and Target position (far left to far right) as factors. For a second analysis, Task (bisecting vs. pointing) was added as a factor. Significant interactions were explored using the Newman-Keuls procedure (Kirk, 1982). In the second analysis, Target position also refers to the correct midpoint between two targets in bisection.

Because dependent measures were occasionally lost due to the obscuring of an IRED or the occurrence of an infrared reflection, means of each dependent measure were calculated, collapsed across trials. If no data points were available for a given subject by hand by hand visibility by task by target cell, then the subject's grand mean for that dependent measure was substituted in order to balance the design.

2.3 Results

2.3.1 Pointing

Cell substitution was only necessary in 4 of 1120 cells (0.4%). Means and standard deviations for each dependent measure as a function of Hand, Hand visibility and Target appear in Table 2.1.

Movement Onset Time and Movement Duration.

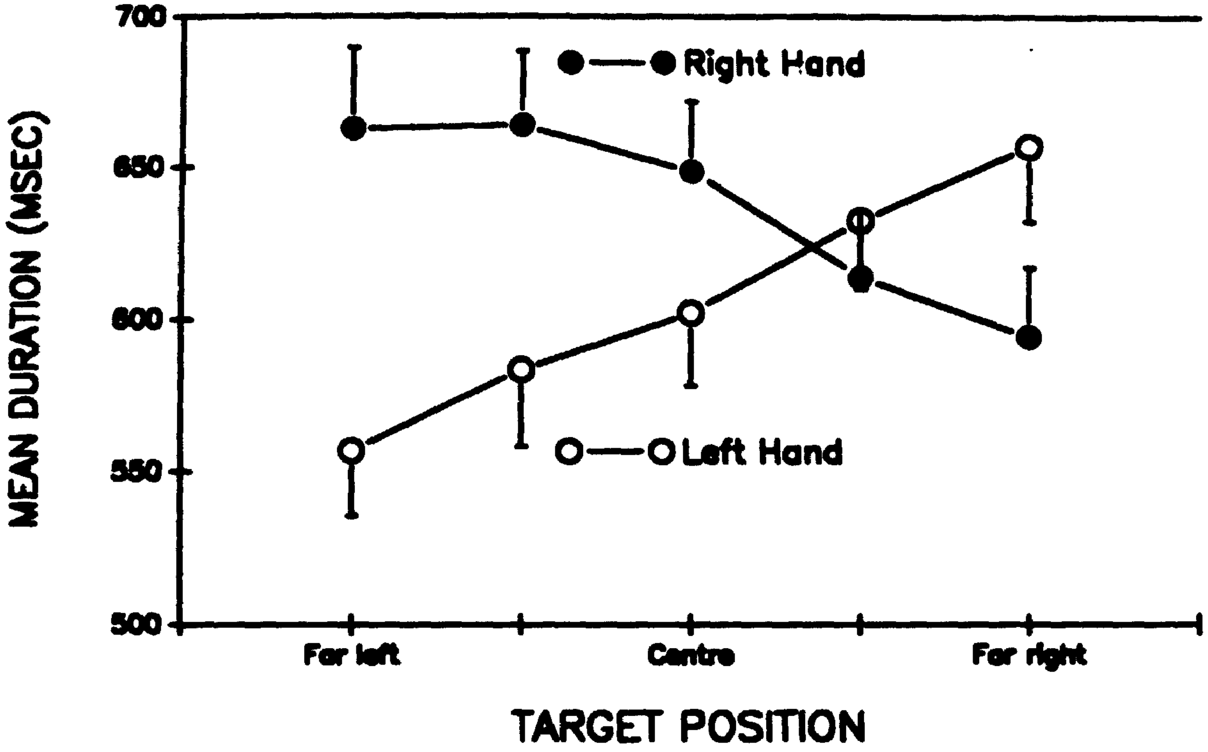
The mean movement onset times were not significantly affected by the Hand used ($F_{(1,13)}=0.50$, $p<0.49$) or any higher-order interactions involving Hand. The removal of visual feedback about limb position increased mean movement onset time (268 msec to 302 msec; $F_{(1,13)}=7.49$, $p<0.02$). This increase may have been due to the decreased luminance of the LED targets when viewed through the green filter.

An unexpected trend towards shorter movement durations in the left hand was found, but only approached statistical significance ($F_{(1,13)}=4.39$, $p<0.06$). Movement duration was influenced by Target position ($F_{(2.6, 34.0)}=4.29$, $p<0.015$) which interacted with Hand ($F_{(2.9, 37.8)}=31.59$, $p<0.0001$). Examination of the mean movement durations seen in Figure 2.1 suggests that subjects complete their movements more rapidly in the ipsilateral

Table 2.1 Mean kinematic variables (w. standard errors) for single target pointing.

	Hand			
	Left		Right	
	Visible	Invisible	Visible	Invisible
Movement Onset	270 (8.7)	306 (11.5)	267 (6.7)	296 (8.9)
Duration	647 (17)	614 (15)	665 (16)	658 (16)
Peak Velocity	89 (2.0)	97 (3.1)	85 (2.3)	95 (3.4)
Percent. Decel.	65 (1.0)	60 (1.4)	58 (1.2)	61 (1.2)
Absolute err.	0.94 (.1)	3.53 (.33)	0.80 (.1)	1.89 (.1)
Constant err.	0.48 (.1)	2.14 (.4)	0.03 (.1)	0.04 (.2)
Variable err.	0.4 (.03)	1.4 (.1)	0.4 (.05)	1.1 (.05)

Figure 2.1 Mean movement duration (msec) as a function of Target position and Hand. In this and all subsequent figures error bars represent standard errors of estimate.



700
650
600
550
500
MEAN DURATION (MSEC)
●—● Right Hand
○—○ Left Hand
Far left
Centre
Far right
TARGET POSITION

hemispace, and that this effect was more pronounced in the left hand (left-handed reaches to the far left target were significantly shorter than all other hand/target combinations). There was no evidence for speed-accuracy trade-offs in these rapid left hand-left target reaches (CE and Duration $r=-0.01$, NS, hand-visible; CE and Duration $r=-0.12$, NS, hand-invisible). The Hand by Position interaction was not significantly different (Hand-visible vs. Hand-invisible conditions, $F_{(1.9,24.4)}=0.74$, $p>0.05$).

Normalized Peak Velocity

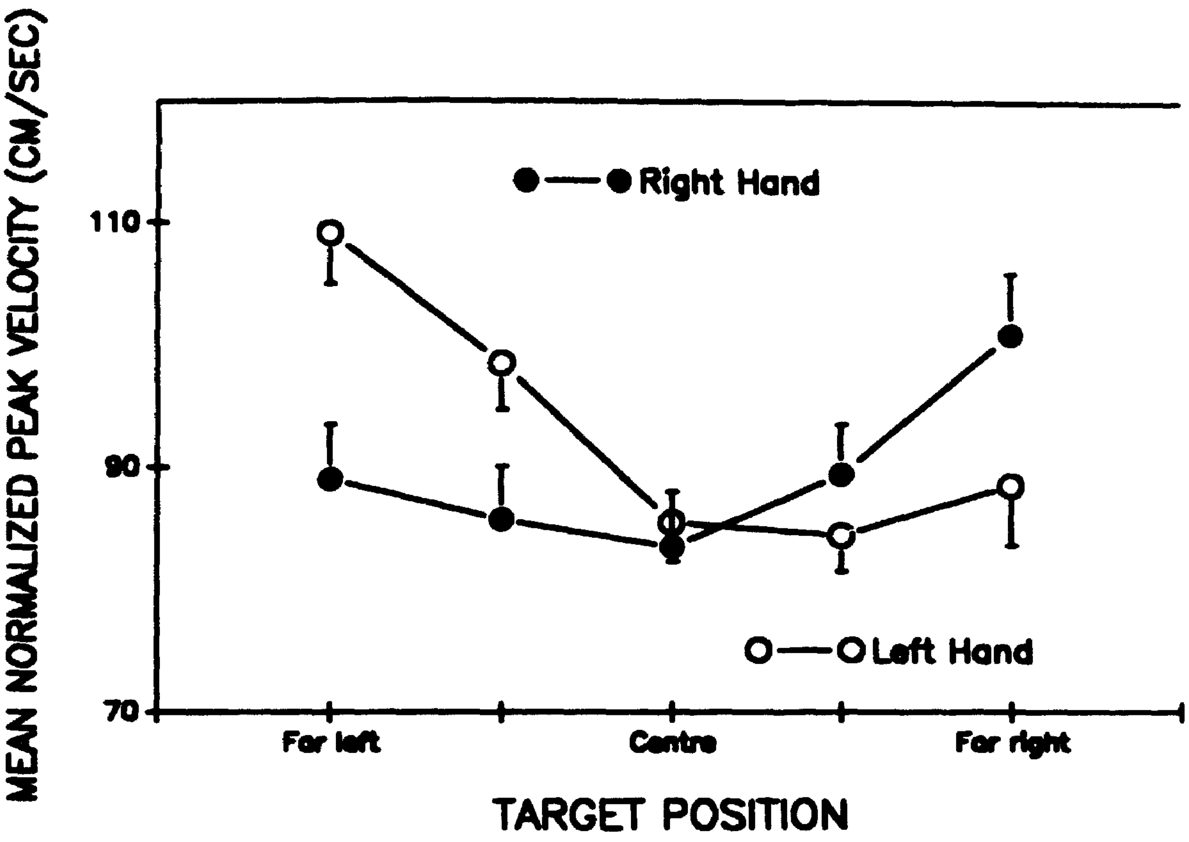
Peak velocity was affected by Position of the target ($F(_{(1.7,21.9)}=8.37$, $p<0.003$), which interacted with Hand ($F_{(2.3,29.3)}=2.25$, $p<0.0001$; Figure. 2.2). The position effect is a consequence of higher peak velocities to peripheral targets. Post-hoc tests suggest that subjects reach higher peak velocities in ipsilateral hemispace (left-handed pointing to the two left sided targets and right-handed pointing to the far right target resulted in higher peak velocities than all other hand/target combinations; all q's $p<0.01$ except one= $p<0.05$).

Percentage of the Reach Decelerating

Numerous investigators consider that the portion of the reach spent decelerating is that in which most visual feedback-driven error correction can occur (Paillard, 1982; but see Jeannerod, 1986 for an alternative view). For example, the duration of this portion of the movement is increased when target size is decreased (Todor & Cisneros, 1985; Soechting, 1984; Zaal & Bootsma, 1993).

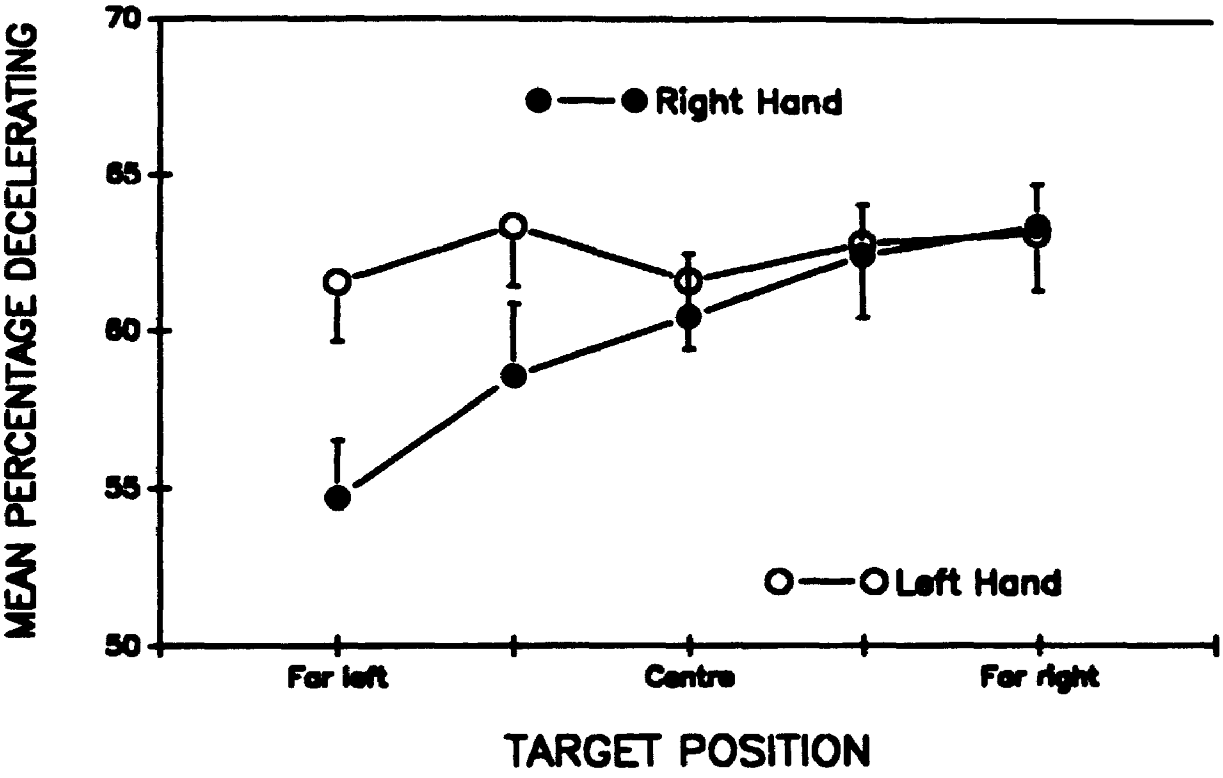
In this study deceleration duration was affected by Target position ($F_{(1.9,24.7)}=3.94$, $p<0.03$). The mean percentage decelerating tended to increase for targets appearing in right space relative to targets located to the left of the body midline (Figure 2.3; Newman Keuls shows that far left target mean is less than the near and far right means at the .05 level). This trend appears more pronounced in the right hand, but the Target by Hand interaction was not significant ($F_{(2,25.3)}=3.12$, $p<0.0525$).

Figure 2.2 Mean normalized peak velocity (cm/sec) as a function of Hand and Target position.



MEAN NORMALIZED PEAK VELOCITY (CM/SEC)
110
90
70
● — ● Right Hand
○ — ○ Left Hand
Far left
Centre
Far right
TARGET POSITION

Figure 2.3 Mean percentage decelerating as a function of Hand and Target position.


70
65
60
55
50
MEAN PERCENTAGE DECELERATING
● — ● Right Hand
○ — ○ Left Hand
Far left
Centre
Far right
TARGET POSITION

A significant Hand by Hand visibility interaction ($F_{(1,13)}$=5.53, $p<0.04$) suggests that when vision of the reaching limb is available, the left hand spends considerably more of the movement decelerating than does the right (Figure 2.4). Post-hoc tests reveal that this difference was the only pairwise comparison which approached significance ($q=3.79$, $p<0.078$).

Endpoint Accuracy Measures

Absolute Error

The particular measure of constant error on which Guiard et al. (1983) found a left hand advantage in was "the distance between the virtual position of the target on the grid-patterned printed circuit and the point corresponding to the mean coordinates of the responses" (p. 112). Because the distance was unsigned (see their Table 1), the most appropriate measure for comparison in the present study is the absolute error. All of the main effects and every one of the four possible interactions were statistically significant. Absolute error as a function of Hand, Target Position, and Hand visibility appears in Figure 2.5. Accuracy as indicated by this measure was decreased in hand-invisible conditions, ($F_{(1,13)}$=26.50, $p<0.0002$), in the left hand relative to the right ($F_{(1,13)}$=6.55, $p<0.02$), and for the two far right targets relative to the others (Target position, $F(_{1.4,18.7)}$=4.88, $p<0.03$). Newman Keuls examination of the means as a function of Hand, Hand visibility and Target Position ($F_{(1.4,18.5)}$=7.72, $p<0.007$) suggests that the two right-sided targets yielded the most dramatic increases in absolute error for the left hand in the dark (greater than all other means at the $p<.01$ level).

Constant Error

Given that target position varied only in the horizontal axis, arguably the most appropriate measure of error based on the use of vision to determine target location is the signed error in this axis. All main effects and all interactions except the three-way had significant effects on the constant error of the subjects' reaches. Examination of the mean constant errors in Figure 2.6 between Hand, Hand visibility and Target Position shows

Figure 2.4 Mean percentage decelerating as a function of Hand and Hand visibility.

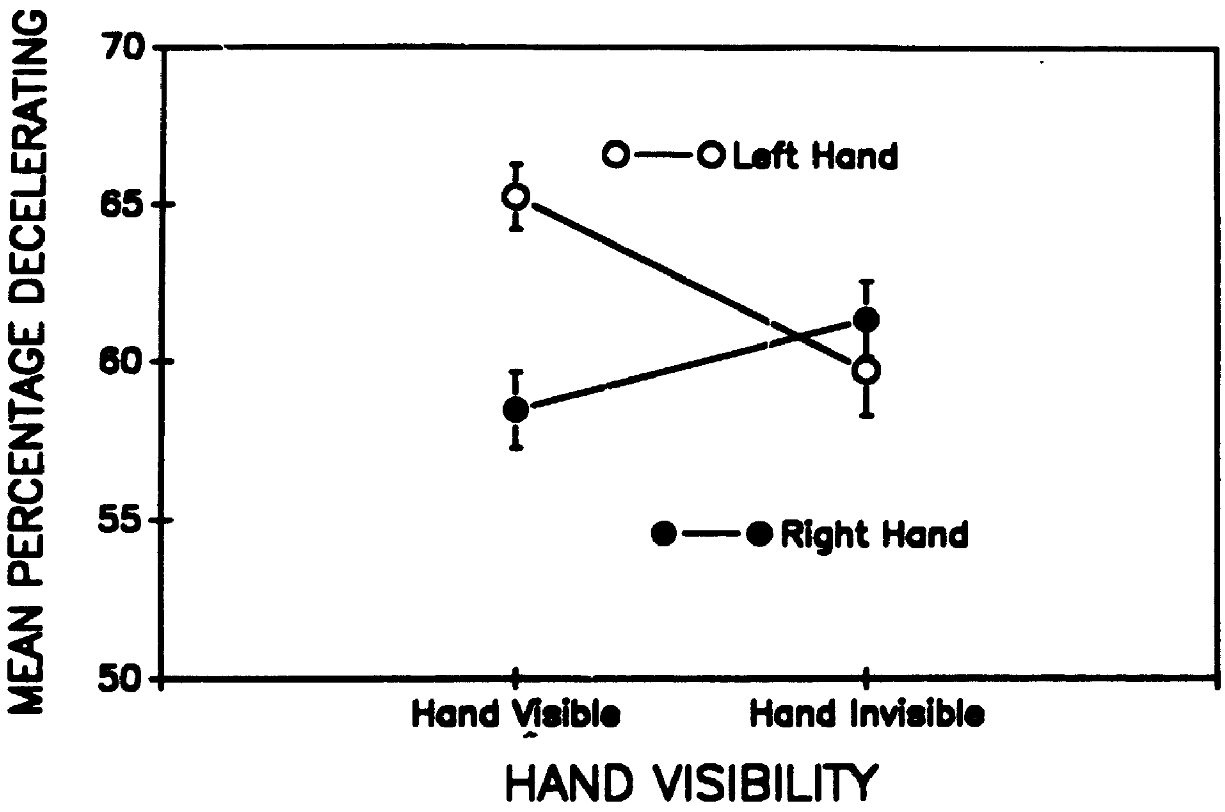

MEAN PERCENTAGE DECELERATING
70
65
60
55
50
Left Hand
Right Hand
Hand Visible
Hand Invisible
HAND VISIBILITY

Figure 2.5 Mean absolute error as a function of Hand, Hand visibility and Target position.

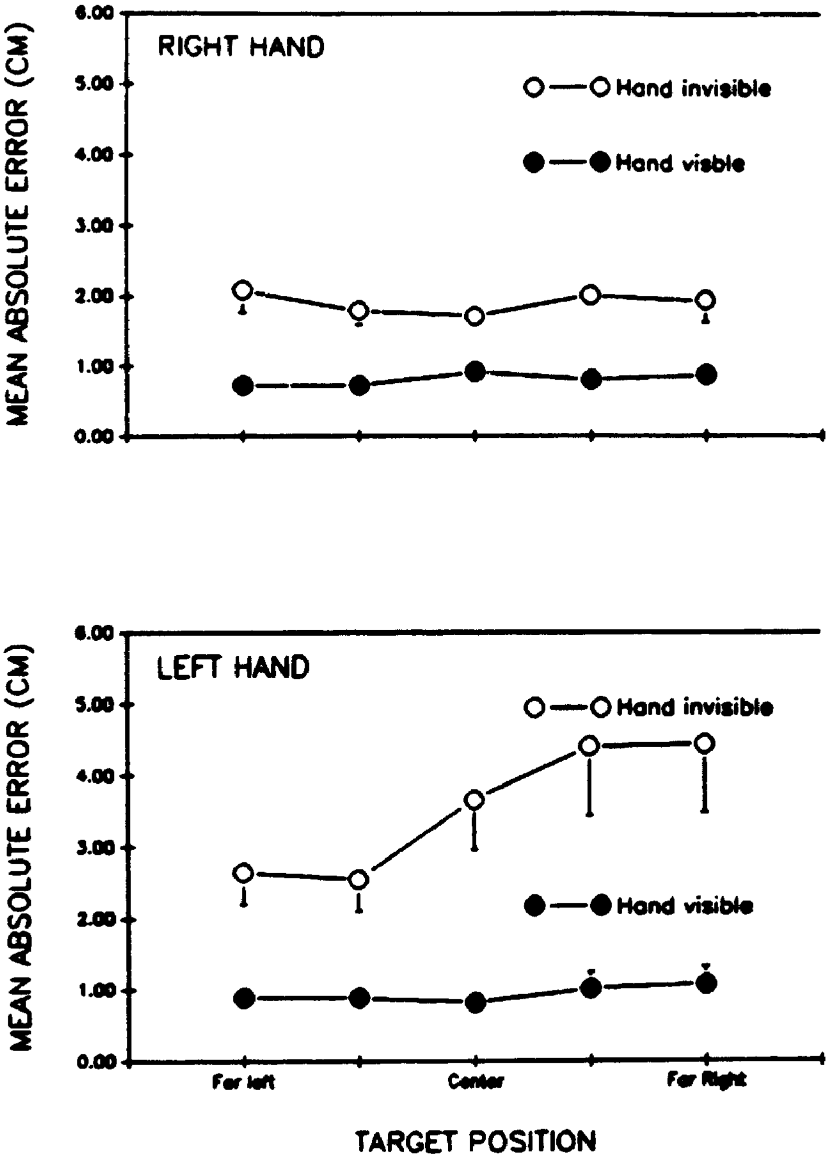
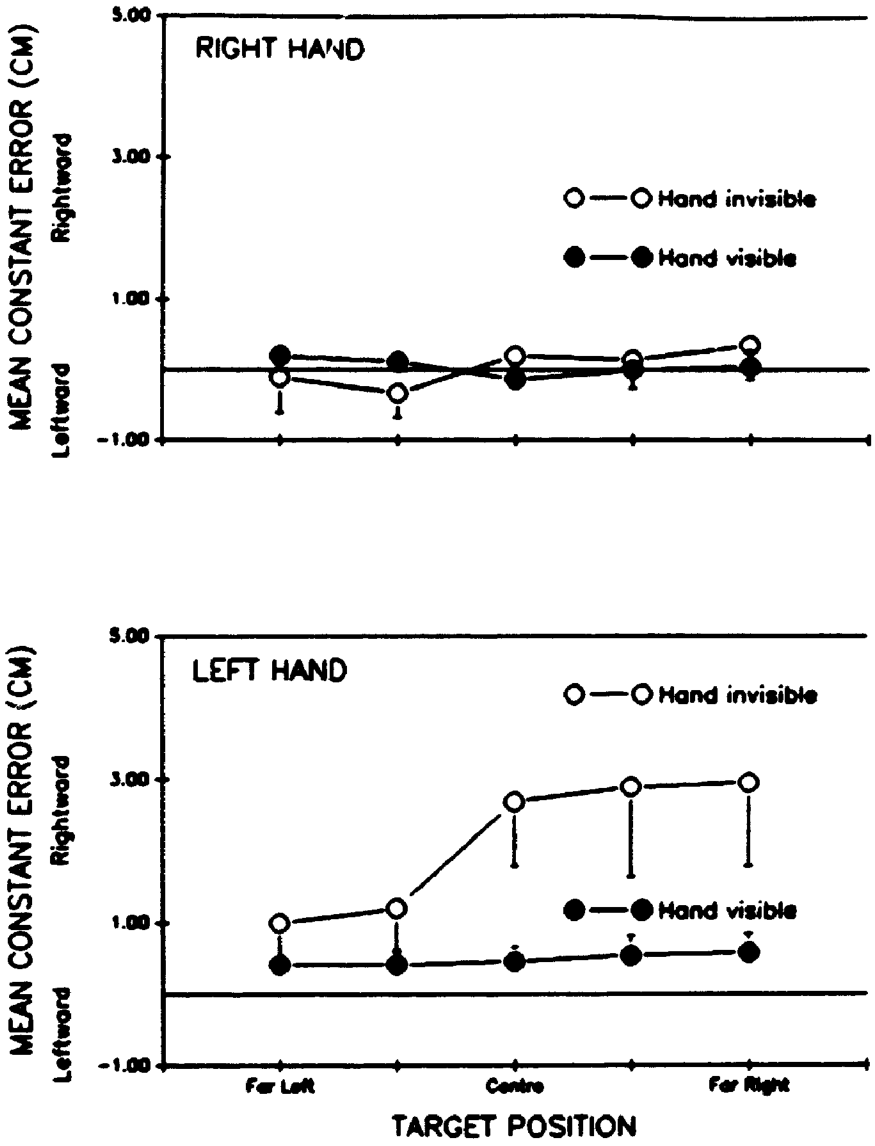

RIGHT HAND
Hand invisible
Hand visble
MEAN ABSOLUTE ERROR (CM)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
LEFT HAND
Hand invisible
Hand visible
MEAN ABSOLUTE ERROR (CM)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
Far left
Center
Far Right
TARGET POSITION

Figure 2.6 Mean constant error as a function of Hand, Hand visibility and Target position.


RIGHT HAND
MEAN CONSTANT ERROR (CM)
Leftward
Rightward
5.00
3.00
1.00
-1.00
○—○ Hand invisible
●—● Hand visible
LEFT HAND
MEAN CONSTANT ERROR (CM)
Leftward
Rightward
5.00
3.00
1.00
-1.00
○—○ Hand invisible
●—● Hand visible
Far Left
Centre
Far Right
TARGET POSITION

that much of the absolute error seen in Figure 2.5 is accounted for by error in the horizontal plane. This suggests that the task does indeed sample endpoint accuracy based on visual localization of the targets, and was not a consequence of general inaccuracy during hand-invisible reaching, since errors in X and Z axes were minimal relative to errors in Y. Large intra-subject variability in the magnitude of these hand-invisible reaching constant errors was found, including some subjects who were relatively unaffected in such conditions. Nevertheless, all main effects and interactions are statistically signficant for constant error, and essentially reproduce the pattern of results for absolute error.

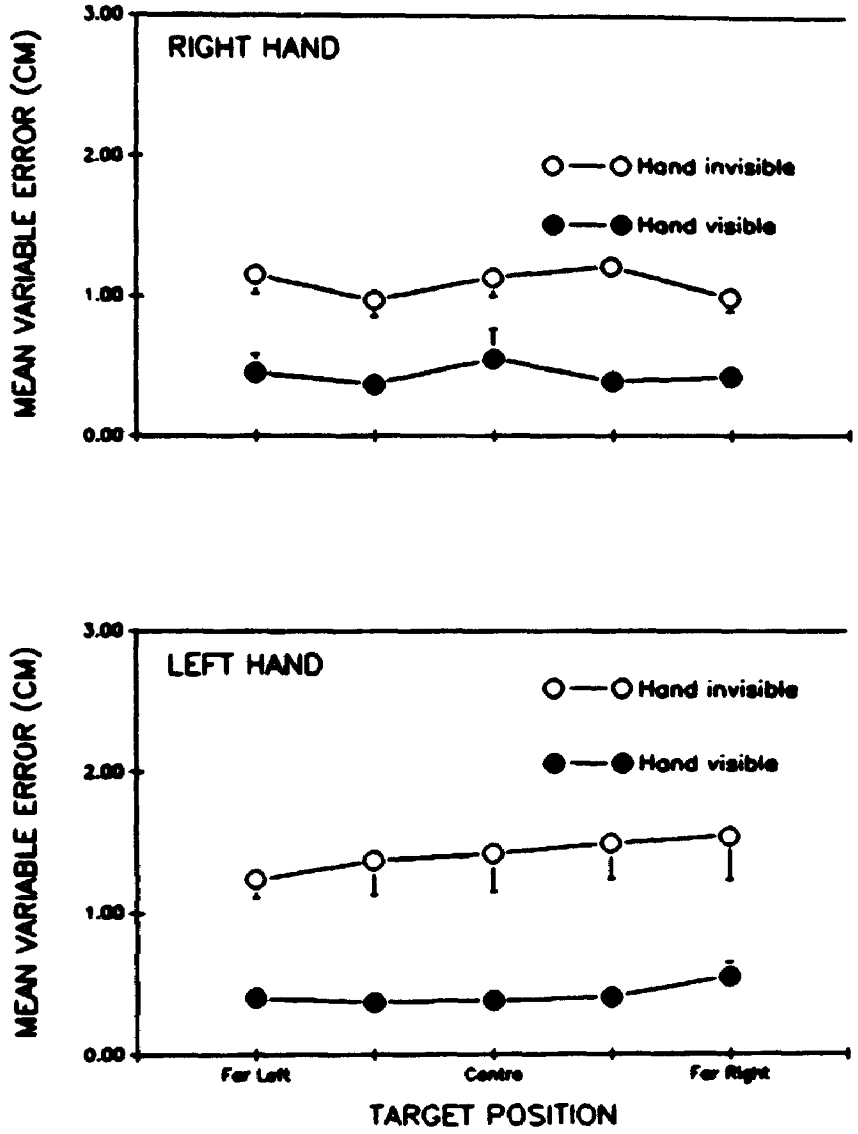
Variable Error

A final measure of endpoint accuracy revealed an unsurprising increase in endpoint variability (as estimated by the standard deviations of constant errors) with the removal of visual feedback of the reaching limb ($F_{(1,13)}=54.0$, $p<0.0001$). Although examination of Figure 2.7 appears to suggest that the left hand was more affected during hand-invisible reaching than the right, the effect of Hand did not reach significance ($F_{(1,13)}=2.53$, $p<0.14$), and it did not interact with Hand visibility ($F_{(1,13)}=2.63$, $p<0.13$), Target position ($F_{(2.7,34.9)}=0.37$, $p<0.75$) or Hand visibility by Target position ($F_{(3.8,50)}=0.93$, $p<0.45$).

