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Characteristics And Control Of Bilateral Arm Movement In Humans

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CHARACTERISTICS AND CONTROL
OF
BILATERAL ARM MOVEMENT IN HUMANS

by

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

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ABSTRACT

Many of our daily normal activities require a close matching and coordination of movements of the two arms. In the present study an attempt was made to answer the following questions: 1) How precisely are movement properties matched for the two arms? 2) Is matching of movements of the two arms affected by visual information? 3) Are movements of one arm affected by kinesthetic information arising from the contralateral arm? 4) Does alteration in the motor performance of one arm affect movement performance in the other arm?

Studies were made of step-tracking movements in normal humans. During experiments, subjects grasped a vertical rod attached to a horizontal manipulandum bar. The subject's shoulder was abducted to 90 deg with the wrist semi-pronated. The manipulandum bar was pivoted above the subject's elbow and could be rotated in the horizontal plane. Subjects made flexion/extension movements about the elbow. Both simultaneously (using two manipulanda) and independently made movements of the two arms, performed at the subject's own speed, were studied.

During simultaneous arm movements, movements of the two arms were initiated at the same times. The degree of matching of movement parameters as amplitude, duration and

peak velocity was dependent on visual information from the arms. In the absence of visual information, these parameters were exactly matched in simultaneous movements of the two arms. When visual information was provided by displaying the position of right or left arm to the subject, the movements of the "non-displayed" arm were consistently of greater amplitudes and velocities than those of the "displayed" arm. Movement durations were affected only when the left arm position was visually displayed and showed asymmetry for handedness. The relation between movement peak velocity and movement amplitude was linear for each arm and was the same (matched) for both arms under all visual conditions. This matching in movement velocity-amplitude relation was seen for both the simultaneous and the independent movements.

In some experiments the normal motor performance of the left (non-preferred) arm was experimentally altered. During trials on simultaneous movements, a weight (1 lb or 12 lb) was added to the manipulandum during the experiment. During trials on independent movements, subjects continuously wore a 1 lb weight on their left forearm for one week. In both conditions, loading altered the slope of the peak velocity-amplitude relation in movements of the left (loaded) arm. In both cases, similar changes occurred in the velocity-amplitude relation of the right (non-loaded) arm.

The effect of proprioceptive input on arm movement performed without visual information was also tested. High frequency (120 Hz) mechanical vibration of muscle tendons was used to stimulate muscle spindles of the biceps or triceps brachii muscles. The effects of this vibration on movements of the opposite arm were studied. Vibration of the stretched triceps muscle of a stationary arm (arm flexed) produced overshooting of the intended flexion end-position by the opposite (moving) arm. Vibration of the lengthening triceps muscle of one arm produced: i) undershooting of the intended flexion end-position by the same arm and ii) overshooting of the intended flexion end-position by the opposite (non-vibrated) arm. The data show that vibration of the muscles in one arm affects movements being made at the same time with the opposite arm. The changes in movements of the non-vibrated arm are opposite to those occurring in the vibrated arm.

It is concluded that the motor actions of the two arms are functionally linked and the two arms work as an ensemble. Matching of movements made by the two arms may reflect the operation of a common motor command or program which can be modified by visual and kinesthetic information.

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INTRODUCTION

In many normal motor activities, such as walking, jumping, swimming and flying, etc., matching and co-ordination between the movements of the opposing limbs is a necessity for the movement to be successfully performed. A bird, for example, has to make exactly similar movements with both wings in order to fly. It is also obvious that overall step lengths, speeds, durations, etc. must be the same for the two legs to enable an individual to make a straight balanced walk. The same must be true in an activity such as rowing a boat; any consistent mis-match in movement performance of the two arms causes the boat to move in a circle.

Bilateral multi-limb movements are older than unilateral (unimanual) movements in phylogenetical development. Motor centres as low as the spinal cord have been shown to have the capability to generate the neural patterns needed for such multi-limb movements as in walking (Grillner, 1981). The skilled movements performed by one limb (unimanual movement) in man and in the primates can be considered as an extension of an evolutionary process, emerging from the development of the original multi-limb movements.

So far studies on bilateral limb movements are relatively few as compared to the amount of research devoted to the studies and understandings of mechanisms underlying single limb movements. In these studies, some investigators have compared movements of the two limbs with the aim of determining whether there were consistent differences related to handedness. Such differences have been found in tests requiring either simultaneous or independent movements (e.g., Flowers, 1975; Peters and Durding, 1978; Wyke, 1967, 1968, 1969). Many of these studies involved a tapping task, often as a variant of Fitts'paradigm (Fitts, 1954).

Movements made by the preferred limbs, either right or left, were more accurate, faster and less variable than those made by the non-preferred limb. Interesting exceptions to this were found by Flowers (1975) and Kelso, Putnam and Goodman (1983). Flowers, for example, found preferred hand performance was better in a Fitts tapping task but no differences when a pattern of tapping was required. He suggested that the latter consisted of ballistic movements and the former of feedback-controlled movements and that differences in performance of the two limbs were speed related. Kelso et al.(1983) found no differences in reaction time or movement time for independent tapping movements. They also found that movement trajectories were the same for both limbs during simultaneous bimanual movements. If the limbs were to be moved to targets of different sizes (i.e., the movements were of different difficulty, cf. Fitts, 1954) the arm moving to the "easy" target slowed while that moving to the "hard" target speeded up.

Many studies have also been made on simultaneous arm movements (e.g., Kelso, Southard and Goodman, 1979 a,b; Marteniuk and MacKenzie, 1980) and of tightly linked limb movements as in walking (e.g., English, 1979, 1980; Stuart, Withey, Wetzel and Goslow, 1973). In many of these studies, interest has been focussed on the space-time structure of inter-limb co-ordination or on the patterning of movements in the limbs during walking. English (1979), for example, showed that the duration of EMG activity in the same muscles of the two fore- or hindlimbs was identical during the walking cycle in the cat. In other studies related to walking movements, it has also been found that within the mammalian spinal cord there are neuronal circuits that regulates stereotypical and rhythmical movements of the hind limbs (Grillner,1981; Blerkinblit, Deliagina, Feldman, Gelfand and Orlovsky, 1978; Selverston, 1980). These neuronal circuits, called central pattern generators (CPGs), set the periodicity, intralimb synergies, and interlimb coordination.

In one of the more theoretically interesting studies, Kelso and his colleagues studied simultaneous cyclic movements of the index fingers of the two hands (Kelso, Holt, Robin and Kuglet, 1981). They reported that there was a tight phase coupling of movements by the two fingers. In addition, the frequencies and amplitudes of free movements were the same for the two digits. Studies have also been made on the effects of altering the motor performance of one limb on movement performance by the contralateral limb. Movements of an intact limb are impaired by concommitant attempts to move the contralateral paralytic limb (Cohn, 1951; Hausmanowa-Petrusewicz, 1959). Cohen (1970) reported changes in the sequence of rhythmic movements of one limb when rapid movements is started by the contralateral limb. More recently, Kelso et al., (1981) showed that the phase relation between simultaneous finger movements in the two hands remained constant even in the face of external mechanical perturbation. Indeed, they showed that movements of the two sides tend to become entrained with one another. Kelso and his colleagues interpreted their findings in terms of the properties of non-linear, limit-cycle oscillators (see also Stein, 1976). It is clear therefore from all the evidence presented above that movements of the opposing limbs are very closely interrelated.

In the present investigation, this interrelation between the movements of the opposing limbs was examined. The characteristics of movements made either simultaneously or independently by the two arms "at the subject's own speed" were studied. An attempt was also made to investigate the mechanism behind the control of these bilateral arm movements using unilateral short- and long-term loading as well as unilateral muscle-tendon vibration.

HISTORICAL REVIEW

I. Control of Multi-limb Movements

A. Locomotion

Many movements by man and animals are parts of co-ordinated activities of two or more limbs. In activities such as flying, swimming or walking, movements of one wing or limb are tightly linked with those of the other wing or limbs. It has long been recognized that many co-ordinated motor behaviours can occur independent of the brain as a whole. The phenomenon of the chicken with its head cut off running about the backyard is well established in popular languages.

A more formal description of this phenomenon, that is, reflex stepping in decapitated or spinalised cats and dogs was given before the days of Sherrington (Denny Brown,1979). It was believed that the stepping obtained in those preparations was a rhythmic series of reflex responses excited by continuous stimulation applied either to various peripheral points outside the limb or to the cross-section of the cord itself (Denny Brown, 1979). The role of peripheral signals from the limbs in initiating and maintaining walking movements was considered essential because of the observation of serious impairment in walking ability of monkeys following dorsal root section (Mott and Sherrington, 1895). It was hypothesized, therefore, that the process of walking was a 'chain of reflexes' that would continue once initiated and for which afferent input from the limbs was an essential requirement.

An early observation was that stepping movements could also occur under deep anaesthesia when peripheral reflexes were abolished. Brown (1911, 1912, 1914) showed that alternating rhythmic activity of ankle flexor and extensor muscles could be generated by the isolated spinal cord after bilateral transection of the lumbosacral dorsal roots. He postulated the existence of two centres of neuronal networks in the spinal cord, one centre for each limb, that were responsible for the rhythmic walking. This postulate was tested more than fifty years later by many workers (see below) and proved to be a basic concept in the physiology of locomotion.

The understanding of the mechanisms of locomotion was advanced following the studies of Orlovsky and co-workers. They demonstrated normal walking movements in decerebrate cats following electrical stimulation of an area of the brain just caudal to the section made for decerebration

(Shik, Severin and Orlovsky, 1966). They called this area the mesencephalic locomotor region (MLR). The mesencephalic cat preparation was of great use in the research on locomotion since it allowed stimulation, recording and drug adminstration on a well controlled animal that could be made to walk in place on a treadmill as desired.

Deafferentation or curarisation, which excluded all movement-related feedback were used to demonstrate locomotion in the mesencephalic cat preparation in the absence of peripheral feedback (Grillner and Zangger, 1975, 1979). The rhythmic muscle activity in the absence of movement in the curarized animal was termed fictive locomotion (Grillner and Zangger, 1979). Thus the concept was established of centres in the spinal cord that can generate the motor output for locomotion. These centres were referred to as central pattern generators (CPGs). It was shown later that, although these centres can generate a motor output by themselves, they were affected both by peripheral feedback (cf. Duysen and Pearson, 1980) and by descending neural signals from supraspinal structures (cf. Orlovsky, 1972). It was also found that ascending pathways supply higher structures (via ventral spinocerebellar pathway) with information by relaying an efference copy of the CPGs activity (Arshavsky, Berkinblit, Gelfand, Orlovsky and Fukson, 1972; for further references see Grillner, 1981).

Thus, the basic network of neural circuitry for locomotion is present in the spinal cord. This network is capable of generating neural patterns to the limbs to initiate and maintain walking movements even in the absence of central commands from higher centres or centripetal feedback input.

In the awake walking cat, electric stimulation applied to one hindlimb induced changes in the duration of the stance and swing phases of the contralateral as well as the ipsilateral limb (Duysens and Stein, 1978). Similar results were obtained with mechanical perturbation applied to the paw dorsum of one forelimb in the awake or decerebrate walking cat (Matsukawa, Kamei, Minoda and Udo, 1982). Thus peripheral feedback is needed for fine co-ordination in the act of locomotion and for adjustment of timing during the step-cycle.

B. Inter-limb reflex studies in reduced animal preparations

That activity in one limb can affect the contralateral limb has long been recognized. Understanding of the physiological mechanisms involved largely came from studies of reflex activity. These studies were of three main types. I) Studies of Sherrington and his colleagues on the decerebrate cat, these studies unravelled the neuronal basis of such phenomenon as the crossed extension-reflex (cf. Sherrington, 1910). 2) Electrophysiological studies aimed at specifying the receptors originating in one limb which are responsible for modifying reflexes occurring in the contralateral limb (e.g. Perl, 1957, 1958, 1959; Holmqvist, 1961). 3) Studies utilizing tendon vibration in decerebrate cats to activate crossed reflexes by selective activation of muscle spindle receptors or Golgi tendon organs (Baxendale and Rosenberg, 1976, 1977).

Sherrington (1909) showed that lengthening and shortening reactions of muscles in one limb were frequently accompanied by reflexes in the contralateral limb. Forcibly stretching the extensor muscles of the knee and ankle in the decerebrate cat produced contraction of the extensor muscles of the opposite side. This crossed excitation accompanying ipsilateral inhibition had originally been described by (Philippson, 1905) and Sherrington in fact called it Philippson's reflex. Sherrington also showed that noxious stimulation, applied to either skin or muscle of one limb produced crossed extension of the contralateral limb, the crossed extension-reflex (Sherrington, 1910). He indicated the importance of this cross linkage in the usual mode of progression such as the walking and running step. When both limbs are engaged in reflex stepping the extensor phase of the step in one limb is reinforced by a crossed extension reflex whose stimulus arises in the flexion of the other limb; and similarly the flexion phase is reinforced by a crossed flexion-reflex derived from the other limb. Although he went on to show that both the ipsilateral and contralateral reactions during the so called Philippson's reflex depend on receptors lying within muscles, the problem of specifying the receptors activated during these reflexes as well as the central connections underlying the crossed reflexes were left unresolved at that time.

Perl (1957) demonstrated in the spinal and decerebrate cat that a single shock applied to a peripheral nerve containing cutaneous fibres evoked a discharge in contralateral ventral roots. Using graded electrical stimulation of muscle nerves or applying graded loads to the muscle tendon, he attempted to separate out the effects of group I components of muscle nerves on the contralateral limb reflexes (Perl, 1958, 1959). He concluded that the Ia fibres of any particular muscle produced an inhibition of the motoneurones of the corresponding muscle on the contralateral side. Activation of Ib fibres, which inhibited the motor neurones of the muscles of origin, produced excitation contralaterally. Using decerebrate cats, Holmqvist (1961) tested the action of conditioning volleys on contralateral monosynaptic reflex discharge recorded from cut ventral roots. She showed that the contralateral actions of Ia and Ib fibres could not in general, be separated. In the few cases where separation was possible, the activity in Ia fibres produced a crossed facilitatory action. This was not in accord with the conclusions of Perl that crossed actions from Ia and Ib systems of the knee extensors and flexors are organized in a double reciprocal fashion. More recently, Baxendale and Rosenberg(1976, 1977) utilizing tendon vibration, were able to selectively activate Ia and Ib neurones in the decerebrate cat. They demonstrated that the activity in Ia axons from the soleus muscle exerted a contralateral inhibitory action on both flexors and extensors of the contralateral knee and ankle whilst Ib activation produced the reverse effects. These conflicting resules might be attributed to the level of decerebration used in these various studies as well as the intensity of the stimulation used. In any case, it is clear from these different physiological studies that reflexes of muscle and cutaneous origin on one side of the body have modulatory effects on the motoneurones of the contralateral side.

C. Inter-limb reflex studies in man

Activities in muscles of different limbs following cutaneous stimulation as well as muscle stretching have also been shown to occur in normal humans. Kearney and Chan(1979) demonstrated that reflex responses to cutaneous electrical stimulation of the foot can be detected in both leg and arm muscles of normal human subjects by averaging stimulus-related changes in tonic electromyographic (EMG) activity. Proprioceptive stimulation produced by ankle displacement in man also evoked interlimb reflexes demonstrated as modulation in tonic EMG activity of arm and contralateral leg muscles (Kearney and Chan, 1981). The interlimb responses, evoked by ankle displacement, were greater in magnitude and shorter in latency than those obtained with cutaneous stimulation.

Similar findings were reported by Meier-Ewert, Homme and Dahm (1972). Electrical stimulation of the sole of the foot, the finger tips and the base of the fingers produced bilateral and widespread changes in EMG activity. These changes occurred at latencies suggesting they might be produced through long-loop reflexes (Shimamura and Livingston, 1963; Shimamura, Mori, Matsushima and Fujimori, 1964; Gassel, 1970). EMG responses of similar amplitudes and latencies (50 ms) from right and left leg muscles (tibialis anterior) in man were also obtained following brisk anterior tilt of one side (Dietz and Berger, 1982). This relatively short latency indicated that a right-left co-ordinated leg muscle activation at a spinal level providing a symmetrical leg muscle activation during balancing. Thus, as seen in reduced animal preparations, there is evidence that the musculature of the different limbs are linked and that activity in muscles of one limb may affect activity in other limbs in intact humans.

D. Role of muscle receptors in humans

As discussed above, changes in the length of muscle in one limb can produce changes in muscles of the other limbs. These effects may be related to activation of muscle spindles, the length-sensitive receptors in the muscle. In intact humans, muscle spindles may be activated experimentally through vibration of the muscle tendon. Granit and Henatsch (1956) found that high frequency muscle vibration induced strong, sustained activation of muscle spindle primary afferents. The influence of vibrating a passively held muscle initiated a sustained contraction due to reflex motoneurone discharges (Eklund and Hagbarth, 1965). This vibration induced reflex contraction was called the tonic vibration reflex (TVR).

Knowledge about the effect of muscle vibration accumulated following various experimental studies in three stages. Originally, Echlin and Fessard (1938) reported that mechanical vibration of muscle tendons with a tuning fork resulted in activation of muscle spindle receptors leading to neural discharge from a whole nerve in animals. Vibration was shown to selectively activate the primary Ia afferents from muscle spindles in the cat (Brown, Engberg and Matthews, 1976; Matthews, 1973). This responsiveness of muscle spindles to mechanical vibration has been used to investigate the central actions of Ia afferents.

Goodwin, McCloskey and Matthews (1972,a,b) showed that vibration of the muscle tendons around the elbow joint in man produced a subjective sensation of arm position which was different from the actual joint position. Subjects perceived their arm as moving in the direction that would be associated with stretch of the vibrated muscle. For example, if the biceps muscle was vibrated and the forearm was prevented from moving into flexion, apparent extension of the forearm was experienced. It was later found possible to elicit illusory motion of the body in nearly any desired direction by vibrating the appropriate muscles (cf. Lackner and Levine, 1979). These findings were consistent with activation of length sensitive receptors such as the ones (primary spindle endings) excited by the vibratory stimulus.

Some studies have been made of the effect of vibration applied during voluntary movements in humans (Capaday and Cooke, 1981, 1983). These experiments showed that vibration of the muscle antagonistic to the movement produced a significant undershoot of the required target position for that movement. It was shown, for example, that biceps vibration applied during forearm extension resulted in an undershoot of the required extension target. However, the same vibration applied during flexion when the biceps was shortening had no effect on the attainment of the required flexion target. This latter result was explained by the sudden decrease of muscle spindle discharge during rapid muscle shortening (Vallbo, 1973; Goodwin and Lushei, 1975).

More recently it was found that muscle vibration applied to one arm influences the position sense of the opposite arm in humans (Lackner, 1984). Vibration of the right biceps brachii muscle with the right arm position fixed, affected the apparent position of the left arm. In the absence of visual feedback, subjects placed their left (non-vibrated) arm at a more extended elbow angle (more than 90 deg for example) than required (90 deg) by the experimenter.

II. Hand Preference

Most of the work which has been done on comparing movements of the two arms has been in the context of hand preference which is accompanied by differences in the motor skill of the two hands. Early studies by Woodworth (1899) for example, described "superiority" of the right hand over the left hand in performing voluntary movement whether the subject made the movement with the eyes open or closed. Woodworth found that increased movement speed severely decreased movement accuracy of the left hand as compared to the right hand.