Summary

The removal of visual feedback regarding limb position increased movement onset time, but not the overall duration of the movement. The percentage of the movement spent decelerating when vision of the limb was unavailable appears to decrease for left-handed movements and remains unchanged (or increases slightly) for right-handed movements. Movements to right-sided targets had longer deceleration phases, and this trend appeared larger in the right hand of these right-handed subjects. Peak velocity tended to be greatest in the ipsilateral field for each limb, but was not significantly increased or decreased when reaching in the dark. Movement duration was affected primarily by an interaction between hand and hemispace; ipsilateral movements were

Figure 2.7 Mean variable error as a function of Hand, Hand visibility and Target position.


3.00
2.00
1.00
0.00
MEAN VARIABLE ERROR (CM)
RIGHT HAND
○—○ Hand invisible
●—● Hand visible
3.00
2.00
1.00
0.00
MEAN VARIABLE ERROR (CM)
LEFT HAND
○—○ Hand invisible
●—● Hand visible
Far Left
Centre
Far Right
TARGET POSITION

completed more quickly than contralateral movements (with no evidence of a speed-accuracy trade off). Accuracy decreased for all three dependent measures in hand-invisible conditions; but the increases in absolute and constant errors were larger in the left hand. In Absolute error this effect was most dramatic in the left hand for the rightward (contralateral) targets.

Hemispatial effects were demonstrated for movement durations and normalized peak velocities; each hand spent less time in motion and achieved higher peak velocities in its own hemispace. There was also a suggestion in the data that more of a movement is spent decelerating towards the target in right hemispace relative to left hemispace.

2.3.2 **Pointing and Bisecting**

After adding the bisecting data, 4 additional cells required mean substitution, bringing the total to 8 out of 2240 (0.4%). Mean dependent measures as a function of Hand visibility and Hand for bisecting appear in Table 2.2.

Movement Onset Time and Movement Duration.

Movement onset times were significantly shorter for central targets relative to peripheral ones (Target position, $F_{(1.95,25.3)}=3.84$, $p<0.04$; the three central targets significantly shorter at $p<0.01$) and for pointing relative to bisecting ($F_{(1,13)}=7.56$, $p<0.02$). A Hand by Target position effect was not significant ($F_{(2.5,32.8)}=0.73$, $p<0.52$) but the Hand by Task by Target position interaction was ($F_{(2.8,36.2)}=2.95$, $p<0.05$). One plausible interpretation is that ipsilateral reaction time advantages are attenuated in the left hand while bisecting (Left hand: in pointing, a 14 msec advantage for leftward movements, in bisecting a 3 msec advantage for leftward movements. Right hand: in pointing, a 15 msec advantage for rightward movements, in bisecting a 16 msec advantage for rightward movements). The data do not suggest any generalized decrease in movement onset time in contralateral space during bisecting for the left hand. For movement durations, an

Table 2.2 Mean kinematic variables (w. standard errors) for two target bisecting.

	Hand			
	Left		Right	
	Visible	Invisible	Visible	Invisible
Movement Onset	311 (10)	310 (11)	306 (11)	320 (10)
Duration	649 (18)	652 (17)	669 (16)	697 (14)
Peak Velocity	93 (2.0)	100 (3.3)	90 (2.6)	92 (2.7)
Percent. Decel.	64 (1.2)	62 (1.3)	63 (.99)	60 (.88)
Absolute err.	1.10 (.1)	3.46 (.3)	1.03 (.1)	2.35 (.1)
Constant err.	0.44 (.1)	1.15 (.4)	0.20 (.1)	0.60 (.2)
Variable err.	.64 (.04)	1.3 (.1)	.68 (.05)	1.1 (.05)

expected Hand by Target position interaction ($F_{(2\ 5,32\ 9)}=30.36$, $p<0.0001$) was found; associated posthocs reveal that movement durations were shorter for each hand into its own hemispace. Left-handed movements to far left-sided targets were shorter than all other movements (.05 relative to near left targets, .01 relative to all other targets). This effect was not the same across task ($F_{(3\ 3,43\ 3)}=3.31$, $p<0.02$). Figure 2.8 shows mean movement duration as a function of Hand, Task and Target position. Ipsilateral movement duration advantages tend to be larger in the left hand (90-100 msec) and less affected by Task than the ipsilateral duration advantages in the right hand (66 msec in pointing, 27 msec in bisecting).

Normalized Peak Velocity.

No main effects or interactions related to task were found in the normalized peak velocity data. Reaching movements to the far left targets resulted in significantly higher peak velocities than the two right sided targets ($q=2.51$ and $q=4.79$, both p's<0.05; Target position; $F_{(1\ 4,18\ 4)}=4.13$, $p<0.05$). Target position interacted with hand ($F_{(1\ 5,19)}=21.86$, $p<0.0001$). Peak velocities were higher in each hands' own hemispace, and this advantage was larger for the left hand (near ipsi targets, $q=3.89$, $p<0.05$; far ipsi targets, $q=4.57$, $p<0.01$; Figure 2.9).

Percentage of the Reach Decelerating.

Position of the target significantly affected the percentage of the movement spent in deceleration ($F_{(1\ 6,21\ 4)}=4.17$, $p<0.036$). As in Pointing, posthocs still suggest that deceleration duration is less for targets in the left hemispace (far left target less than left, near right and far right targets according to Newman Keuls testing; Figure 2.10). A significant Hand by Position interaction was obtained ($F_{(1\ 4,18)}=5.42$, $p<0.023$) where right-handed movements to the far left target had significantly shorter deceleration durations than all other hand/target combinations (Figure 2.11). Left hand deceleration duration did

Figure 2.8 Mean duration as a function of Hand, Task and Target/Midpoint position.

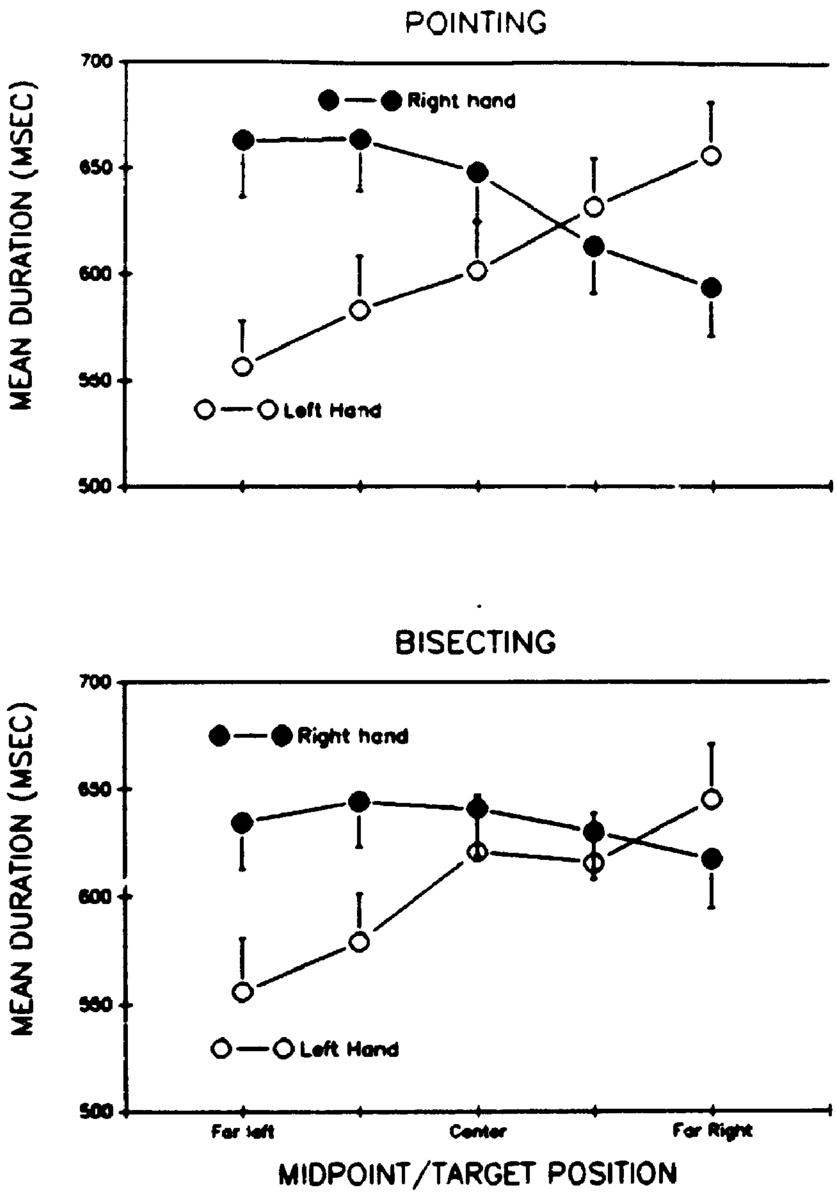

POINTING
MEAN DURATION (MSEC)
700
650
600
550
500
Right hand
Left Hand
BISECTING
MEAN DURATION (MSEC)
700
650
600
550
500
Right hand
Left Hand
Far left
Center
Far Right
MIDPOINT/TARGET POSITION

Figure 2.9 Mean normalized peak velocity as a function of Hand and Target/Midpoint position.

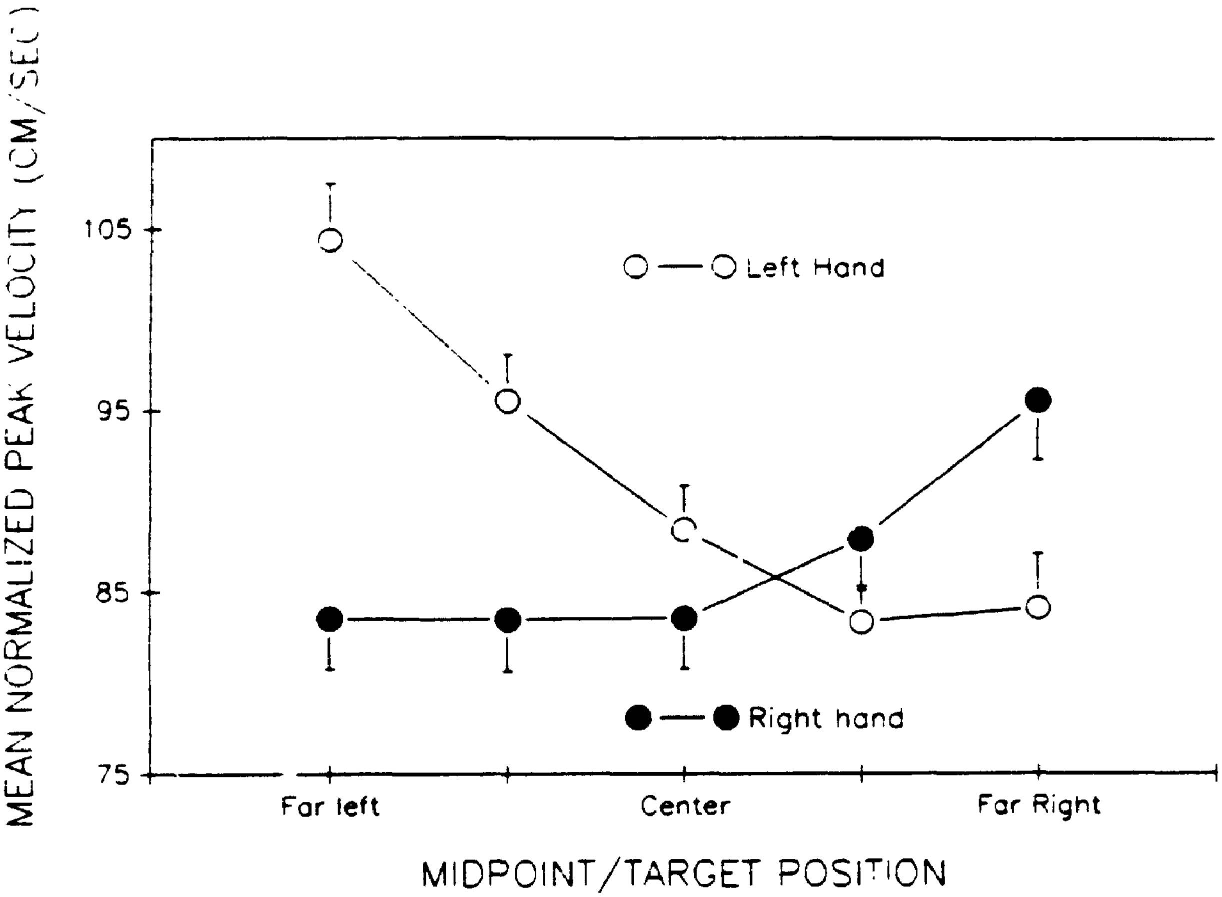

MEAN NORMALIZED PEAK VELOCITY (CM/SEC)
105
95
85
75
○—○ Left Hand
●—● Right hand
Far left
Center
Far Right
MIDPOINT/TARGET POSITION

Figure 2.10 Mean percentage deceleration as a function of Target/Midpoint position.

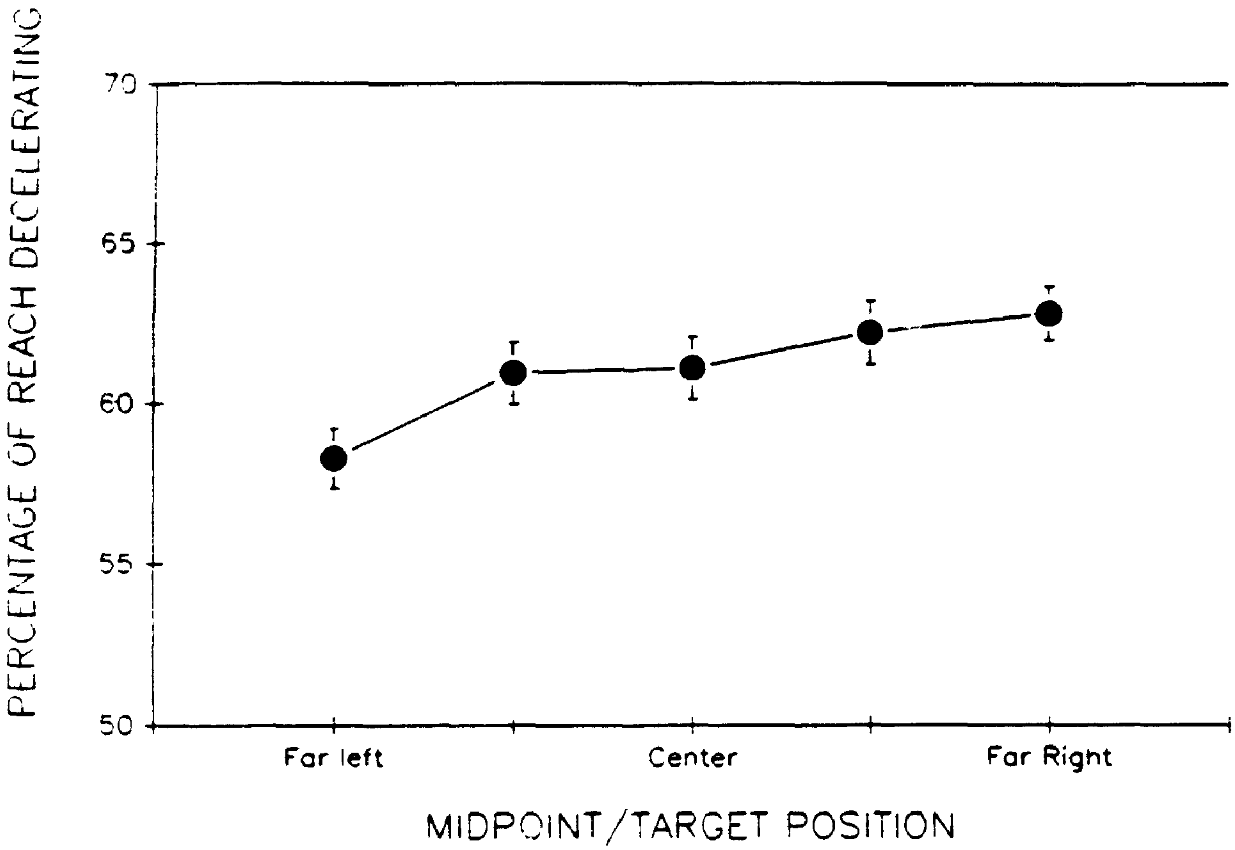
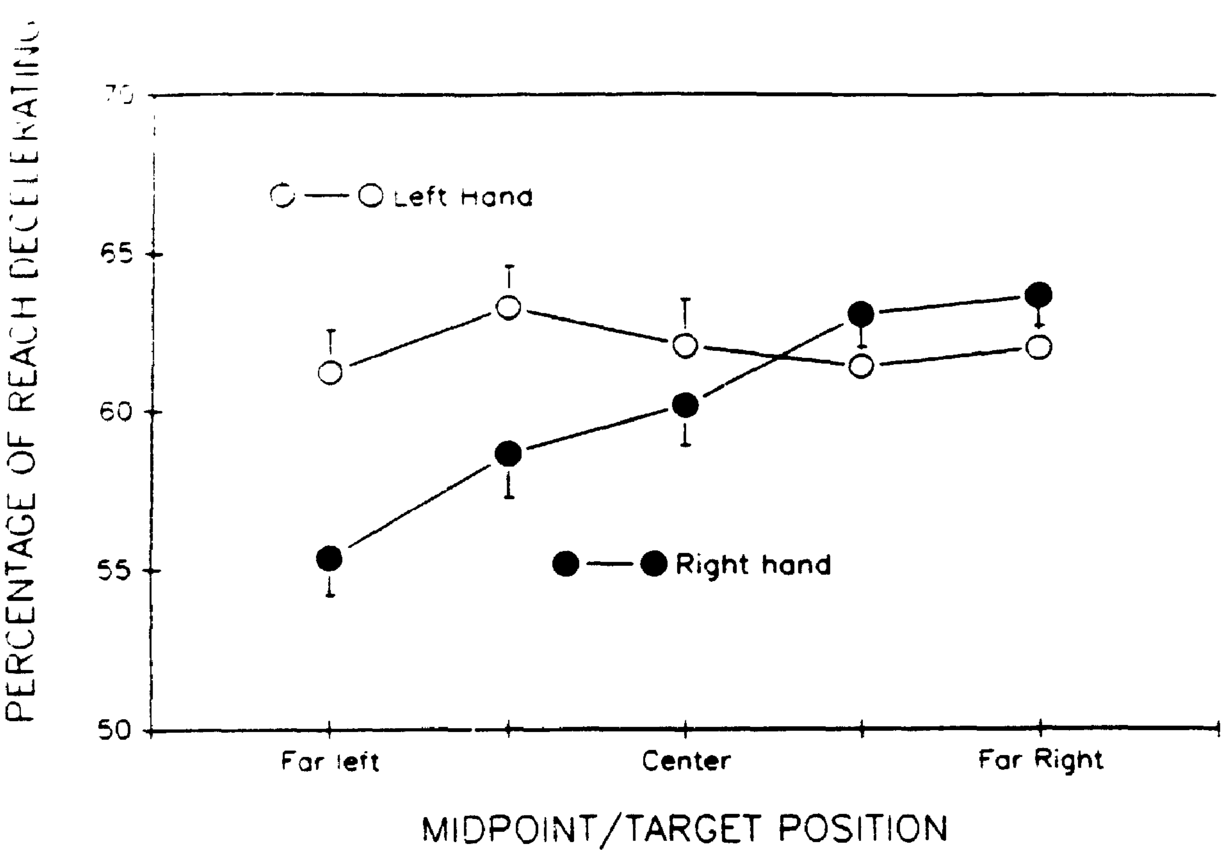

PERCENTAGE OF REACH DECELERATING
70
65
60
55
50
Far left
Center
Far Right
MIDPOINT/TARGET POSITION

Figure 2.11 Mean percentage decelerating as a function of Hand and Target/Midpoint position.


PERCENTAGE OF REACH DECELERATING
70
65
60
55
50
○—○ Left Hand
●—● Right hand
Far left
Center
Far Right
MIDPOINT/TARGET POSITION

not vary across hemispace. This Hand by Position did not interact with Task ($F_{(3.1,40.7)}=1.76$, $p<0.17$) or Hand visibility ($F_{(3.2,41.9)}=0.39$, $p<0.77$).

Endpoint Accuracy Measures

Absolute error

When bisecting data were added to the analysis of Absolute error, hand-invisible movements continued to be less accurate ($F_{(1,13)}=29.09$, $p<0.0001$) as did left-handed movements relative to right-handed movements ($F_{(1,13)}=4.76$, $p< 0.05$). A significant interaction between Task and Target position ($F_{(2.7,35)}=3.38$, $p<0.03$) is consistent with left-sided absolute error advantages which are significant in pointing but not in bisecting (left targets < all others at .01 level in pointing; near left target less than near right and far right in bisecting).

Target position also interacts with Hand ($F_{(1.5,20)}=7.93$, $p<0.005$) Figure 2.12 shows that the right hand tends to be uniform across space, and the left hand is better in its own hemispace (the left hand movements to far left targets and right-handed movements to all five targets displayed signifcantly less Absolute error than the central and right targets in the left hand $p<0.01$). Hand by Target position interacts with Hand visibility ($F_{(1.3,17.5)}=9.90$, $p<0.003$), suggesting that this effect is primarily accounted for by hand-invisible conditions.

Unfortunately, absolute error was not affected by a Hand by Task interaction ($F_{(1,13)}=1.77$, $p<0.20$), although the difference in the two hands was in the predicted direction (0.89 cm in pointing, 0.59 cm in bisecting).

Constant error

No simple main effects of task, hand visibility or position resulted from this analysis. Two of the significant interactions are pertinent to the hypotheses being tested here. A significant Hand by Task interaction ($F_{(1,13)}=5.11$, $p<0.04$; Figure 2.13), and subsequent post-hoc analysis, suggested that the discrepancy between the two hands in accuracy was significant in pointing ($q=6.58$, $p<0.002$) but not in bisecting ($q=2.07$,

Figure 2.12 Mean absolute error as a function of Hand, Task, Hand visibility and Target/Midpoint position.

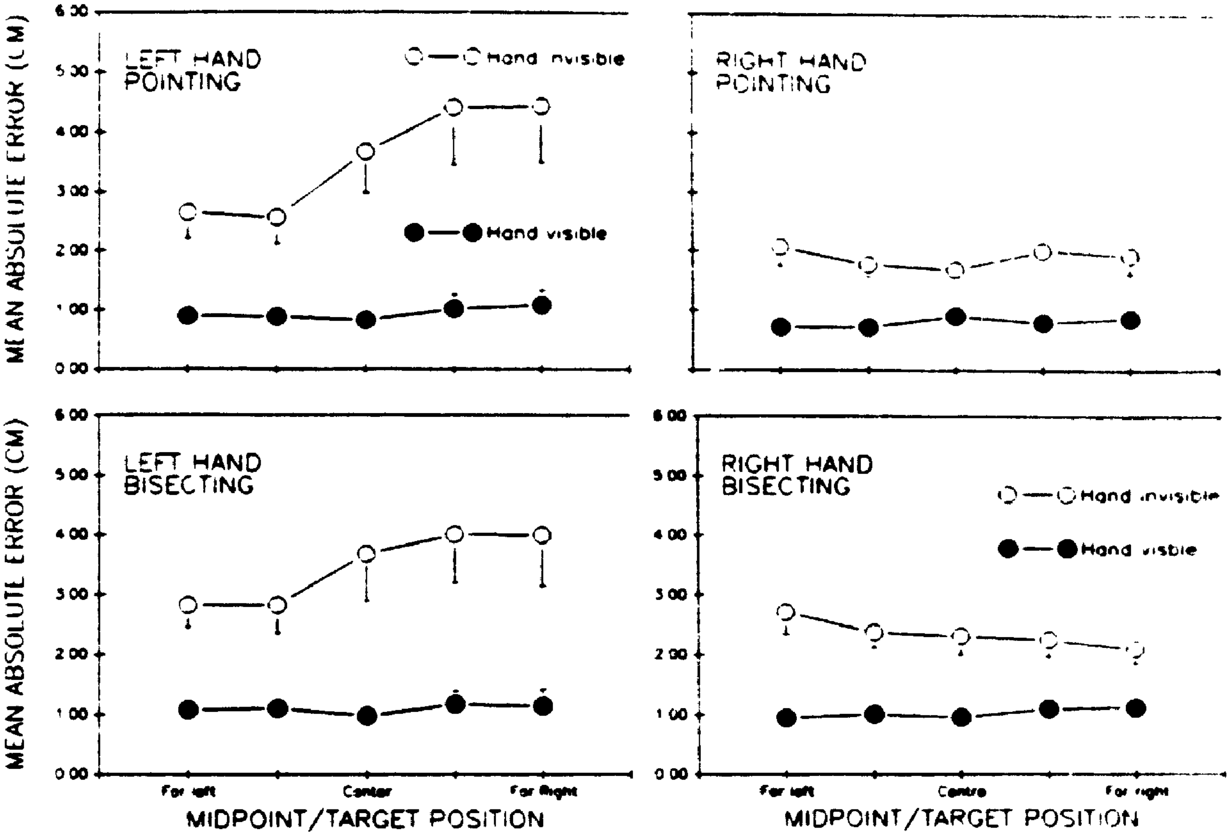
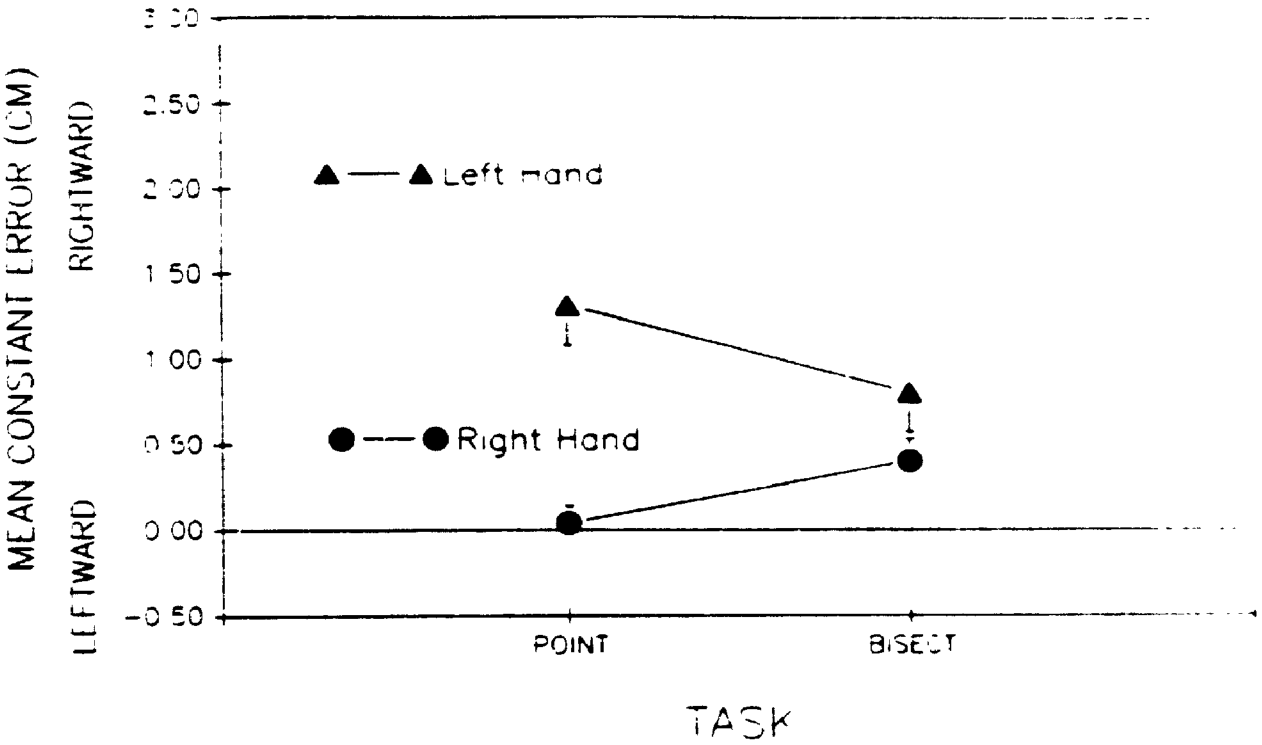

MEAN ABSOLUTE ERROR (CM)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
LEFT HAND POINTING
Hand invisible
Hand visible
RIGHT HAND POINTING
LEFT HAND BISECTING
RIGHT HAND BISECTING
Hand invisible
Hand visible
Far left
Center
Far Right
MIDPOINT/TARGET POSITION
Far left
Centre
Far right
MIDPOINT/TARGET POSITION

Figure 2.13 Mean constant error as a function of Hand and Task.


MEAN CONSTANT ERROR (CM)
RIGHTWARD
LEFTWARD
3.00
2.50
2.00
1.50
1.00
0.50
0.00
-0.50
Left Hand
Right Hand
POINT
BISECT
TASK

$p<0.17$). A Hand by Target position interaction ($F_{(2,28)}=3.48$, $p<0.04$) suggests poor performance by the left hand in contralateral space, while the right hand is relatively uniform across space. None of the right hand means differ significantly. The constant errors in the left hand to the central and right-sided targets are larger than all right-handed mean errors and the ipsilateral targets/left hand errors.

Variable error

As in the pointing analysis, an unsurprising increase in endpoint variability is found in hand-invisible conditions ($F_{(1,13)}=73.09$, $p<.0001$). A three-way interaction between Hand, Task and Target Position ($F_{(3\ 3,42\ 7)}=$[illegible], $p<0.009$) was not easily interpreted so will not be discussed further.

Although the trend was again for smaller between hand descrepancies in bisecting (a .08 cm right hand advantage) than in pointing (a .16 cm right hand advantage), these differences were so small that the Hand by Task interaction was not significant ($F_{(1,13)}=0.45$, $p<0.51$).

Summary

Visual feedback

Removal of visual feedback of the hand produced increases in movement onset time, endpoint variability and absolute error. Hand visibility interacted with several other factors for some of the dependent measures.

Hemispatial effects

As in the analysis of the pointing data alone, the proportion of the movement spent decelerating toward the target tended to be less towards left sided targets, particularly in the right hand. This effect was seen for pointing and bisecting movements. Movement durations and normalized peak velocities were also influenced by target hemispace: Movements had shorter durations and higher peak velocities when they were made into the ipsilateral hemispace. Movement onset times showed some evidence for ipsilateral advantages (although not in the left hand while bisecting).

Endpoint accuracy was either unaffected by hemispace or tended to be smaller in ipsilateral hemispace. Peak velocities were higher in movements to left-sided targets, and this effect was due to a larger ipsilateral left hand advantage relative to the right hand advantage for right-sided targets.

Task effects

Increases in movement onset times but not movement duration were found when subjects bisected two targets relative to pointing to single targets. The predicted decrease in movement accuracy advantages for the right hand was found in constant error; this trend in absolute error may have been obscured by variance accounted for by higher-order interactions. In variable error, small hand and task differences were dwarfed by the huge increase in variable error produced by removing visual feedback from the moving limb. In the left hand, hemispatial effects on movement accuracy and movement onset times may have been attenuated in bisecting relative to pointing.

2.4 **Discussion**

Unlike Guiard, et al. (1983), no kinematic variable or any endpoint-based measure of accuracy favored the performance of the left hand over that of the right. Peak velocity was not greater in the left hand overall, but was higher for ipsilateral targets than right-handed movements to right-side targets. Variable error did not differentiate the hands in our study or in Guiard et al. (1983). The opposite result for Constant and Absolute error was found; a significant increase in the horizontal constant error when vision of the limb was removed in the left hand relative to the right. This finding is consistent with previous reports of right hand advantages in movement accuracy across a number of different task conditions (Fisk & Goodale, 1985; Elliot, 1991).

Several explanations for the difference between this study and Guiard et al. (1983) are possible. One discrepancy was their use of only two different target positions (3 deg.

left and 3 deg. right). In such a situation, the appearance of a particular target might be used for a "go right" vs. "go left" type of decision, while other nonvisual types of sensory feedforward and feedback information (such as efference copy, proprioception, kinesthesis, etc.) might substantially contribute to the final produced position of the limb. Practice trials (and, perhaps even the early trials in the test sequence) might allow the hand/hemisphere systems to employ increasing degrees of nonvisual information for limb positioning.

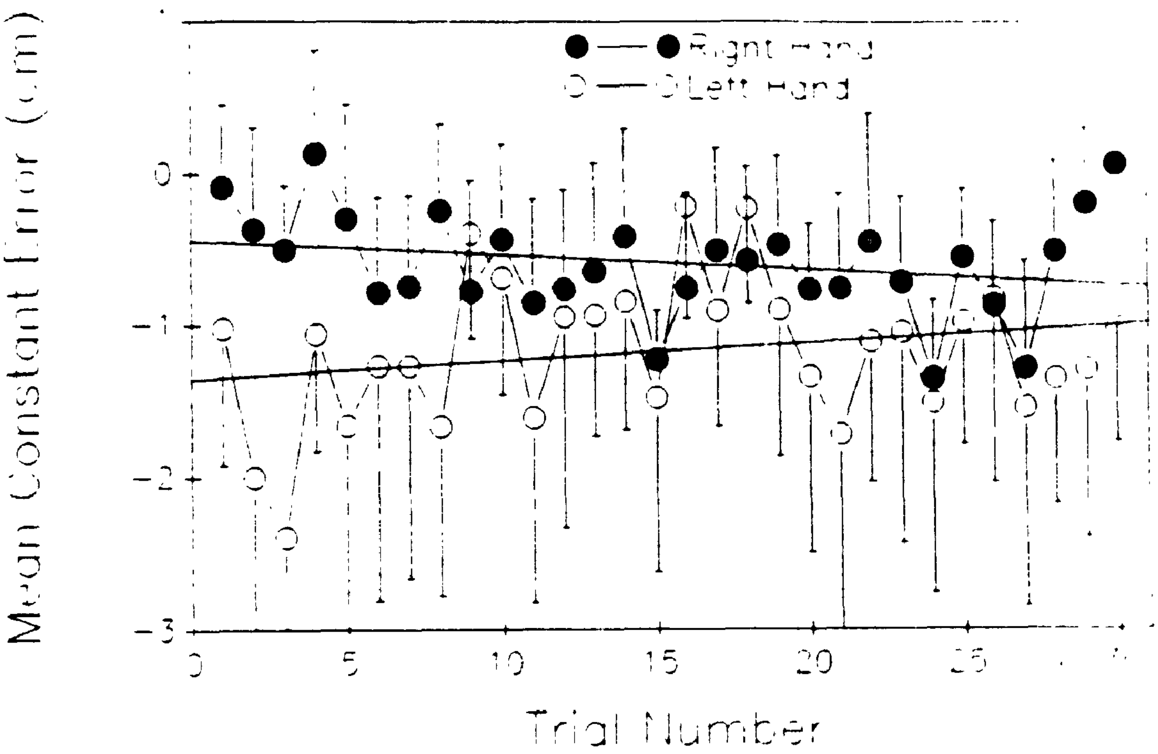
For example, a motor memory task performed by Carson et al. (1990b) was used to show that the reproduction of static limb positions without vision of the limb was performed with equal proficiency with either hand in right-handed subjects. Their interpretation of these data was in terms of the spatial complexity of the task causing a shift away from the usual right-hand advantage for movement accuracy. An alternative interpretation of their data would be that a reduced right-hand advantage on such a task reflects a greater use of proprioceptive/kinesthetic processing than more standard aiming movements typically require. There is a suggestion in the literature that right hemisphere and/or left hand systems may be superior in the processing of somatosensory sources of information than the left hemisphere and/or right hand (Benton, Varney, & De Hamsher, 1978; Carson et al., 1990b; Kimura & Vanderwolf, 1970; Leonard & Milner, 1991a,b; Milner & Taylor, 1972; Nachson & Carmon, 1975; Roy & MacKenzie, 1978).

The significance of the shifts in constant error above and beyond increases in endpoint variability remains unclear. The somewhat larger rightward errors for the far right targets are difficult to explain in terms of range effects (i.e., movement overshooting of relatively near targets and undershooting of more distant targets; see Jeannerod, 1988). An intriguing possibility is that, although noisy, these constant error shifts in the present sample reflect a drift in the register between visual and motor "maps" in the absense of any chance for recalibration of action by vision. This possibility will be addressed in the next chapter.

A difficulty in interpreting these shifts is that in many other studies of aiming movement control, hand-invisible trials are produced by eliminating illumination of the hand after movement is initiated. In the present study, subjects spent each hand-invisible block in complete darkness. Perhaps the constant errors seen in the left hand occur towards the end of the block, after a sufficient period of time has elapsed. Figure 2.14 suggests that this was not the case; mean constant error does not appear to increase as a function of trial number. SPSS Linear Regression analysis of these data reveals that the slopes for the right ($b=-0.0097$, $t(1,28)=-1.33$, $p<.195$) and the left hands ($b=0.012$, $t(1,28)=1.17$, $p<.254$) are both not different from zero. The effects of hand visiblity on the percentage of the movement spent in deceleration differed for the two hands. The right hand seemed to produce shorter deceleration phases for the contralateral targets when vision of the limb was available, while the left hand tended to spend more of the movement decelerating across the whole hemispace under the same conditions. Although this interaction between Hand, Target Position and Hand visibility was not significant in pointing, it was significant in bisecting (although not easily interpretable). It is interesting to note that the right hand makes slower movements with lower peak velocities into the same hemispace, without substantial decrements in accuracy (Figures 2.5 and 2.6). Smit et al. (1987) find that saccades to remembered targets and anti-saccades (saccades to equivalent positions on the side opposite to the target) have longer durations and lower peak velocities than regular saccades to targets. This type of control may reflect a compensatory mechanism within the left hemisphere which reduces endpoint errors in the more "difficult" hemispace without producing an increased reliance on terminal feedback. The removal of visual feedback regarding position of the right limb may increase the length of the deceleration phase somewhat, while the movement onset time was unchanged (Figure 2.1) and endpoint accuracy is relatively preserved (Figures 2.3, 2.4, and 2.5).

By contrast, the aiming movements of the left hand show a uniform decrease in deceleration duration and a trend towards shorter movement duration when vision of the limb is unavailable, perhaps reflecting a shift towards a more ballistic type of control process. Yet in spite of claims in the literature regarding superior programming of ballistic movements by left- hand/right hemisphere systems, there is a dramatic increase in terminal error across all of the hemispace, but in particular in the more "difficult" contralateral hemispace when the left hand reaches in the dark. Perhaps the right hand,

Figure 2.14 Mean constant error as a function of Hand and Trial number.


Right Hand
Left Hand
Mean Constant Error (cm)
0
-1
-2
-3
0
5
10
15
20
25
Trial Number

within its preferred field, is able to shift towards a control strategy that relies on a longer lasting perceptual representation of the exact location of a target when terminal positional feedback is not available (i.e., like saccades to remembered positions, Smit, et al. 1987).

Although bisecting attenuated right hand advantages in endpoint accuracy, it is not clear what other kinematic markers are related to hand performance differences in that task. Few other task-related effects were found in the present study. There was a suggestion that hemispatial effects in the left hand may be attenuated during bisection (i.e., movement onset time, and perhaps terminal accuracy). Given that the more dramatic hemispatial effects are not yet fully understood, interpretation of these changes is unlikely to provide significant insight into right hemisphere contributions to visually-guided aiming.

CHAPTER 3 - EXPERIMENT 2: MARATHON.

Abstract

Extended periods of hand-invisible reaching were run in this experiment to examine differential drifting in the reach endpoints of the two hands, following a suggestion made by Jeannerod (1992). Eleven right-handed subjects bisected two LEDS in a series of 800 trials in 50-trial blocks. The hypothesis that the right hand would be more resistant to drift than the left hand was not supported, although the mean constant errors of right-hand marathons were left of true midpoint position while the constant errors of the left-hand marathons were rightward. Hemispatial differences in peak velocities and movement durations tended to remain stable throughout the marathons, in spite of the long period of time without visual feedback from the moving limb.

3.1 Introduction

The results of Experiment 1 did not produce accuracy advantages for the left hand relative to the right in the 14 subjects I tested. In fact, the mean absolute and constant errors were significantly larger in left-handed reaches. The large rightward errors in the left hand were seen across the entire hemispace and were not anticipated. Previous reports of directional errors in normal subjects usually consist of so-called "range effects"-subjects overshoot near targets and undershoot more distant ones. Other directional errors include undershooting towards the side of the lesion in patients with unilateral brain damage (i.e., Ratcliff & Davies-Jones, 1972). An explanation for the directional effects in Experiment 1 might be related to the way in which visual feedback was eliminated. Subjects did not view their hand at any time during the hand-invisible trials. In other studies (Carson et al., 1990a; Carson et al., 1993; Prablanc et al., 1979) ambient illumination has been removed upon movement initiation: Therefore in such situations subjects have a view of their hand at the start position which could be used to recalibrate visual and motor systems between actual movements made in the dark. Prablanc et al. (1979) found greater constant and variable errors when subjects did not have an opportunity to view the static hand before a hand-invisible trial. Unfortunately, their results cannot be directly compared to those of Experiment 1 because they collapsed across side of target. Jeannerod and colleagues have long argued for a calibration process which maintains the register between proprioceptive and visual "maps". By maps he means computation of target position in visual space and limb position in body-centred space (Jeannerod, 1988; 1991; Jeannerod & Biguer, 1987). Jeannerod has commented that the time course of this calibration process is as yet unknown; "in the absence of such data, one can only speculate that, *without vision of the hand, the two maps will drift with respect to each other* and position sense will lose its calibration with respect to visual space" (Jeannerod, 1991, pg. 287, italics mine). Although the non-significant slopes of constant error as a function of trial (see Figure 2.14) do not suggest a time- or trial-related effect in Experiment 1, it is conceivable that with longer durations without feedback, the right hand might begin to shift in the dark (as the left does immediately in hand-invisible reaching).

The right hand showed only slight shifting during hand-invisible reaching in Experiment 1. There are two possible reasons why right hand performance remained so robust. Right hand/left hemispheric mechanisms may be relatively independent of visual feedback for long term visuomotor calibration, and therefore would show increased variability in reach accuracy but no systematic changes in constant error, regardless of the number of trials spent in hand-invisible conditions. A second possibility is that directional shifts would occur, but would require a greater period of time in the dark (or number of trials without visual feedback) to manifest themselves. In other words, the calibration of the right hand by vision might be more stable than the calibration of the left hand. The present experiment was designed to differentiate between these two possible explanations by requiring subjects to reach in an extended series of trials without visual feedback.

Independent of whether or not the right hand shifts is the question of whether or not any shifts in reach endpoints are a function of changes in subjective egocentre. That is, the midline of the body (the sagittal plane which cuts the body into two symmetrical left and right halves) has been suggested by many to serve as an important reference axis for the generation of visually-guided movements of the limbs (although others argue for a shoulder-centred coordinate system; see Soechting & Flanders, 1993, and associated commentaries for a detailed discussion). Jeannerod has claimed that when subjects have to indicate the plane coincident with their own midline in the dark, they tend to make errors to the left of their true objective midline (Jeannerod & Biguer, 1989). These authors note that these shifts are related to the phenomenon of "pseudoneglect", where normal subjects tend to bisect lines slightly to the left of true midpoint either visually (Bowers & Heilman, 1980) or tactually (in the absence of visual feedback; Bradshaw et al. 1983). Gras et al. (1993) have reported contralateral shifts in perceived egocentre for the left and right hands in the absence of visual feedback. Chokron & Imbert (1993) recently reported similar contralateral shifts in tacto-kinesthetic bisection tasks, which were exacerbated when the subjects deviated their gaze towards the side of the hand. In order to examine possible drift of perceived midline during each session, subjects were required to indicate the projection of their perceived midpoints periodically by pointing to their estimate of this position on the target wedge in complete darkness.

Finally, other kinematic variables and their relationships to hemispace might depend on routine visuomotor recalibration, even if movement accuracy (as measured by constant error) does not. For example, some of the ipsilateral movement "advantages" might be dependent on vision of the moving limb on a trial-to-trial basis or on occasional calibration of motor systems by vision. If such is the case, the magnitude (or indeed, presence of) of ipsilateral limb movement advantages might depend on periodic vision of the limb.

To examine these issues and any potential differences between the hands in long-term reaching without visual feedback of the hand, 11 right-handed males participated in two 800-trial reaching sessions in complete darkness. After every 50 trials, subjects indicated their perceived midline position in hand-invisible conditions. Finally, after some adaptation to dim illumination (with no vision of their limbs and minimal eye movements), 10 of the 11 subjects pointed with visual feedback for a small number of trials after the marathon was completed, to examine the possibility of different mechanisms of recalibration in the two hands.

3.2 Methods

Subjects

Subjects were eleven University of Western Ontario graduate students, Research Assistants and senior Undergraduates who were paid either $20.00 or $25.00 for each session. Subjects were right-handed as assessed by the Hand preference inventory.

Procedure

Subjects participated in two separate sessions, one for each hand. After positioning the subjects as comfortably as possible in the chinrest, five calibration trials were collected as in Experiment 1. Subsequently subjects performed a "midline" trial calibration with their hand visible to them. For this and all subsequent midline trials, subjects were asked to reach out and place the tip of their index finger on the target wedge at the position directly in line with their body midline. The subjects did so from their standard position in the chinrest, and were told to restrict any other contact with the table surface. When they verbally indicated their satisfaction, a 1.5 sec 100 Hz sample of that position was collected.

After a 5-minute dark adaptation period, subjects received five practice trials (one to each target) and then testing began. Subjects were given a ready signal from the experimenter, and then two LED targets were illuminated for 400 ms. This short presentation time was used to minimize the potential visual feedback which would occur if the subject partially occluded one or both of the targets at any point in the movement, while still providing sufficient time for the movement to be initiated before target extinction in the majority of trials. Bisection was used for a similar purpose; if on some trials movements were completed before 400 msec, occlusion (or non-occlusion) of target position could provide some visual feedback about final position of the limb.

Subjects reached in 50-trial blocks. At the end of each block, most subjects were asked to perform a midline trial (see above) and then received a self-paced rest period. Subjects were not informed of the number of trials in a block, the number of blocks, or duration of the session at any time.

After 16 blocks of trials were completed, subjects were instructed to close their eyes and re-position themselves in the chinrest. The ambient room illumination was then turned on, and subjects were required to direct their attention to the centre of the target wedge, which was indicated by an auditory cue provided by the experimenter. They were asked to restrict any eye movement as much as possible. Subjects were not instructed to open their eyes until their reaching hand was in the start position (and invisible to the subject due to the position of the chin rest) and their other limb was off the table surface. These preparations were undertaken in an attempt to minimize potential visual reafference prior to the hand-visible post marathon trial block.

Subjects were given a few minutes to adjust to the light levels, and during this period they were instructed that a block of trials under hand-visible conditions were to be collected, and that they should, as before, reach quickly and accurately to the targets as they appeared, and to remain in their landing position until instructed to return to home (see Figure 3.1 for a schematic of the procedure).

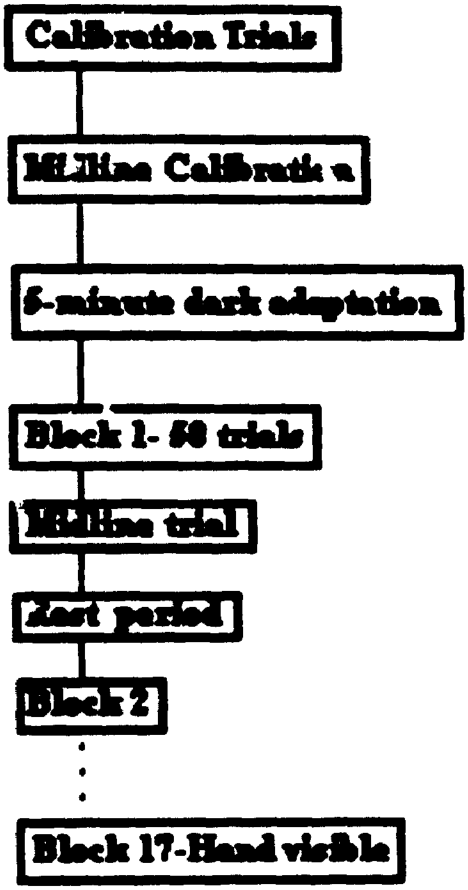
Sessions were separated by at least a 10-day period. An attempt was made to run the subject at the same hour of day, and to pace rest breaks such that the marathons did not differ substantially in duration. Because subjects performed in a self-paced fashion, intra-individual differences were minimal (although actual durations between individuals varied from approximately two to three hours).

Data Analysis

Mean values for each dependent measure were calculated for the sixteen 50-trial blocks. For the univariate analyses, means as a function of 50-trial block were computed; for a second analysis, means were calculated as a function of side of target (central trials were excluded). Perceived midlines were compared to the calibration trial for the central target, which lay on a direct line from the midline when the subject was positioned in the chinrest. The signed deviations of the midline trials were compared to mean constant error as a function of block.

In addition to those kinematic variables reported in Experiment 1, the peak positive and peak negative acceleration (averaged over three frames, in dm/sec^2), and the time to

Figure 3.1 Schematic of the procedure for the Marathons.


Calibration Trials
Midline Calibration
5-minute dark adaptation
Block 1- 50 trials
Midline trial
Rest period
Block 2
Block 17-Hand visible

peak positive and peak negative acceleration (normalized for the duration of the movement) were also recorded and analyzed (for a sample velocity profile identifying these measures, see Figure 3.2). SPSS MANOVA repeated measures analysis of variance was performed using the dependent measures, with Hand and Block as the within-subjects factors in the first analysis.

For a second analysis, ipsilateral "advantage" ratio scores were calculated from the block means, to examine potential changes in the hemispatial advantages usually elicited for movement onsets, durations, and peak velocities. These scores were calculated using the following formula (after Harshman & Lundy, 1988):

[(Ipsi-Contra)/(Ipsi+Contra)]*100

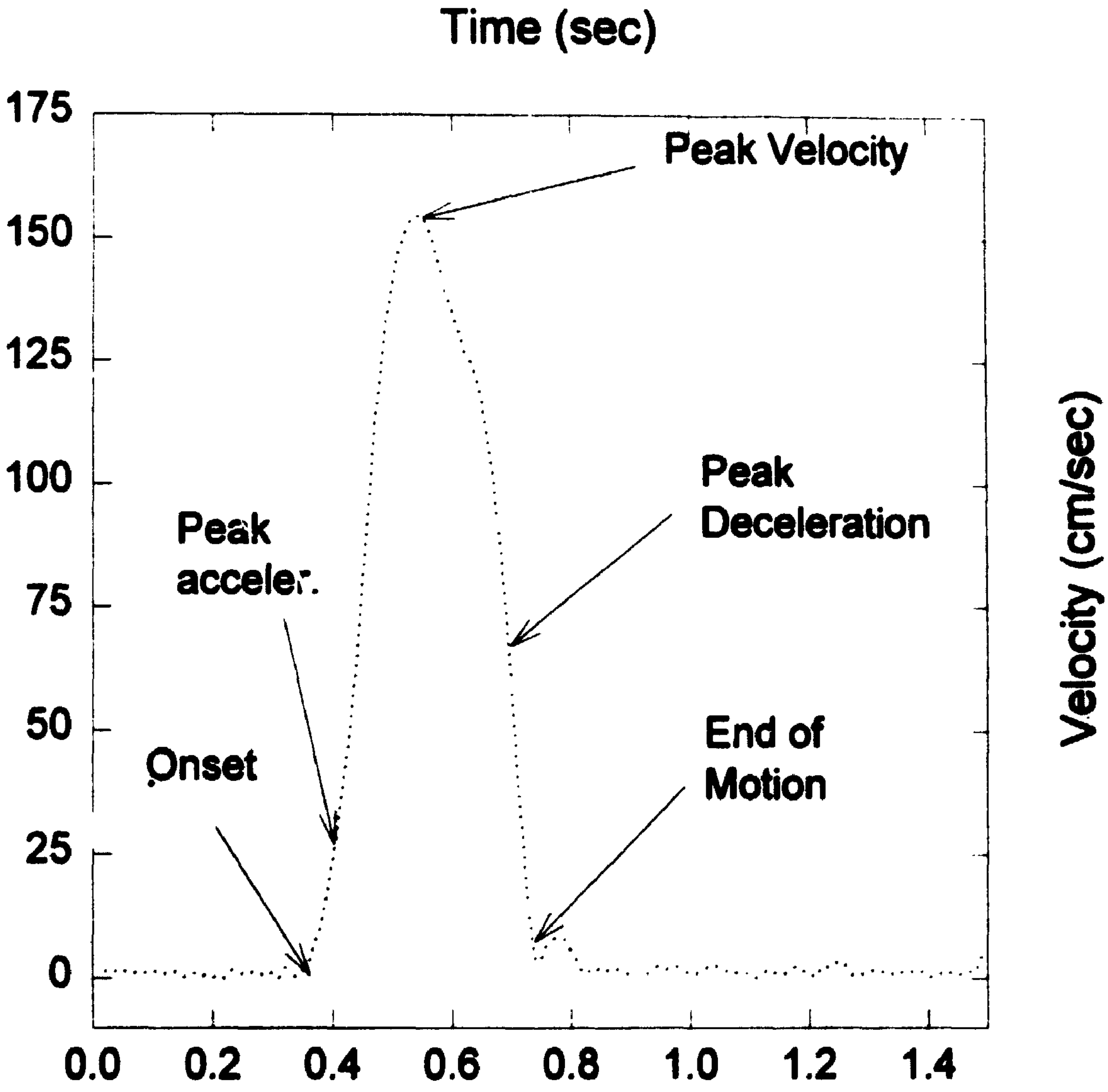
This measure gives an estimate of ipsilateral advantage in a percentage scale, and was calculated separately by hand. These scores were then subjected to an analysis of variance with Block and Hand as factors as described above.

Mean constant error for each 50-trial block was correlated with perceived midline position for each subject by hand. In addition, the movement kinematics of the first five trials of the hand-visible Block 17 were compared to the last five trials of the hand-invisible block 16 by correlated t-tests.

3.2 Results

Because subjects' rest breaks were self-paced, there were some differences in the durations of particular marathons (but these differences were usually larger across subjects than within subjects). When accurately timed, marathons were completed within 2 to 3 hours. Although midline trials were not collected for all of the subjects (and some were inadvertently lost), data were analyzed for 9 of the 11 right hand marathons and 7 of the 11 left hand marathons.

Figure 3.2 A sample velocity profile showing the relevant computed kinematic variables. This particular movement was sampled at 100 Hz and smoothed with a 7-Hz Butterworth filter.


Time (sec)
175
150
125
100
75
50
25
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Peak Velocity
Peak Deceleration
Peak acceler.
Onset
End of Motion
Velocity (cm/sec)

3.3.1. *Univariate Analyses*

Movement Onset, Movement Duration, and Total Movement Time.

Mean movement onset times were significantly shorter in the left hand relative to the right (264 msec vs. 292 msec; $F_{(1,10)}=8.41$, $p<0.16$) and were affected by Block ($F_{(15,150)}=2.41$, $p<0.004$). Examination of these onset times shown in Figure 3.3 suggests a trend towards decreasing onset times over the sessions. This effect did not differ between the two hands ($F_{(15,635)}=0.19$, $p>0.05$). Mean movement durations were significantly affected by Hand used ($F_{(1,10)}=22.72$, $p<.001$) and an interaction between Hand by Block ($F_{(15,150)}=1.79$, $p<0.04$). Unlike in Experiment 1, the right hand produced shorter movement durations than the left. The interaction has numerous interpretations, but it appears that the trend for decreasing durations is somewhat more pronounced in the right hand data (Figure 3.4). Another interpretation is suggested by performing an ANOVA on the data from the first 5 blocks alone, based on the observations that changes in some of the kinematic variables (see constant error analysis below) are completed within that stage of the marathons. Such an analysis produces a significant Hand by Block interaction ($F_{(4,40)}=4.32$, $p<0.05$). Newman Keuls analysis suggests that in the first 100 trials, the hands are not significantly different but in blocks 3, 4, and 5 the right hand is consistently shorter in durations of the movement than the left hand (all associated p values significant at the .03 level or lower).