Hand preference has been attributed to asymmetries in cerebral organization possibly linked with whatever underlies the tendency of most humans to develop speech in the left hemisphere (Annett, 1972, 1975). Motor deficits resulting from lateralized damage to either the right or left hemisphere were studied by Wyke (1967, 1968, 1971). In one study Wyke (1967) examined a left hemisphere lesion group, a right hemisphere lesion group and a control group on two tasks designed to measure rapidity of arm movement independently for each of the two arms. The first task measured speed of arm movement prior to depression of a telegraph key; the second measured rate of repetitive, alternating tapping. Similar results were obtained for both tasks. For the control group (all right-handed), the right arm performed significantly faster than the left. The right hemisphere lesion group was significantly slower than the control group in terms of left arm performance only (i.e., the arm contralateral to the cortical lesion). In contrast, the left hemisphere lesion group had significantly slower performance than the control group for both arms, although the right arm (contralateral to the lesion) was slower than the left.

In a later study (Wyke, 1971) found that patients with left hemisphere lesions took significantly longer time in learning a motor task and made more errors compared to normal group in performing it. Patients with right hemisphere lesion showed minor deficiencies early in practice, but did not show a significant difference from control subjects in the proficiency attained. Wyke concluded from these results that the left hemisphere was specialized for bilateral motor control as well as the organization of motor programming.

Many investigators have associated the typical right hand superiority in tasks such as rapid finger tapping, or reciprocal tapping involving arm movements, to the tendency of the left hemisphere for sequential processing (Peters and Durding, 1979; Todor and Doane, 1978; Todor and Kyprie, 1980). This idea is supported by studies showing that simultaneous verbalization produces a profound decrease in the performance of the right hand (Hicks, Provenzano and Rybstein, 1975; Lomas, 1980). Apparently, this effect is due to the intrahemispheric interference between the left hemisphere's involvement in speech production and its motor control of the right hand (Kinsbourne and Hicks, 1978; Lomas and Kimura, 1976). Similarly, a left hand superiority in tasks such as tactile discrimination and position reproduction have been attributed to a right hemispheric superiority for visual spatial ability or parallel precessing (Ingram, 1975; Kimura and Archibald, 1974; Young and Ellis, 1979). Hence, the left hemisphere is superior in processing information with a sequential or temporal structure, i.e., where the processing of current information is in reference to prior information. In contrast, the right hemisphere is superior to the left when the task needs parallel processing, i.e., where items of information are simultaneously processed such as in spatial judgements.

III. Cross Education

Another approach which has been taken to study the influence of activity in one limb on motor performance of the contralateral limb has been through the phenomenon of cross education or cross transfer of strength from the exercised ipsilateral muscles to the unexercised contralateral muscles. Scripture, Smith and Brown (1894) studied cross education experimentally in relation to the speed, strength and accuracy of relatively simple movements. They reported that after a period of exercise involving the right hand, concomitant improvement was experienced in the unpracticed left hand. They attributed this effect to what they termed "indirect practice". Davis (1898), conducting similar research in the same laboratory, coined the term "cross education" to describe the effects that he observed and postulated that some central mechanism must be operating in transferring the effects between the two sides. Wissler and Richardson (1900) also found evidence of cross education when training two subjects, suggesting that there was a diffusion of motor impulses from the exercised arm to the unexercised contralateral arm.

Hellebrandt, Parrish and Houtz (1947) reported a concurrent training effect of the contralateral muscles in subjects who exercised the knee extensors, the elbow flexors and other muscles of the arm. Hellebrandt, Houtz and Krikorian (1950) had subjects made maximal voluntary wrist extension, and found that the contractile power and endurance of the non-exercised band were increased. They suggested that cross education is the outcome of irradiation and tonic postural reflexes arising in and acting on the limbs leading to diffusion of motor impulses to the unpracticed side. This reflected the possible connection between the isometric cocontraction of the muscles of the unpracticed side and the degree of the effort exerted by the subjects in order to preserve balance and to avoid the shifting of the centre of gravity. In support of this view, other investigators demonstrated that action potentials in the contralateral muscles could be detected during involvement of the ipsilateral side with physical activity (Gregg, Mastellone and Gersten, 1957; Sills and Olson, 1958) indicating radiation of nerve impulses to extremities other than the active ones.

Slater-Hammel (1950) administered 3 weeks of right arm flexion exercises and showed that the subjects gained significantly over a control group in the contralateral, (left) arm. Although he could not rule out the possibility that bilateral effects resulted from raising the subject's tolerance to fatigue, he suggested that exercise of one arm produces a positive and significant improvement in the muscular performance of the other arm and recommended it for treatment of patients with joint immobilization.

Some investigators have compared the effects of isotonic and isometric training on cross education. Rasch and Morehouse (1957), for example, reported that their subjects showed significant improvement on the unexercised side with isotonic but not with isometric exercises. There is some histological evidence supporting the concept of cross education from isotonic exercise. Reitsma (1969) performed surgical procedures on three groups of white rats so that in the first group the rectus femoris was the only extensor, in the second group, the plantaris was the only flexor, and in the third group, the soleus was the only flexor. As a result of 3 weeks running for a maximum of 12 hours/day, 5.5 days/week, there was evidence of muscle fibre regeneration in the same muscle of the non-operated side.

The physiological mechanism of cross education has therefore, not yet been fully explained. It might be that during motor activity on one side of the body, irradiation of neural activity from cortical motor areas to contralateral symmetrical cortical areas (i.e. direct interhemispheric interaction of motor corollary outflow) causing trans-callosal facilitation that accounts for part of the mechanism. Evidence for such a postulate awaits further experimental studies.

IV. Co-ordination of Two-Handed Movements

The ultimate goal of studying interaction between activities of two or more limbs is of course to understand principles and mechanisms underlying motor control and coordination of complex movements involving multi-degrees of freedom. Movements of the two arms were among those studies that received some attention recently. One of the interesting conclusions reached by workers on co-ordination of two-handed movements in humans was that of Kelso and colleagues. From experiments based on Pitts' paradigm (Fitts, 1954) they found that simultaneous motor actions of the two arms in man are linked by a common parameter, movement duration (Kelso et al, 1979a,b, 1983). In these experiments subjects moved an index finger from a starting position to tap a plate in response to a command signal. Single as well as simultaneous arm movements were used. Movements of short distance to large target (termed easy) were compared with movements of long distance to narrow targets (termed difficult). In all situations movements of the two limbs started and ended at nearly the same time in spite of one being made easy and the other, made at the same time, being made difficult. The concept that emerged fro these experiments was that simultaneously performed actions as two arm movements share a common clock even when the other features of the movement (movement kinematics) are different. Based on Kelso's work and also some experiments performed by Schmidt and colleagues (Schmidt, Zelaznik, Hawkins, Frank and Quinn, 1979) the latter proposed a model for the processes leading to the two-handed aiming response. According to this model, the first step in the process is program selection. The next step would be the specifications of parameters common to movements of both sides, the overall movement time according to the findings of Kelso et al (1979a,b). Finally parameters are added that specify features such as movement amplitude for each of the two arms. Figure 1 shows these steps as proposed by Schmidt et al (1979) for two-handed aiming response.

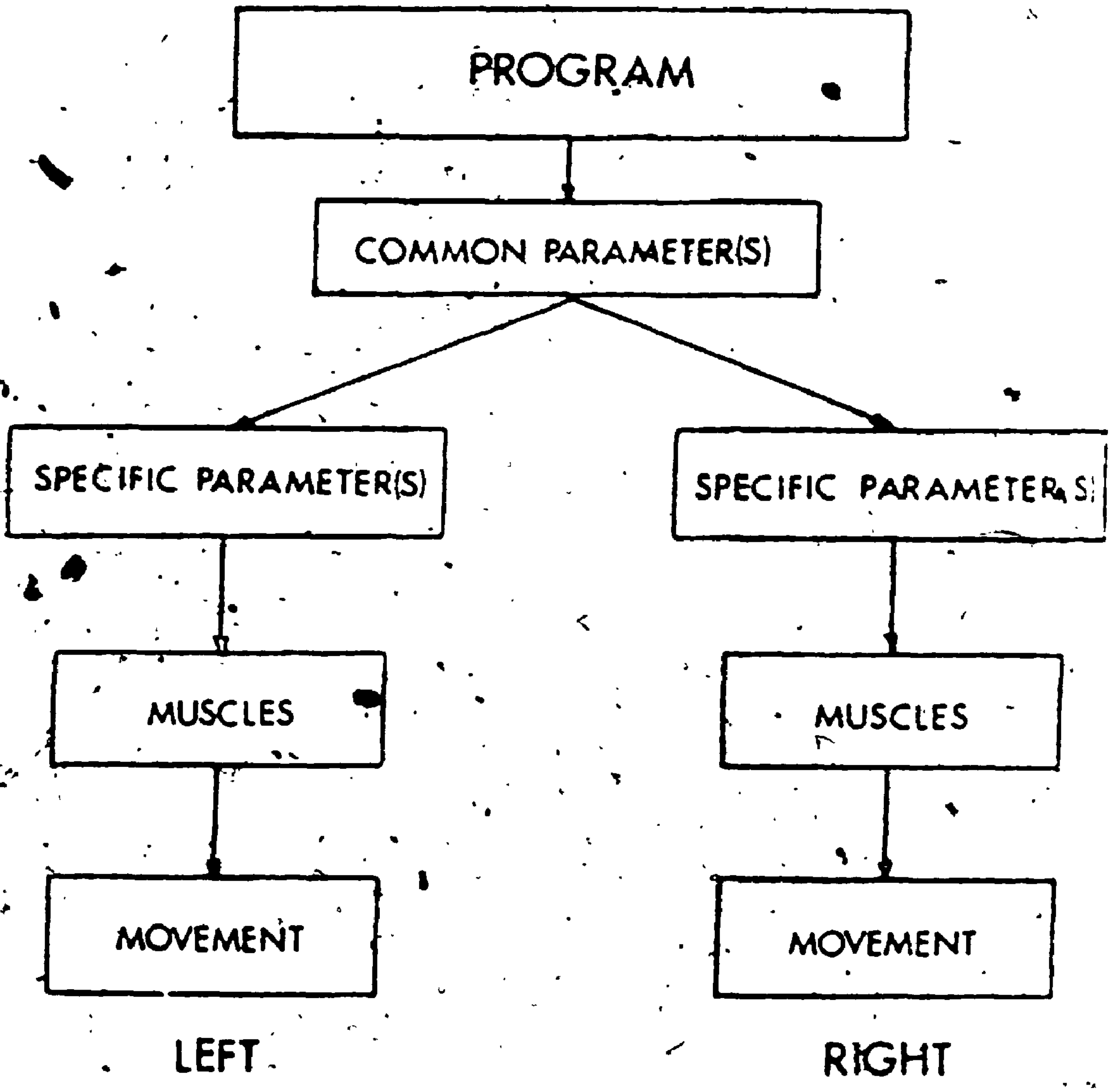
Peters (1981), on the other hand, suggested two possible models for co-ordination of movements of the two hands. In the one model, there would be independent control of the two limbs. That is, there would be two separate, central control systems. In the other model, there would be a single central system which acts on both limbs. Thus, in the one case there would be two, independently controllable command systems for movements of the two limbs whereas in the other there would be a single command that would be distributed to both limbs. Peters' data supported the notion that one single system initiates and terminates movement in two subsystems, each of which guides one hand. This hypothesis is basically similar to the one mentioned earlier by Schmidt et al (1979).

V. Analysis of Simple Movement

It has long been known since work by Woodworth (1899) that limb movements by human subjects are performed with increasing error as the subject moves the limb faster. That is to say, movement to a determined destination can be made more accurately given a longer time. This speed-accuracy

Figure 1

Motor program and order of addition of parameters that result in a two-handed aiming response. (Schmidt et al, 1979)


PROGRAM
COMMON PARAMETER(S)
SPECIFIC PARAMETER(S)
SPECIFIC PARAMETER(S)
MUSCLES
MUSCLES
MOVEMENT
MOVEMENT
LEFT
RIGHT

interrelation of movement performance was carefully examined by Fitts in 1954 and was, for the first time, systematically defined by a simple equation. The equation that is now known as Fitts' Law states:

$$MT = a+b \log_2 (2D/W)$$

where MT is movement time, D is the distance moved, W represents accuracy expressed as target width and a and b are constants that represent complexity of the movement under study.

Fitts and Peterson (1964) extended this study and found that this equation accounted for 99% of the variability in movement time for various combinations of movement amplitudes and movement precisions. It was later found by many workers that this equation was applicable to movements made by old as well as by young people, for movements made by monkeys and in a variety of other situations (see a review by Keele, 1981 for ref.). These studies were done on movements made with visual feedback and it was suggested that this feedback was an important factor for Fitts equation. This was because the accuracy of translating visual perception of the distance to be moved into actual movement was believed to affect the movement time. It was found that movements lasting longer than 250 msec were under visual control. However, accuracy for very fast movements (<250 msec) was still found to be related to speed. Schmidt, Zelaznik and Frank (1978) and Schmidt et al (1979) postulated that movement amplitude depended on the amount of force generated during the movement. In their opinion, the required accelerative and decelerative forces for movement are programmed. They found that the variability in movement end point was proportional to the ratio of distance/movement time. According to Schmidt and co-workers, since the forces determine the distance for the limb movement, then movement distance was programmed. This hypothesis gained support from experiments performed by Hallett, Shahani and Young (1975) that showed electromyographic activity in the form of pulses corresponding to the accelerative and decelerative forces (the triphasic emg pattern). In addition to the pulses necessary to cover the movement distance, the triphasic emg pattern of Hallett and co-workers also contained a final sustained agonist activity which was assumed to hold the joint in the new position (see below for programming final movement position).

Bizzi, Polit, and Morasso (1976) on the other hand showed that what may be programmed is not movement amplitude but rather the final position of the movement. They made their conclusion following experiments on deafferented, vestibulectomized monkeys. They tested head movements in this monkey preparation in the dark where targets for final position were switched off once the animal moved the head. It was found that the animal, in spite of total deprivation of feedback was able to attain the correct final position with the head movement. In addition Bizzi et al (1976) showed that if the head was loaded during the movement with a spring load the animal undershot the final position as long as the load was maintained but immediately attained the correct position once the load was removed. Similarly, inertial loading of the head did not prevent the monkey from reaching the final correct position. They suggested that the end position of the movement was determined by setting ahead of time the stiffness in the opposing muscles around the joint (agonist and antagonist muscles) for the new position. This was later confirmed by Bizzi and Polit (1979) using arm movements in the monkey, by Kelso (1977) and Kelso and Holt (1980) for finger movements in human subjects and later by Schmidt (1980) for rapid arm movements in humans. These experiments strongly supported the theoretical analysis of Feldman (Astrayan and Feldman, 1965) that suggested that the location of the moving limb can be programmed independently of the distance by presetting the stiffness in the opposing pair of muscles around the moving joint.

Cooke (1980) showed that movements similar to human movements can be reproduced using a model that simulated the human arm as a damped spring having a mass. The model consisted of a pair of opposing springs that represented the agonist and antagonist muscles of the arm. Movement could be produced by a step change in the stiffness of these springs. The model also showed that there was a strong linear relationship between movement peak velocity and movement amplitude and that the slope of this relationship was an estimate of the stiffness of the systems, which can be adjusted by changing the length-tension relation between agonist and antagonist muscles. It should be noted that the velocity-amplitude relation is determined not by programming distance but merely by setting stiffnesses of the opposing springs for a terminal location.

Schmidt's analysis that the force was the timed variable in ballistic movements gained support from experiments by Freund and Budingen (1978) on finger movements in humans and by Ghez and Vicario (1978) in the cat. Freund and Budingen found that subjects moving the forefinger as rapidly as possible showed the same movement time for different distances of finger flexion. When the forefinger was isometrically flexed as quickly as possible the time to peak force developed by the flexion force was the same for different isometric forces. This was achieved by linearly increasing the rate of increase in the force of the finger.

Ghez and Vicario (1978) showed similar results for the time to peak force in forelimb movement of the cat.

For fast (ballistic) movements, therefore, the underlying mechanism can be explained by combining the two hypotheses: the distance programming of Schmidt and colleagues for the first part of the movement that corresponds to the initial emg pulses of Hallett et al.(1975) and the final position programming of Bizzi and coworkers that correspond to the final sustained agonist activity in the Hallett et al. emg pattern. On the other hand for slow movements the final equilibrium point hypothesis of Bizzi provides sufficient explanation since the emg pattern for the slow smooth movement contains a tonic activity in the agonist muscle alone.

METHODS

I Subjects:

A. Normal subjects

A total of 27 human subjects were studied in the various aspects of this thesis. Subjects were of either sex and ranged in age between 16 and 45 years. They were all right-handed. Handedness was determined by asking the subject which hand he/she preferred to use for normal daily activities. Two female subjects were patients wearing an orthopaedic cast on their left forearms (see description of patients below). The rest of the subjects (25) were healthy individuals with no known history of motor disorders. All subjects and patients gave their informed consent to the study.

B. Patients with orthopaedic cast:

The orthopaedic cast of the following two patients was an ordinary plaster cast used for supporting bone fractures. Each patient had the cast on the left forearm starting from the elbow joint (joint not included) and extending over the whole forearm and wrist joint (joint included). The cast therefore, did not interfere with the movements examined in this study (elbow flexion-extension movements).

(i) K.G. : This 21 year old right-handed female had sustained an accidental fracture of her left scaphoid bone. One day following the accident, her left forearm was put in a plaster cast weighing 0.45 kg . She was first introduced to the experimental study 11 weeks following her injury with the cast still on her left forearm. There were no signs or symptoms of left arm dysfunction or pain when her arms were first examined for motor performance. She was tested 23 times (total) over a period of 5 months for movements made independently by the two arms (see below). The cast was removed for a period of one week in the middle of the 5 month period and was replaced by a light weight (.18 kg) cast. The patient was tested four times during the week the cast was off. The patient was also tested twice with the new cast on and for four times after it was permanently removed at the end of the 5 months.

(ii) U.B. : This 45 year old right-handed female had a Smith's fracture (fracture of the radius near its lower articular surface with displacement of the fragment toward the palmer aspect) of her left arm following a fall. Her left forearm was put in a 0.55 kg plaster cast one day following the accident. There was no pain or other signs or symptoms when she was first examined for bilateral, independently made arm movements (see below). The cast had been in place for one month when she was first tested. She was tested 7 times over a period of 7 weeks with the cast on and once after the cast was removed.

II. General Procedures

A. Experimental paradigms:

All experiments were done in a quiet room at a comfortable environmental and temperature conditions. During experiments, subjects were comfortably seated in a modified dental chair..The forearm was positioned horizontally with the upper arm abducted and the elbow resting on a support. The subject grasped a vertical rod attached to a horizontal manipulandum handle that was pivoted just above the elbow. The subject could then rotate the manipulandum in the horizontal plane by making flexion/extension movements about the elbow joint. Using such movements, the subject was required to follow a target displayed as a vertical bar on an oscilloscope placed 1m in front of him. The target switched every three seconds between two fixed but adjustable positions. The width of the bar indicated the target width. The targets were not mechanically detectable and were not bounded by mechanical stops. The positions of both targets could be independently varied. In all the experiments described below the target width was 3 degrees and the target changed position every 3 seconds. The task was not a "reaction time" task; the subject was not required to minimize his/her reaction time to the change in target position. This instruction resulted in movements that were clearly "step-like in nature", having a smooth rise in velocity to a single peak which then decreased smoothly to zero again (Brooks, Cooke, and Thomas, 1973; Brown and Cooke, 1981).

The angular position of the manipulandum handle (and thus of the forearm) was displayed to the subject as a thin vertical line on the same oscilloscope. Handle position was obtained from a precision potentiometer at the axis of rotation of the handle. The subject was thus required to superimpose the handle cursor on the target bar, in this visual, step-tracking paradigm.