Given that fatigue was likely to play a factor in these long reaching sessions, an estimate of overall response speed was calculated to examine such effects. Total movement time was calculated by adding movement onset times and durations. Total movement time did not appear to increase over the session in either hand (Hand: $F_{(1,10)}=1.31$, $p<0.28$; Hand by Block $F_{(15,150)}=0.54$, $p<0.92$). In fact, a significant Block effect ($F_{(15,150)}=3.02$, $p<0.001$) is most easily interpreted as a slight decrease in this measure over the session (see Figure 3.5).

Figure 3.3 Mean movement onset time, collapsed across Hand.

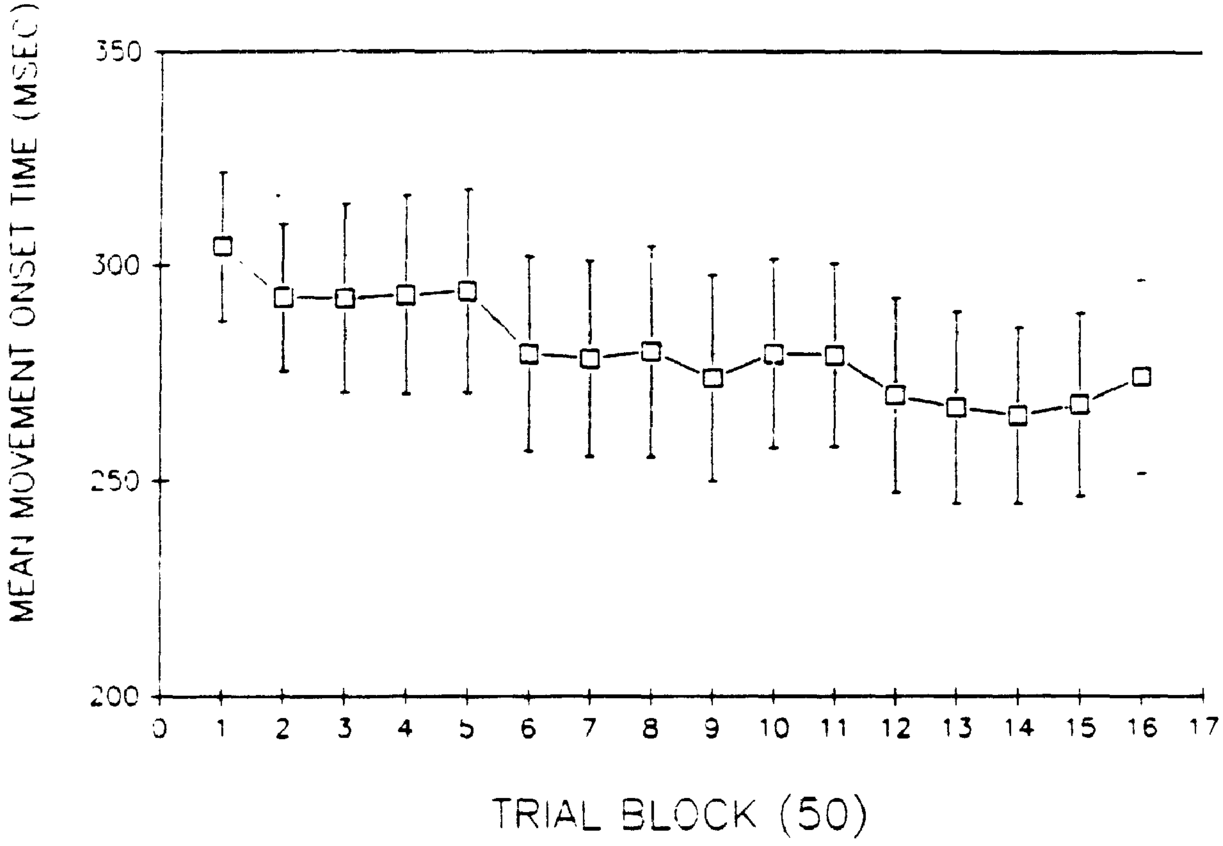

MEAN MOVEMENT ONSET TIME (MSEC)
350
300
250
200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Figure 3.4 Mean duration as a function of Hand and Block.

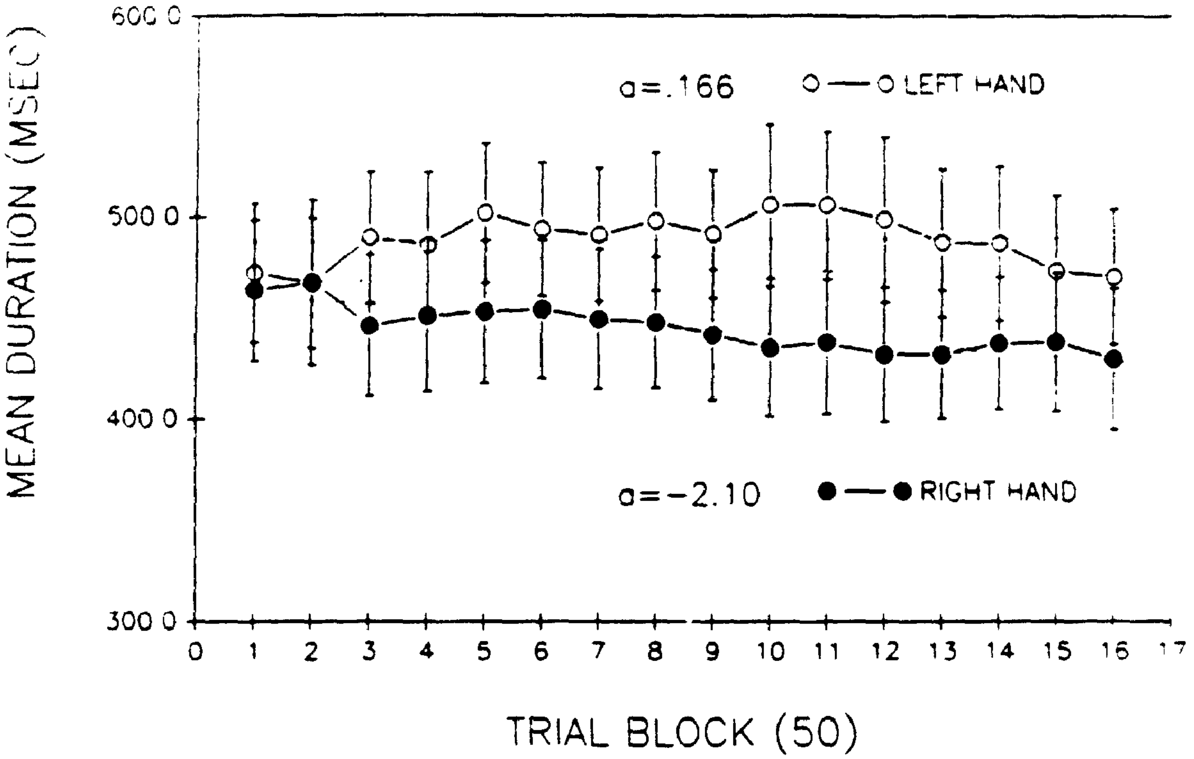
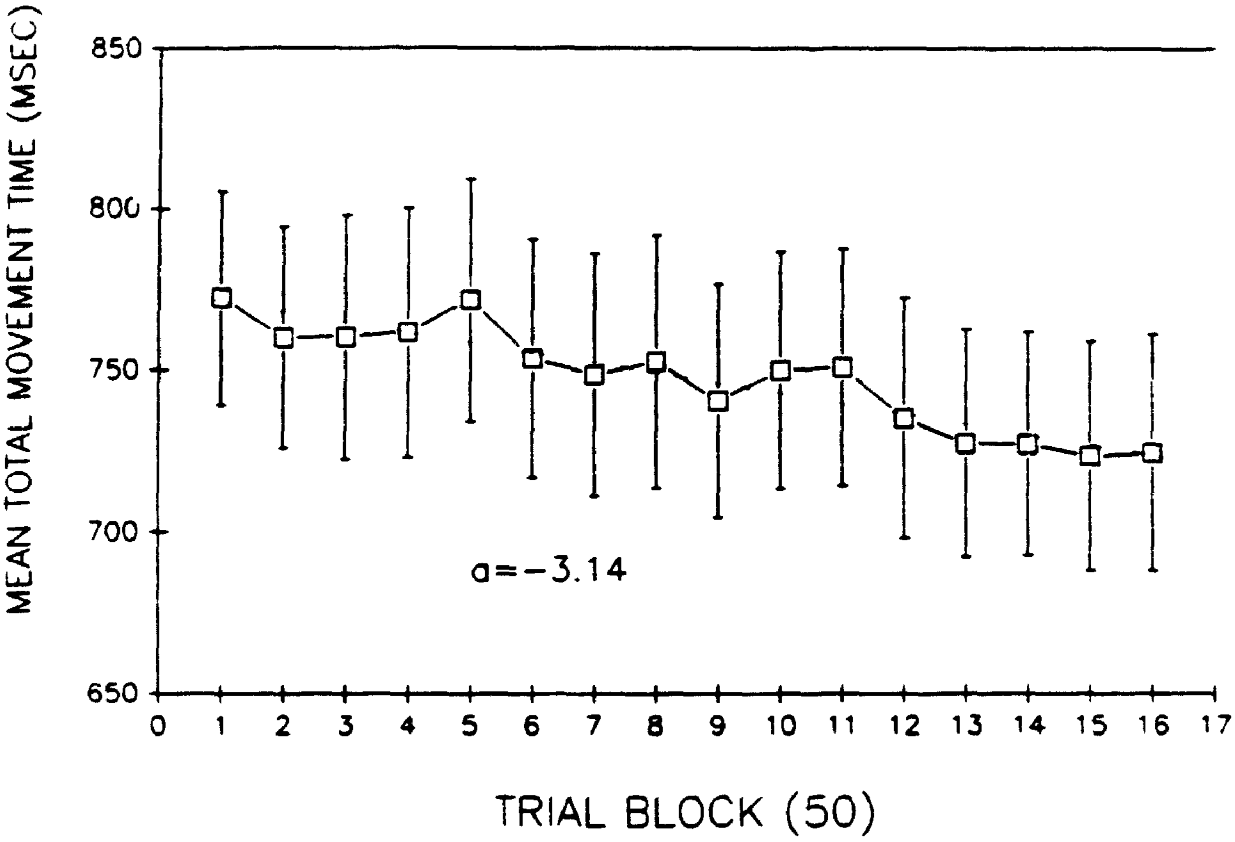

MEAN DURATION (MSEC)
600.0
500.0
400.0
300.0
a=.166
LEFT HAND
a=−2.10
RIGHT HAND
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Figure 3.5 Mean total movement time (movement onset time + duration) as a function of Block (collapsed across hands).


MEAN TOTAL MOVEMENT TIME (MSEC)
850
800
750
700
650
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)
a=−3.14

Movement Length.

No significant difference between the hands was found ($F_{(1,10)}=0.04$, $p<.85$) but a Block effect ($F_{(15,150)}=2.13$, $p<0.011$) and a Hand by Block interaction ($F_{(15,150)}=1.82$, $p<0.036$) affected mean length of the movement. Again, high degrees of variability between subjects make multiple interpretations of this interaction possible. There is at least a suggestion in the data that the path lengths were gradually increasing in the two hands, and this effect may have been larger in the left hand marathons (Figure 3.6).

Peak Velocity and Time to Peak Velocity.

An apparently higher peak velocity in the right hand (mean=140.6 cm/sec) relative to the left (mean=127.8 cm/sec) was not statistically significant ($F_{(15,150)}=4.06$, $p<0.07$). A significant block effect appears in Figure 3.7 ($F(15,150)=3.47$, $p<0.001$) and was not significantly different between the two hands ($F_{(15,150)}=1.05$, $p<0.41$). There was a trend for time to peak velocity to increase over the course of the marathon (Block $F_{(15,150)}=2.17$, $p<0.01$) which appeared to be slightly more pronounced in the left hand, but this trend was not significant ($F_{(15,150)}=1.63$, $p<0.07$) nor was there any overall difference between the two hands ($F_{(1,10)}=0.19$, $p<0.67$; Figure 3.8).

Peak acceleration, deceleration, and percentage time to peak acceleration and deceleration.

Although peak acceleration appeared to be higher in the left hand ($X=202$ dm/sec^2) relative to the right ($X=153$ dm/sec$_2$), this trend did not reach statistical significance ($F_{(1,10)}=3.37$, $p<0.096$). Block was not a significant factor for this measure ($F_{(15,150)}=1.01$, $p<0.45$), but a Hand by Block interaction ($F_{(15,150)}=2.09$, $p<0.013$) was obtained. The trend may be towards increasing peak accelerations in the left hand but not the right hand marathons (see Figure 3.9). Percentage time to peak acceleration was affected by Block ($F_{(15,150)}=2.68$, $p<0.01$) but not Hand ($F(1,10)=.10$, $p<0.76$) or Hand by Block ($F(15,150)=1.25$, $p<0.24$). In general this trend is for peak acceleration to be reached slightly later in the movements in the later portions of the marathons.

Figure 3.6 Mean path length as a function of Hand and Block.

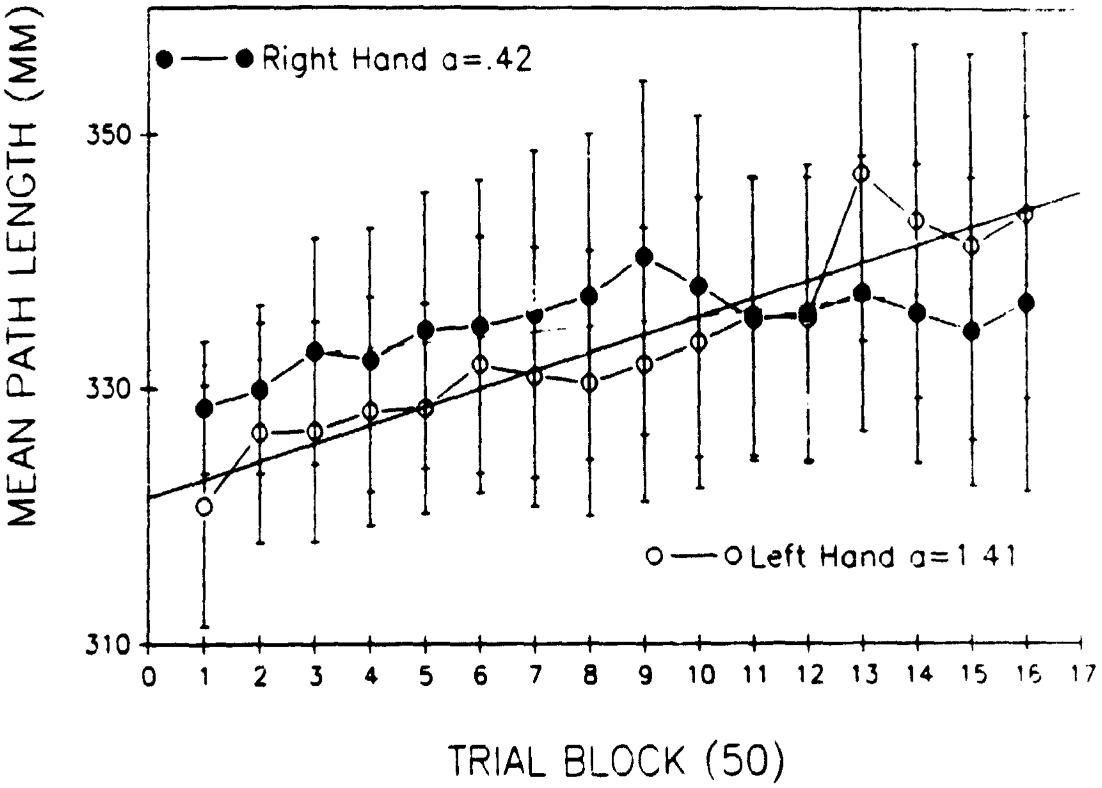

Right Hand a=.42
Left Hand a=1.41
MEAN PATH LENGTH (MM)
310
330
350
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Figure 3.7 Mean peak velocity as a function of Hand and Block.

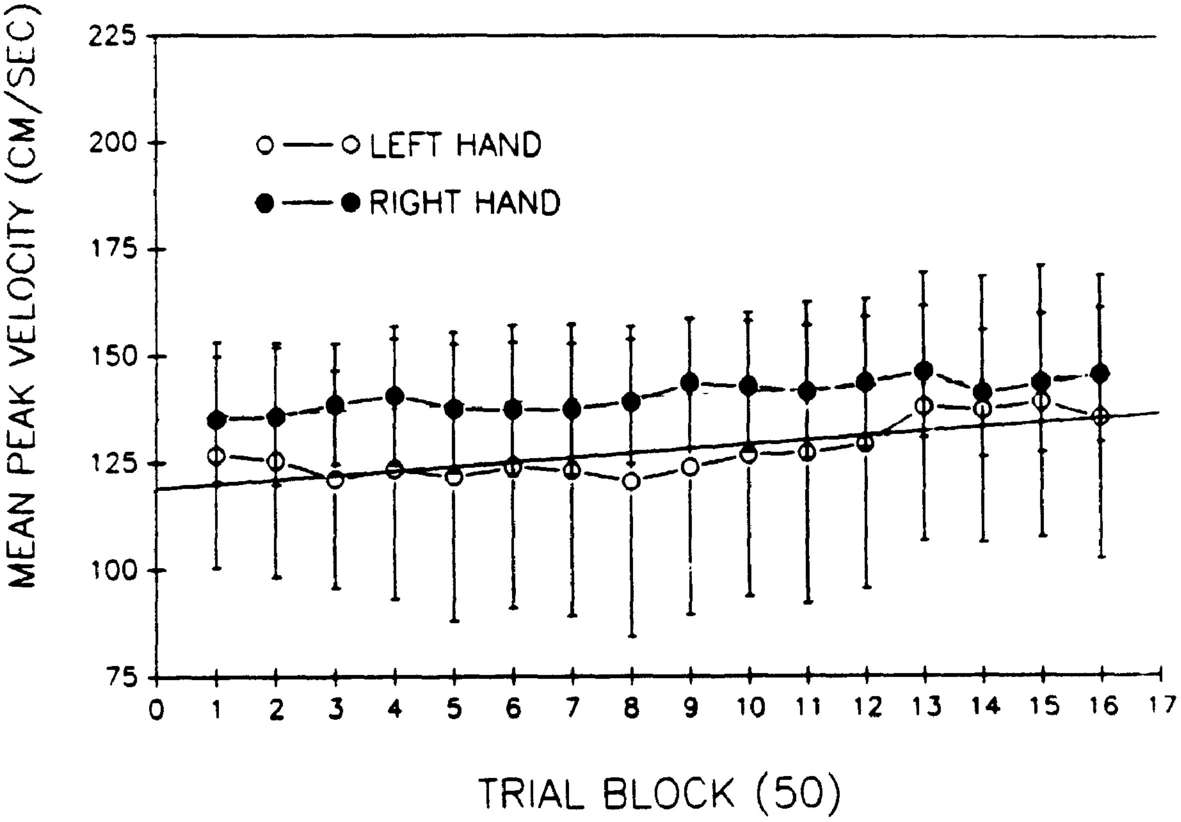

MEAN PEAK VELOCITY (CM/SEC)
225
200
175
150
125
100
75
○—○ LEFT HAND
●—● RIGHT HAND
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Figure 3.8 Mean time to peak velocity as a function of Block collapsed across hands.

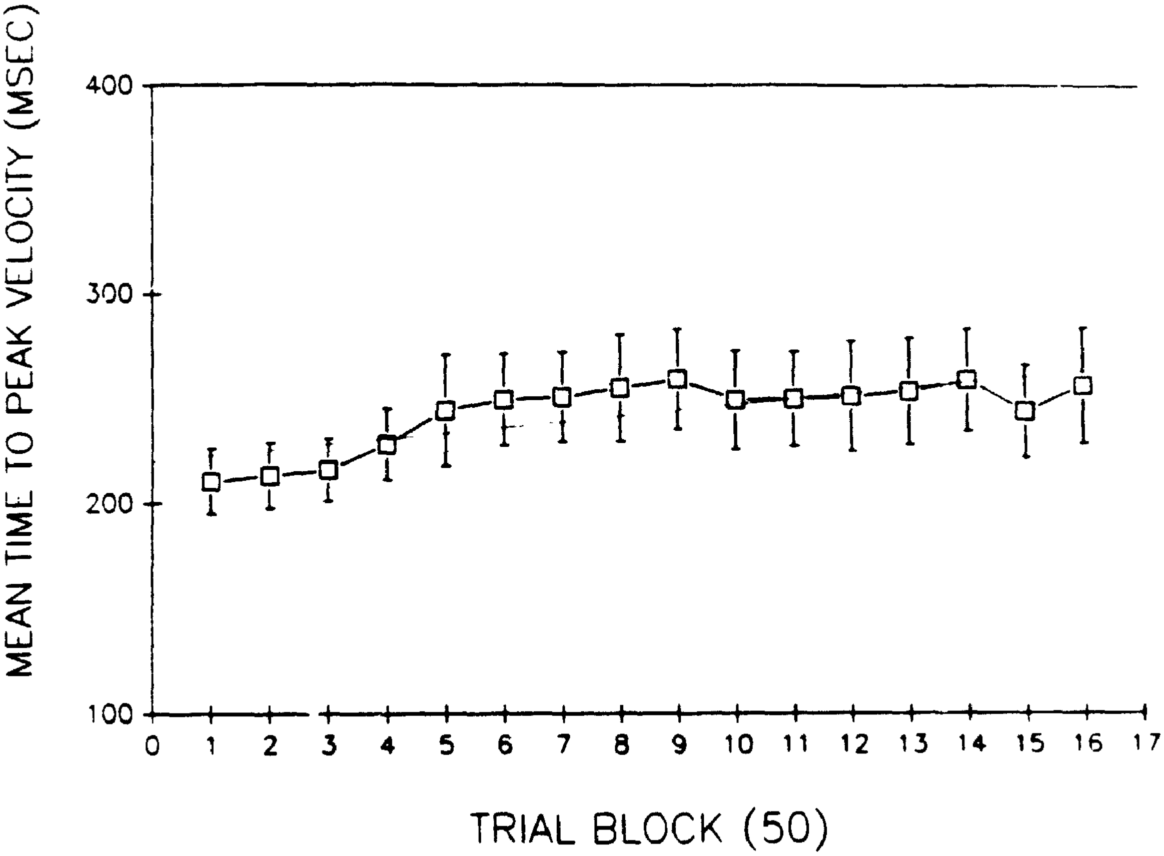
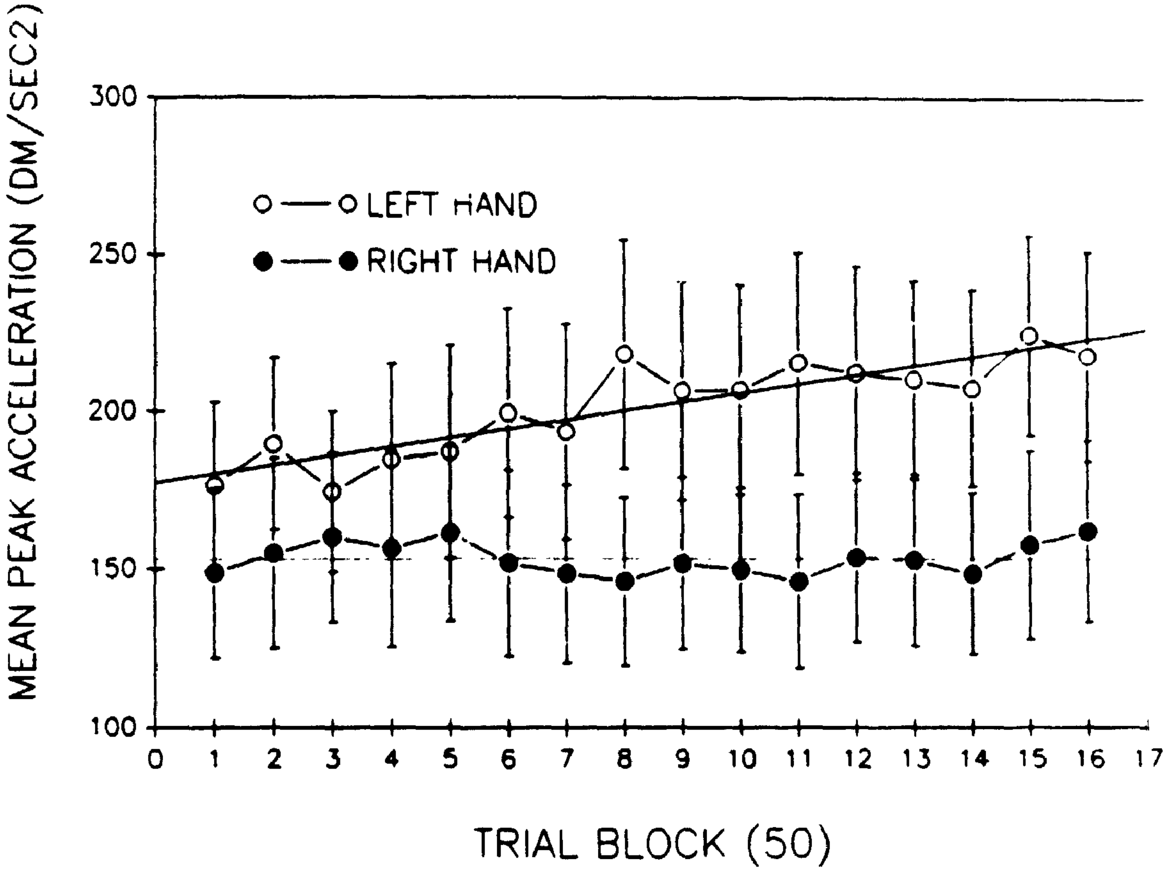

MEAN TIME TO PEAK VELOCITY (MSEC)
400
300
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Figure 3.9 Mean peak acceleration as a function of Hand and Block.


MEAN PEAK ACCELERATION (DM/SEC2)
300
250
200
150
100
○—○ LEFT HAND
●—● RIGHT HAND
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)

Significant hand differences ($F_{(1,10)}=0.16$, $p<0.70$) or a Hand by Block interaction ($F_{(15,150)}=0.73$, $p<0.75$) were not found in the peak deceleration data. A block effect ($F_{(15,150)}=5.46$, $p<0.0001$) was statistically significant and suggests an increase in peak deceleration as marathons progressed (Figure 3.10--note that decreasing slopes indicate greater rate of deceleration). Percentage time to peak deceleration was not affected by Hand ($F_{(1,10)}=4.83$, $p<0.53$), Block ($F_{(15,150)}=1.57$, $p<0.88$) or the interaction ($F_{(15,150)}=1.09$, $p<0.37$).

Accuracy Measures

Constant error

Given Jeannerod's comments on the viability of visuomotor calibration processes and the constant errors obtained in Experiment 1, changes in endpoint accuracy are of particular importance. Figure 3.11 shows mean constant error as a function of Hand and Block. Repeated measures ANOVA reveals a main effect of Hand ($F_{(1,10)}=19.02$, $p<0.001$) and a Hand by Block interaction ($F_{(15,250)}=2.38$, $p<0.004$). Errors for the left hand are rightward and asymptote after approximately 200 trials (although there is considerable inter-subject variability). A similar asymptote is seen in right hand constant error, but these means show consistent leftward deviations from true target position. The Hand by Block interaction is difficult to interpret but may have resulted from the greater separation of the two functions after the first few blocks of trials. For this reason, an additional analysis of variance was performed, comparing the two hands across the first five blocks of trials only, as was done with duration data (see above). This analysis revealed a significant Hand ($F_{(1,10)}=15.76$, $p<0.003$) and Hand by Block effect ($F_{(4,40)}=7.90$, $p<0.0001$). The differences between the two hands across blocks is largely a function of the sign in the constant errors; when left-handed constant errors have the sign changed, these two effects are no longer significant (Hand, $F_{(1,10)}=0.83$, $p>0.05$; Hand by Block $F_{(4,40)}=1.26$, $p>0.05$). These results do not support the hypothesis that the two hands might show differential increases in constant errors across the marathons.

Figure 3.10 Mean peak deceleration as a function of Hand and Block.