In some experiments, movements made independently by the two arms were examined, i.e. the right or left arm was tested first and the opposite arm was tested later after a short rest period. For these independently made movements, the chair and manipulandum were reversed (rotated 180 degrees) following examination of one arm to allow recording from the opposite arm using the same manipulandum.

In other experiments, movements made simultaneously with the two arms were examined using two similar manipulanda. The manipulandum, for the right arm, contained a torque motor in addition to the other recording equipment with which the left was provided. Control experiments were performed to ensure that the presence of the torque motor did not affect the recorded data. Experiments were performed with the chair and manipulanda in the normal position, and the same tests were then repeated with the chair and manipulanda in the reverse position. That is, the manipulandum originally moved with the right arm was now moved with the left arm and vice versa. The results from the two experiments were not different.

In the studies utilising the two manipulanda, the position of either the left or the right arm could be displayed to the subject together with the target. Therefore there were three conditions where the subject could make the movements: a) by moving while the position of the right handle was displayed, b) moving while the position of the left handle displayed or c) moving without any of the two handle positions displayed on the screen.

B. Movements made independently

A total of 8 subjects of either sex (6 normal subjects and 2 patients wearing orthopaedic cast on the left forearm) were examined in this study. As noted above, a single manipulandum was used. Each subject was required to make a series of 20 movements (10 flexion alternating with 10 extension movements) at each of five different inter-target distances (5, 10, 20, 30 and 40 degrees), the whole series of movements was first made with one arm and then after a short rest period repeated with the other arm. Movements made at one amplitude were separated from those at the next amplitude by a 1 or 2 minute rest period. Once movements of all amplitudes were completed with one arm, the subject rested for 5-10 minutes before recording from the other arm was started. Whether the right or left arm was tested first was random and depended on how the apparatus had been left the previous day. The order in which movement amplitudes were presented to the subject was also randomized and was the same for the two limbs.

C. Unilateral long-term loading

For some experiments a light weight of 1 lb (0.45 kg) was strapped to the subject's forearm just proximal to the wrist. The weight was enclosed in soft material and fastened to the forearm by velcro straps. Subjects were requested to wear the weight 24 hours a day, removing it only during washing. They were particularly requested to wear it during all their normal daily activities. The weight was put on the subject's non-dominant arm (left arm in all subjects) in order to interfere as little as possible with their normal activities. All six subjects studied wore the weight for at least one week. They were tested, as described above, on a number of days before the weight was attached and were tested daily while the weight was on. Testing during the period of loading was made with the load on the forearm during the experimental session. Testing was continued for a variable period following removal of the weight. The two patients with the fractures were tested in a similar way but for periods of loading longer than one week. The patients were examined with the cast on for a number of times on different days and then immediately following removal of the cast. Testing also continued for the patients for few days after the cast was removed.

D. Simultaneous movements

A total of 10 subjects of either sex were studied in these experiments. The subject was seated on the chair and held handles on the end of two manipulanda. Each subject was instructed to make the movements with the two arms simultaneously and as identical to each other as possible. In general, each subject was required to make a series of 20 flexion-extension movements (10 flexion alternating with 10 extension movements) at each of 6 different inter-target distances (6, 12, 18, 36, 54 and 72 degrees). A series of movements at one amplitude would be separated from the series at the next amplitude by 1-2 min rest period.

The subjects first made movements with visual guidance, the position from the right arm and the target being displayed on the oscilloscope screen. The same series of movements was then repeated with the position of the left arm displayed. A third set of movements was then performed without any visual guidance. For these movements, the oscilloscope was switched off and the subject closed both eyes. During this third series of movements, the subject was required to move in response to an auditory cue that signaled the time of change of target position. The instruction was also to make identical movements with the two arms and keep the same amplitude throughout the session. In the non-visually guided trials, the subject was required to make movements of three different amplitudes :- small, medium and large (approximately 20, 50 and 70 degrees respectively) as described by the experimenter. The order in which movements amplitudes were presented to the subject was randomized and was the same for all subjects.

E. Unilateral short-term loading:

Six subjects paticipated in these experiments. As described above, subjects made simultaneous, non-visually guided movements of the two arms. Subjects were instructed to start the movements of the two arms at the same time and to make them as identical as possible. Each subject made a series of 20 flexion-extension movements at each of 5 different amplitudes (ranging between 15-70 degrees) as directed by the experimenter. A series of control movements of all amplitudes and with no visual guidance were first obtained. The whole sequence was then repeated with a weight of 1 lb (0.45 kg) attached to the manipulandum being moved by the left arm. Following this series, a third series was performed with a weight of 12 lb (5.4 kg) attached to the handle being moved by the left arm. A rest period of 10-15 min was allowed between experimental conditions.

F. Muscle tendon vibration

Tendon vibration was used to stimulate muscle spindle receptors in the biceps and triceps brachii muscles. A small (6x4x2 cm), light weight (<100 g) vibrator with a vibration frequency of 120 Hz was used. The vibrator was placed over the distal tendon of the biceps or triceps brachii muscles and strapped around the upper arm with Velcro straps. The vibratory stimulus was applied either as continuous vibration for periods up to 15-20 seconds, or as brief bursts of vibration. In the latter case, vibration was applied only when movement velocity was greater than a pre set value. Thus vibration for example, would be applied only during flexion or extension movements.

All the studies with tendon vibration were conducted without visual guidance. The subject was first made familiar with the feeling of the vibration. Before testing the effects of vibration on movement performance, subjects were required to practice movements of a given amplitude (usually 40 degrees) with their eyes open. For this practice session which lasted 10-15 minutes the target and handle cursor were displayed to the subject on the oscilloscope. The subject then attempted to make the movements with his eyes closed. Trials testing the effects of vibration were started when the subject could perform the movements in a consistent manner without visual guidance (see RESULTS).

In some experiments the effect of tendon vibration on movements performed by the opposite arm was investigated. First, subjects made flexion-extension movements with one arm while tendon vibration was applied to the biceps or triceps muscles of the opposite, stationary arm. Following these trials, subjects made simultaneous bilateral movements. Tendon vibration was applied to the biceps or triceps muscles of one arm. Various combinations of the muscle vibrated and whether vibration was applied during flexion or extension movements were used in various subjects. In 7 subjects out of 13, a systematic study was conducted where the left triceps brachii muscle was vibrated and the effects on flexion movements of the opposite (right) arm were examined. The flexion end position attained by the right arm during a. unilateral and b. bilateral arm movements were studied. For these 7 subjects, sessions consisting of 20 flexion alternating with 20 extension movenments were made and tendon vibration was apllied successively in brief bursts triggered by the flexion movements during the last 10 flexions. This procedure was repeated in each subject for a. unilateral, and b. bilateral arm movements.

III. Data Recording

Handle (and thus forearm) position for the two arms were obtained from precision potentiometers mounted at the axes of rotation of each manipulandum handle. The angular velocities of each handle were obtained from tachometers also mounted at the axes of rotation of the manipulanda.

Data was digitized in real time using a PDP 11/44 computer having 12 bit analog to digital converters. Data were stored on disc during the experiment and were later transferred to digital tape for off-line analysis and archiving. In some experiments, data was recorded on paper as it was collected using a multi-channel recorder (GOULD RECORDER ES1000). Surface EMGs (if recorded) were obtained from the biceps and lateral head of triceps brachii muscles using silver disc electrodes, 9 mm in diameter. The electrodes were placed 3-5 cm apart on the muscle belly. EMGs were amplified, full wave rectified and filtered (low cutoff 20 Hz, high cutoff 1 kHz) before sampling. If EMGs were recorded a sampling rate of 500 Hz was used. For other experiments when EMGs were not recorded a sampling rate of 200 Hz was used.

IV. Data Analysis and Statistical Methods:

Data was analysed using a computer based system. Using this system, raw data (for example information about arm position and velocity during each movement) were analysed. This was done by specifying a threshold level for movement acceleration (120 deg/sec/sec, see APPENDIX 1). Then the following details about individual movements were determined:

a. movement start (for time).
b. movement end (for time).
c. movement start position.
d. movement end position.
e. movement peak velocity.

Details for statistical analyses will be given with the specific experiments in the section on RESULTS.

RESULTS

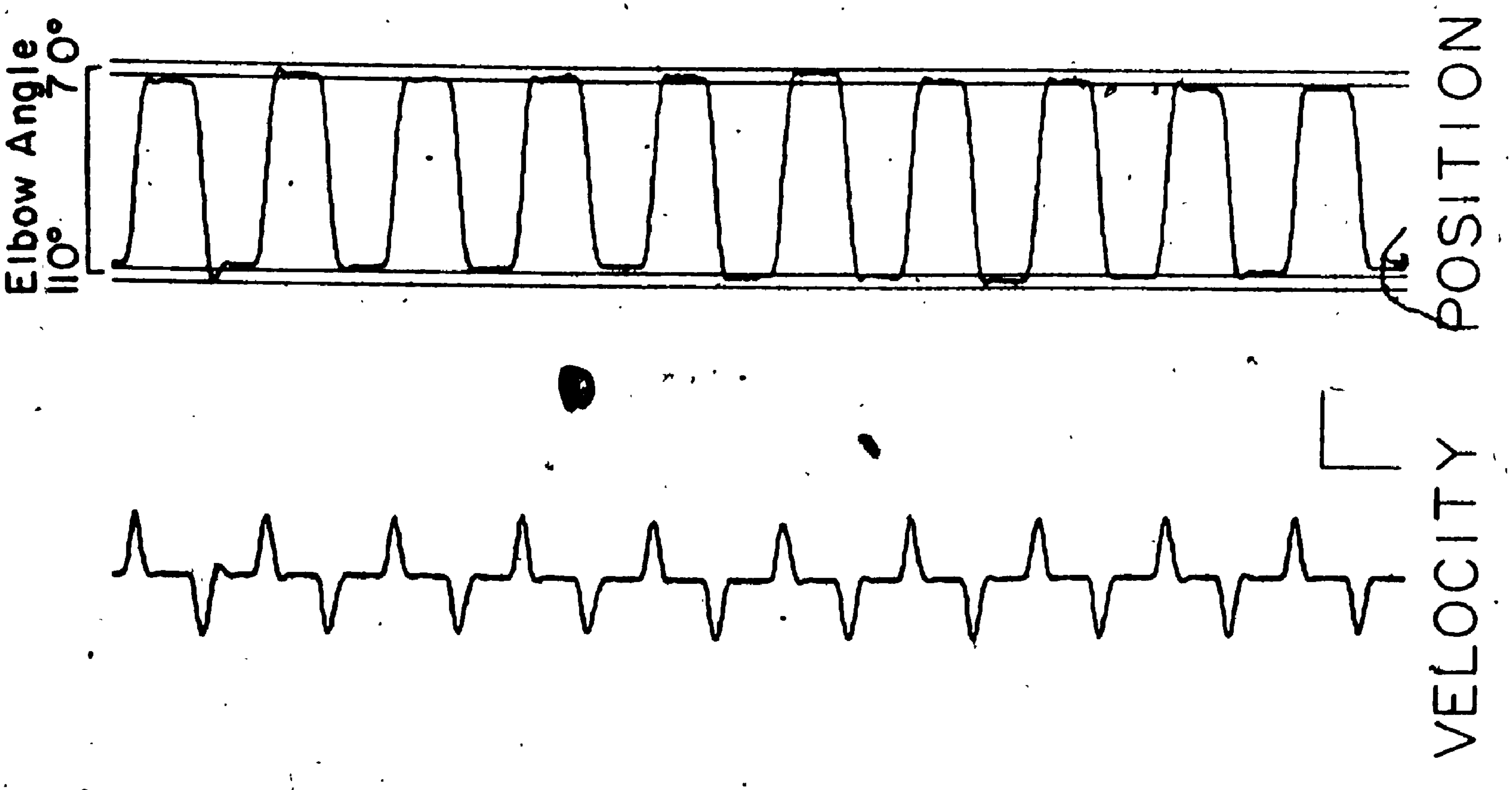
I. Visually and Non-Visually Guided Movement

For many of the experiments in this study, it was necessary for the subjects to make movements without visual guidance. Experiments were performed to ensure that the subjects could reliably perform required movements under this condition. Representative data from one subject is shown in Figure 2. The subject was first given a practice period during which visual guidance was provided. As described in METHODS, target positions were displayed as vertical bars on an oscilloscope. Manipulandum (and thus forearm) position was displayed as a thin vertical line on the oscilloscope. In this example, the target switched between two positions separated by an elbow angle of 40 degrees. The subject started by making movements of the required amplitude with visual guidance. After this practice period, he was instructed to close his eyes and to continue making the same movements in response to an auditory cue. He was given a practice period during which he could visually check the accuracy of his movements. Once the subject felt he 'knew' the movement, he was instructed to continue making movements without visual guidance. As shown in Figure 2, he

Figure 2

Unilateral arm movement made without visual guidance. The two pairs of lines around the position record represent the intended flexion (upper) and extension (lower) target positions. The inter-target distance was 40 degrees. The subject made these continuous flexion-extension movements without visual guidance following a session of practice to make the same movements (40 degrees) with the eyes open. Such control records without visual guidance were always obtained prior to further testing when visual guidance was to be excluded. Vertical calibration represents 15 degree for position and 150 degrees/sec for velocity. Horizontal calibration bar represents 1.5 sec.(VN)

UNILATERAL ARM MOVEMENT



continued to make movements of the same amplitude and speed without visual guidance.

In some subjects, movement amplitude altered following the withdrawal of visual guidance. Movement amplitude could either increase or decrease in these subjects. The change in general was not large and once a movement amplitude was established it was maintained for the duration of the non-visually guided trial.

II. Simultaneous Bilateral Movements

A. Movement kinematics and durations

As discussed in the introduction, it was expected that normal subjects would match the movements of the two arms when the movements were made simultaneously. In the first series of experiments, subjects were given a visual display of both the target and the position of the right arm. The subject was instructed to make the "same" movements simultaneously with the two arms. Movements were performed at the "subject's own speed"; movement peak velocity was well below the maximum that the subject could produce with either arm.

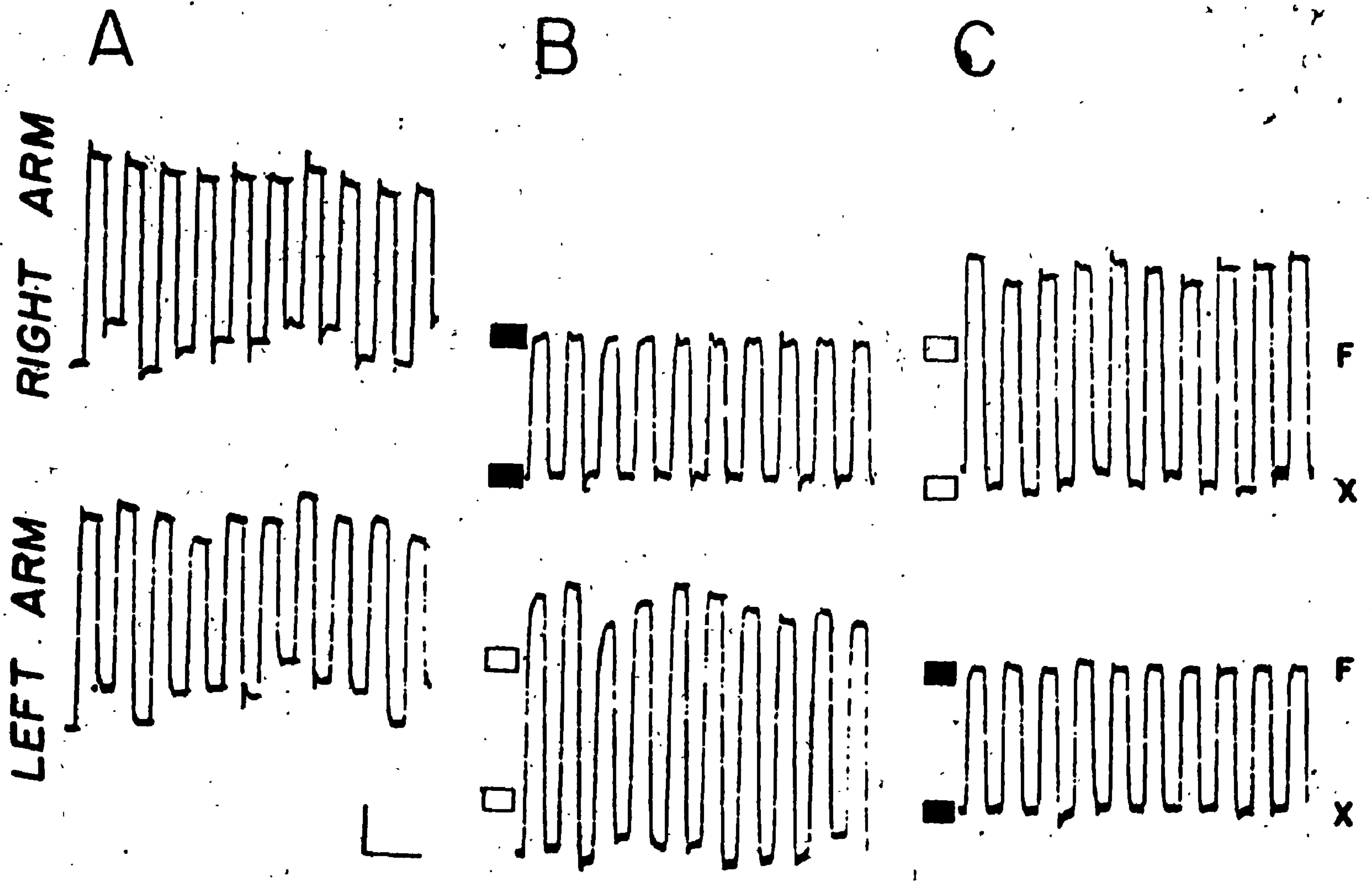
Representative data from one subject is shown in

Figure 3B. As expected, movements of the visually guided (right) arm were made consistently between the required targets (indicated by the solid bars). The movements made simultaneously with the other (left) arm, however, were consistently larger than the required inter-target distance (open bars). In general the non-visually guided arm overshot the required target in both flexion and extension directions. Thus movement of the non-visually guided left arm were larger than those of the visually guided right arm.

This unexpected difference in movement amplitude between the two arms was found to be independent of which arm was used for the visual feedback to the subject. For Figure 3C the visual presentation was switched to the left arm, the inter-target distance remaining the same as in part B. In this case, movements of the visually-guided (left) arm were made accurately between the required targets. However, movements of the non-visually guided (right) arm were again greater than those of the visually-guided arm. In some subjects, such as the example given in Figure 3C, movements of the non-displayed arm showed an increase in movement amplitude in only one direction (either flexion or extension). This unidirectional increase was not systematically shown for all movement amplitudes used in the same subject and was not consistently seen in all subjects.

Figure 3

Bilateral simultaneous arm movements. Traces represent position records for movement made with the right (upper traces) and the left (lower traces) arms at the same time. In "A" the subject made the movements without visual guidance. In "B" and "C" the subject was shown a target (filled squares) and the position of either the right "B" or left "C" arms on the oscilloscope screen. The squares indicate target positions: filled squares indicate the arm where position was visually displayed to the subject; empty squares indicate no visual guidance from that arm. Each pair of squares represents flexion (top) and extension (bottom) target positions. Vertical calibration bar represents 12 degrees for position and horizontal 10 sec. (PR).


A
B
C
RIGHT ARM
LEFT ARM
F
X
F
X

The results indicated that the visual information given to the subject markedly affected his ability to make the simultaneous movements the same with the two arms. Experiments were therefore performed to test subjects' ability to match movements of the two arms in the absence of visual guidance. The subject was instructed to close his eyes and to continue to make movements simultaneously with the two arms. The subject was given an auditory cue as to when to start movements.