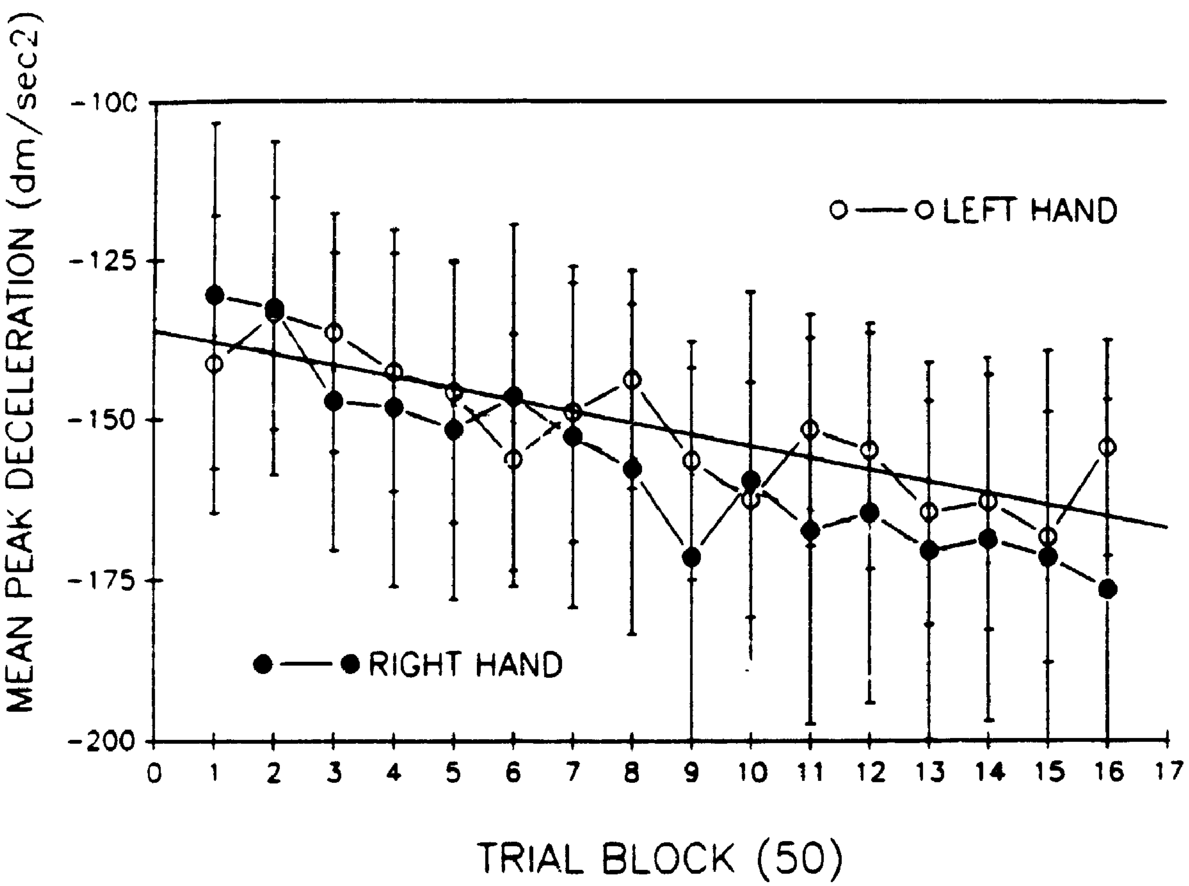
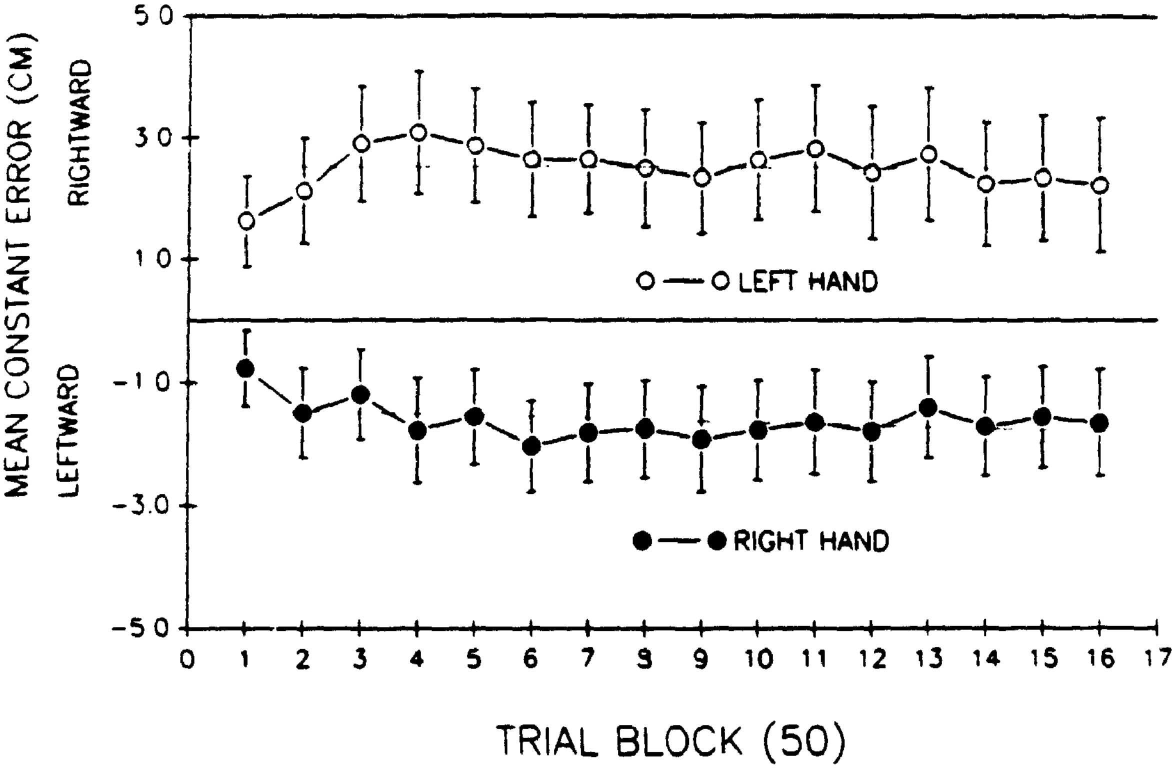

MEAN PEAK DECELERATION (dm/sec2)
-100
-125
-150
-175
-200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)
○—○ LEFT HAND
●—● RIGHT HAND

Figure 3.11 Mean constant error as a function of Hand and Block.


MEAN CONSTANT ERROR (CM)
RIGHTWARD
LEFTWARD
5 0
3 0
1 0
-1 0
-3.0
-5 0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)
O — O LEFT HAND
● — ● RIGHT HAND

Absolute error

Unlike in Experiment 1, the pattern of results for absolute error is not identical to that found for constant error (see Figure 3.12): No effect of Hand ($F_{(1,10)}=0.57$, $p<0.48$) or Hand by Block ($F_{(15,150)}=0.45$, $p<0.96$) were elicited. However, it should be noted that in the majority of blocks the right hand was producing smaller mean absolute errors than the left. A significant effect of Block ($F_{(15,150)}=4.95$, $p<0.001$) is consistent with a gradual increase in this measure over time.

Variable error

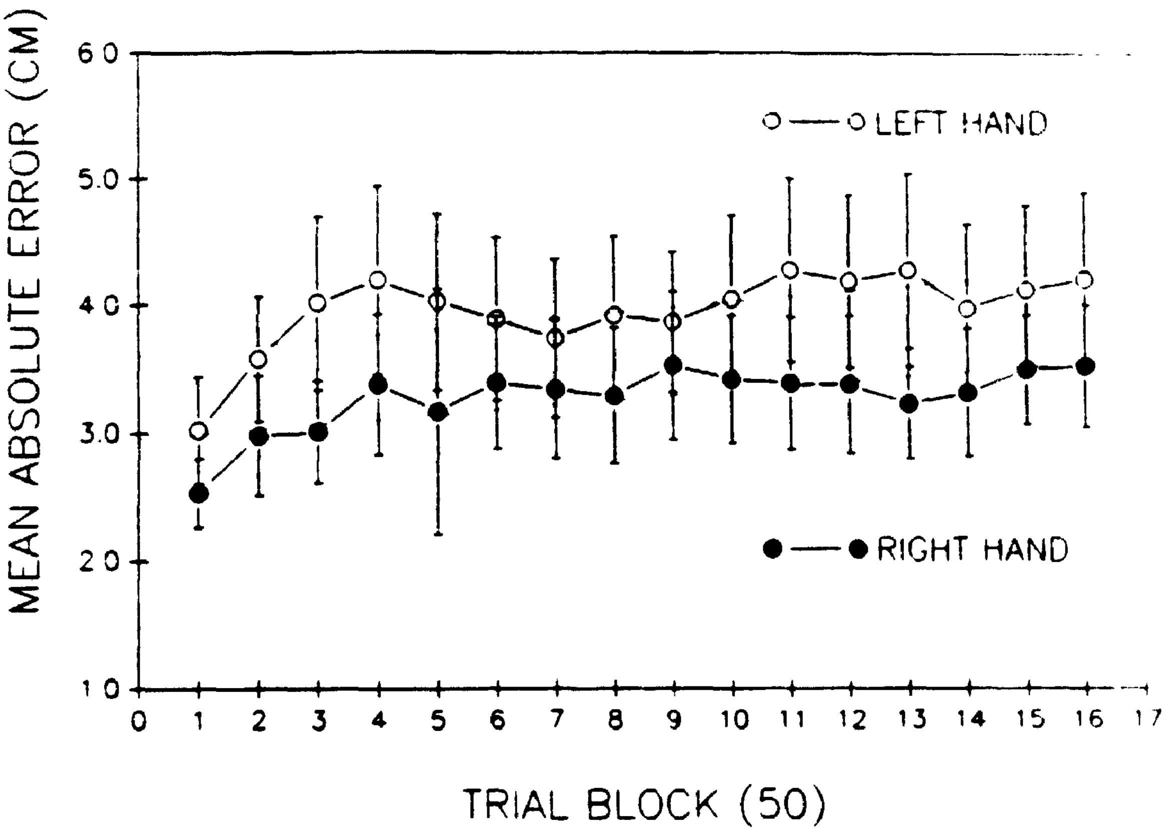
No significant effects of Hand, Block or the Hand by Block interaction were found.

Summary of Univariate Analyses.

Shorter movement onset times were found in the left hand relative to the right, and shorter movement durations in the right hand relative to the left. The left hand advantages in onset time did not change over the course of the marathons, but in the duration data, the right hand seemed to make movements of slightly shorter durations as the marathons progressed. As in Experiment 1, constant errors were somewhat larger in the left hand relative to the right, but the difference between the hands was primarily due to the sign difference, given that absolute error did not differentiate between hands.

Movement onset times decreased in both hands as the sessions progressed. Total times (onsets and durations combined) mimicked this tendency (although durations seem to decrease in the right hand only). Movement length tended to increase as a function of block, and this trend may have been greater in the left hand relative to the right. Peak velocities increased slightly and in an equivalent manner in the two hands (again, the trend was for this effect to be greater in the left hand, but the interaction was not significant). Peak accelerations increased (slightly more in the left hand), and occurred slightly later in the reach during the later blocks of the marathon. Peak decelerations also tended to increase as a function of trial block. (Duration seems to be a controlled

Figure 3.12 Mean absolute error as a function of Hand and Block.


MEAN ABSOLUTE ERROR (CM)
6.0
5.0
4.0
3.0
2.0
1.0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRIAL BLOCK (50)
○—○ LEFT HAND
●—● RIGHT HAND

variable; in spite of longer path lengths durations did not change as a function of trial block).

3.3.2 *Ipsilateral Advantage Ratio Analyses*

These ANOVAs were performed in order to examine the stability of ipsilateral movement advantages found for movement durations, onset times, and peak velocities seen in previous investigations and experiment 1. These percentage scores were originally devised by Harshman, who describes their statistical properties in Harshman and Lundy (1988). Positive values reflect a percentage increase in a measure for ipsilateral movements relative to contralateral movements.

Movement onset times and durations.

Ipsilateral advantage scores in movement onset times obtained in this sample were inconsequential (approximately .5% overall in each hand) and were not significantly different between hands ($F_{(1,10)}=0.01$, $p<0.93$) or across blocks ($F_{(15,150)}=1.14$, $p<0.32$). The Hand by Block interaction was also not significant ($F_{(15,150)}=0.76$, $p<0.72$). Although Fisk and Goodale report ipsilateral onset advantages, other investigations suggest that this advantage is less robust than that seen in movement duration and peak velocity data.

Movement duration advantages were consistent across blocks ($F_{(15,150)}=1.11$, $p<0.35$) and between hands ($F_{(1,10)}=1.41$, $p<0.26$) at approximately 5-7% of total movement duration. Again, no Hand by Block interaction was obtained ($F_{(15,150)}=0.92$, $p<0.54$).

Peak Deceleration and Percentage Decelerating.

Peak deceleration difference scores were not significantly different between hands (Right 3.65%, Left 3.86%; $F_{(1,10)}=0.01$, $p<0.91$) or blocks ($F_{(15,150)}=0.62$, $p<0.86$) and the Hand by Block interaction was also non-significant ($F_{(15,150)}=1.54$, $p<0.10$). Percentage decelerating did not produce consistent ipislateral/contralateral differences (1.67% overall) but a trend towards a Hand effect was found ($F_{(1,10)}=4.25$, $p<0.07$) with a trend towards the left hand spending slightly more of the movement decelerating in its own hemispace (left hand=3.8%, right hand=-0.49%). There was no effect of Block ($F_{(15,150)}=1.06$, $p<.40$) or an interaction between hand and block ($F_{(15,150)}=1.18$, $p<0.30$) in the percentage deceleration data.

Peak velocity.

A significant effect of Hand was found in the analysis of peak velocity ipsilateral advantage scores ($F_{(1,10)}=6.66$, $p<0.027$), showing larger ipsilateral advantages for the right hand (8.75%) relative to the left (2.44%). This effect did not interact with Block ($F_{(15,150)}=1.35$, $p<0.18$) and there was no main effect of Block on this measure ($F_{(15,150)}=0.80$, $p<0.67$).

3.3.3 *Midline Analyses*

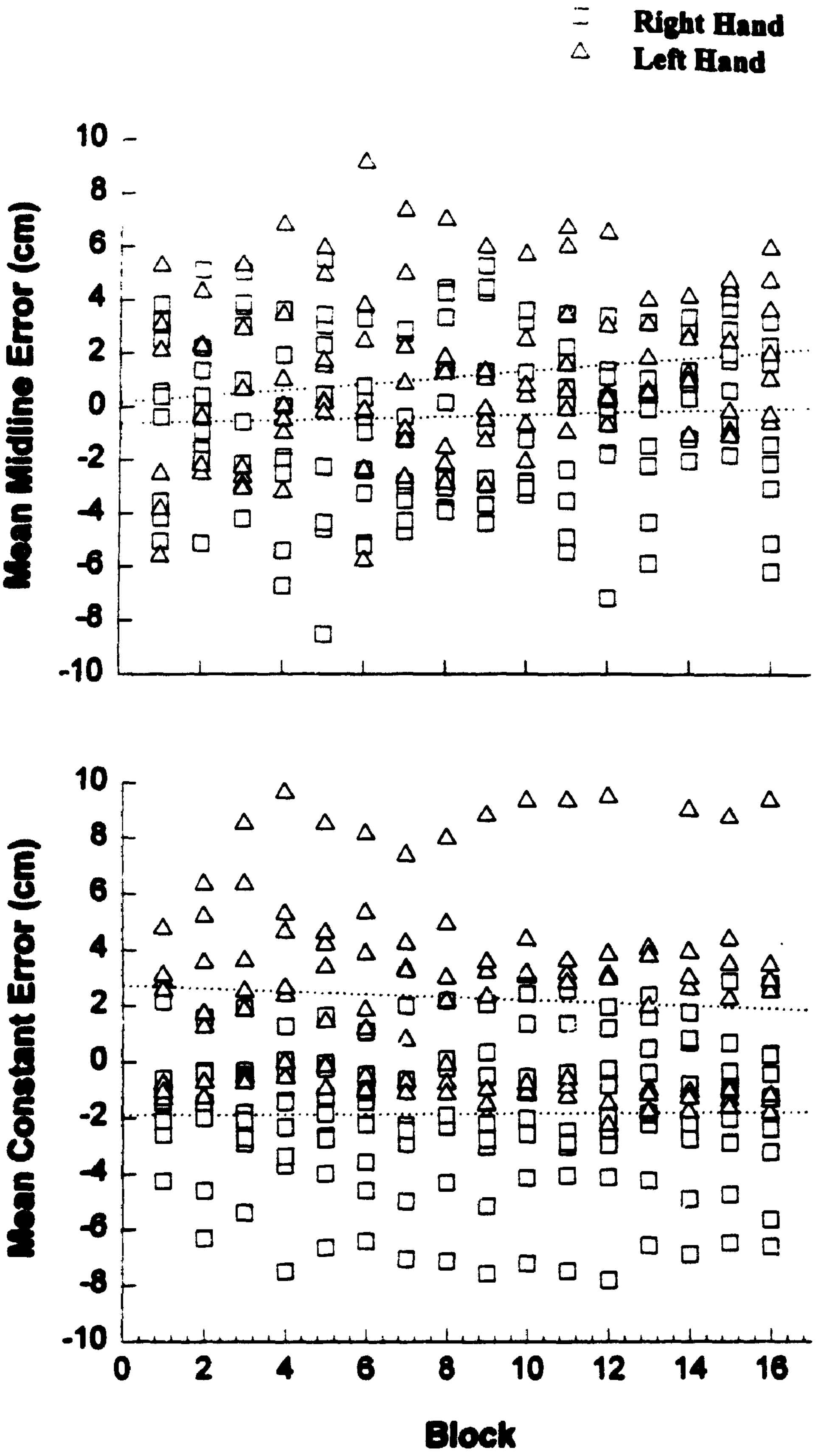
Midline errors were calculated by comparing each midline trial y-coordinate to the position supplied by the subject for the central target calibration trial (which is aligned with the centre of the chinrest and the start position). Individual midline trials are plotted in Figure 3.13 for 9 right hand marathons (open squares) and 7 left hand marathons (filled triangles). Mean constant errors from the same subjects appear in the lower part of the same figure. Pearson product moment correlation coefficients were calculated between mean constant error and midline error. For both hands, these two measures were significantly correlated: Right hand $r=.51$, $p<0.01$; Left hand $r=.69$, $p<0.01$). Excluding the subjects for whom no left hand midline data were available in the right hand correlation drops the value slightly (Right hand $r=0.495$, $p<0.01$).

Many of the largest errors in the left hand (in CE especially) were produced by two subjects, so the correlation was recalculated excluding subject no. 6 (see Table 3.1). Even with data from only 6 remaining subjects, the correlations remain significant ($r=.46$, $p<0.01$ for the right hand and $r=.46$, $p<0.01$ for the left hand).

Table 3.1 Mean constant and midline error as a function of Subject and Hand (all measures in cm; +=rightward).

Subject	Left Hand Constant error	Left Hand midline err	Right Hand Constant Error	Right Hand midline err
01	3.18	0.15	-0.76	0.95
02	-1.09	-0.82	-2.13	1.82
03	8.69	NA	-2.49	-2.61
04	4.45	1.79	-0.22	-1.26
06	8.30	5.45	0.21	3.26
08	-1.08	-0.72	2.04	2.22
09	-0.50	NA	-4.05	-3.01
10	-0.09	-1.52	-6.70	-2.42
11	2.90	3.79	-2.49	-1.67
Mean (7 subjects)	2.37	1.16	-1.96	-0.30

Figure 3.13 Mean midline error (top) and constant error as a function of Hand and Block. Data from 9 right hand marathons and 7 left hand marathons.


□ Right Hand
△ Left Hand
Mean Midline Error (cm)
10
8
6
4
2
0
-2
-4
-6
-8
-10
Mean Constant Error (cm)
10
8
6
4
2
0
-2
-4
-6
-8
-10
0
2
4
6
8
10
12
14
16
Block

3.3.4 *Post marathon hand-visible trials*

Given that systematic shifts in constant error (analogous to prism adaptation shifts) did not occur, it seemed less likely that evidence of recalibration in any kinematic measure would be seen in the post-marathon block of hand-visible trials. The sample size for this analysis is even smaller than that for the marathon study itself, so interpretations have be made cautiously. Nevertheless, some changes in movement kinematics were obtained between the trials at the end of the marathon and the first five trials made in hand-visible conditions (see Table 3.2 and 3.3). Not surprisingly, absolute error decreased substantially in the first five trials of the hand-visible post marathon block relative to the last five trials in block 16 of the marathon. In these trials, of course, visual information about limb position and the visual surround was available (although with 400 msec presentation total movement times would still preclude much useful feedback about the terminal position of the limb relative to the target). This attenuation of terminal error was also seen in the constant error, although little gains were to be made in this measure for the right hand. Movement onset times decreased in the right hand only, while duration of movement decreased in hand-visible conditions for the left hand only. The movement paths were somewhat shorter in both hands in the post-marathon hand-visible block. Time to peak velocity decreased in the left hand in hand-visible conditions to levels similar to the right hand in both blocks.

3.4 **Discussion**

Analysis of the constant, variable and absolute errors did not suggest any appreciable difference across blocks in either hand. As in Experiment 1, the left hand was dramatically right-shifted in its movement endpoints. This shift did not change over the course of the marathons. Unlike in Experiment 1, a small shift was seen in the constant error data in the right hand. It was shifted leftward of true midpoint position, and this trend did not increase over the course of the marathon. Although these shifts are remarkably variable between subjects (as endpoint errors are in most aiming movement

Table 3.2 Summary of correlated t-tests for the right hand trials, last five trials of Block 16 vs. first five trials of Block 17.

DV	Block 16 (dark)	Block 17 (light)	Obtained t	p value
Movement onset (msec)	279	248	2.08	.043
Duration (msec)	422	410	1.20	.235
Length (cm)	327	307	2.97	.005
Constant Error (cm)	-1.22	-1.36	0.32	.75
Absolute error (cm)	3.70	1.85	6.77	.001
Peak velocity (cm/s)	145	145	.08	.94
Time to PV (msec)	25.6	22.3	1.33	.19
Peak accel (dm/sec^2)	36.4	38.6	-.41	.69
%time to peak accel	27.5	23.3	1.44	.16
Peak decel (dm/sec^2)	-18.1	-17.4	-0.66	.51
% time to peak decel	74.2	74.3	-.03	.98

Table 1.3 Summary of the correlated t-tests for the left hand trials, last five trials of Block 16 vs. the first five trials of Block 17.

DV	Block 16 (dark)	Block 17 (light)	Obtained t	p value
Movement onset (msec)	245	243	.16	.88
Duration (msec)	487	415	3.87	.001
Length (cm)	340	310	4.04	.001
Constant Error (cm)	2.75	-0.27	4.55	.001
Absolute error (cm)	4.16	1.65	5.05	.001
Peak velocity (cm/s)	137	128	1.90	.064
Time to PV (msec)	31.0	24.1	3.35	.002
Peak accel (dm/sec^2)	44.2	37.7	1.17	.25
%time to peak accel	27.5	25.3	0.95	.345
Peak decel (dm/sec^2)	-15.8	-14.7	-1.34	.189
% time to peak decel	74.6	79.2	-1.15	.26

studies, see also Zipser, 1992), I have to conclude that there is no evidence to suggest that the constant errors of the pointing movements drift over time. Although some replication of this finding is necessary, at present the data suggest that in the first 50 trials whatever changes in the relationship between visual and proprioceptive systems (see the general discussion of the issue of proprioceptive and visual "maps") have already taken place and are not affected by further movements made in the absence of visual feedback. It also seems quite unlikely that these shifts are some sort of artifact related to instability of the WATSMART workspace, since Block 17 data reveals increased movement accuracies as measured with our calibration and measurement procedures.

In spite of large variance in the data, ipsilateral movement advantages were elicited for movement durations, peak velocities, and percentage of the movement spent in deceleration. Although there is the suggestion that these advantages (or perhaps contralateral disadvantages) may be larger in the right hand for two of the three measures, in none of the three variables was a Block effect obtained (or Hand by Block effects that are not explainable as variation about a stable central tendency). The relative stability of these advantages suggests that they are not related to visual feedback utilization in any obvious way. That is, since they are not attenuated or enhanced as the marathons continue, it is unlikely that hemispatial effects are due to differential utilization of visual feedback. If ballistic vs. feedback-driven explanations of hand movements are valid, it seems reasonable to expect some change in hand-hemispace interaction as a function of trial block. Instead, the data are at least suggestive of a motor programming type of explanation of the kinematic differences across the hemispace. This question will be addressed in the final experiment reported in the thesis.

I know of no other study which has attempted to address the "mapping" issue as stated by Jeannerod (see introduction). Although there have been some studies of movements made with an extended number of trials, these have tended to utilize tasks where movement times are strictly controlled, the subject uses a hand-held stylus, etc. (e.g., Proteau et al., 1987; Abrams & Pratt, 1993). Proteau and colleagues (1987) have maintained that extensive practice in one type of visual feedback condition biases the subjects towards performance in that exact condition. That is, performance on their task in a "no visual feedback" (during acquisition) was actually detrimentally affected by adding visual feedback in a test phase. Of course, such task-specific training may indeed result in a transient reduction in level of performance when additional information is made available to the subject; it certainly would have been surprising if the same was true of my subjects in hand-visible reaching after completion of a marathon.

The mean constant errors seen in this study do not appear to increase over the course of the marathons. This lends support to the suggestion made in the discussion of the previous chapter (see Figure 2.14) that the errors are not related in any obvious way to the period of time that visual information has remained unavailable. This finding does little to help explain why these directional errors occur at all in hand-invisible reaching. Several static alignment studies report effects that suggest some relationship exists between hand used and hemispace and directional error. For example, Jeannerod and Biguer (1989) report that when right handers have to point straight ahead in the dark, when using the right hand they show a small but statistically significant bias to the left of their true sagittal midline. No such bias was found in the left hand of these subjects. In a second study, when subjects were required to direct their gaze to fixation points to the right or left of their body midline, perceived egocentric midline deviated to the same side. A similar report has been made by recently by Chokron and Imbert (1993). Nevertheless, other studies have described somewhat different patterns of directional error in normal subjects in the two hands and two (or three) hemispatial positions. The norm seems to be large intra-subject variability, and this study is no exception to that general rule.

Of course, some of the effects obtained in this study might have to do with the short target duration that was used; perhaps on trials with longer reaction times the primary and corrective saccades are not completed quickly enough to allow foveation of the target. Jeannerod et al. (1965; cited in Jeannerod, 1988) recorded saccades made in the dark towards previously learned target locations. They found hypermetric saccades--subjects tended to overshoot target positions. Rightwards overshooting in ipsilateral space for the right hand and leftwards overshooting in the left space for the left hand could result from hypermetric saccades, but this hypothesis presupposes that saccades are asymmetrically regulated depending upon which hand makes the subsequent aiming movement. There is some suggestion that that is the case in movement onset times of saccades, depending on whether or not a given eye movement is coupled with an ipsilateral or contralateral arm movement (Fisk & Goodale, 1985). However, I found no correlation between the absolute errors of movements and movement reaction times ($r=0.045$, $p>0.05$), suggesting that short target duration is unlikely to be a major factor in determining endpoint error.

Unlike the suggestion that eye movements to disappearing targets may be part of the explanation is the idea that constant errors might help manual control systems achieve better terminal accuracy under normal (i.e., hand and target visible) conditions. Several authors have argued that error correction is facilitated if movement amendments are in the same direction as the original large- amplitude movement (Carlton & Carlton, 1987; Quinn & Sherwood, 1983; but see Jakobson & Goodale, 1989). Leftward shifting in the right hand and rightward shifting in the left hand would result in target undershooting for ipsilateral targets, and under normal conditions, when visual feedback is available, might indeed facilitate error correction in the "advantaged" hemispace. If such a suggestion is true, it is surprising that such a mechanism seems invariant in spite of the absence of visual feedback for such an extended period of time. In this study, several measures related to the velocity profile did indeed show small but significant changes over time, but no evidence for any change in movement undershooting or overshooting is suggested by the constant error data. Such effects might be contained within this rather variable data, but certainly seem unlikely to account for all of the variance in constant error. Additionally, the lack of ipsilateral aiming movement advantages in constant error do not suggest undershooting in each hands' own hemispace, where a movement undershooting would produce the leftward and rightward errors in ipsilateral space for the left and right hands, respectively.

CHAPTER 4 - EXPERIMENT 3: ANTIPOINTING.

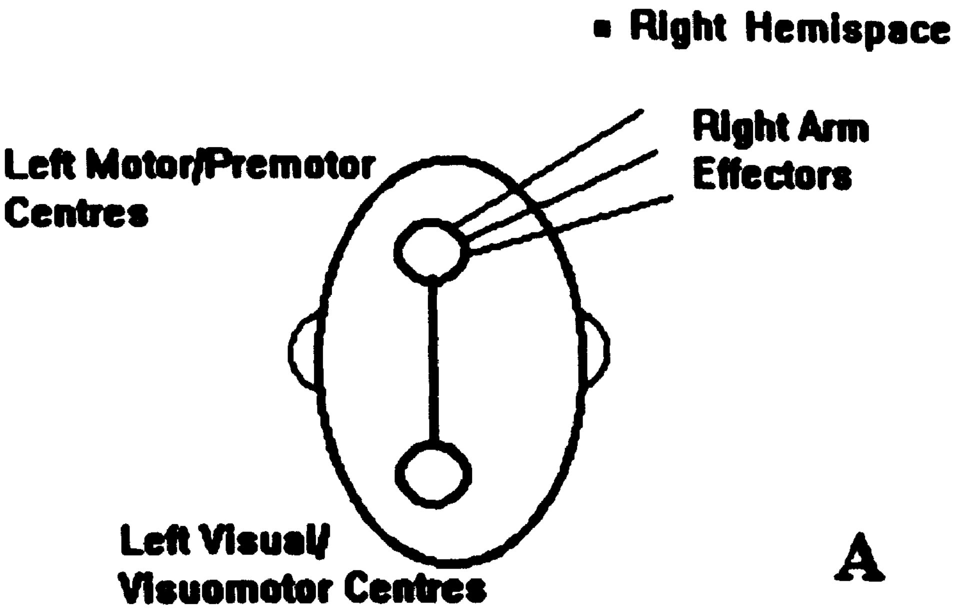
Abstract

In the final experiment of this thesis, 26 right-handed subjects were required to reach to single targets in one block of trials and to reach to the mirror symmetrical position on the side opposite of target presentation (relative to a centrally-placed fixation light) in a second block of trials. This manipulation was designed to determine if hemispatial differences in measures like duration and peak velocity were related to the side of stimulus presentation or the side of subsequent motor response. As predicted by Fisk and Goodale (1985), the side of subsequent motor response seemed to determine ipsilateral/contralateral differences in duration, peak velocity and the percentage of the movement spent in deceleration. Subsidiary hypotheses regarding attenuated right-hand advantages in antipointing relative to pointing, and sighting dominance as playing a role in the pattern of constant errors in hand-invisible reaching, were not supported by the obtained data.

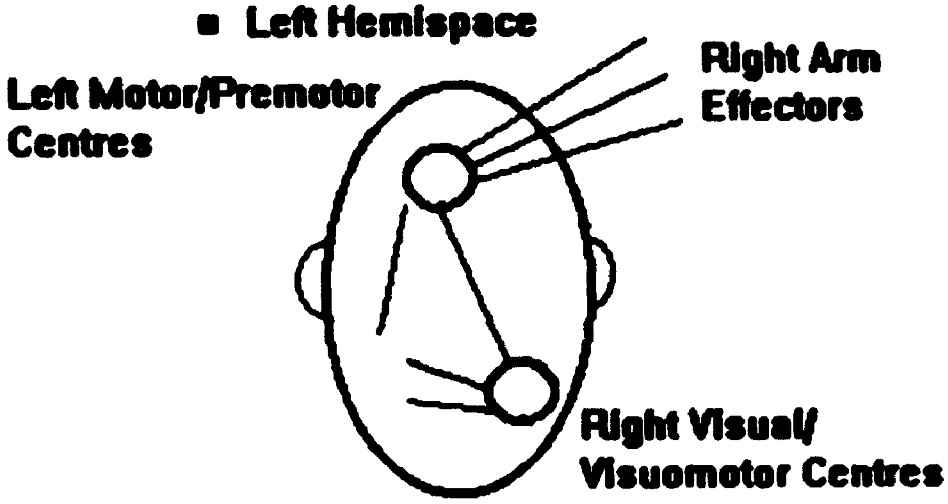
4.1 Introduction

Experiments 1 and 2 replicated many of the typical hemispatial advantages found in movements made to ipsilateral targets (Carson et al., 1992; Fisk & Goodale, 1985; van Der Staak, 1975). Such targets are processed initially in the same hemisphere as the motor and somatosensory cortices with direct connections to the reaching hand. The advantages for ipsilateral targets may be related to the side of stimulus presentation or the side of the motor response. In none of the past experiments, however, was the side of stimulus presentation dissociated from the side of the required motor response. The typical ipsilateral movement advantages for movement onset, peak velocity, duration and accuracy can be explained in two alternative ways. Fisk & Goodale (1985) offered the suggestion that kinematic advantages stem from the fact that, if the programming of the limb movement is largely contralateral, then visual information about targets which are contralateral has to cross the corpus callosum to reach the motor programming centres necessary to generate the movement (Fig 4.1). On the other hand, the effect might not

Figure 4.1 Ipsilateral targets are processed in the same hemisphere which processes the initial visual stimulus. (A) A right-sided target and the left hemisphere. (B) A left-sided target and the left hemisphere. Information for the left motor/premotor may cross the callosum in a number of different locations.


Right Hemispace
Left Motor/Premotor Centres
Right Arm Effectors
Left Visual/ Visuomotor Centres

A


Left Hemispace
Left Motor/Premotor Centres
Right Arm Effectors
Right Visual/ Visuomotor Centres

B

have to do with processing the visual input per se, but instead be a by-product of some sort of biomechanical constraints on contralaterally directed movement. Fisk and Goodale suggest that this explanation might be too simple: In their study the more contralateral targets resulted in movements with higher peak velocity than less eccentric contralateral target locations (although it should be noted that they do not report normalizing for distance, which may be relevant because peak velocity scales for movement distance, and their more peripheral targets were more distant). To date, no study has investigated differential muscle activity in ipsilateral versus contralateral movements (identical in distance and direction from the body midline) to identify differential motor programming requirements. Nevertheless, movement kinematics might reveal whether or not input or output stages of the visuomotor transformation are crucial, by dissociating the side of input from the side of response.

The present experiment dissociates stimulus position from motor response by requiring subjects in two of four blocks of trials to reach to the mirror symmetrical position on the opposite side of the fixation point from the presented stimulus position ("antipointing", after Guitton et al.'s 1985 "antisaccades"). This task should allow for better description of the relative contributions of processing stimulus location from executing motor responses. Particular emphasis in this study will be placed on reaction time, movement time, and movement accuracy -- kinematic markers which often show advantages for ipsilateral movements.

An additional advantage of this task is that, arguably, it may rely more heavily on visuospatial processes, and thus may engage the right hemisphere more than a simple pointing task. If the right hemisphere does contribute more when a subject is antipointing relative to pointing, a Hand by Task interaction like that obtained in Experiment 1 should be found, such that right hand advantages in pointing should be attenuated in antipointing.

A final goal of this experiment was to examine a potential contribution of sighting dominance to the pattern of constant errors produced in hand-invisible conditions in Experiment 1 and Experiment 2. The sighting eye has been linked to saccadic control by Money (1972), and Foley (1977) and Foley and Held (1972). These investigations have implicated sighting dominance as an important factor in the pattern of constant errors in reaching without vision of the limb. Similarly, constant errors might be explainable by saccadic errors in each hands' own hemispace, and might be exacerbated or attenuated in subjects who sight with their left rather than their right eye.

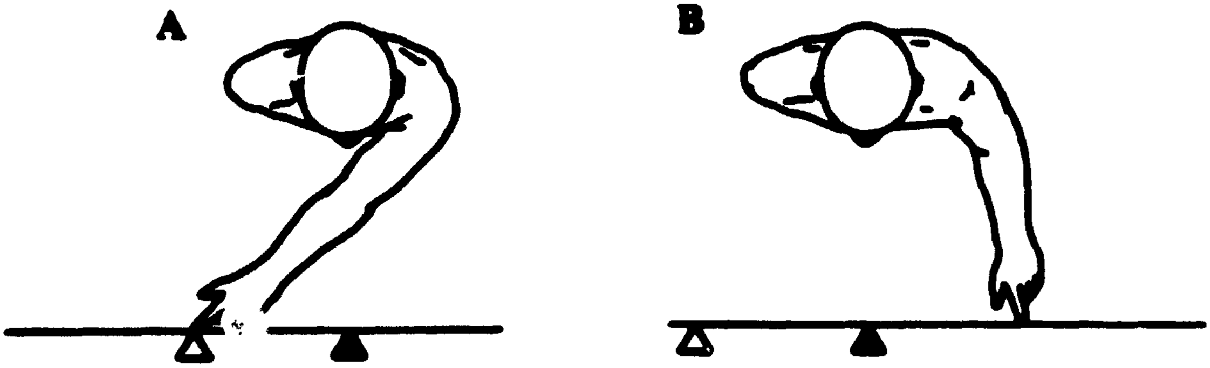
4.2 Methods

For this experiment, new calibration software from Northern Digital allowed for recording of mean root square error for any given calibration of the workspace. This value represents measurement error of the positions of IREDs in a 24-IRED calibration cube. For this study, all sessions had a mean root square error of less than 2.00 mm from a minimum of 21/24 IREDs.

Subjects

Subjects were 26 graduate, senior undergraduate, and research assistants from the University of Western Ontario. Subjects were male, right-handed, and had a mean age of 26.5 (range 22-32 years of age) at time of testing. In this experiment, sighting dominance was assessed by requiring subjects to fixate (binocularly) a point target approximately 5-6 metres distant. After acquiring the target, subjects were required to bring together two floppy disks held at arms length until they were viewing the target through a narrow slot defined by the disks. Subjects then closed one eye (or the experimenter covered it as required) and then the other. Occlusion of the sighting eye eliminated viewing of the target while occluding the other eye did not. This procedure was repeated at least two times before both test sessions. Subjects were subsequently assigned to right sighting or left/anomalous sighting groups. For this analysis, 12 subjects composed the left/anomalous group, the remaining 14 were right sighters. It should be noted that due to the higher proportion of right-sighting subjects in the general population (Porac & Coren, 1976), to achieve approximately equal sample sizes this sample includes a much higher proportion of non-right sighters than a random sample of right-handers would.

Figure 4.2 The antipointing task required the subject to reach to a mirror symmetrical position on the opposite side of fixation (B) and was contrasted with pointing directly to the target.


A
B

Procedure

Subjects were positioned as comfortably as possible in the chinrest and the black glove with the two attached IREDs was worn as before. In this study, the central target was used as a fixation light and two additional targets were added to each hemispace. As in Experiment 2, target presentation was restricted to a 400 msec period, again intending to minimize potential visual feedback during hand-invisible reaching. Additional light restrictions in the room, coupled with shorter time periods for subjects to dark adapt (relative to Experiment 2) allowed for subjects to be tested without wearing the goggles.

The two inner-most targets were 3 cm away from the fixation light (5.4 degrees); the additional three targets in each hemispace were 6 cm apart (16.1, 26.9 and 37.6 degrees from the fixation light). Eight calibration trials were collected as in Experiments 1 and 2. Subjects reached in four forty-trial blocks: once in each combination of hand visible/invisible and pointing/antipointing. For the antipointing trials, subjects demonstrated their comprehension of the task by showing what would be correct movements to positions manually indicated by the experimenter. Order of blocks was completely randomized. At the beginning of each block, subjects received eight practice trials prior to data collection. During each block, subjects were frequently reminded of the appropriate task for that block. Subjects were also instructed to report any instructional set errors (i.e., antipointing during a pointing block or vice versa) for subsequent deletion of those trials. Subjects used one hand in each session, and sessions were separated by at least two days.

Data Analysis

Data were analyzed much as in Experiment 2, with the exception that, for antipointing trials, accuracies were calculated relative to the symmetric target position on the opposite side of fixation. For this analysis, means were collapsed across all four targets on the same side of the fixation light. Because target position was no longer a factor, and the two sides were balanced for target distances, no normalization was carried out to control for the longer target distances of the more peripheral targets. Repeated measures ANOVAs with Hand, Hand visibility, Task, Sighting dominance (right eye dominance vs. anomalous dominance), and Side (left vs. right sided *target presentation*) were performed.

4.3 Results

Means and standard errors of the kinematic markers appear in Tables 4.1 and 4.2.

Movement onset time.

Mean movement onset time advantages were found for the left hand (306 msec) relative to the right (338 msec; $F_{(1,24)}=7.71$, $p<0.01$) and hand-visible reaches (297 msec) relative to hand-invisible reaches (347 msec; $F_{(1,24)}=110.48$, $p<0.0001$). Not surprisingly, reaction times for pointing movements were shorter (299 msec) than for the antipointing movements (344 msec; $F_{(1,24)}=27.06$,$p<0.0001$). A main effect of Side was also found; left-sided *targets* (318 msec) produced shorter movement onset times than right- sided *targets* (326 msec; $F_{(1,24)}=24.45$, $p<0.0001$). A Hand visibility by Side interaction($F_{(1,24)}=10.4$, $p<0.004$) suggested that this left-sided advantage may have been larger in hand-invisible conditions (Figure 4.3; hand-visible left side < hand-visible right side, $q=3.38$,$p<0.05$; hand-invisible left side < hand-invisible right side, $q=9.84$, $p<0.01$).

If movement onset time advantages for ipsilateral targets were dependent to any extent on factors related to the arm movement rather than target position per se, then an interaction between Hand, Task and Side should have occurred, such that for antipointing the usual "ipsilateral faster than contralateral" relationship would have been reversed (or attenuated if side of stimulus and side of motor response both play a role). This interaction was significant ($F_{(1,24)}=5.47$, $p<0.03$). But since the pointing data did not provide any evidence for ipsilateral target-movement onset advantages, it is impossible in this dataset to see any evidence of attenuation of such advantages in the antipointing trials. Movement onset time seems to be a variable where ipsilateral advantages are not always obtained (cf. Carson et al., 1992; M. Harvey, personal communication; Fisk and Goodale, 1985, Experiment 2 -- except in the condition where central fixation was maintained throughout the movement).

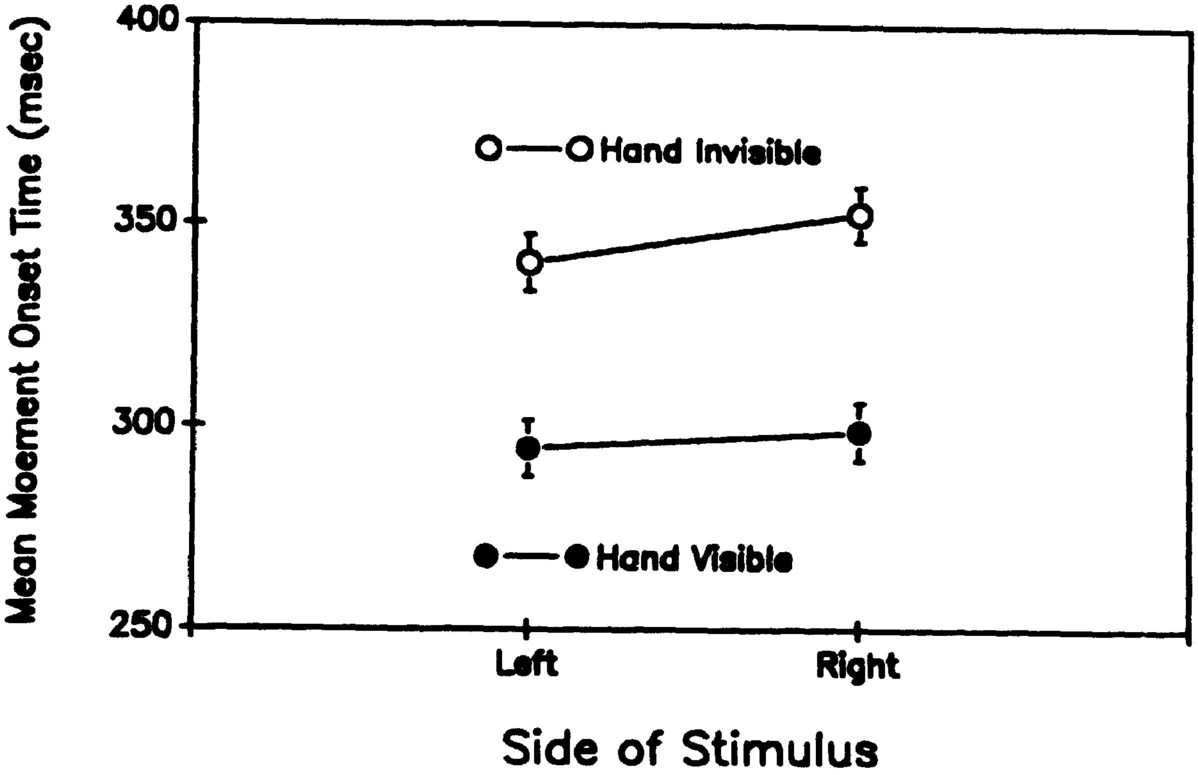
Table 4.1 Mean kinematic markers (w. standard errors) by Hand, and Hand visibility for single target pointing.

	Hand			
	Left		Right	
	Visible	Invisible	Visible	Invisible
Movement Onset	263 (6.9)	309 (7.0)	282 (7.1)	343 (7.5)
Duration	392 (7.4)	421 (8.7)	376 (7.6)	391 (7.5)
Path Length	325 (4.0)	344 (5.2)	333 (1.7)	345 (2.3)
Peak Velocity	144 (4.2)	143 (4.0)	156 (5.1)	154 (5.2)
Percent. Decel.	58.1 (1.1)	59.4 (1.3)	56.6 (.97)	56.2 (1.0)
Peak + Accel.	182 (10.7)	194 (11.4)	168 (8.5)	161 (8.3)
%Time Peak + Accel.	18.5 (0.7)	17.6 (0.7)	19.9 (0.6)	18.9 (0.7)
Peak - Accel.	-149 (7.6)	-154 (8.3)	-145 (8.9)	-145 (9.5)
%Time Peak - Accel.	69.1 (2.1)	64.5 (2.8)	80.2 (1.1)	79.7 (1.3)
Absolute Error	1.01 (.04)	2.95 (.21)	0.97 (.07)	2.73 (.18)
Constant Error	0.01 (.09)	0.80 (.04)	0.20 (.08)	0.01 (.08)
Variable Error	0.75 (.05)	1.55 (.10)	0.72 (0.05)	1.42 (.05)

Table 4.2 Mean kinematic markers (w. standard errors) by Hand, and Hand visibility for antipointing.

	Hand			
	Left		Right	
	Visible	Invisible	Visible	Invisible
Movement Onset	301 (6.9)	351 (7.1)	341 (14)	384 (13)
Duration	407 (7.6)	437 (8.9)	414 (9.5)	425 (8.6)
Path Length	323 (3.7)	338 (4.3)	330 (2.1)	347 (2.8)
Peak Velocity	136 (4.0)	134 (3.6)	137 (4.3)	141 (4.4)
Percent. Decel.	57.4 (1.2)	60.0 (1.3)	56.6 (1.0)	57.1 (.97)
Peak + Accel.	172 (10.9)	173 (10.9)	140 (7.6)	141 (6.3)
%Time Peak + Accel.	18.7 (0.6)	17.4 (0.7)	18.7 (0.7)	18.6 (0.7)
Peak - Accel.	-142 (7.3)	-144 (7.7)	-118 (7.1)	-127 (7.3)
%Time Peak - Accel.	68.6 (2.6)	65.0 (2.8)	80.8 (1.1)	79.5 (1.3)
Absolute Error	2.20 (.08)	3.42 (.15)	2.20 (.10)	3.48 (.17)
Constant Error	-0.47 (.21)	-0.41 (.39)	0.80 (.20)	0.82 (.37)
Variable Error	2.12 (.80)	2.87 (.70)	2.08 (.70)	2.86 (.13)

Figure 4.3 Mean movement onset time as a function of Hand visibility and Side of Stimulus presentation (collapsed across Task).


Mean Moement Onset Time (msec)
400
350
300
250
○—○ Hand Invisible
●—● Hand Visible
Left
Right
Side of Stimulus

Duration

As expected, movements were shorter when pointing (395 msec) relative to antipointing (421 msec; $F_{(1,24)}=25.51$, $p<0.0001$) and in hand-visible conditions (397 msec) relative to hand-invisible conditions (418 msec; $F_{(1,24)}=41.01$, $p<0.0001$). An interaction between Hand and Task ($F_{(1,24)}=5.11$, $p<0.03$) and associated post hocs suggested that the duration advantages for the right hand were attenuated in antipointing relative to pointing (right pointing significantly less than all three other hand/hand visibility combinations). The Hand by Side interaction ($F_{(1,24)}=8.20$, $p<0.009$) suggests that there was an ipsilateral *target* advantage in the left hand ($q=3.46$, $p<0.05$) but not the right ($q=2.26$, $p>0.05$; but see below).

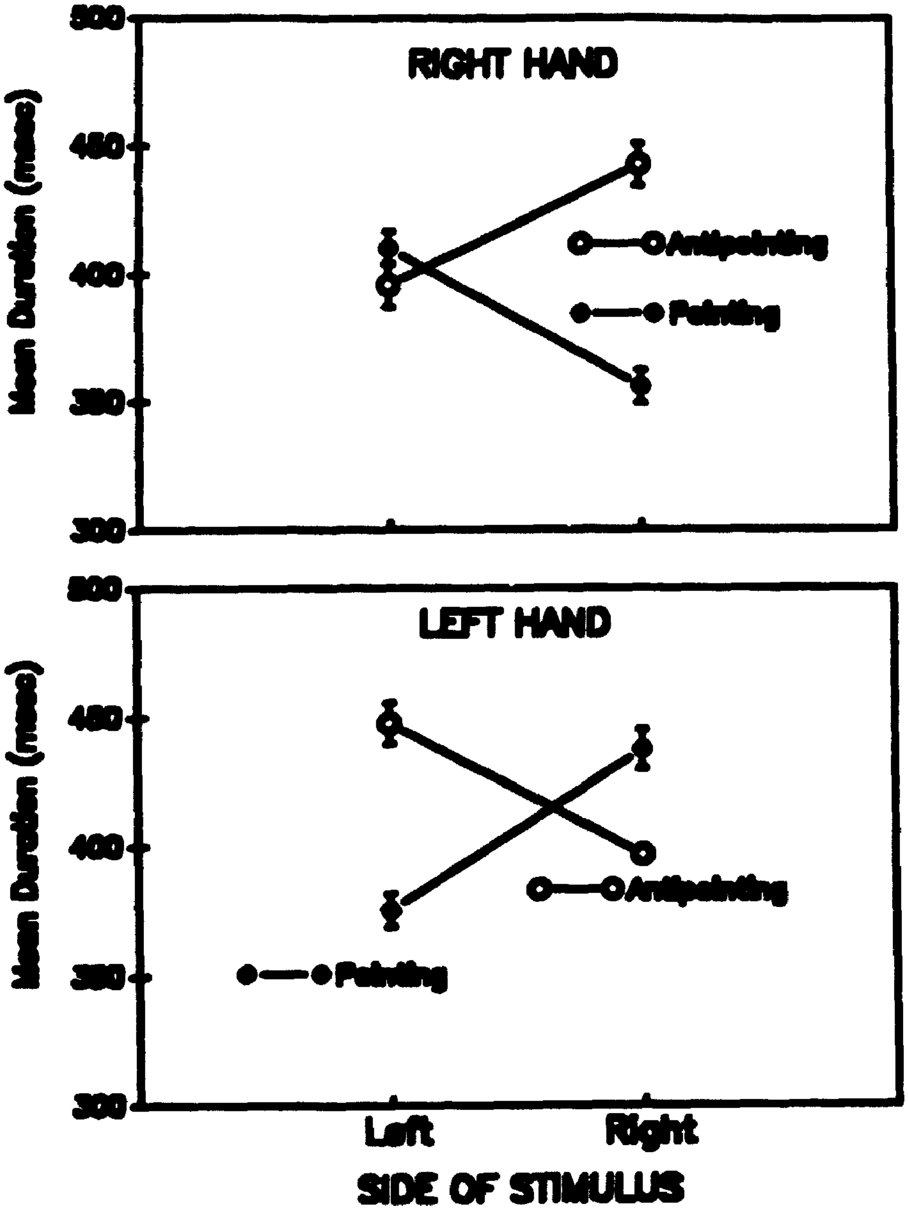
Movement durations provide very strong support for the importance of hemispace of the movement rather than target position being the crucial variable (Figure 4.4). The Hand by Task by Side interaction ($F_{(1,24)}=398.05$, $p<0.0001$) and post hoc tests revealed that antipointing reversed the normal movement duration advantages seen in pointing to ipsilateral targets. For both hands, pointing into the ipsilateral side of space produced significantly shorter durations than pointing into contralateral space (all p's < 0.01). In fact, the ordering of the means was exactly as predicted for ipsilateral *side of movement* and right-hand advantages.

Peak velocity

In these right-handed subjects, right-handed movements (147 cm/sec) had significantly higher peak velocities than left-handed movements (139 cm/sec; $F_{(1,24)}=4.33$, $p<0.05$).

A Hand by Task interaction ($F_{(1,24)}=6.43$, $p<0.02$) revealed no significant difference in peak velocities between side of target in antipointing ($q=2.62$, $p>0.05$) while pointing responses were faster on the right than the left side of stimulus presentation ($q=7.68$, $p<0.01$). A Task by Side interaction ($F_{(1,24)}=59.69$, $p<0.0001$) suggested that the fastest peak velocities were in the pointing movements when the target appeared on the right ($p<.01$ against all other means) and the slowest in the antipointing task when the targets appeared on the right ($p<0.01$ against all other means). In other words, movements into

Figure 4.4 Mean duration as a function of Hand, Task and Side of Stimulus presentation.


RIGHT HAND
Mean Duration (msec)
500
450
400
350
300
Antipointing
Pointing
LEFT HAND
Mean Duration (msec)
500
450
400
350
300
Antipointing
Pointing
Left
Right
SIDE OF STIMULUS

right hemispace achieved higher peak velocities than movements into left hemispace in both tasks.

Movements made towards the contralateral side of the body were different from movements into the ipsilateral hemispace. A significant Hand by Task by Side interaction ($F_{(1,24)}=111.08$, $p<0.0001$; Figure 4.5) and associated post hocs showed that pointing in ipsilateral hemispace produced higher peak velocities, independent of stimulus hemifield ($q=11.45$, $p<0.01$, for right-handed pointing; $q=10.24$, $p<0.01$ for right-handed antipointing; $q=3.81$, $p<0.05$, for left-handed pointing; $q=4.30$, $p<0.05$, for left-handed antipointing).

Accuracy

Constant error

In this experiment, constant errors were not different in the two hands ($F_{(1,24)}=3.19$, $p<0.08$). Although a Hand by Task interaction was found ($F_{(1,24)}=28.17$, $p<0.0001$), it was not easily interpretable as an attenuation of a right-hand advantage in pointing (which was predicted for the more "spatial" antipointing task; Figure 4.6). Newman Keuls tests suggested significant changes in constant error from pointing to antipointing in the left ($q=5.75$) and right hands ($q=4.86$, $p<0.01$). If the absolute value of the constant error is considered, then arguably right-hand performance is more detrimentally effected than left-hand performance (but see Absolute error analysis below). Regardless, these constant errors were quite small in relation to those obtained in Experiment 1, again suggesting that they were largely idiosyncratic (26 subjects contributed to the means of this experiment, while only 14 contribute to the means analyzed in Experiment 1).

Even though in half of the trials movements were made to the opposite side of space, the main effect of Side of stimulus presentation was significant ($F_{(1,24)}=22.55$, $p<0.0001$; left= -0.26 cm; right= 0.70 cm). This factor interacted with Task ($F_{(1,24)}=17.64$, $p<0.0003$) in a manner which suggested right shifts in response to right targets and left shifts in response to left targets in pointing ($q=7.80$, $p<0.01$), but no significant difference

Figure 4.5 Mean peak velocity as a function of Hand, Task and Side of Stimulus presentation.