In this situation (Figure 3A) movements of the two arms were of the same amplitude. Note that there was no target shown in this case (subjects were instructed to move the two arms simultaneously with no relation to any target) and that the subjects's eyes were closed. Note also that although movement amplitude varied from movement to movement, the same variation occurred in each arm. Thus a larger movement by the right arm was matched with a larger movement by the left arm. In Figure 4 are shown averaged records of simultaneous bilateral movements made without visual guidance. Movement amplitudes and speeds were similar for the two arms. Extension movements made with the left arm were somewhat more variable than those made with the right arm in this example.

These results are summarized for averaged data in Figure 5. Both position and velocity records are shown in

Figure 4

Bilateral simultaneous arm movements made without visual guidance. Each set of traces represents averaged records of position and velocity of movements made by the left (A & C) and right (B & D) arms at the same time. A,B for flexion and C,D for extension movements. All traces represent the average of 10 movements. The dotted lines on either side of the average show the standard deviations. The vertical calibration in D represents 20 degrees for position and 170 degrees/sec for velocity. Horizontal calibration bar represents 500 ms. (VN).

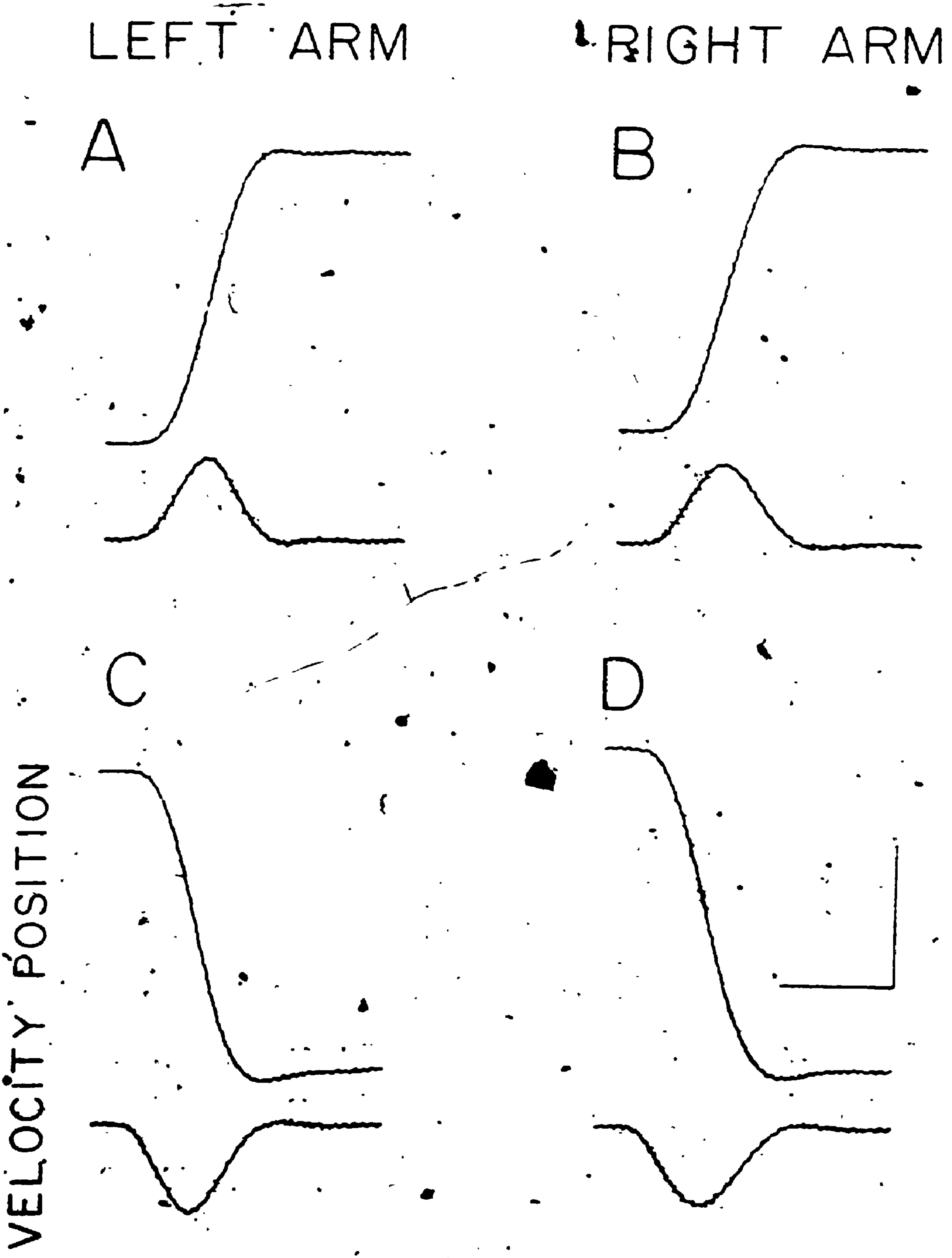
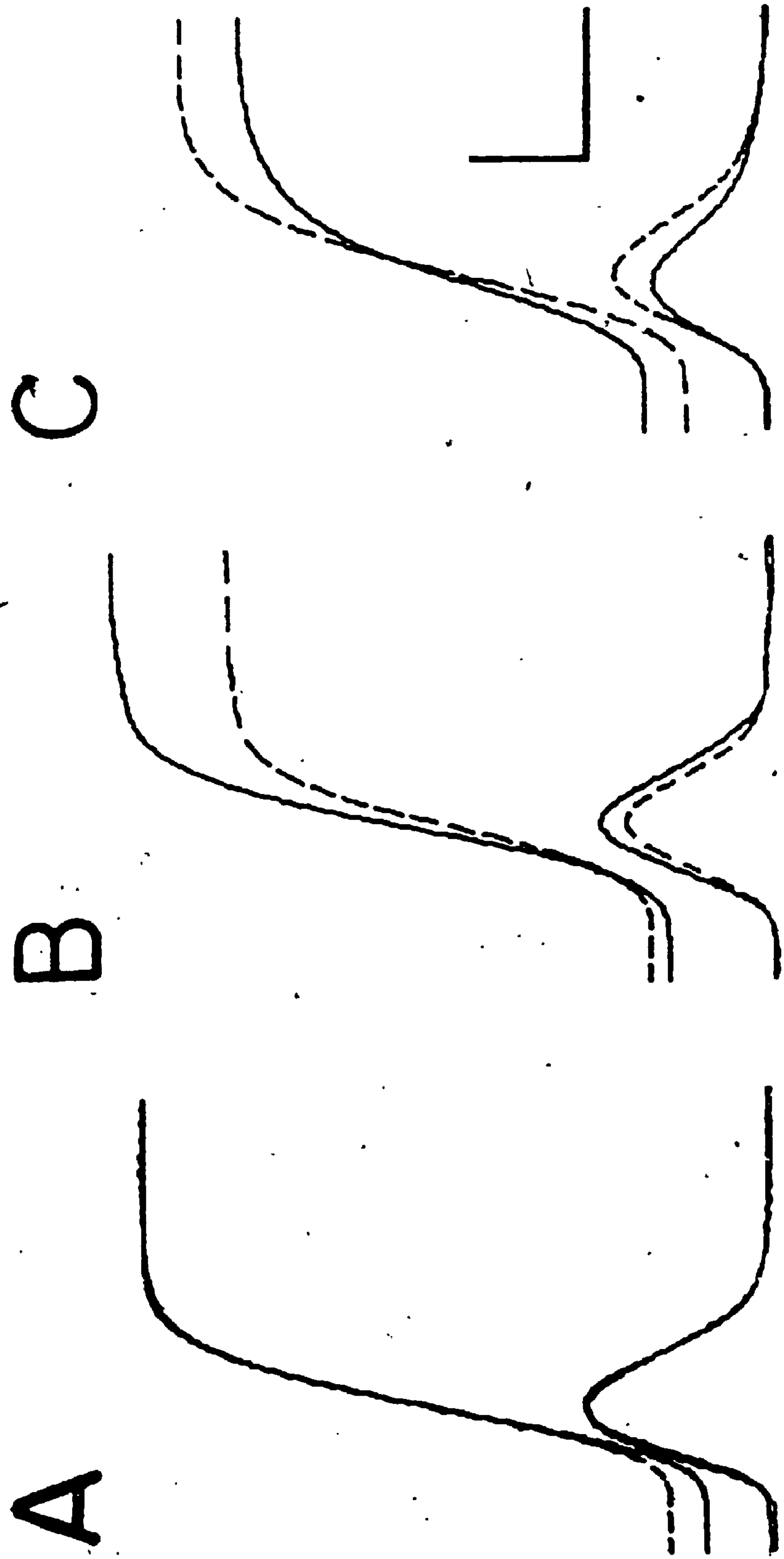

LEFT ARM
RIGHT ARM
A
B
C
D
VELOCITY POSITION

Figure 5

Effects of visual feedback on bilateral simultaneous arm movements. Each set of traces represents records of position and velocity made by the left (solid traces) and right (dashed traces) arms at the same time. All traces represent the average of 10 flexion movements. In "A" the subject made the movements without visual feedback. In B & C the subject was shown a target and the position of either the right "B" or left "C" arms on the oscilloscope screen.The target for B & C was made to switch at 54 degrees of inter-target distance. Vertical calibration represents 15 degrees for position and 150 degrees/sec for velocity. Horizontal calibration represents 400 ms. (KS).


A
B
C

this figure, solid traces being for the left and dashed traces for the right arm. As described, presentation of visual information about the position of either arm led to a gross mis-match of movement amplitudes. As shown in this figure, there was an associated mis-match in movement peak velocities. Thus, peak velocities of movements of the two arms were identical when the movements were performed without visual guidance (Figure 5A). When visual guidance of one arm was given (B,C), the peak velocity of the movements of the other arm increased. Thus, movement peak velocity increased with the increase in movement amplitude of the non-visually guided arm. It should be noted, however, that in this example the subject started movements of the two arms from a slightly unmatched extension position as seen in the averaged records in A. Such slight differences were encountered in some subjects but they were not systematically related to handedness.

Averaged data from ten subjects is given in Tables 1 - 3. These tables compare the kinematics of movements of the two arms made without visual guidance (Table 1), with display of right arm position (Table 2) and with display of left arm position (Table 3). Movement amplitude, duration and peak velocity and time to peak velocity are compared under each condition. The tables give the mean ratios and standard deviations of these various parameters from the two

Table 1

Ratios represent movement kinematics and durations for right arm/left arm in non-visually guided movements.

	20 deg	50 deg	70 deg
Amplitude	.96	.92	.95
(SD)	(.07)	(.17)	(.11)
Duration	1.01	1.03	1.07
(SD)	(.11)	(.05)	(.11)
Peak Velocity	1.00	.99	.97
(SD)	(.21)	(.17)	(.09)
Time to Peak Velocity	1.07	1.04	1.04*
(SD)	(.11)	(.06)	(.03)

* mean ratio is significantly different from 1.00 (mean falls outside confidence limits of 95 percent).

Table 2

Ratios represent movement kinematics and durations for left arm/right arm in movements with the right arms displaved.

	6 deg	12 deg	18 deg	36 deg	54 deg	72 deg
Amplitude	1.76*	1.50*	1.43*	1.44*	1.41*	1.33*
(SD)	(.39)	(.21)	(.41)	(.24)	(.21)	(.12)
Duration	1.08	1.04	1.03	1.10*	1.04	1.00
(SD)	(.14)	(.08)	(.08)	(.08)	(.08)	(.03)
Peak Velocity	1.64*	1.26*	1.17	1.18*	1.18*	1.22*
(SD)	(.56)	(.30)	(.23)	(.21)	(.15)	(.16)
Time to Peak Velocity	1.11	.95*	.93	1.04	1.01	1.00
(SD)	(.16)	(.04)	(.10)	(.05)	(.04)	(.06)

* mean ratio is significantly different from 1.00 (mean falls outside confidence limits of 95 percent).

Table 3

Ratios represent movement kinematics and durations for right arm/left arm in movements with the left arm displayed.

	6 deg	12 deg	18 deg	36 deg	54 deg	72 deg
Amplitude	1.79 *	1.60 *	1.41 *	1.30	1.16 *	1.14 *
(SD)	(.32)	(.54)	(.51)	(.50)	(.20)	(.12)
Duration	1.16 *	1.16 *	1.21 *	1.28 *	1.26 *	1.13 *
(SD)	(.19)	(.18)	(.24)	(.22)	(.11)	(.12)
Peak Velocity	1.53 *	1.50 *	1.35 *	1.31 *	1.13 *	1.19
(SD)	(.51)	(.49)	(.33)	(.42)	(.22)	(.35)
Time to Peak Velocity	1.28 *	1.39 *	1.29 *	1.23 *	1.13 *	1.08 *
(SD)	(.19)	(.36)	(.35)	(.18)	(.07)	(.08)

* mean ratio is significantly different from 1.00 (mean falls outside confidence limits of 95 percent).

arms. A movement amplitude ratio of 1.0 indicates, for example, that movements of the two arms were of the same size. Calculation of the confidence limits was used to determine whether the observed mean ratio was significantly different from 1.00. Note that in Tables 2 & 3 the ratio is of non-displayed/displayed arm (left/right in Table 2 and right/left in Table 3). Each table contains data from movements of all amplitudes tested.

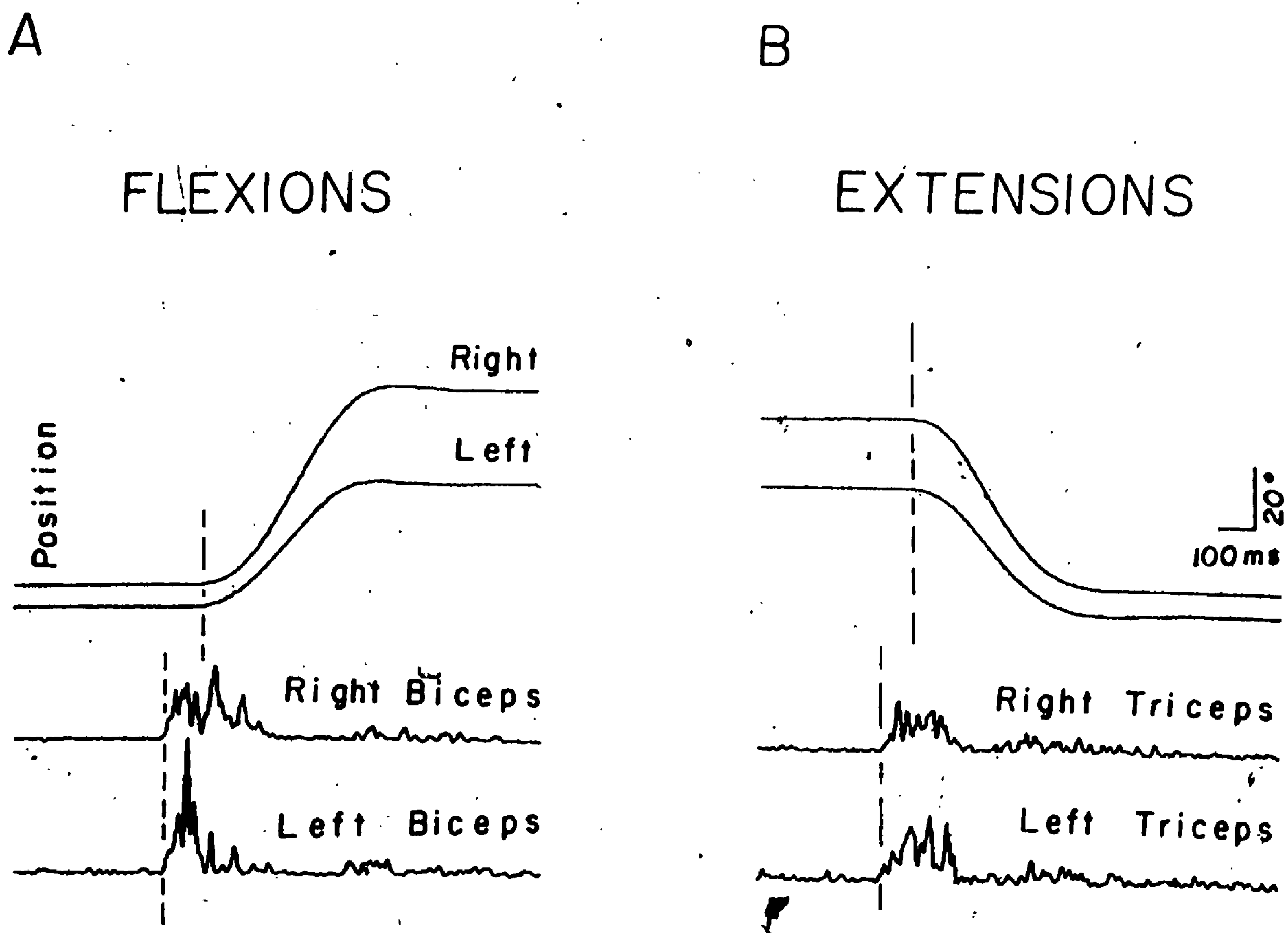
.With no visual feedback, the mean ratios for movement amplitude, peak velocity, duration and time to peak velocity were not significantly different from 1.00 ($p > .05$, the t-value was less than 2.262, n=10). With visual feedback from either arm, the mean ratios (non-visually guided/visually guided) for movement amplitude and peak velocities were significantly greater than 1.00 ($p < .05$, the t-value was greater than 2.262, n=10) (Tables 2 & 3). Movement duration and time to peak velocity showed some bias to handedness in these visually guided movements. In Table 2 (right arm displayed) the mean ratios for movement duration and time to peak velocity were not significantly different from 1.00. Therefore movement durations for both arms were not significantly different as measured from each other. In contrast, when the left arm was visually displayed, Table 3, the mean ratios for movement duration and time to peak velocity were significantly greater than 1.00. Therefore movement duration was longer for movements of the right (undisplayed) arm. This difference, dependent on which arm was visually displayed, was seen even after repeating the experiment with the chair reversed so that the right handle was used by the left hand and vice versa. Again the movement duration and time to peak velocity ratios were greater when the left arm was visually displayed. The difference between the ratios for movement duration for the two conditions (right arm display versus left arm display) was statistically significant ($F = 29.1$; df = 1,9 ; $P < 0.001$).

In spite of the gross differences in movement amplitudes and peak velocities of the two arms when the position of one arm was visually presented, the movements of the two arms were initiated at the same time. This is illustrated in Figure 6 which shows records of single trials during simultaneously made movements. As seen from the position records, the two arms started moving at the same time during flexions (A) and extensions (B). In this example, the left arm position was visually presented to the subject. The synchronous onsets of movements of the two arms was not influenced by visual guidance and was observed in all subjects studied whether the movements were visually-guided or not.

Figure 6 shows that the initial EMG burst recorded

Figure 6

Movement onset for simultaneous bilateral arm movements. Each set of traces represents (from top to bottom) single records of right arm position, left arm position, right agonist EMG (right biceps brachii in "A" & right triceps brachii in "B") and left agonist EMG (left biceps brachii in "A" & left triceps brachii in "B"). The movements in A & B are made with visual feedback. The subject was shown the target and the position of the left arm on the oscilloscope screen. The inter-target distance for both flexion "A" and extension "B" movements was 36 degrees. The interrupted vertical lines indicate movement initiation (position traces) and agonist muscle activation (EMG traces). (JS).


A
B
FLEXIONS
EXTENSIONS
Position
Right
Left
Right Biceps
Left Biceps
Right Triceps
Left Triceps
20°
100 ms

from the agonist muscle of one arm started synchronously with that recorded from the agonist muscle of the opposite arm. In Figures 7 and 8, this timing of the bilateral agonist muscle activation is shown for an uninterrupted series of 10 bilateral flexions (Figure 7) alternating with 10 extensions (Figure 8). The synchronism in movement onset, shown above, was determined by visually aligning each pair of records for individual trials of the two arm movements. This was done both for movement position and agonist emg activity. By inspection of these records it was found that the movement onset for the two arms occurred at the same time. Results from all subjects tested showed this synchronism at this level of analysis.

B. Movement peak velocity-amplitude relation

From studies on single arm movements, it is well known that movement peak velocity increases as movement amplitude is increased. The relation between movement peak velocity and movement amplitude is linear (Bouisset and

Figure 7

Onset of biceps muscle activation during simultaneous bilateral flexion movements. Each pair of traces represent surface EMG records from the right (upper trace) and left (lower trace) biceps brachii muscle during single successive trials of flexion movements. All movements were done with visual feedback. The target together with the position of the left arm was shown to the subject on the screen of the oscilloscope. The inter-target distance used was 36 degrees. The vertical interrupted lines are drawn to mark the onset of biceps activation for the two arm movements. (JS).

BILATERAL FLEXIONS

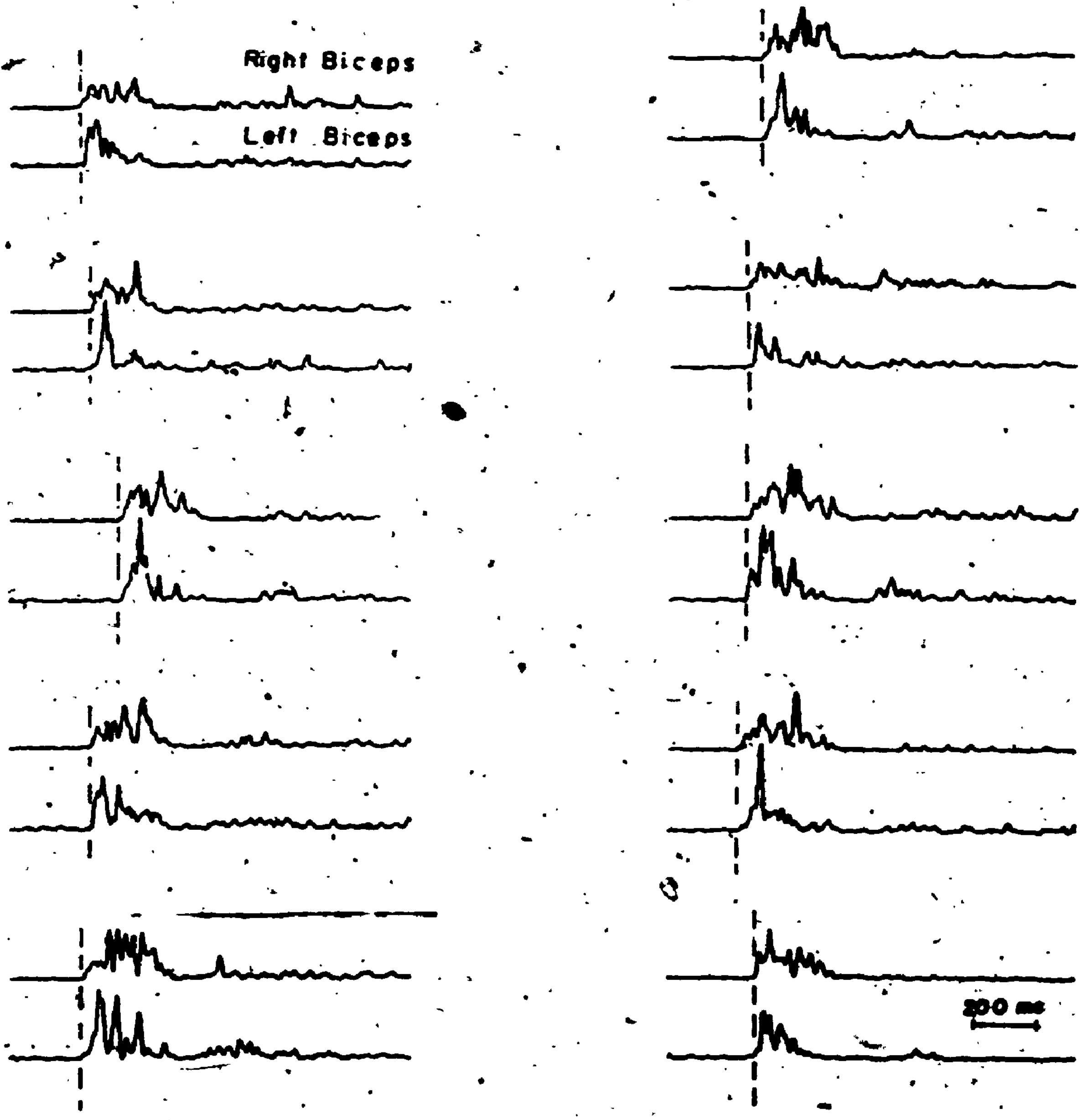
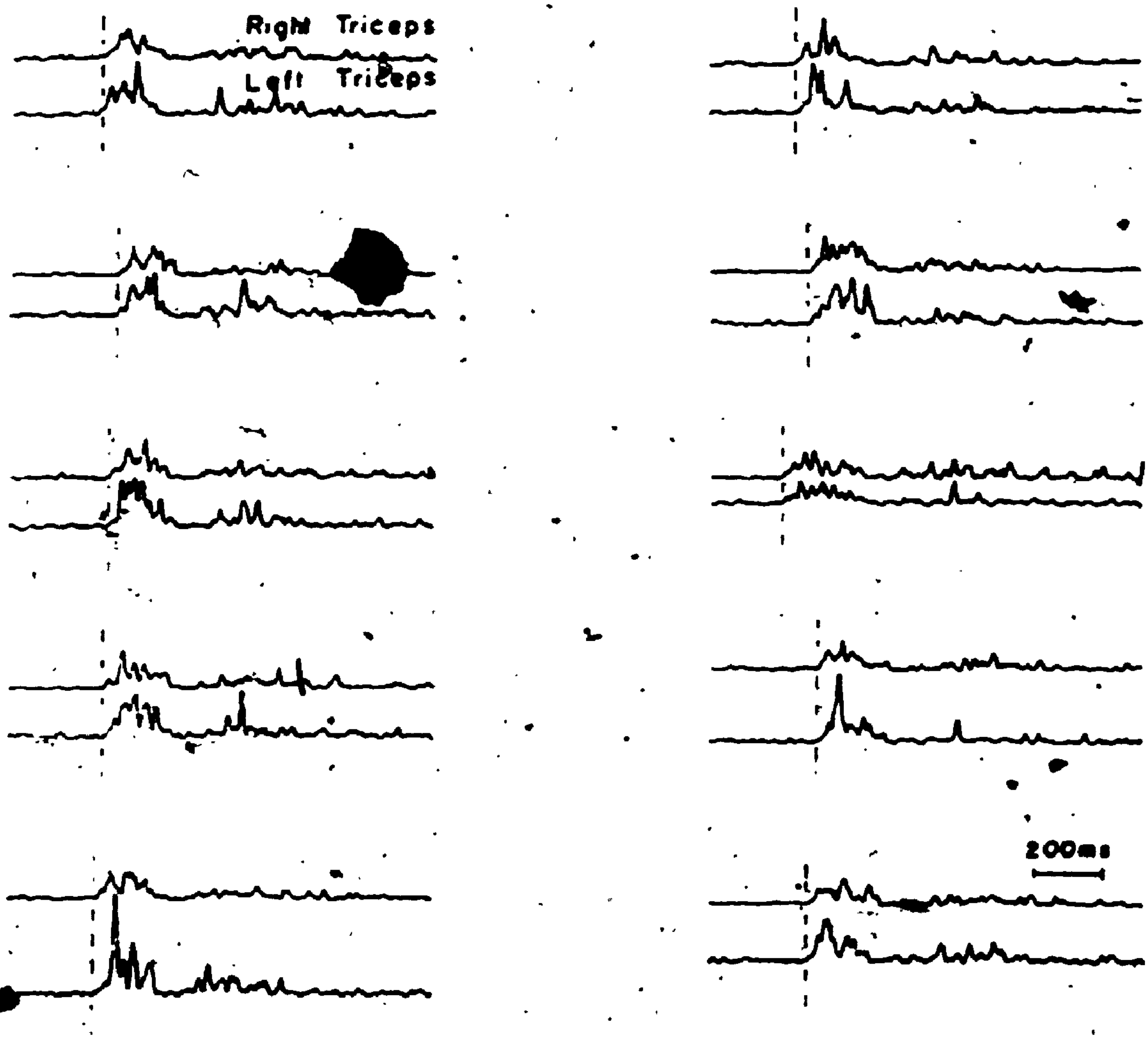


Figure 8

Onset of triceps muscle activation during simultaneous bilateral extension movements. Each pair of traces represents surface EMG records from the right (upper trace) and left (lower trace) triceps brachii muscles during single successive trials of extension movements. All movements were done with visual feedback. The target together with the position from the left arm was shown to the subject on the screen of the oscilloscope. The inter-target distance used for all movements shown was 36 degrees. The vertical interrupted lines are drawn to mark the onset of triceps activation for the two arm movements. (JS).

BILATERAL EXTENSIONS



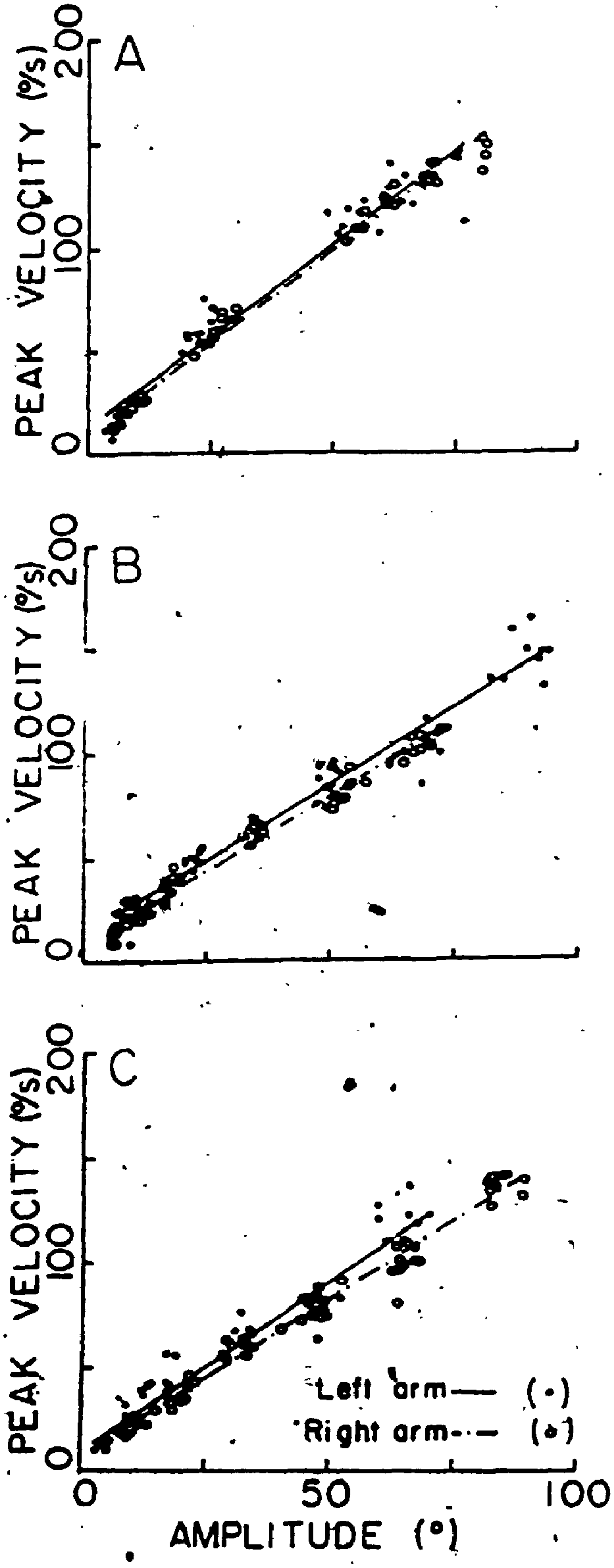
Lestienne, 1974; Cooke, 1980). Figure 9 shows this velocity-amplitude relation from one subject. In this subject, peak velocity increased linearly with movement amplitude (correlation coefficients 0.95 or greater). As can be seen in A,B and C there was no striking difference between the two arms (asterisk symbols are for the left and circles are for the right arm). The slopes of the regression relations appeared similar for the two arms (solid lines for the left and dashed lines for the right arm). Note that the matching in peak velocity-amplitude relations between the two arms remained unchanged whether the right arm was visually presented (B); the left arm visually presented (C) or in the absence of the visual guidance (A). This matching in velocity-amplitude relation was seen for all subjects (n=10) tested in this series and was not affected by directing visual attention to one arm or the other.

C. Dynamic matching:

The data presented has shown that movements made simultaneously by the two arms are similar in some of their kinematic properties. It was not, however, possible to tell from these results whether the movements of the two arms were also matched on a moment-to-moment basis throughout the whole movement. The movements in the two arms could be started at the same time and terminated at the same time

Figure 9

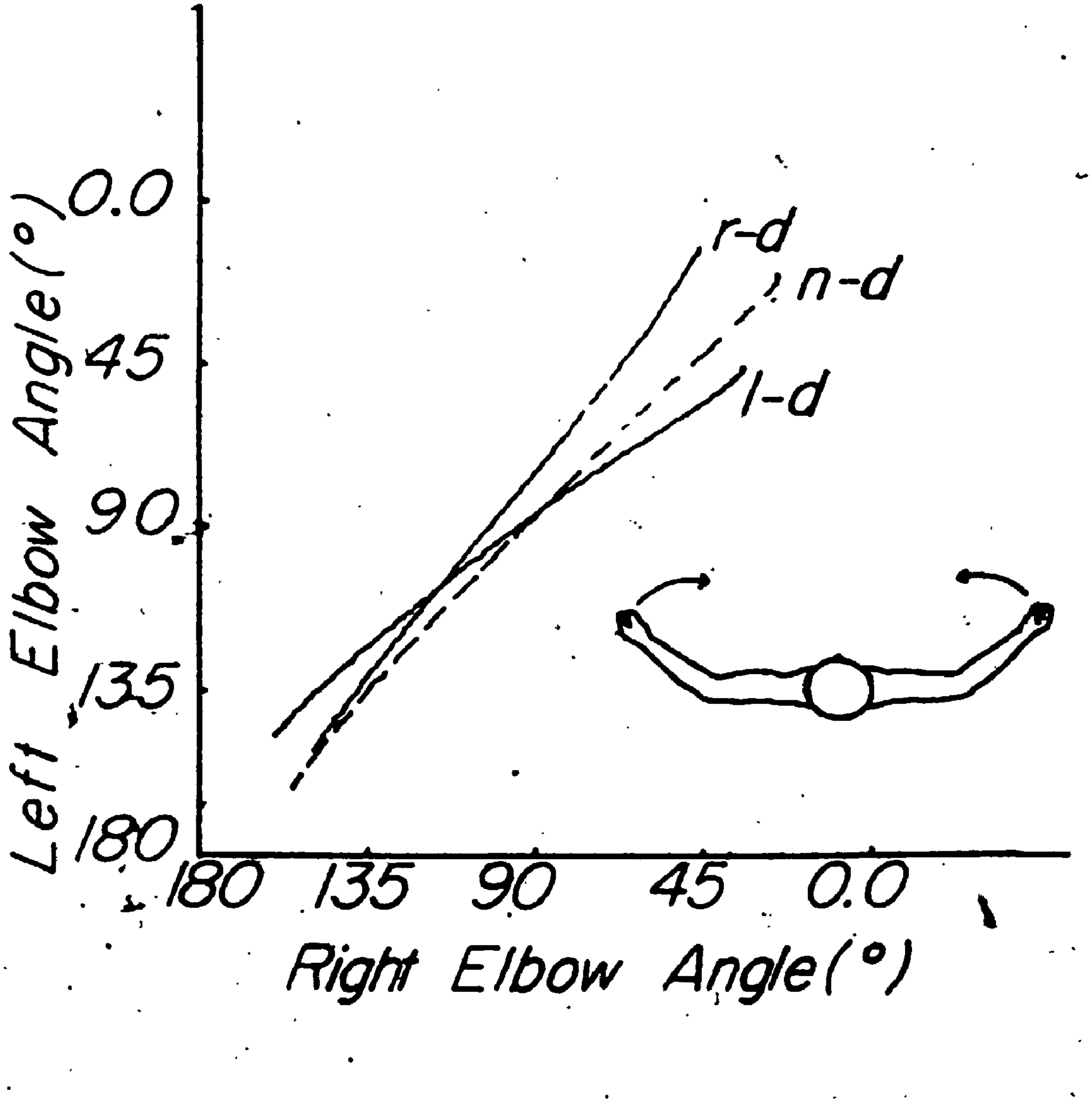
Movement peak velocity-amplitude relations for the right and left arms. For each graph movement peak velocity is plotted as a function of movement amplitude for flexion movements made simultaneously by the right (circles) and left (asterisks) arms. In "A" the subject made the movements without visual feedback. In B & C the subject was shown the target and the position of either the right "B" or left "C" arms on an oscilloscope screen. In "A" 4 different movement amplitudes were made. In B & C 6 different movement amplitudes were made by the subject. For each movement amplitude tested the subject made 10 flexion movements by the two arms at the same time. The straight lines in each graph represent the best-fit regression relations. Solid lines are obtained from movements of the left and dashed lines from movements of the right arms. The slope in each case was determined from the least squares, best-fit linear regression equation. In all cases, the correlation co-efficient of the linear regression equation was .95 or greater. (KS).


A
B
C
PEAK VELOCITY (°/s)
0
100
200
0
50
100
AMPLITUDE (°)
Left arm —— (•)
Right arm -·- (∘)

yet, during the course of the movement each arm movement could have been performed differently. For Figure 10 the position of left arm has been plotted as a function of the right arm position during simultaneous movements. Each trace is from the average of 10 flexion movements. The figure shows data from 3 different visual-display conditions: r-d, position of right arm displayed; l-d, position of left arm displayed, and n-d, no visual display from either arm was shown to the subject. All curves are linear (r>0.95). The slopes of the lines are 1.28, 0.77 and 1.04 for r-d, l-d and n-d respectively. A curve that has a correlation co-efficient of 1.00 and a slope of 1.00 represents the relation which would be obtained if the positions of the two arms were exactly matched at every point during the movements. A slope less than 1.00 indicates that the right arm leads the left while a slope greater than 1.00 indicates that the left arm leads the right. In the right-display condition, for example, the slope was 1.28. Thus, throughout the movement, the left arm was at a more flexed position than the right arm. Note also that curvature in these lines indicates phase delays between the two arms. Thus, if the line is concave upward, the right arm has started moving and completes its movement before the left arm. For the movements illustrated in Figure 10 the correlation of 0.95 or greater indicate that there was little phase delay between the two arms. To examine this moment-to-moment matching

Figure 10

Dynamic relations for movements made simultaneously with the two arms. The moment-to-moment changes in positions of the two moving arms are correlated. Each curve shows the least squares best-fit regression line for averages of 10 bilateral flexion movements made with the two arms at the same time. Data from 3 visual-display conditions are shown: r-d, position of the right arm displayed; l-d, position of the left arm displayed and n-d, no visual display (without visual feedback) was shown to the subject. All correlations are linear (r>.98). The slopes of the lines are 1.28, .77 and 1.04 for r-d, l-d and n-d respectively. The correlation for the left and right arm positions was made at 5 ms intervals. (PR).