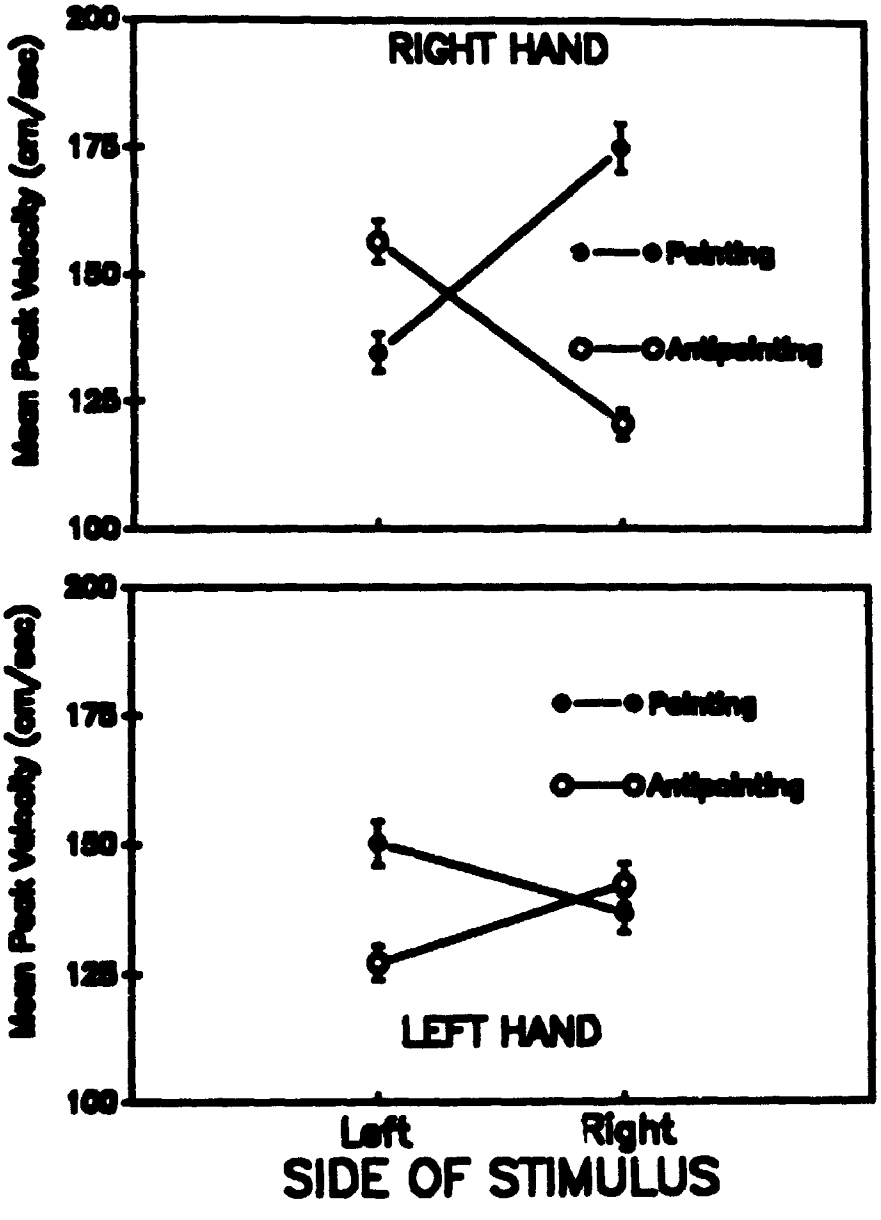
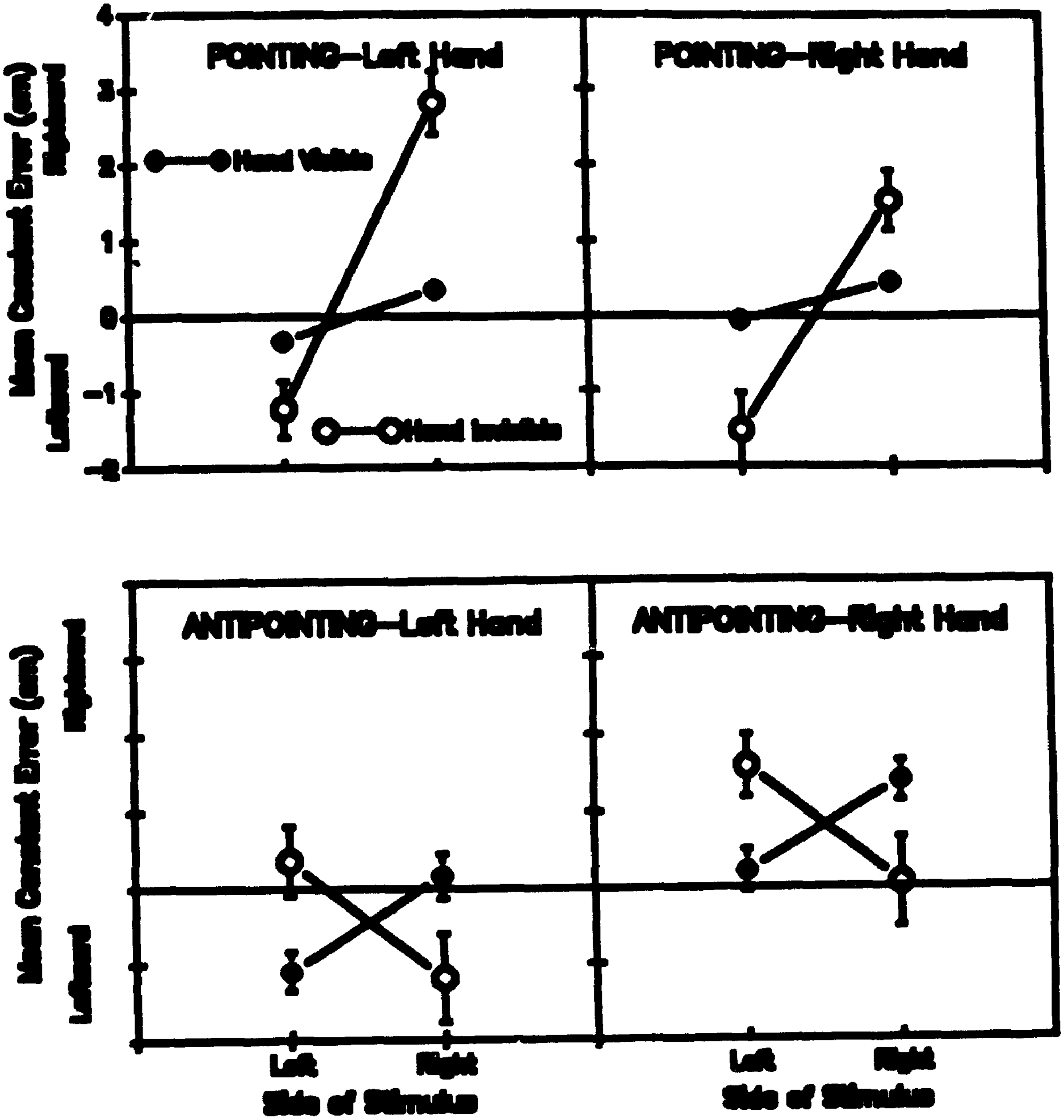

RIGHT HAND
Mean Peak Velocity (cm/sec)
200
175
150
125
100
Painting
Antipainting
Mean Peak Velocity (cm/sec)
200
175
150
125
100
Painting
Antipainting
LEFT HAND
Left
Right
SIDE OF STIMULUS

Figure 4.6 Mean constant error as a function of Hand, Task, Side of Stimulus presentations and Hand visibility.


POINTING—Left Hand
POINTING—Right Hand
ANTIPOINTING—Left Hand
ANTIPOINTING—Right Hand
Mean Constant Error (cm)
Rightward
Leftward
Hand Visible
Hand Invisible
4
3
2
1
0
−1
−2
Left
Right
Side of Stimulus
Left
Right
Side of Stimulus

in constant error shifts between right and left target positions in antipointing ($q=0.60$, $p>0.05$).

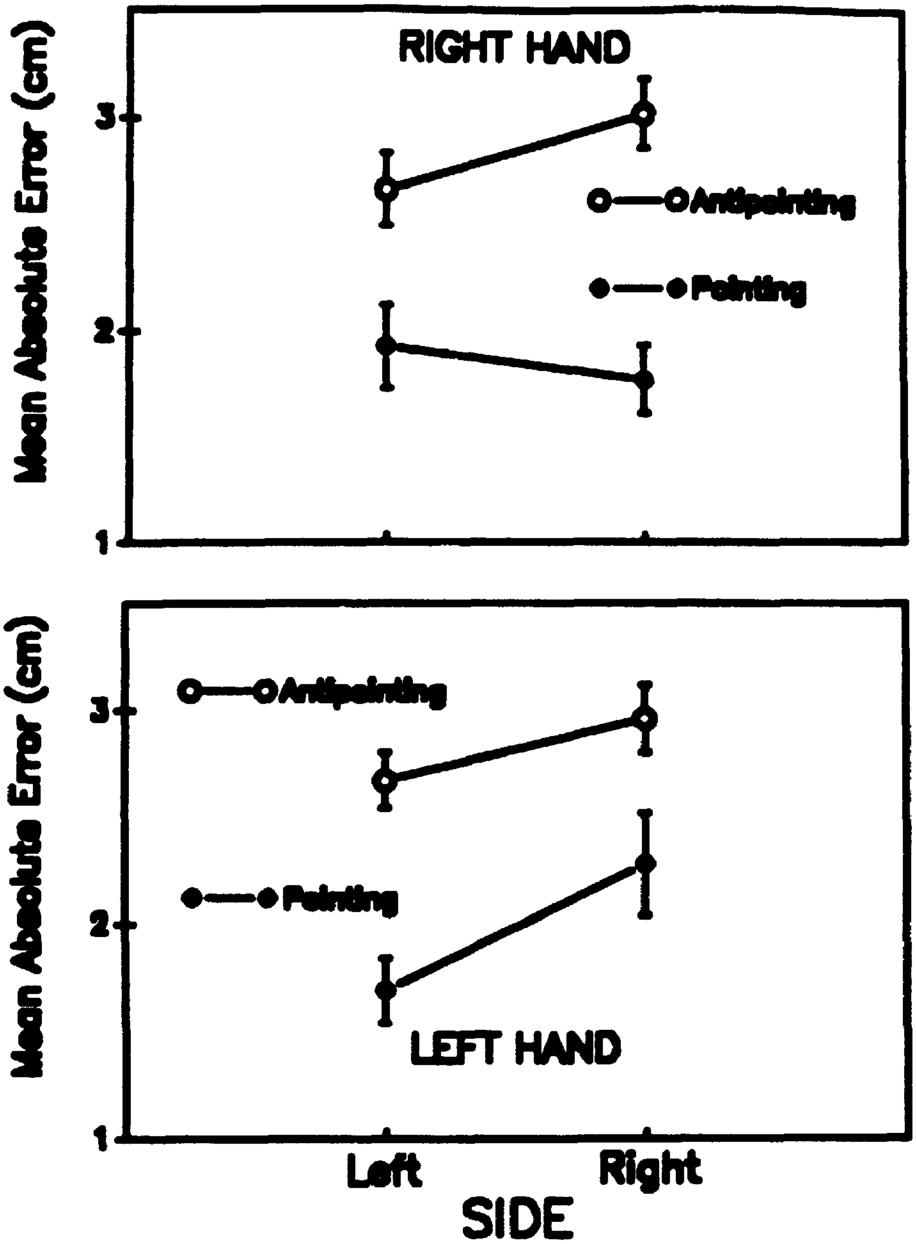
A Task by Side by Hand visibility ($F_{(1,24)}=39.95$, $p<0.0001$) interaction has a number of possible interpretations; the most likely appears to be that the discrepancy in constant error between right and left targets was seen in hand-invisible pointing (right side= 2.18 cm., left side =-1.38 cm, $q=11.20$, $p<0.01$), while in hand-invisible antipointing this trend for *side of movement* overshooting was maintained but was not as large (right-sided targets=-0.55 cm, left sided targets=0.97 cm, $q=4.80$, $p<0.05$). The remaining two cells in this interaction, hand-visible pointing ($q=1.92$, $p>0.05$) and hand-visible bisecting ($q=3.79$, $p>0.05$) did not contain significant differences between left- and right-sided targets. This three-way interaction did not interact with Hand ($F_{(1,24)}=1.02$, $p>0.05$).

This dataset also allows for testing the possible influence of sighting dominance on constant errors in dark reaching, after the findings of Held & Foley (1972) and Foley (1977). If sighting dominance was related to the pattern of constant errors in dark reaching, main effects and/or interactions related to sighting dominance would have been significant. Sighting dominance did not affect constant error in any obvious way in the present dataset ($F_{(1,24)}=0.45$, $p<0.50$) as a main effect; and no interaction was found with an associated probability of less than 0.12. Although sighting dominance did interact with a number of factors in the other kinematic variables, because they were not predicted they will not be analyzed further.

Absolute error

As in constant error, if antipointing depended on right hemispheric mechanisms more than simple pointing, then a privileged access account would predict attenuation of right hand advantages in antipointing relative to pointing. Although the Hand by Task effect was not statistically significant ($F_{(1,24)}=1.09$, $p>0.05$) the Hand by Task by Side interaction was significant ($F_{(1,24)}=4.76$, $p<0.03$). The mean absolute error for these conditions appear in Figure 4.7. The right hand showed a slight trend towards increased accuracy in its own hemispace in both tasks, although these two pairwise differences (left

Figure 4.7 Mean absolute error as a function of Hand, Task and Side of Stimulus presentation.


RIGHT HAND
Antipointing
Pointing
Mean Absolute Error (cm)
3
2
1
Antipointing
Pointing
LEFT HAND
Mean Absolute Error (cm)
3
2
1
Left
Right
SIDE

vs. right side of target within task) were not significant. The left hand showed a strong ipsilateral advantage in its own hemispace in pointing but not in antipointing.

A significant Hand by Hand visibility by Side interaction ($F_{(1,24)}=8.54$, $p<0.008$) suggested that the right hand was equivalently worse moving in either hemispace in hand-invisible conditions ($q=0.06$, $p>0.05$; Figure 4.8). The left hand was significantly more impaired in endpoint accuracy when the movements were directed by right-sided targets ($q=7.13$, $p<0.01$). This effect did not interact with Task ($F_{(1,24)}=0.01$, $p<0.97$).

Absolute error was significantly greater in antipointing (2.95 vs. 1.96 cm; $F_{(1,24)}=54.4$, $p<0.00001$) and in hand-invisible conditions (1.72 vs. 3.19 cm; $F_{(1,24)}=207.2$, $p<0.00001$).

Variable error

As expected, removing visual feedback about hand position dramatically increased endpoint variability (from 1.42 cm to 2.18 cm; $F_{(1,24)}=167.35$, $p<0.0001$). Antipointing (2.49 cm) produced larger endpoint variability than pointing (1.11 cm; $F_{(1,24)}=284.28$, $p<0.0001$). Finally, movements in response to left-sided targets (1.72 cm) resulted in smaller variable error than movements to right-sided targets (1.87 cm; $F_{(1,24)}=8.35$ $p<0.008$). As with constant error, if right hand advantages in accuracy were attenuated in antipointing relative to pointing, a Hand by Task interaction should have resulted. This was not the case, as the hands were fairly similar in pointing on this measure and antipointing produced rather large increases in variable error in both hands (Hand by Task, $F_{(1,24)}=0.21$, $p>0.05$).

Percentage decelerating

A significant Task by Side ($F_{(1,24)}=5.29$, $p<0.03$) interaction may be explained by a tendency to spend more of the movement decelerating when left-sided movements were made compared to right-sided movements. This two-way effect interacted with Hand (Hand by Task by Side $F_{(1,24)}=34.99$, $p<0.0001$). The ordering of the cell means is perfect for contralateral movements and the right hand spending less of the movement decelerating than ipsilateral movements and the left hand (Figure 4.9). Newman Keuls

Figure 4.8 Mean absolute error as a function of Hand, Hand visibility and Side of Stimulus presentation.

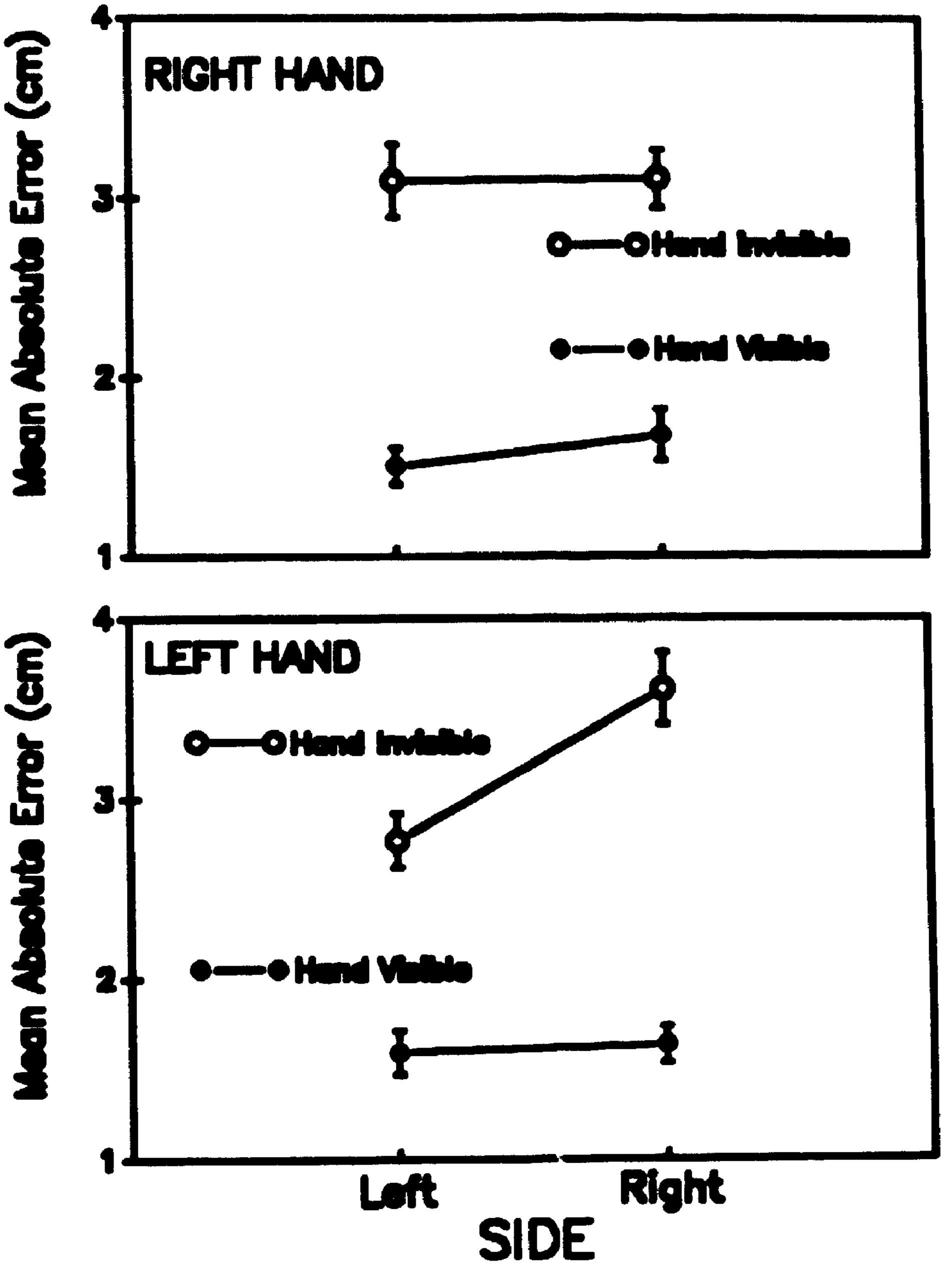
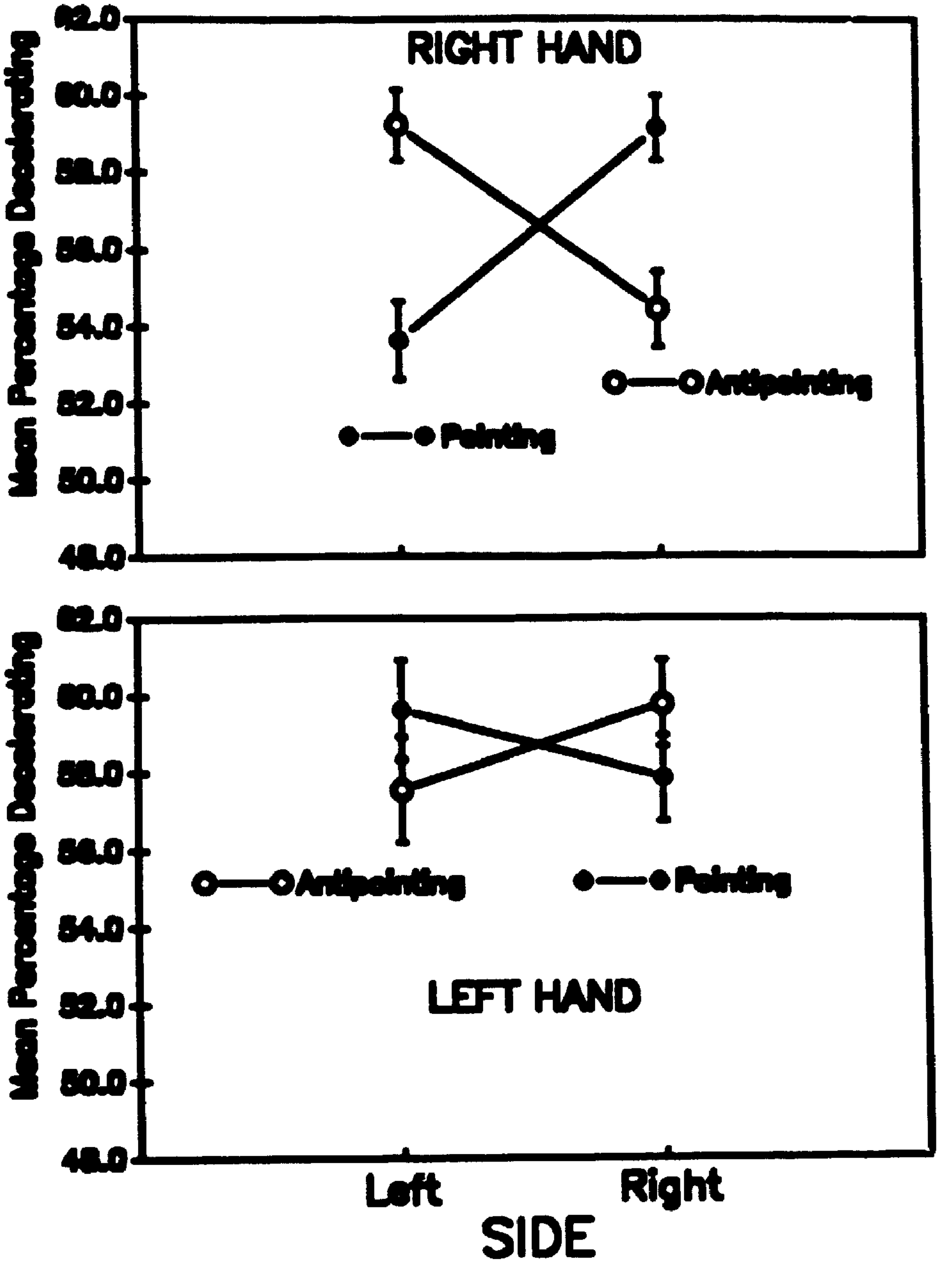

RIGHT HAND
LEFT HAND
Mean Absolute Error (cm)
Mean Absolute Error (cm)
1
2
3
4
Hand Invisible
Hand Visible
Left
Right
SIDE

Figure 4.9 Mean percentage decelerating as a function of Hand, Task and Side of Stimulus presentation.


RIGHT HAND
Mean Percentage Decelerating
62.0
60.0
58.0
56.0
54.0
52.0
50.0
48.0
Antipointing
Pointing
LEFT HAND
Mean Percentage Decelerating
62.0
60.0
58.0
56.0
54.0
52.0
50.0
48.0
Antipointing
Pointing
Left
Right
SIDE

results suggest that only right-pointing/left targets and right-antipointing/right targets (i.e., movements into contralateral hemispace for the right hand) were significantly less than all other means ($p<0.05$).

Summary

In one of the few occasions in this set of experiments, an advantage in a movement-related measure favoured the left hand: A movement onset time advantage was found for the left hand relative to the right. Unsurprising advantages for pointing relative to antipointing were found in a number of measures, including movement onset times, durations, absolute error, and variable error. A suggestion (although a weak one) from this dataset is that constant error in the right hand was differentially increased by antipointing relative to pointing, while the left hand was equivalent (although opposite in sign) across the two tasks. By far the largest effects in this analysis had to do with effects of Hand, Task and Side. In the case of deceleration duration, movement duration, peak velocity, and to a limited extent endpoint accuracy, when ipsilateral advantages in pointing were obtained, the effect was reversed in antipointing. When these effects were not equivalent in the two hands, they were always more obvious in the right hand (i.e., peak velocity, absolute error, percentage decelerating).

In the accuracy measures, the story is less clear (perhaps because mean accuracy in most cells is so good), although there is a suggestion of movement overshooting in each side of space in the constant error data.

Finally, contrary to expectations, no effect of sighting dominance on the pattern of constant error was found.

4.4 Discussion

In comparison to Experiment 1, the evidence for increased right-hemisphere participation in antipointing relative to pointing was at best rather scant. Duration advantages for the right hand were attenuated in antipointing relative to pointing (However, it has to be noted that duration was not significantly shorter in the right hand in pointing in Experiment 1-if anything there was a trend for left-handed movements to have shorter durations). There are three possible explanations likely to account for the differences between antipointing and bisection, and to a lesser extent, why right hemispheric mechanisms were unlikely to be more engaged when antipointing. The first possibility is that the attenuation of constant and absolute error advantages for the right hand in Experiment 1 was spurious. Carson and colleagues have also failed to find attenuated right-hand advantages with a manipulation they claimed was a spatial one (Carson et al., 1992). Indeed, understanding of the processes involved in bisection performance is still relatively poor (Milner et al., 1993), and the characterization of bisection as spatial may well be the consequence of a circular argument in the first place (see General Discussion).

A second possible reason for the failure to replicate Experiment 1 might relate to the more "cognitive" nature of the antipointing task. The arbitrary nature of antipointing might require decision-making processes which are less lateralized, and less likely to reflect normal, relatively automatic visuomotor processing. Bisection, although perhaps more cognitive than simple pointing, still requires aiming-movement responses in the direction of the stimuli. In fact, the bisection task could be solved as a large single target task where accuracy is characterized by movements to the centre of the "target". Georgopoulos and colleagues have argued for a "mental rotation" operation playing a role in a task which has some similarity to antipointing. In a series of experiments, monkeys were trained to make movements towards a visual target in some trials and 90 deg away from a target in others, depending on the brightness of the visual target. Based on the responses of single units in motor cortex, he argues that the population vector is rotated as the movement 90 deg away from the target unfolds (Georgopoulos, et al. 1989). An alternative interpretation of the same data has been made by Giacomo Rizzolatti, who notes that distinct populations of visual cells and motor cells could produce the same result. That is, an initial burst of activity in the direction of the target based on visual cell activity, followed by activation of cells specific for the 90 deg. movement direction (D. Perrett & M. Oram, personal communication). The mechanisms behind performance on antipointing and similar tasks remain to be elucidated.

A third possibility for the lack of evidence for increased right hemisphere participation in antipointing is related to eye movements. Although the direction of primary and secondary saccades in bisecting is unknown, in antipointing the possibility of double (or even multiple) saccades in opposite directions seems quite likely. Another possibility is that subjects adopt a strategy during antipointing, in which they maintain approximate fixation at target fixation, in order to facilitate their estimates of eccentricity of the initial target and their estimate of an equivalent point in the opposite hemispace (in fact one subject spontaneously reported such a strategy).

The more encouraging results of this study are related to its primary goal: To dissociate side of stimulus presentation from side of motor response. On each measure where ipsilateral aiming movement "advantages" were obtained in pointing (duration, peak velocity, and percentage decelerating), these advantages were for the opposite side of stimulus presentation in the antipointing task. These results are consistent with the prediction made by Fisk and Goodale (1985), that ipsilateral spatial advantages are related to side of motor response rather than side of stimulus presentation. In a second experiment reported in Fisk and Goodale (1985), they dissociated visual field from hemispace, by having the subjects fixate eccentrically on selected trials. Their results strongly supported the importance of target hemispace--but they did not dissociate hemispace of target appearance from hemispace of subsequent response. That is, independent of eye position, the targets in those experiments always appeared in the hemispace to which a subsequent movement would be made. From computational principles alone, it is obvious that gaze position signals allow for reconstruction of target position in space when the eyes are not in primary position. Neurophysiological investigations have show that gaze coding influences single unit responsiveness in areas of cortex crucial for visuomotor control (i.e., the lateral intraparietal area (LIP) in parietal cortex -Andersen et al., 1990; Colby et al., 1993; dorsolateral frontal cortex -Boussaoud et al., 1993).

In Fisk and Goodale's Experiment 2, the strongest hemispatial effects were found for peak velocities and durations. These variables showed the largest hemispace-related effects in this experiment. Movement onset times showed the effect only in their condition which required subjects to maintain fixation. In the present study, the effects of side of motor response on movement onset time could not be properly examined, since significant advantages for ipsilateral targets were not seen. As noted previously, movement onset advantages are not reliably obtained in other studies in the literature.

Hemispatial effects were not always equivalent in the two hands in this experiment. In fact, the data suggest that more often than not, the strength of the reversal from ipsilateral to contralateral target is larger in the right hand of these right handed subjects than in their left hands. There are three possible reasons for this asymmetry. One possibility is that the right hemisphere plays a large role in localizing targets relative to the body midline, and as such is less influenced by the requirements of subsequent motor response. A second possibility is that variation in left-handed movements obscures hemispatial effects equivalent to those seen in the right hand. Finally, given the right-handed privileged access to the left hemisphere, movements into the right hemispace are the least variant with respect to parameters related to motor control. These alternatives will be discussed in the general discussion.