Left Elbow Angle(°)
0.0
45
90
135
180
Right Elbow Angle(°)
180
135
90
45
0.0
r-d
n-d
l-d

between movements that were simultaneously made by the two arms, positions as well as velocities of the two arms were correlated, i.e. right arm position versus left arm position and right arm velocity versus left arm velocity, at 5 ms intervals throughout the entire movement. Table 4 shows the correlation co-efficients and slopes for correlated positions and correlated velocities of movements of the two arms for one subject. As noted above, the correlation co-efficient is indicative of how much the two movements were in phase with each other while the slope is a measure of equality of the two movement parameters for the two arms.

D. Summary :

In the absence of visual feedback, simultaneous, bilateral arm movements were closely matched at each point during the movements. Movement amplitudes, durations and onset times were the same. Providing visual feedback from one arm markedly influenced the matching in movement kinematics so that the non-visually guided arm was moved faster and for a greater distance than the visually-guided arm.

E. Response to unilateral short-term loading:

The above results clearly indicated a close matching

Table 4

Moment-to-moment comparison of positions and velocities for movements of the two arms made simultaneously.

	POSITION		VELOCITY	
	Cor.Co.	Slope	Cor.Co.	Slope
NO VISUAL DISPLAY	1.00	.99	.97	.95
	1.00	.97	.99	.85
	1.00	1.07	.97	.97
	1.00	1.00	.90	1.02
	1.00	1.06	1.00	1.17
	1.00	.99	.95	1.00
	1.00	.95	.96	.90
	1.00	1.09	.99	1.04
	1.00	1.13	1.00	1.18
	1.00	1.06	1.00	.97
RIGHT ARM VISUALLY-DISPLAYED	1.00	..39	.99	1.32
	1.00	1.28	1.00	1.29
	1.00	1.72	1.00	1.52
	1.00	1.45	.99	1.42
	1.00	1.40	1.00	1.36
	1.00	1.30	.98	1.19
	1.00	1.26	.99	1.46
	1.00	.99	.98	1.02
	1.00	1.10	.99	1.07
	1.00	1.21	1.00	[illegible]
LEFT ARM VISUALLY-DISPLAYED	1.00	.91	1.00	1.00
	1.00	.92	.99	[illegible]
	1.00	.78	1.00	[illegible]
	1.00	.75	.95	.67
	1.00	.71		
	.99	.75	.97	.78
	1.00	.72	.99	.79
	1.00	.77	1.00	.85
	1.00	.71	.99	.71
	1.00	.74		

of movements made simultaneously by the two limbs. The relation between movements of the two arms was, however, affected by visual feedback from the movements. The next series of experiments were designed to test whether the relation between the arms was affected by kinesthetic feedback from the limbs themselves during movement. Movements of one arm were modified by applying a load to the arm and then having the subject perform simultaneous movements with the two arms as described. Since it was found that visual information seriously affected the subject's ability to match the movements of the two arms the effects of loading were tested in the absence of visual guidance.

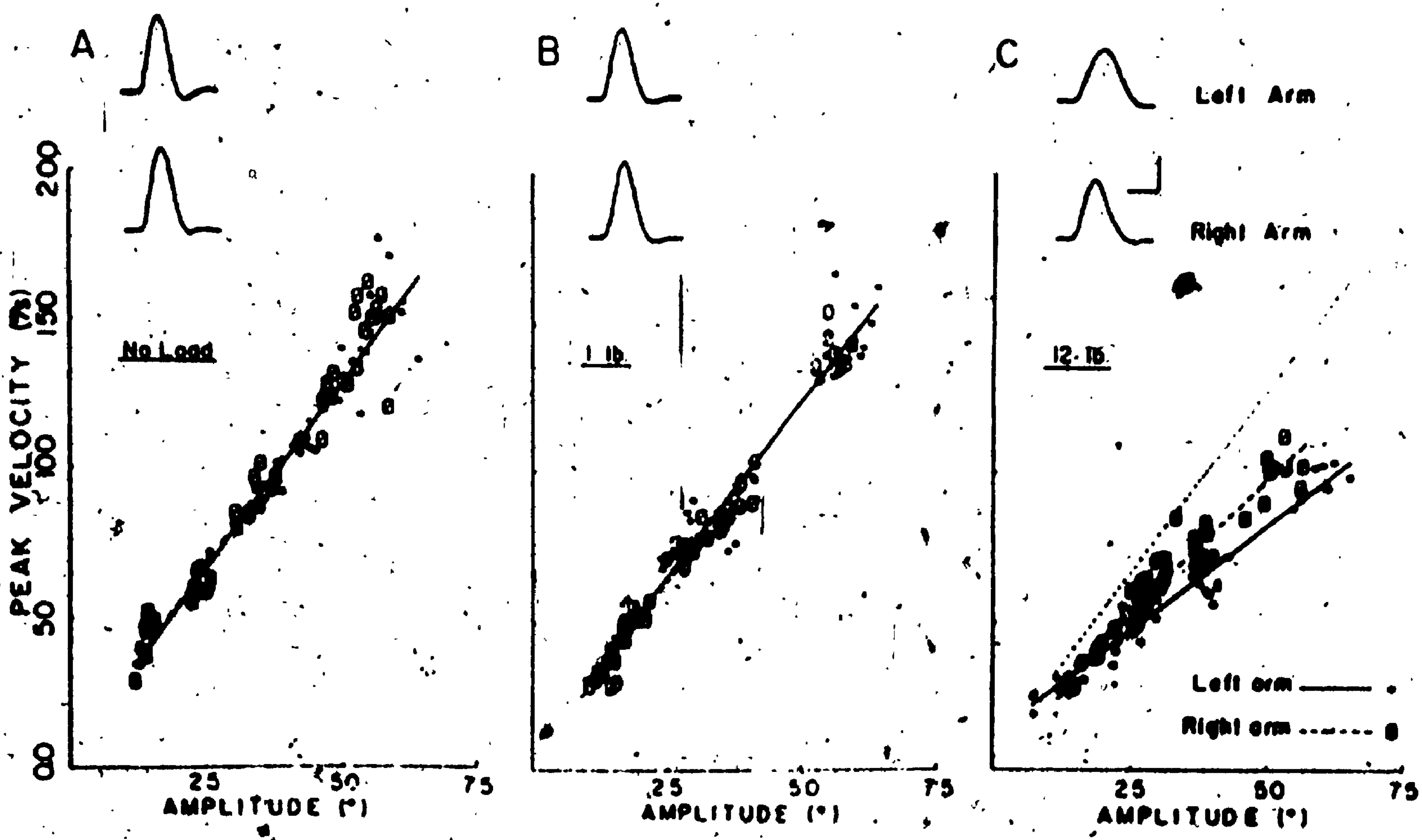
Movements of five different amplitudes were tested both with and without the load attached to the manipulandum in 6 subjects. As shown earlier, the subjects made bilateral movements that were matching in movement kinematics before loading. With a small load (1 lb) applied to the left manipulandum, no significant effect was observed on the performance by either arm and the subject as usual made matching movements with the two arms. A significant effect was observed when a heavy load (12 lb) was applied to the left manipulandum. The peak velocity of movements by the left arm was markedly reduced at each of the movement amplitude tested. Most interesting was that this effect was also seen in the movement performance of the right (unloaded) arm, although to a lesser degree. Figure 11 shows an example of this effect. Note that the peak velocity (traces of averaged velocities) for the largest movement amplitude used decreased in C for both left (loaded) and right (unloaded) arms as compared to A & B. In order to show the effect on motor performance of the two arms under the three different conditions, the peak velocity-amplitude relations were plotted for each condition (graphs in Figure 11). In Figure 11A the relation is shown for the movements without any load. In (B) and (C) the relations are shown during left side loading with 1 lb and 12 lb respectively. Note firstly that the two arms have similar relations to each other in Figure 11A and B. Secondly, this matching in relation between the two arms persisted during application of the light load (1 lb) to the left side and thirdly that the heavy load (12 lb) affected the loaded side as well as the unloaded side in performimg the movement (Figure 11 C).

F. Summary :

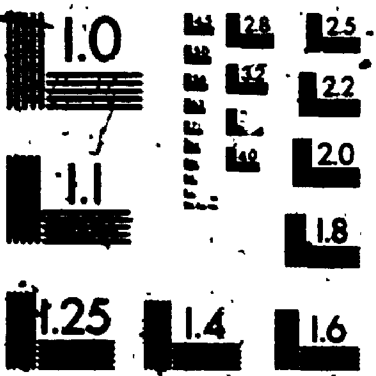
Loading of one arm during simultaneous bilateral arm movements caused a decrease in the velocity of that arm. The velocity of the opposite, non-loaded arm was also decreased during that loading. Similar velocity-amplitude relations were obtained for movements of the two arms with the light

Figure 11

Movement peak velocity-amplitude relations for the two arms with unilateral loading. For each graph, movement peak velocity is plotted as a function of movement amplitude for flexion movements made simultaneously with the two arms. In "A" the subject made the movements without loading. A load of 1 lb and 12 lbs was applied to the left manipulandum in B & C respectively. All movements were made without visual feedback. For each graph 5 different amplitudes of movement were made. For each movement amplitude performed the subject made 10 flexion movements with the two arms at the same time. The straight lines in each graph represent the best-fit regression relations. Solid lines are obtained from movements of the left (loaded in B & C) and dashed lines from the right (unloaded) arms. Movements from the left arm are represented by asterisks and those from the right arm by circles. For ready comparison, the dotted lines in B & C show the control relation for the left arm from A. The traces at the top represent velocity records for the left (upper trace) and right (lower trace) arm movements. Each record is the average of 10 flexion movements taken from ~~the~~ largest series of movements performed (70 degrees). Vertical calibration line represents 60 degrees/sec for velocity. Horizontal calibration line represents 400 ms (DF).


A
B
C
Left Arm
Right Arm
No Load
1 lb.
12 lb.
PEAK VELOCITY (°/s)
0
50
100
150
200
25
50
75
AMPLITUDE (°)
AMPLITUDE (°)
AMPLITUDE (°)
Left arm
Right arm

2 OF/DE 2



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

weight (1 lb.). When the weight applied during movements was 12 lbs., the effect seen was on the two arms. The value of the slope of the peak velocity-amplitude relation of movements of the loaded arm decreased when that arm moved with the load on. A decrease in the value of the slope of the relation for simultaneous movements of the opposite, non-loaded, arm was also obtained.

III. Movements Made Independently by the Two Arms

A. Movement kinematics and durations :

The experiments on simultaneous bilateral arm movements in this study revealed the existence of an intimate relation between movements made by the two arms. Movements were tightly linked in their time of onset and were closely matched in their kinematic features. This suggested that these simultaneously performed movements of the two arms may utilise a shared or common motor program. If the same motor program is used to organize movements of the two arms, one might expect that movements of the two arms would share some characteristics even if they were performed independently. This hypothesis was approached by comparing motor performance of the two arms when subjects were asked to make the movements with each arm independently.

In the experiments to be described, the subject first made a series of movements with one arm and then after a rest period of 10-15 minutes, the same series of movements was repeated by the subject using the other arm (see METHODS for details). Figure 12 shows typical averaged records of flexion movements from one subject. Each set of traces shows averaged records of position and velocity of movements of three amplitudes made independently by the right (A-C) and left (D-F) arms. The position record of each movement shows a smooth translation of the arm from one position to another. Since visual feedback was provided to the subjects, movements of either arm started within one target zone and ended within the other target. Movements were made at well below the subject's maximum speed and there was thus only small over- or undershoot of the targets. Movement amplitudes were therefore the same for the two arms. For all movements, movement velocity started from zero, increased to a single peak and decreased to zero again.

In all subjects, movement duration increased with movement amplitude. Figure 13 shows data on movement durations from the six subjects studied in this series. In each graph, the open symbols are data from right and closed symbols from the left arm. Each plotted point is the mean from 10 flexion movements. Standard deviation bars are shown.

Figure 12

Comparison of movements made by the two arms independently. Each set of traces shows averaged records of position and velocity of flexion movements made by the right (A-C) and left (D-F) arms. Each trace is from the average of 10 movements; the dotted lines on either side of the average show the standard deviations. Movement amplitudes were 10 degrees (A,D), 30 degrees (B,E) and 40 degrees (C,F). The vertical calibration in F represents 10 degrees for position and 75 degrees/sec for velocity. Horizontal calibration bar represents 200 ms. (AS).

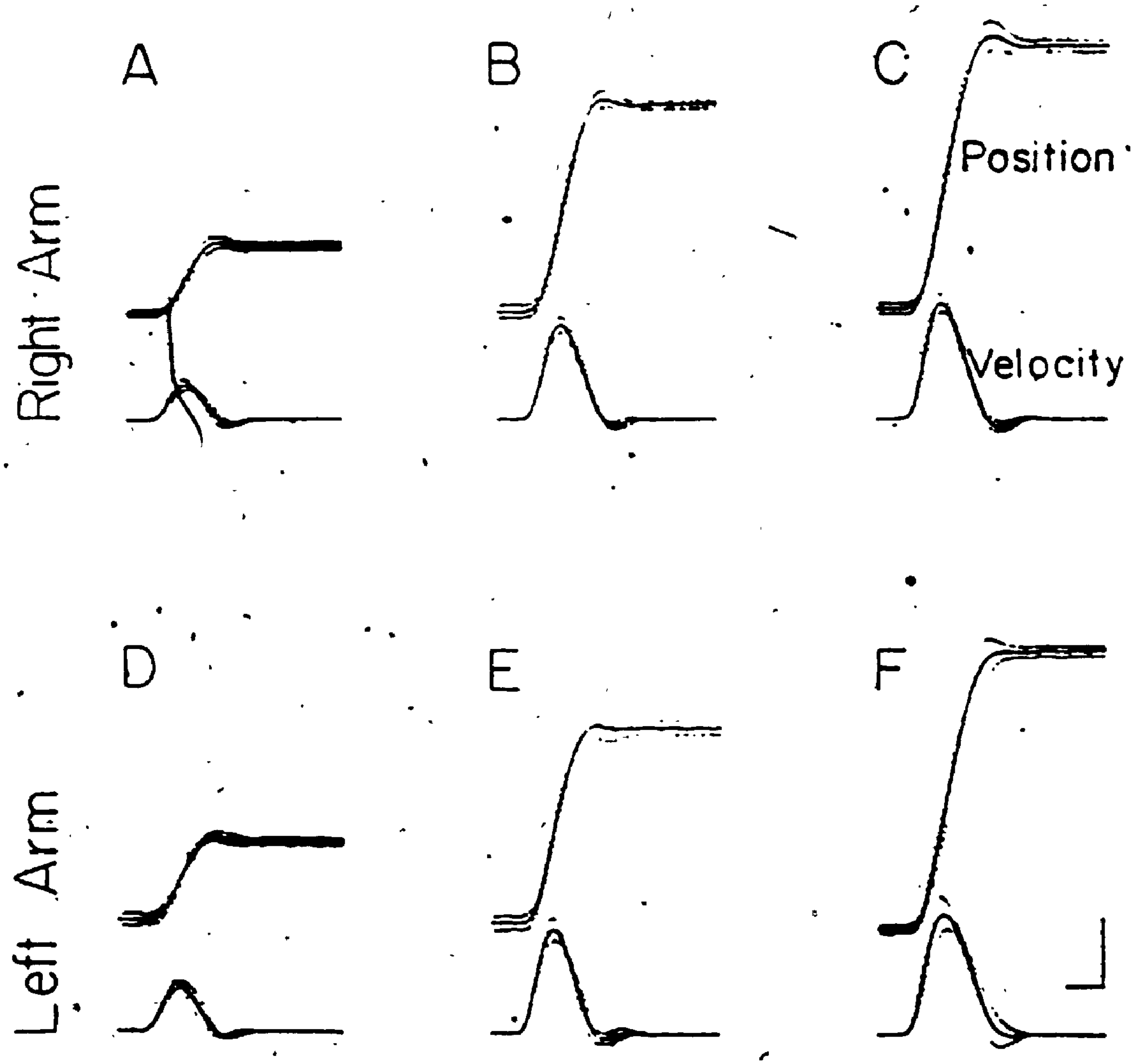
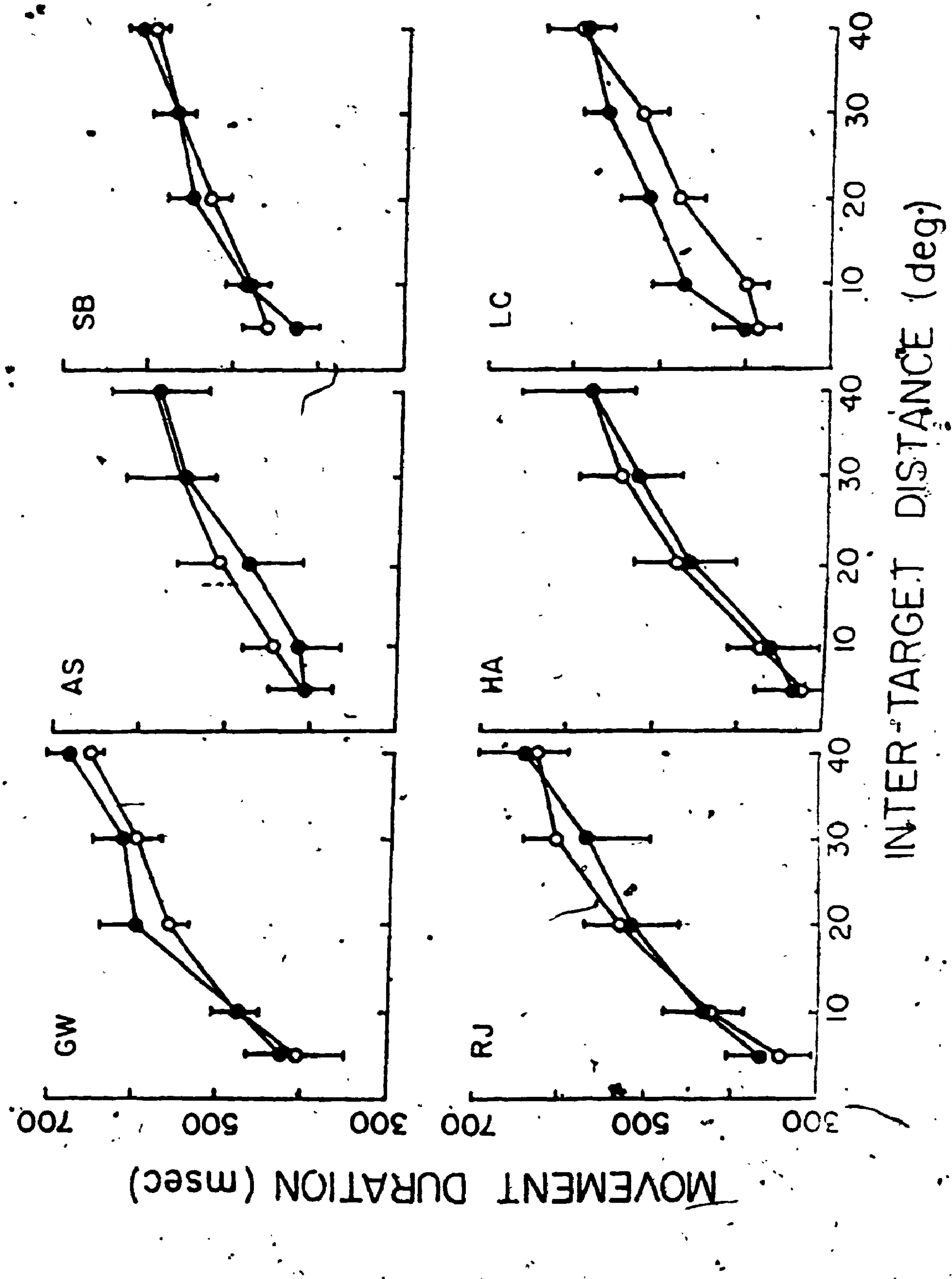

A
B
C
Position
Velocity
Right Arm
D
E
F
Left Arm

Figure 13

Duration-amplitude relations of movements made independently by the two arms. Data are presented from 6 subjects. Movement duration is plotted as a function of inter-target distance for movements made independently by the right (open symbols) and left (closed symbols) arms. Each point represents the mean of 10 flexion movements with the standard deviations.


GW
AS
SB
RJ
HA
LC
300
500
700
10
20
30
40
MOVEMENT DURATION (msec)
INTER-TARGET DISTANCE (deg)

There was no consistent difference between the two arms. Thus, movements of the right (preferred) arm were not consistently of shorter duration than those of the left (non-preferred) arm. As indicated in Figure 12, the variability of the movements was similar for both arms. That is, movements of the preferred (right) arm were not less variable or better reproduced than those of the non-preferred (left) arm. Variabity of the durations of movements made with right arm was not significantly different from that of the left arm. In Table 5, are given the ratios of the variances of movement durations (right arm/left arm). F-Test showed that there was no significant difference between the variances of the durations for the two arms in the six subjects studied (F value was less than 1.7 for all movement amplitudes, df=54,5, p>.05).

B. Movement peak velocity-amplitude relations :

As described earlier for simultaneously performed movements, these independently performed movements were also characterized by an increase in movement peak velocity as movement amplitude was increased. Figure 14 shows velocity-amplitude data from 6 subjects. Here, peak velocity is plotted as a function of inter-target distance because the latter will correspond to actual movement amplitude in these visually-guided movements. Each point in Figure 14 is from

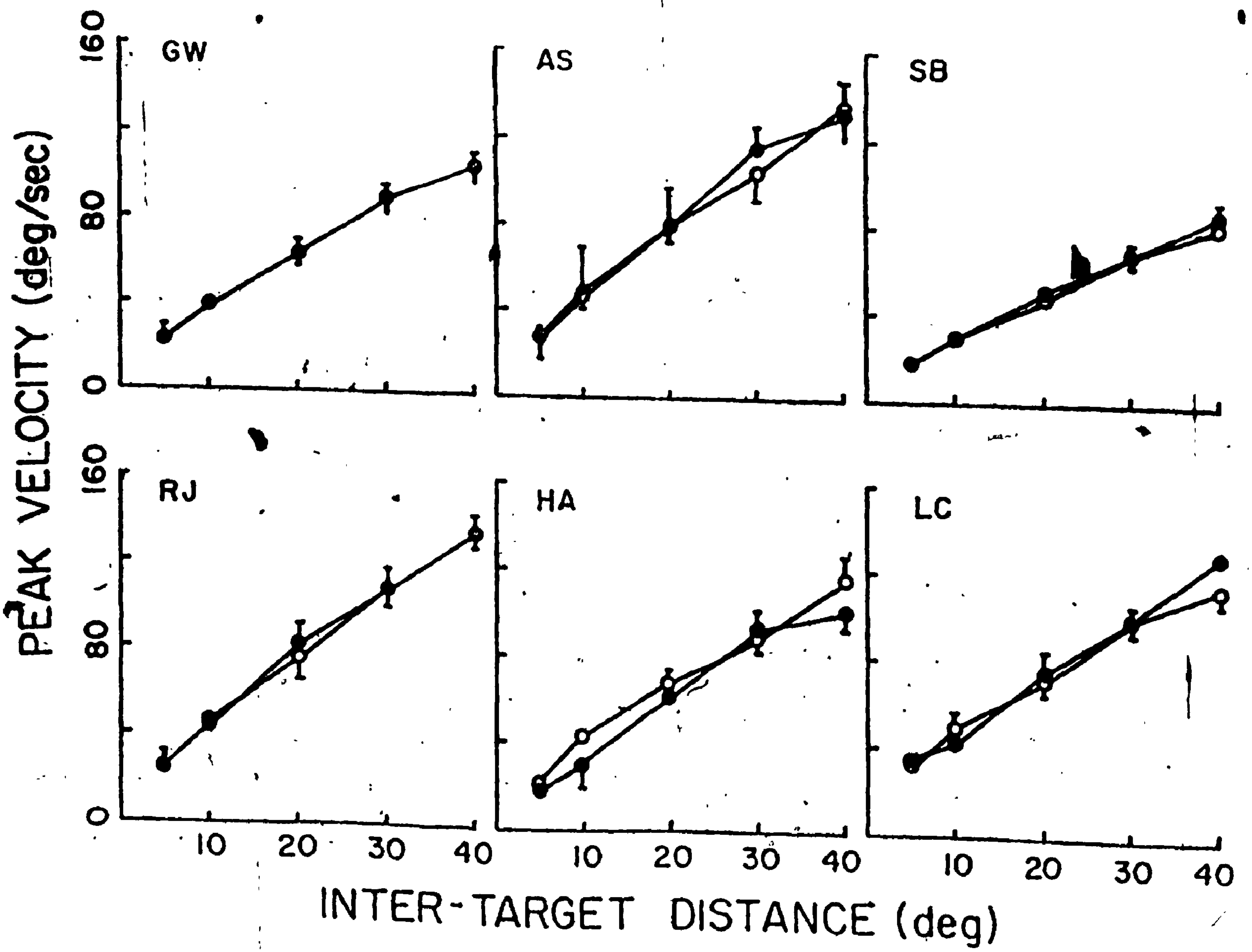
Table 5

Ratios of variances of movement duration (right arm/left arm) for independently made movements of the two arms.

Subject	5 deg	10 deg	20 deg	30 deg	40 deg
GW	1.42	.94	.37	.90	.26
AS	.81	.49	.59	3.03	.87
SB	1.82	.59	.69	.46	1.59
RJ	1.06	.69	.69	.32	.34
HA	.85	[illegible]	.81	.94	2.02
LC	.52	.52	.76	1.19	3.50
F-test					
$F_{54,5}$	1.079	1.658	1.534	1.141	1.427

Figure 14

Velocity-amplitude relations for movements made independently by the two arms. Data from 6 subjects are shown. Peak velocity is plotted as a function of inter-target distance. Each point is the average of 10 flexion movements with standard deviations; open symbols from the right arm and closed symbols from the left arm.

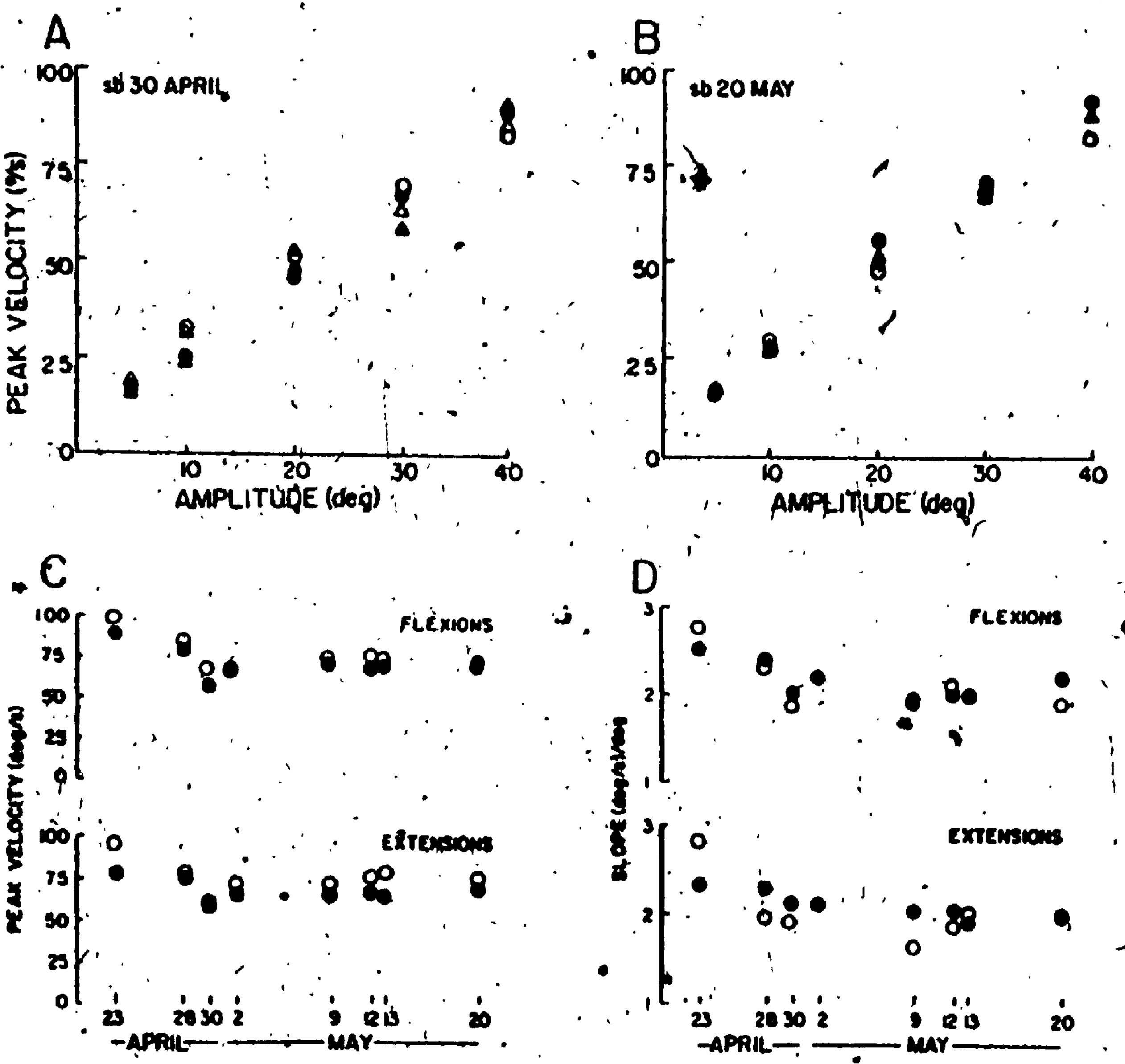

PEAK VELOCITY (deg/sec)
160
80
0
GW
AS
SB
RJ
HA
LC
10
20
30
40
INTER-TARGET DISTANCE (deg)

the average of 10 flexion movements: open symbols from the right arm and closed symbols from the left. In all subjects, peak velocity increased linearly with movement amplitude (correlation coefficient 0.95 or greater). There was no systematic difference between the performance of the two arms. To test the similarity between the velocity-amplitude relations of the two arms, the slopes of the regression relations were compared for the two arms in all 6 subjects. The unsigned difference between the slopes relative to the slope for the right arm was not significantly different from zero (t=1.79, n=6). The slopes of the regression relations were therefore the same for the two arms.

Similar data from one subject is shown in Figure 15A. In the graphs in this figure, movement peak velocity is plotted as a function of movement amplitude for movements made by the right and left arm (open and closed symbols respectively). Data shown as circles were obtained from flexion movements and that as triangles from extension movements. Each point represents the average from 10 movements. The SE of the mean was smaller than the plotted points in every case. Two points should be noted. First, for each arm the relation was the same for both flexion and extension movements (circles and triangles). Second, the relation was the same for both arms (open and closed symbols). Thus, in terms of the relation between movement

Figure 15

Peak velocity-amplitude relations for movements made independently by the two arms. A & B show data from two test days for the same subject: open symbols-right arm, closed symbols-left arm, circles-flexions, triangles-extensions. C shows peak velocities of 30 degree movements on 8 different test days. D shows the slope of the velocity-amplitude relation on the same days shown in C. (SB).


A
sb 30 APRIL
PEAK VELOCITY (%)
100
75
50
25
0
10
20
30
40
AMPLITUDE (deg)
B
sb 20 MAY
100
75
50
25
0
10
20
30
40
AMPLITUDE (deg)
C
FLEXIONS
EXTENSIONS
PEAK VELOCITY (deg/s)
100
75
50
25
0
23
28 30 2
9
12 13
20
APRIL
MAY
D
FLEXIONS
EXTENSIONS
SLOPE (deg/s)/deg
3
2
1
23
28 30 2
9
12 13
20
APRIL
MAY

amplitude and velocity, this subject performed these independently made movements identically with both arms.

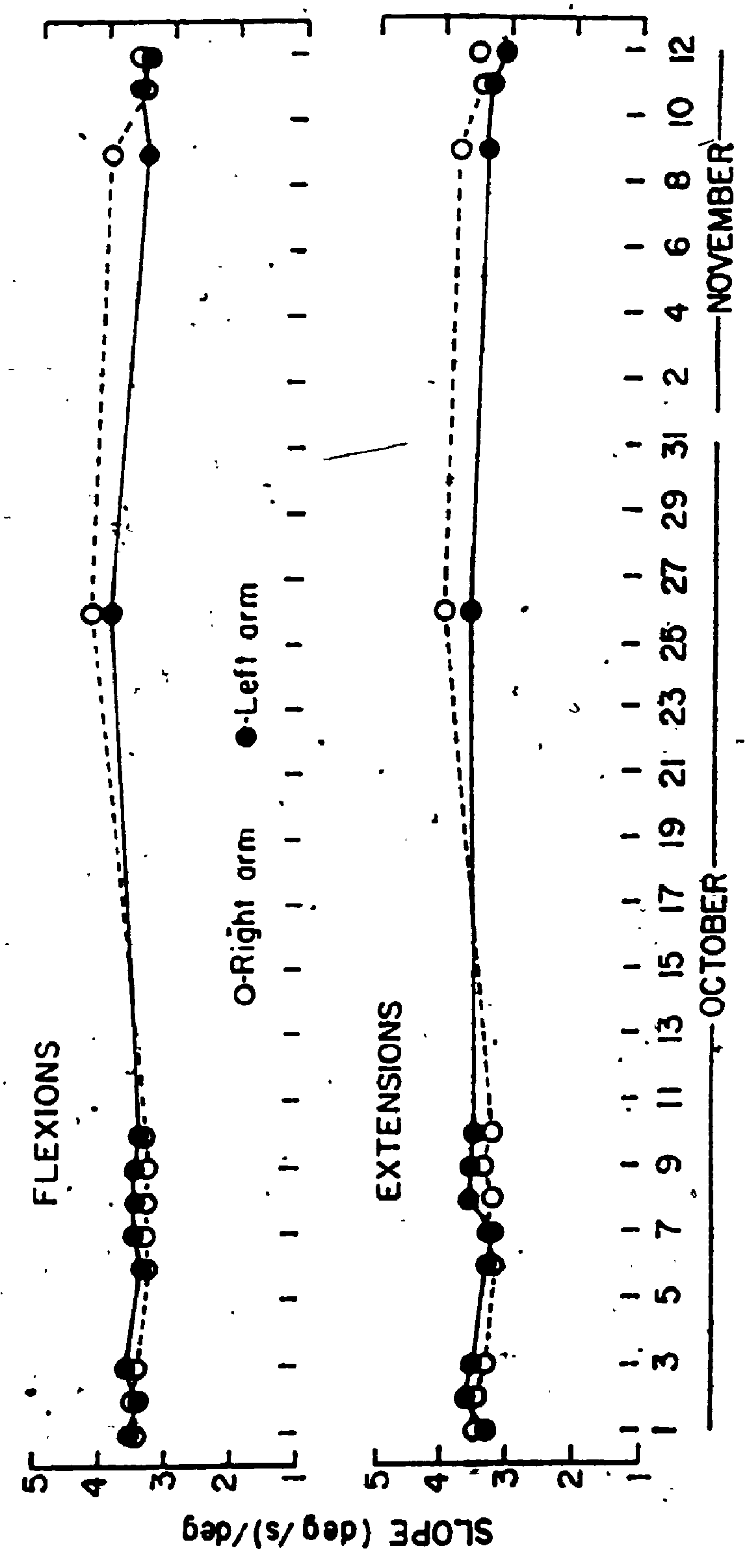
Repeated determination of this relationship showed that it was stable over long periods of time. For example, the data shown in <u>Figure 15A</u> was obtained on 30 April. In <u>Figure 15B</u> is shown analogous data, obtained from the same subject three weeks later on 20 May. There was again, a linear relation between movement velocity and amplitude with no marked differences between flexions and extensions, or between right and left arms. Moveover, the slope of the relation appeared very similar to that obtained three weeks previously (A).

In order to determine the time course of any changes in this peak velocity-amplitude relationship and compare these changes for the two arms, experiments were performed with this same subject on the eight experimental days indicated at the bottom of <u>Figure 15 C,D</u>. These experimental days spanned a period of 4 weeks. In <u>Figure 15C</u> the peak velocity of movements of 30 degrees amplitude is plotted for flexions (upper records) and extensions (lower records). As before, open symbols are from movements made by the right arm and closed symbols from movements by the left arm. Over the first few days of testing the peak velocity of these movements decreased to a level (30 April) which was then maintained over the next three weeks. Note that the peak velocities of movements by the right and left arms changed in the same way from one test day to another. This linked change in the performance of movements by the two limbs is reinforced in Figure 15D where the slope of the peak velocity-amplitude relation is plotted for the same experiments as in C. The slope in each case was determined from the least squares, best-fit linear regression equation. In all cases, the correlation co-efficient of the linear regression equation was 0.95 or greater. As seen with the individual movements (30 degrees, Figure 15C), the slope of the velocity-amplitude relation decreased over the first week of testing, reaching a new level that was maintained thereafter. As before, there were parallel changes in the right and left arms, the slope of the relation becoming the same for both arms.

Figure 16 shows data from another subject tested over a period of 6 weeks. This subject was examined 12 times during this period as indicated on the figure. The slope of the velocity-amplitude relation for movements of the right arm was compared to that of the left arm using the "paired" t-test. There was no significant difference between these slopes over the 6 week period (flexion movements: $t=1.4937$, $df=11$, $p>0.1$; extension movements: $t=2.1953$, $df=11$, $P>0.05$).

Figure 16

<u>Comparison of movements made independently by the two arms over a 6 week period.</u> The slope of the peak velocity-amplitude relations is plotted for each of the experimental sessions over the six week period for the same subject. Open symbols show data from right and closed symbols from the left arms. (GW).


FLEXIONS
EXTENSIONS
O-Right arm
●-Left arm
SLOPE (deg/s)/deg
5
4
3
2
1
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
2
4
6
8
10
12
OCTOBER
NOVEMBER

C. Summary :

For movements made independently by the two arms, movement peak velocity increased linearly with movement amplitude. This relation was identical for flexion and extension movements of the same arm as well as for movements made by the right and left arms. This matching in independently made movements was maintained over periods of time, up to two months.