CHAPTER 5 - GENERAL DISCUSSION

5.1 Hand Advantages and the Left Hemisphere

This series of investigations was designed to examine hand and hemispace differences in the production of aiming movements to visual targets. Many studies of unimanual movement have been concerned with specifying the relative contributions of each hemisphere to motor control. Typically researchers have attempted to manipulate stimulus characteristics in some way in order to attenuate or enhance right-hand advantages in measures of movement accuracy or speed. The assumption behind such manipulations has been that, for instance, increased right-hemisphere involvement would enhance left-hand performance in some way, thereby reducing right-hand advantages in right-handed subjects. Contrary to previous suggestions in the literature, in no instance did I find a consistent advantage for the left hand relative to the right, except for movement onset time advantages (which were present in two of the three studies). This is in spite of the fact that the use of several target positions (5-8) required localization of targets in visual space to a greater degree than in many other studies of aiming (cf Carson et al., 1993; Roy & Elliot, 1986). Although Guiard et al. (1983) has been cited fairly frequently, other investigators have not replicated the left-side and left-hand advantages for hand-invisible reaches reported by those investigators. These failures have not been completely conclusive, however, because of many methodological differences across experiments and laboratories. For example, in many studies the subjects were required to make movements of a particular duration or to only one target position (e.g. Roy & Elliot, 1986).

In the present investigations several targets were used and no particular constraints beyond reaching "quickly and accurately" were imposed on the subjects. Despite the fact that three experiments in this thesis involved reaching in the dark without visual feedback, I did not find any advantage for the left hand on measures of endpoint accuracy. In most cases the right hand, not the left, was less affected by removal of visual feedback in terms of variable, constant and absolute error (in the remaining instances the hands were affected equivalently). It seems unlikely that these findings can be explained by practice effects or strength advantages for the right hand of these right-handed subjects; when visual feedback was available throughout the movement, left hand performance was comparable to right-hand performance in terms of accuracy. When reaching behaviours of left-handed subjects were compared with reaching behaviours of right-handed subjects, there was little difference between preferred- and non-preferred hands in terms of speed (duration) and accuracy in the left-handed subjects (Goodale, 1988). Yet it seems unlikely that the left-hander's left hand is less practised, at least for simple tasks that require minimal participation of the distal musculature, than the right-hand of a right-hander. The "odd-man out" in terms of speed and accuracy is the right-hand of a right-handed subject.

5.2 Privileged Access and Aiming Movements

A popular interpretation of right handedness and right-hand advantages is the "privileged access" theory. This theory suggests that because the motor outflow and somatosensory inflow related to right-hand performance are associated with the left hemisphere, this hand has within-hemisphere connections to a praxis system important for motor control on both sides of the body. Although this theory is difficult to test directly, recent PET studies showing ipsilateral and contralateral contributions to unimanual movements are for the most part consistent with the position (cf Kim et al., 1993). For example, left premotor cortex tends to be activated during either left or right-handed movements, while right premotor cortex is only significantly activated during left-handed movements (Kim et al., 1993; Kawashima et al., 1993).

This example and others from the PET literature suggest that the greatest degree of contralateral activation is produced by discrete movements of the fingers, although only a few laboratories have compared proximal and distal movements directly. In the aiming movements examined here, participation of muscles controlling index finger position (i.e., the first dorsal interosseous, the second lumbrical, the Palmarus longus and others; Darling et al., 1994; see Fig. 1.2) was unlikely to have played a large role in the determination of final position or movement kinematics, relative to the proximal musculature. This is in sharp contrast to the importance of digit movement and coordination in tasks which require manipulation or grasping (Jakobson & Goodale, 1991; Johansson & Cole, 1992; Muir, 1985).

This more prominent role of the proximal musculature in aiming movements underlies a problem for a simple version of a privileged-access interpretation for aiming-movement advantages for the right hand. If more proximal muscles are involved in the control of one class of movements relative to another (like aiming movements compared with grasping movements), it would be reasonable to expect more ipsilateral involvement in the former case and consequently smaller asymmetries between the hands. This may indeed turn out to be the case, but given large intra-subject variability in motor tasks, a within-subjects design comparing two tasks would be necessary to show such an interaction. I know of no study which compares the kinematics of pointing versus grasping in the same subjects to date (although see Carnahan et al., 1993), but the most likely outcome of such an experiment would be greater right-hand advantages in some measures related to grasping than in pointing. Nevertheless, I have found some (but not many) indications of right-hand advantages in pointing, especially in accuracy-based measures.

The simple response to this difficulty for a privileged-access explanation of aiming movement advantages for the right hand is to argue for differences in the degree of "contralaterality" of human corticomotoneuronal systems compared to nonhuman primates. Indirect evidence for this position comes from the tremendous asymmetry of hand preference seen in our species relative to other primates, even the great apes. Byrne and Byrne (1990) report a 60% incidence of hand preference (in the one of two handedness factors which showed the "larger" population preference) in gorillas; this figure is hardly comparable to the 90% or greater incidence of hand preference in *Homo sapiens*. Because the biomechanical design of the limbs differs substantially across primate species (cf Fleagle, 1988), differences in neurological control of the upper limb and hand would not be surprising. Examination of manual performance of other primates suggests elaborations present in our species but less developed in the other great apes (e.g., Marzke, et al., 1992). In fact, the most frequently cited experiments concerning contralateral control of the distal but not proximal musculature have been performed on

Macaque monkeys and not in the more closely related great apes (Brinkman & Kuypers, 1972, Haaxma & Kuypers, 1975; Lawrence & Kuypers, 1968). Recent neuroanatomical analysis of the corticospinal tract in Cebus and Squirrel monkeys suggest differences in the laminar terminations of corticomotoneurons in the spinal cord across different primates (Borthoff & Strick, 1993). Nevertheless, data from split-brain subjects (e.g., Gazzaniga et al., 1967) and neurological patients do suggest a proximal-distal gradient in the degree of contralateral control of the musculature (see Introduction).

An alternative solution to the puzzle of a privileged-access interpretation for movements involving proximal muscles is that an aiming movement may depend upon control systems that are normally used to transport the grasping digits into an appropriate position to interact with an object. It is difficult to imagine many situations where a pointing movement using a single digit would be useful in a natural environment (although some foraging for insects might be best achieved by a single digit, for example the middle finger of the Aye-Aye; Jolly, 1985. Other theorists have argued that pointing movements serve a unique communicative function which may or may not be linked spatially with an object of interest, but much of this literature is speculative, at best. See Butterworth, 1991). When a subject performs a simple aiming task, perhaps some preparatory activity takes place in the praxis system for digit manipulation which is never ultimately utilized, but nevertheless influences the control of the movement. This suggestion might be difficult to test, but if true could be supported by PET investigations which contrast grasping and gripping movements with simple aiming tasks of comparable distance and position. If areas of motor and premotor cortex normally associated with grasping and other hand actions were activated equivalently by aiming, this would be indirect evidence for the suggestion of preparatory activity in distal systems even when they are not utilized in the movement. Another possibility is that pointing to a "graspable" target within peripersonal space might involve a slightly different set of neural substrates than those necessary for pointing to a target at a distant location.

A related answer to this problem is that a left-hemisphere praxis system is likely to play a role in the coordination of transport (having more proximal involvement) and grasping (having more distal involvement) phases of movements, even if their control is somewhat independent at the level of primary motor cortex. Although Jeannerod has argued that these two systems are relatively independent (cf Jeannerod, 1983), Jakobson and Goodale (1991) provide evidence to the contrary (see also a recent report by Soechting & Flanders, 1993). Intimate coordination of proximal and distal musculature for normal movements must be an integral part of the control systems which coordinate their activity. Getting the hand into a spatially-correct position for grasping or manipulating requires dealing with a number of complex inertial forces that accompany mulitjointed movements. Motion of any limb segment produces inertial forces in other segments in the arm (Hasan, 1991). This means that computations of whole arm movements must coordinate activities of antagonist-agonist pairs throughout the limb. This problem is compounded by the fact that many muscles in the limb are biarticular and produce torques at more than one joint (such as the biceps; Gielen, 1993; Miller et al., 1990; see Darling et al., 1994 for a discussion of this problem in the intrinsic and extrinsic muscles of the hand). Many of these computational constraints may be dealt with at a programming level (i.e., before the movement is initiated), but there is at least a suggestion in the motor control literature that on-line proprioceptive feedback may be involved in whole arm movements. This suggestion comes from studies of deafferented patients, who show abnormalities in limb segment coordination in spite of (as far as is known) relatively intact motor programming mechanisms (normal strength, and normal movements when performed under visual guidance; see Blouin et al., 1993; Ghez et al., 1990; Sainberg et al., 1993). Nevertheless, computational restraints specified by the biomechanics of the upper limb suggest that any control system will have to coordinate the activities of the proximal and distal musculature. Both feedforward and feedback-related control are likely to be invovled in such coordination (Gracies et al., 1994).

Studies of grip force modulation also provide evidence for close coordination of proximal and distal muscles. Somatosensory inputs from the digits (skin, muscle and joint) surely must have intimate access to proximal effector systems in the trunk and upper arm. Information about surface friction, texture, object mass and inertia must have influence on the control of the proximal muscles when objects are being transported and manipulated once they have been grasped (although some of the control mechanisms are surely mediated by spinal cord reflexes, see Lacquaniti, 1992, for a review). Picking up different masses must call into play feedback-related mechanisms which deal with the new inertias and torques created by a new weight at the end of the effector. These observations also suggest several ways that limb movement control for grasping or aiming movements requires close cooperation of proximal and distal muscles (and therefore crossed and uncrossed brain pathways, even if the contralateral/ipsilateral differences are functionally equivalent between humans and monkeys).

5.3 Visuospatial Analysis and the Right Hemisphere

Some of the hand differences that I found are consistent with differences in the reported movement abnormalities in right and left hemisphere damaged patients. Disordered motor control in the absence of hemiparesis is reported more frequently after left-hemisphere damage then after right-hemisphere damage (cf Kimura, 1993). In the present studies, where accuracy differences are found, they tend to favour the right hand/left hemisphere. Conversely, movement-onset delays have been reported after right-hemisphere damage (Fisk & Goodale, 1988); movement-onset advantages, when obtained, always favoured the left hand in the present experiments. These similarities provide at least some indication that hand performance can, to a limited extent, tell us something about hemispheric contributions to sensorimotor control.

The suggestion that the right hemisphere is specialized for visuospatial function has a long history in experimental psychology and neurology. Of course, the evidence for right-hemisphere advantages in spatial processing is invariably found in perceptual tasks. Evidence for right hemisphere visuomotor processes is almost unheard of, perhaps because of a bias towards viewing sensory systems as perceptual (Goodale, 1983). A few claims have appeared recently which argue for visuomotor control differences between the hemispheres. MacNeilage et al. (1989) argue for greater preference for the left hand for reaching behaviours in infrahuman primates. Bracewell et al. (1990) make a rather bold claim for a right- hemisphere specialization for visuomotor control, based on greater accuracies of saccades to targets presented in the left visual fields. However, their task had a memory component, which might engage visuoperceptual mechanisms, which can be dissociable from mechanisms used for visuomotor control (Goodale, 1993; Goodale et al., in the press).

Guiard et al. (1983) and others have attempted to relate attenuated right-hand advantages to spatial "factors" or "demands". In this thesis, two attempts were made to increase the visuospatial demands of an aiming movement task while requiring an equivalent motor output. In Experiment 1, requiring the subjects to bisect two targets seemed to attenuate the large right hand- advantages in constant and absolute error. Unlike tasks previously claimed to be spatial in nature (beyond the obvious spatial requirements of *any* aiming task when target position is varied), there are two reasons to suspect that, regardless of whether or not it is "spatial" in character, bisecting requires right hemisphere involvement. First, bisection is a task often associated with right-hemisphere processing, because line bisection errors are much more frequently associated with right-hemisphere disease. Second, terminal errors in bisecting have differentiated the performance of right-hemisphere damaged subjects from aged-matched controls, while terminal errors in a pointing task did not (Goodale et al., 1990). Consequently it is tempting to describe bisection as a "spatial" task, because of the commonly held assumption that the right hemisphere is specialized for "spatial" processing. However, many other deficits which could be described as spatial, and can be found after left-hemisphere damage as well as right (constructional apraxia is one obvious example). Kosslyn and his colleagues have argued that the best way to categorize right- and left-hemispheric spatial processes is that the right hemisphere is superior when metrical information about space is provided while the left hemisphere codes for spatial relations in a categorical sense (Brown & Kosslyn, 1993; Kosslyn et al., 1989). Regardless, in spite of claims of right hemispheric superiority for "spatial" tasks, there is still substantial debate in the literature regarding what "spatial" actually means (Landau & Jackendoff, 1993, with associated peer commentaries; Quinn, 1994; Kosslyn, et al., 1989).

My initial hypothesis was that, like bisecting, antipointing might depend on right-hemispheric processes to a greater extent than pointing. Antipointing required estimation of both the eccentricity of the initial target and the required position in the opposite hemispace. I did not obtain any conclusive evidence for increased right-hemisphere involvement in this task, except for a right-hand duration advantage in pointing but not in antipointing. This duration advantage was primarily accounted for by higher peak velocities in pointing in the right hand relative to the left hand. There are several reasons why this study failed to provide good evidence of right-hemispheric participation in antipointing. Unlike bisecting, the antipointing task differs in a number of ways from the pointing task. For example, a strategy which may have been used by subjects would have been to maintain fixation during antipointing trials (to facilitate making an antipointing movement of equivalent extent from fixation into the opposite hemispace) while normal saccades would have been directed to target location during pointing trials. Another possibility is that subjects indeed moved their eyes to target locations, but then directed their eyes back in the opposite direction toward the intended landing position in the opposite hemispace. Given the evidence for the coupling of saccades with manual aiming responses, such trials are unlikely to be directly comparable to trials where responses are made directly towards target location. Of course, the somewhat arbitrary nature of the response required in antipointing might rely on perceptual and/or cognitive mechanisms to some extent, much like making saccades to remembered targets, discussed above. Some neuropsychologists have argued that increasing cognitive demands in tasks tends to attenuate lateral symmetries (cf Moscovitch, 1979).

In summary, right-hand advantages for accuracy and movement durations were found, but not across all three studies for any one measure. Although endpoint error was attenuated somewhat when the subjects were required to bisect rather than point at a single target, left- and right-hand performance was indistinguishable in most other measures. The speed and accuracy of left-handed reaches made by such right-handed subjects is indeed remarkable. Several reasons for this to be so in spite of the good evidence for a left-hemispheric motor control system can be advanced. First, in all of these subjects intrahemispheric pathways are intact and left-hemispheric systems can most certainly direct the activity of the right-hemispheric motor and premotor cortices.

Second, the Kuypers and colleagues' version of the story may indeed be true; reaching movements in humans may require less participation of exclusively contralateral projections to the distal musculature. If there is greater ipsilateral control of proximal muscles of the shoulder and upper arm, right-handed aiming movements might be slightly "disadvantaged" by some right-hemispheric control and left-handed aiming movements might be slightly "advantaged" by some left-hemispheric control.

Hemispatial Differences in Movement Production

In some respects, I have avoided tackling the question of what a hand or hemispatial "advantage" is in the motor control domain. Increased accuracy is fairly obviously an advantage; but is a 50 msec "lead" in movement-onset time? Perhaps, if the decreased movement-onset time is not coupled with a decrease in accuracy. Primates frequently capture insects, snakes, birds and other small prey which are quite capable of rapid avoidance or defensive responses (reviewed in Jolly, 1985). Rapid programming and execution of movements to visual targets could confer obvious advantages in such prey-catching behaviours, as long as they are accurate enough to successfully acquire the prey in a significant proportion of the attempts. For some types of prey ballistic movements might suffice; while for others responsiveness to changes in the position of the intended prey would require rapid adjustments of the movement trajectory. Visual information during locomotion through an arboreal environment would also require accurate and rapid adjustments of the limbs in response to rapidly changing retinal stimulation.

Unlike accuracy, movement onset or movement duration, the significance of hemispatial differences in measures such as percentage of the movement spent decelerating is less clear. The typical suggestion made about deceleration duration is that it is an index of efficiency of visual feedback. The usual description is that vision of the hand relative to the target is used to "home-in" during the final phase of the movement (i.e., Todor & Cisneros, 1985). Shorter deceleration phases in one hemispace could be interpreted as an advantage if longer deceleration phases with equivalent accuracies were obtained in the other. Of course, a longer deceleration phase might just as easily be interpreted as more "efficient", if overall movement duration is maintained (i.e., if peak velocity is achieved more rapidly).

Regardless of how to label differences of this type, they may be related to peripheral biomechanical factors rather than advantages or disadvantages for a hemispace per se. For example, Jeannerod (1983; 1986) has suggested that the deceleration phase is not related to the use of visual feedback in the terminal portion of a movement, because characteristics of that part of the movement are unchanged in hand-invisible conditions. The finding that the length of the deceleration phase does not change over 800 trials when visual feedback was not available (Experiment 2) provides some support for Jeannerod's argument. Indeed, the unchanging deceleration phase in hand-invisible reaching is difficult to reconcile with the commonly-held assumption that during the deceleration phase, hand position and target position differences are minimized based on visual information about the discrepancy. Deceleration duration is not "hard-wired" and therefore invariant with respect to task conditions; it does increase as a function of task difficulty (Soechting, 1984; Todor & Cisneros, 1985) and when subjects are instructed to move accurately rather than quickly (Carson et al., 1993). Nevertheless, in my sample, deceleration duration is unchanged over the course of the marathons, in spite of many trials where terminal visual feedback was not available.

Carson et al. (1993) have suggested a relationship between hemispace and deceleration duration. In their study, ipsilateral movements had shorter deceleration durations than contralateral movements, although only in the left hand. In this thesis, the strongest evidence relating deceleration duration and hemispace was revealed in Experiment 3: Each hand spent *more* time decelerating in its own hemispace, independent of the hemispace of the target. And unlike Carson et al.'s (1993) finding, this effect appeared to be larger in the right hand than in the left. Roy et al. (1994) also report longer deceleration duration in the right hand of their subjects. As is often the case, methodological differences are probably the source of these discrepancies. Carson et al. (1993) varied task instructions to emphasize speed or accuracy, and his hemispatial effect was seen primarily in the accuracy condition. In Experiment 1, the trend towards shorter deceleration duration in contralateral hemispace was also seen in right-handed reaches only. The significance of this effect is as yet unknown, and it is certainly not present in all right-handed subjects. No hemispatial effects on deceleration duration were found in the Experiment 2 dataset (n=11); a modest effect was found in Experiment 1 (n=14) and the largest hemispatial effects, primarily seen in the right hand, were found in Experiment 3 (n=26). As with the other kinematic variables which were affected by hemispace in Experiment 3 (duration and peak velocity), the effects were related to the hemispace of the movement, rather than the hemispace that the target originally appeared in.

For the most part, hemispatial effects occurred in left-handed and right-handed movements in these studies, although, whenever hand differences in the magnitude of hemispatial effects were suggested by the data, it was usually the right hand which showed the larger effects. This observation might be related to higher variability in the performance of the left hand of these right-handed subjects. On the other hand, hemispatial differences in the performance of the right hand might reveal some of the "operating principles" of the praxis system. To differentiate between these two possibilities, left-handed subjects should be tested with an antipointing task. If left-handed subjects do not show a preferred-hand trend for larger hemispatial effects, this would provide some support for the notion that left-hemisphere praxis might be examined in normal subjects by varying hemispace. Other investigators have noted hemispatial effects in patients (Bowers & Heilman, 1980) and in normal subjects (Bradshaw et al., 1983) that may be related to cerebral asymmetries.

In this thesis several hemispatial advantages were found. In Experiment 1, peak velocities were higher in ipsilateral hemispace for both the left- and the right-handed movements. Some accuracy differences were also found for left-handed movements, but these might be better described as contralateral disadvantages rather than ipsilateral movement advantages (the right hand was equivalent in accuracy across the hemispace). In Experiment 2, ipsilateral advantages were found for peak deceleration, duration, and peak velocity (but not accuracy), and did not appear to be attenuated despite a substantial period of time without visual feedback. Many studies have suggested that a view of the limb at starting position is sufficient to maintain accurate visuomotor control. In spite of the lack of such an opportunity throughout the course of each marathon, ipsilateral-contralateral differences remained relatively stable (although with some intra-subject variability).

In Experiment 3, the explicit dissociation of side of motor response from side of stimulus presentation showed for the first time that a suggestion of Fisk and Goodale (1985) is indeed true--the hemispatial effects found in typical aiming-movement studies are related to the output side of visuomotor processing rather than the input side. In the last experiment of their study, Fisk and Goodale (1985) dissociated visual field from side of motor response, by having subjects fixate eccentrically. Their results did not suggest that the visual field that the target appeared in had any effect on obtained ipsilateral advantages. However, their targets always appeared in ipsilateral or contralateral *hemispace*. As long as the visuomotor systems responsible for the aiming response have access to an "eye-in-orbit" signal, then the position of the target relative to the body midline can be derived. In fact, there is substantial evidence that the dorsal stream of visual cortical processing in primates has ample signals of such a kind available. Single-unit neurophysiological study of the lateral intraparietal area and in frontal cortex (e.g., Boussaoud et al., 1993) has shown powerful modulatory effects of the position of the eye in the orbit on single-unit responses to visual stimuli. More recently, Galletti and colleagues (1993) have even suggested that the parietal cortex may extract a signal about target position in craniotopic (head-centred) coordinates. They have found cells in the parieto-occipital area (near the lateral intraparietal area) which seem to be unmodulated by the gaze position of the monkey. That is, the receptive fields are invariant with respect to the head (they could not test the intriguing possibility that such units might actually code target position independent of head position, since restraint of the head is inevitably necessary in single-unit studies of alert animals). Richard Anderson's group have also made a similar claim about cells in posterior parietal cortex (Snyder, et al., 1993).

This notion of extraction of three-dimensional position from retinal, orbital and cranial coordinate frames is reminiscent of Jeannerod's frequent reference to visual and proprioceptive "maps". Jeannerod argues persuasively that vision and motor systems have to be calibrated in order for accurate visuomotor control to be maintained. So far so good. What is less clear is whether he believes that this type of description is of a process, or that actual representations of space are somehow maintained in the neocortex by elaborate visual and somatosensory association processing. To be sure, somatosensory and visual information is indeed represented topographically in primary sensory cortices, but these maps are hardly veridical with respect to the body or the retinal world. Stein (1992) has recently argued that there is no explicit representation of space per se in the posterior parietal cortex, and many other authors who work in visuomotor control tend to agree (see the associated commentaries that accompany Stein's target article).

5.4 Summary and Suggestions for Future Research

Unfortunately this thesis does not go as far as originally intended in describing the nature of hand differences in motor control. Accuracy differences were obtained in hand-invisible reaching in some of the subjects (i.e., the sample of 14 in Experiment 1) but not others (i.e., in the larger sample of 26 in Experiment 3). Movement onset time advantages were seen for the left hand on some occasions, but again, as in the literature, not on all occasions. Similarly, durations tended to be shorter in right-handed movements than in left-handed movements. The largest effects found in this series of experiments seem to be related to the hemispace of the movement, and these may be independent of the availability of visual feedback. Besides the obvious need for replication, some additional experiments might strengthen the position that aiming movements of the left and right hand can be used to reveal some of the contributions each hemisphere makes to visuomotor control.

First, as I suggested earlier, if there are indeed greater hemispatial effects in the performance of the right hand, and these are related to the left-hemispheric praxis system, then larger hemispatial effects should not be seen in the left hand of left-handed subjects. The available neuropsychological data suggest that left-handed subjects should still, in about 65% of the cases, have left-hemispheric praxis (for review, see Bryden 1982). Independent assessment of speech lateralization in a large sample of left-handers by dichotic listening might allow for grouping subjects into those most likely to have left-hemisphere praxis versus those that do not. If the "left-hemispheric" left-handers show larger hemispatial effects in their *non-preferred* right hand, this would suggest that hemispatial effects are indeed related to the operation of the praxis system.

However, Kimura (1993) has recently reported the effects of focal brain damage on manual praxis in a sample of adextral subjects. Her data suggests that manual and oral praxic control may be vested in different hemispheres in adextrals, such that in many left-handers manual praxis does indeed depend more on the *right* hemisphere where oral praxis (as in dextral subjects) may depend more on the left hemisphere. If this hypothesis is true, then adextral subjects may indeed show larger hemispatial effects in the left hand, if these effects are related to the praxis systems. Both independent verification of Kimura's suggestion and replication and extention of the antipointing study will help clarify the issue of praxis and hemispatial effects in motor control.

Second, dissociation of the side of stimulus presentation and the side of subsequent motor response should be attempted in a way which produces equivalent eye movements in the experimental and the control conditions. Reaching with left-right displacing prisms or with a virtual reality display could allow for such an experiment to be undertaken, providing that oculomotor and skeletomotor systems adapted to visual-proprioceptive discordance equivalently. Descriptions of visuomotor coordination when wearing inverting and reversing lens systems suggests that compensatory strategies are evoked in the subject which are rather cognitive (reviewed in Howard & Templeton, 1966). Displacements of the optical array seem much easier to adapt to than reversals and inversions; however the new technologies related to virtual reality systems might allow for a fresh look at this question. My prediction would be that if visuomotor calibration could be achieved for oculomotor and manual systems, kinematics of movements would show the hemispatial effects related to the side of the movement rather than the side of the stimulus, as shown in Experiment 3.

Third, the attempt to attenuate right-hand advantages by manipulating stimulus characteristics should be attempted in a more theoretically vigorous fashion than some of the experiments in the literature to date. The dangers of both Type I and Type II errors in this domain are vast, given that several different conditions can be examined and that the occasional lack of a hand difference in any one of them is incorrectly interpreted as a more "spatially demanding" condition, post-hoc. One solution to this type of problem is to define "spatial" in a highly specific, operational fashion and then examine several conditions which vary along this dimension in the same subjects using the same experimental procedure (crucial when so many different variables have been shown to affect movement kinematics, see the General Introduction). This approach is unlikely to be terribly useful in the near future, given that experimental psychology has yet to reach consensus on what "spatial" really means. Arguably any movement is "spatial" in the sense that it takes place in coordinate spaces which vary from trial to trial).

A second solution to the problem of the "right-hemisphere" approach is to identify mechanisms that are more obviously "right-hemispheric" because they are differentially affected by right-hemisphere disease. Bisection seems a likely candidate for such a task (see Chapt. 3). Manipulations which affect line bisection performance in patients with right- but not left-hemisphere damage should produce changes in the performance of the left-hand in normal subjects, if hand differences in normals are useful tools in exploring hemispheric asymmetries. For example, right-hemisphere damaged patients tend to show increased movement onset times when reaching to targets relative to controls, while once they begin moving the durations of the movement are normal. Left-hemisphere damaged patients show the opposite pattern; normal movements onset times but prolonged durations relative to control subjects (Fisk & Goodale, 1988). In the current experiments, the left-hand tended to have faster onset times than the right-hand, while durations tended to favour the right hand. These results suggest that some of the variance in hand performance in normals is related to the "privileged access" hemisphere for that hand.

Additional investigations of bisection might proceed initially by varying the lengths of the bisections. In right-hemisphere damaged patients with neglect, reducing the length of the line to be bisected reduces the magnitude of the rightward error (and may result in leftwards errors with extremely short lines; Halligan & Marshall, 1988; Marshall & Halligan, 1990). This type of manipulation might produce a similar effect in left-hand performance in visuomotor bisection, or, alternately, could increase the localization demands of the task sufficiently to produce more dramatic differences in the kinematic profiles of the two hands.

Finally, results from this thesis and other investigations of reaching behaviours in normal subjects and infrahuman primates suggest that much work remains to be done regarding the proximal-distal distinction in contralateral motor control. Most of the empirical work on manual laterality where movements have been carefully recorded has been done on simple aiming movements. The few kinematic studies which have required greater participation of the hand have typically looked at dominant (i.e., right) hand performance exclusively (i.e., Jeannerod et al., 1990; Montagne et al., 1993; Servos & Goodale, 1994; Zaal et al., 1993). Carnahan et al. (1993) have compared aiming at single LEDs and grasping illuminated dowels in the same subjects, under conditions where the LED or the illuminated dowel unpredictably changed position during some of the trials. They found differences which included changes in the initial portion of the velocity profile in grasping but not in aiming on trials where the target was displaced during the movement relative to control trials. The authors concluded that grasping vs. aiming movements utilize visual feedback about target positions in different ways (Carnahan et al., 1993). Although this study suggests that kinematic differences between grasping and pointing movements within-subject are likely, unfortunately, the two types of movements were performed using only the right hand in the eight subjects who participated in their experiment.

High-resolution recording of reaching and grasping movements in both hands of a large sample of subjects would be one way to examine the ipsilateral/contralateral distinction in normals subjects. PET and functional MRI might also be useful in determining in what respects the "crossedness" of our motor systems is asymmetrical and related to the operating principles of the praxis system (unfortunately, the majority of the PET studies concerning reaching and/or motor performance to date have tended to examine the performance of the right hand exclusively; i.e., Jenkins et al., 1994; Kawashima et al., 1994). If in many respects we differ from nonhuman primates in this dimension, these types of study could provide great insight into the nature of the praxis system which seems so well-developed in our species.

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