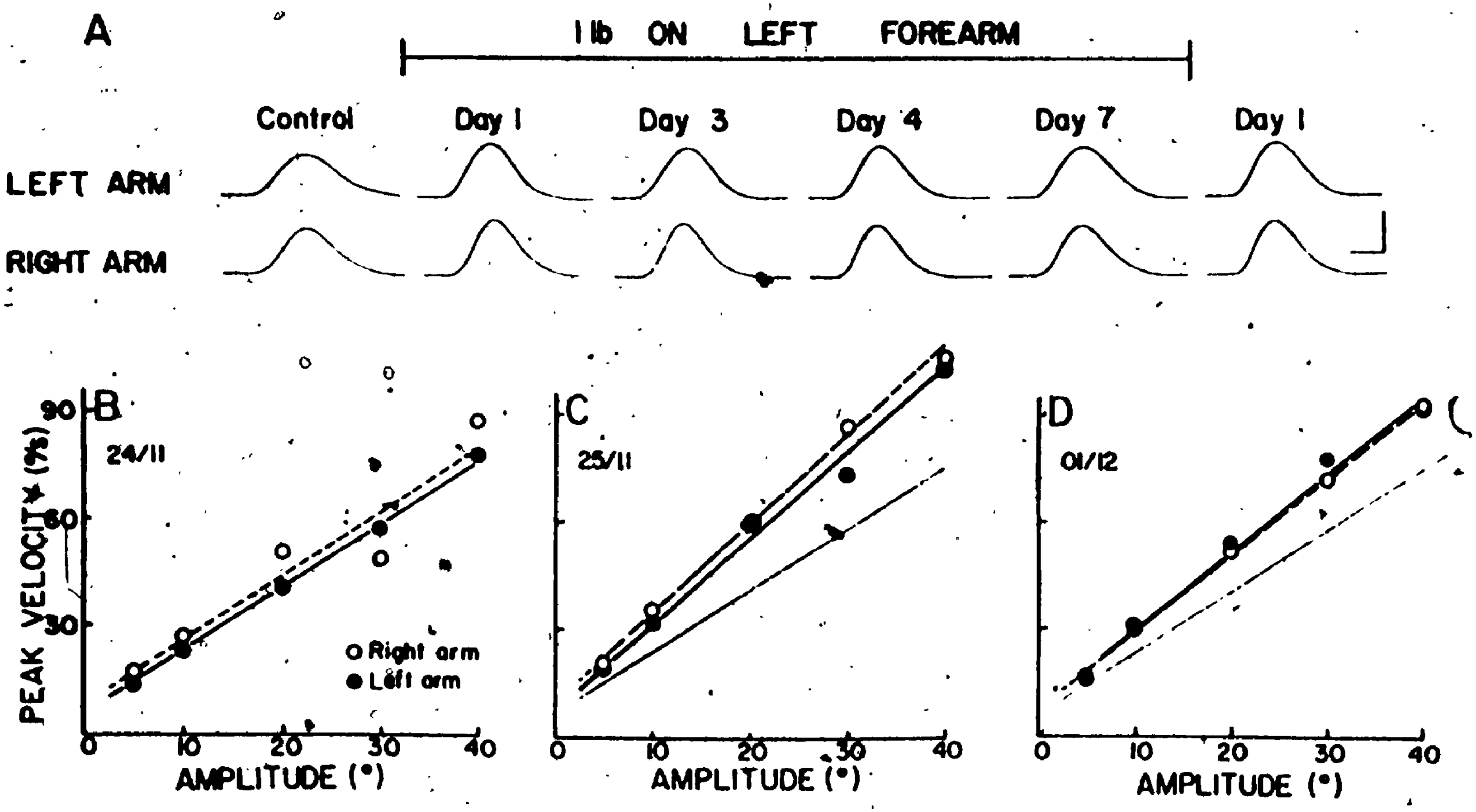
D. Compensation for unilateral long-term loading:

As described in the previous section, the relation between movement velocity and amplitude showed little difference for movements made by the right and left arms and, after an initial "settling down" period, little change over a period of weeks. There was thus an apparent matching of movements of the two arms even though made independently and whichever arm was tested first. This raised the question whether this apparent matching of movement performance by the two limbs was an inherent characteristic in the organization of the motor system. This question was approached by attempting to produce a unilateral, long-term alteration in motor performance and following the time course of changes in movement performance by the two limbs.

In this series of experiments, movement performance was altered by having subjects wear a light (1 lb) weight strapped to the left forearm just proximal to the wrist. As described in METHODS, subjects wore the weight continuously for one week during which movements of the two arms were independently examined daily. Data from one subject is shown in Figure 17. In A are shown records of movement velocity for movements of 40 degrees amplitude. Each record is the average of 10 flexion movements. In this subject, movement velocity of the left (loaded) arm increased on the day immediately following application of the weight and remained above control levels on each testing day thereafter. As may be seen from the traces, the velocity of the right, unloaded arm also increased and was maintained at this new higher level. In B-D are shown peak velocity-amplitude relations for control movements obtained before loading of the arm (B) and for the first (C) and sixth day (D) following application of the weight. Open symbols show data from the right (unloaded) and closed symbols from the left (loaded) arm. All lines are least squares, best-fit regression lines. Correlation co-efficient were 0.95 or greater. For ready comparison, the dotted lines in C and D show the control relation from B. In each case, the velocity- amplitude relation was linear with the slope, for this subject, being greater during loading than for the control movements.

Figure 17

Matching of movements following chronic unilateral loading. In A are shown records of movement velocity for flexion movements of 40 degrees amplitude. Each record is the average of 10 movements. In B & C are shown peak velocity-amplitude relations for control movements before loading of the left arm B and for the first C and sixth day D following application of the weight. Open symbols show data from the right (unloaded) and closed symbols from the left (loaded) arm; solid lines represent the relation for the left and dashed lines for the right arms. All lines are least squares, best-fit regression lines. For ready comparison, the dotted line in C & D show the control relation from B. Vertical calibration bar represents 90 degrees/sec for velocity and horizontal bar 200 ms. (RJ).

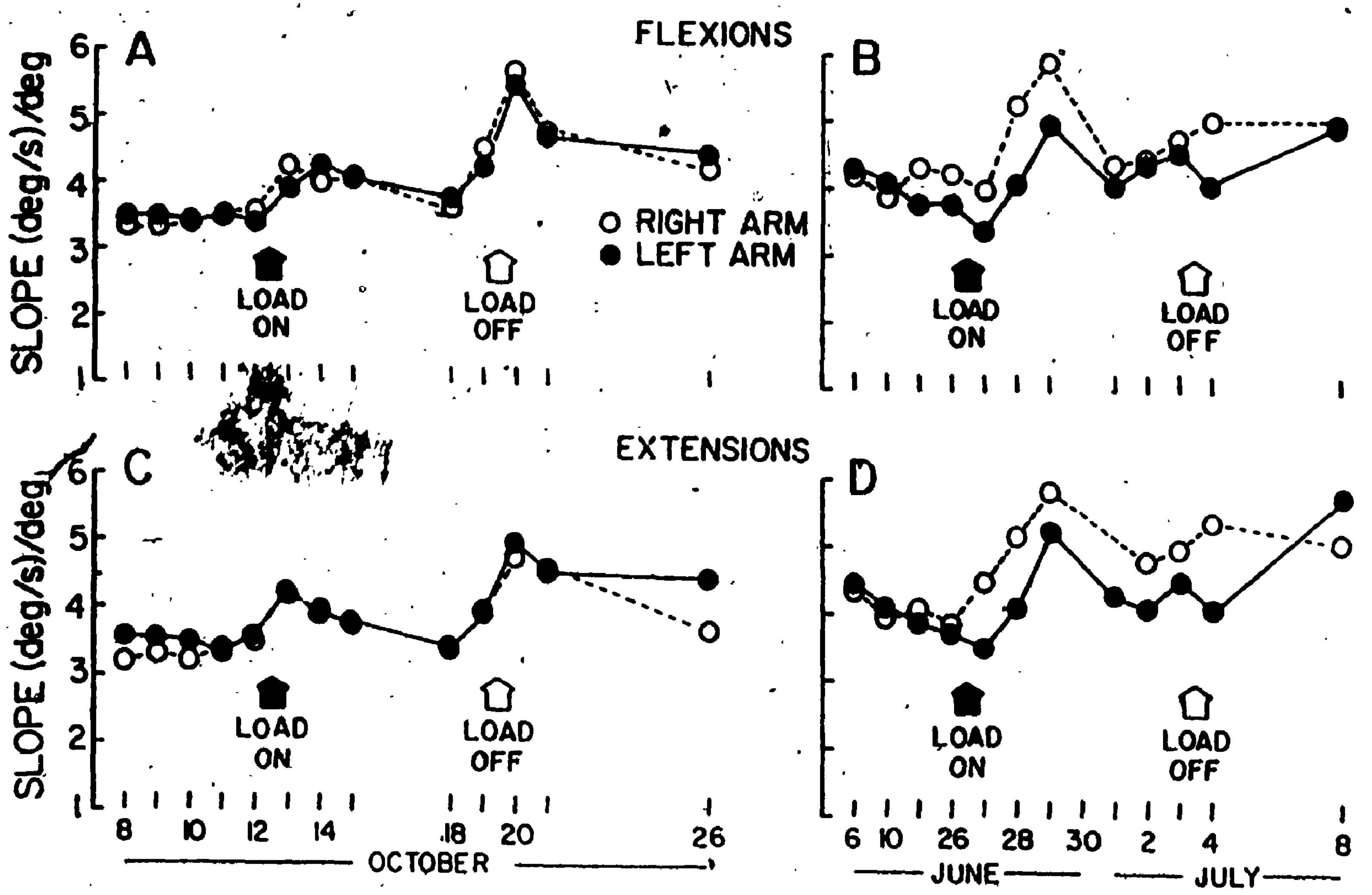

A
1 lb ON LEFT FOREARM
Control
Day 1
Day 3
Day 4
Day 7
Day 1
LEFT ARM
RIGHT ARM
B
24/11
C
25/11
D
01/12
PEAK VELOCITY (%)
90
60
30
0
10
20
30
40
AMPLITUDE (°)
○ Right arm
● Left arm

Moreover, the relations were the same for both arms (open and closed symbols) on each testing day.

Not all subjects showed the same pattern of change in the peak velocity-amplitude relation as did the subject illustrated in Figure 17. However, whatever the specific pattern of change in movement performance produced by wearing the weight, the consistent finding was that the same change was seen in both arms. Data from two other subjects are shown in Figure 18. A and C show data from one subject and B and D from the other. The graphs show the slope of the peak velocity-amplitude curves obtained from the two subjects, data from flexions and extensions being plotted separately. Open symbols show data from the right (non-loaded) arm and closed symbols from the left (loaded) arm. Each subject was tested on several days before application of the load (solid arrow) and on two or more days following removal of the weight (open arrow). In the first subject (A,C), a modest increase in slope occurred upon application of the weight, this increase persisting over several days and being the same for each arm. Most striking in this subject was the large increase in slope of the velocity-amplitude relation upon removal of the weight. This increase occurred identically in both arms and was followed by a gradual, parallel decrease in slope.

Figure 18

<u>Velocity-amplitude relations following unilateral loading.</u> The slope of the peak velocity-amplitude relation is shown from two subjects (A, C and B, D) both before and after they wore a 1 lb weight on the left forearm for one week. Each data point represents the slope of the best-fit linear regression equation obtained from movements of 5 different amplitudes; open circles represent the right (unloaded) and closed circles the left (loaded) arms. The horizontal scale indicates the days on which the experiments were performed. (A,C-GW; B,D-AS).


FLEXIONS
A
B
SLOPE (deg/s)/deg
6
5
4
3
2
1
○ RIGHT ARM
● LEFT ARM
LOAD ON
LOAD OFF
EXTENSIONS
C
D
8
10
12
14
18
20
26
OCTOBER
6
10
26
28
30
2
4
8
JUNE
JULY

In the second subject (B, D), a more striking increase in slope occurred upon loading, with the slope subsequently decreasing somewhat. Although in this subject the two arms were not initially as well matched as in the other subjects, nonetheless the right (unloaded) arm (open symbols) followed a similar sequence of changes as the left (loaded) arm (closed symbols).

To test whether similar changes occurred in the movements of the two arms, the peak velocities of the largest movement performed (40 degrees) were chosen for daily correlation over the period of the loading. The daily mean peak velocity for 10 movements (40 degrees amplitude) of the right and left arms for each of the 6 subjects were correlated over the one week period during which the left arm was loaded. Using the Fisher-Z transformation (Steel and Torrie, 1980), the correlation co-efficients for the six subjects were found to be homogenous ($p>0.25$) and the correlation was therefore pooled into one value for flexions and one value for extensions. The values of the pooled correlation coefficient were 0.88 for flexion and 0.81 for extension movements ($p<0.001$). Thus, for these 40 degrees movements peak velocities for the two arms changed in parallel over the period of the unilateral loading.

E. Unilateral long-term loading with orthopaedic cast :

Data from two more subjects wearing an orthopaedic cast on the left forearm for periods longer than one week were also collected. One patient was tested 8 times over a period of 7 weeks with the cast on and once when the cast was removed. The other patient was tested 19 times over a period of 5 months with the cast on (removed once for radiological checking in the middle of the 5 month period) and 4 times after the cast was permanently removed. The data showed that similar changes in movement performance, produced by wearing and removing the cast, occurred in both arms. A paired t test for the results showed that the changes in the slope of the peak velocity-amplitude relation for each arm were not significantly different from the other over the whole period for each patient, (Patient U.B.: $t=2.1$ $df=8$, $p>0.05$ for flexion and $t=2.2$, $df=8$, $p>0.05$ for extension; Patient K.G.: $t=1.6$, $df=23$, $p>0.1$ for flexion and $t=1.9$, $df=23$, $p>0.05$ for extension).

F. Summary :

Chronic loading of the left arm changed the value of the slope of the velocity-amplitude relation for movements of the left arm. The slope of the velocity-amplitude relation for movements of the right (unloaded) arm changed in parallel so as to remain matched with the slope of the relation for movements of the left (loaded) arm. Re-matching between the slopes of the velocity-amplitude relations for movements of the two arms also occurred following removal of the weight.

Loading and unloading of the left arm led to changes in the movements made by the left arm that were different in different subjects. However, whatever changes occurred to the slope of the velocity-amplitude relation of the loaded arm, the same changes were seen in the movements made independently by the right (unloaded) arm.

IV. The Influence of Kinesthetic Information :

The experiments which have been described showed that there is a strong tendency for movements of the two limbs to be matched. This matching can be disrupted by visual information. However, alteration of movements of one limb by mechanical means leads to changes in movements of the other limb in order to re-establish the matching. The experiments to be described were designed to define more closely the influence of kinesthetic information from one limb on movements made with the other limb. For these experiments vibration was applied to the muscle tendon of one arm both when that arm was stationary and while the subject was performing simultaneous bilateral movements. As discussed under HISTORICAL REVIEW, muscle tendon vibration is a powerful stimulus for muscle spindle receptors. Such vibration will thus provide the nervous system with incorrect information about the actual limb position and velocity.

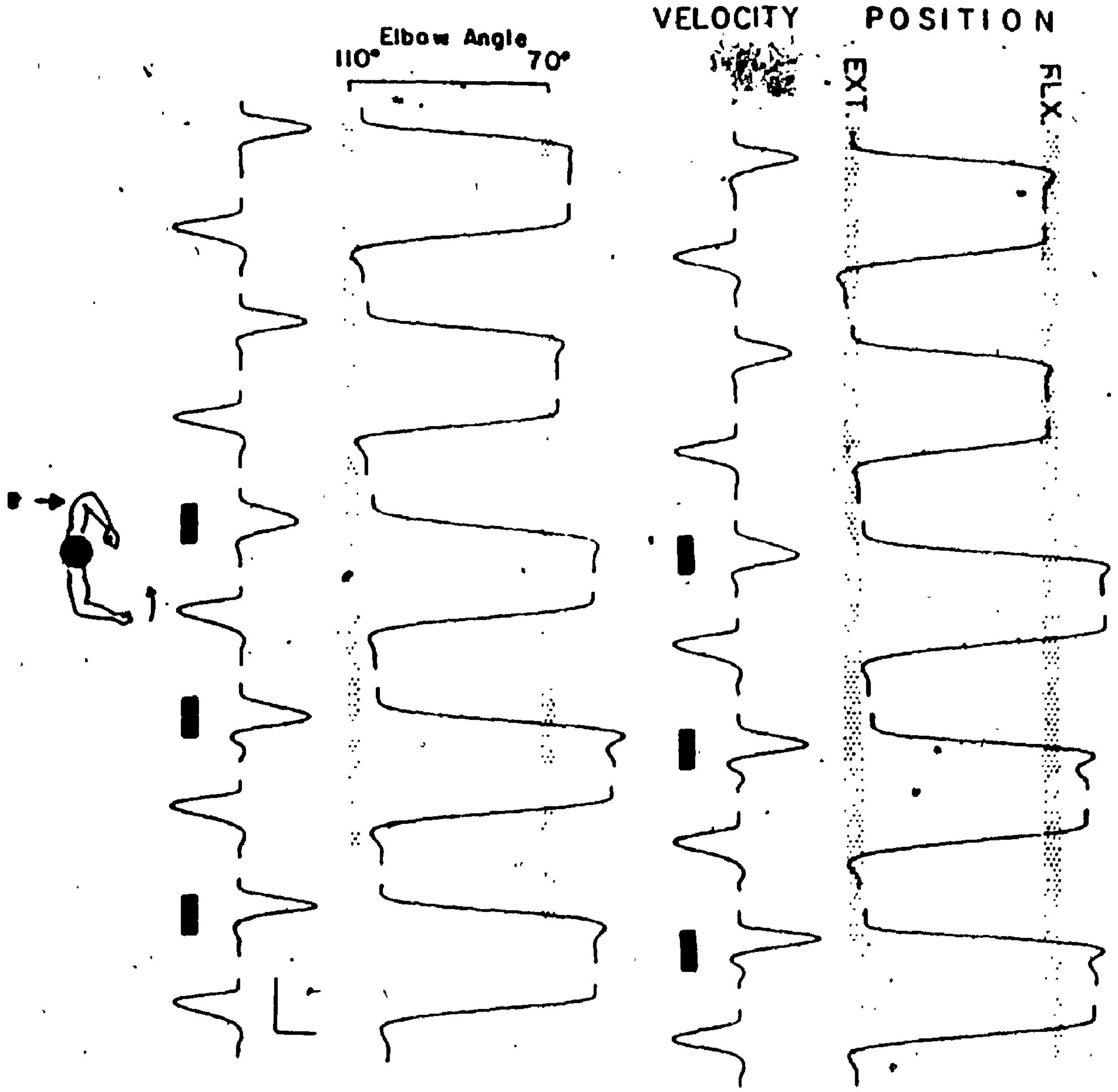
A. Contralateral effects of vibrating muscles in stationary arm :

As described in detail under METHODS, subjects first practiced movements of the one arm with visual guidance. The subjects then performed movements without visual guidance (eyes closed). During these trials, an auditory cue was used to signal when the subject was to move. As described previously subjects were able to attain the required target position equally well with or without visual guidance (cf. Figure 2).

Figure 19 shows records of movements from the right arm of one subject. Brief bursts of mechanical vibration (indicated by solid rectangles) were applied to the tendon of the triceps muscle of the left (stationary) arm. The records are of sequential movements. No vibration was applied during the first two flexions/extensions. The subject moved between the two desired target positions (indicated by the stippled bars). The triceps tendon of the

Figure 19

Effect of muscle-tendon vibration on step-tracking performance by the contralateral arm. The position and velocity records of movements made with the right arm are shown for successive trials of movements. The stippled bars on the position records represent the target (upper bar for flexion and lower bar for extension). The left triceps brachii tendon was vibrated at the time indicated by the solid rectangles below the velocity record. Vibration was applied 6 times during this session and was triggered during the flexion movements of the right arm. The left (vibrated) arm was kept stationary during all this session. All movements were performed without visual feedback. Vertical calibration represents 8 degrees for position and 60 degrees/sec for velocity. Horizontal calibration represents 1 sec. (VN)

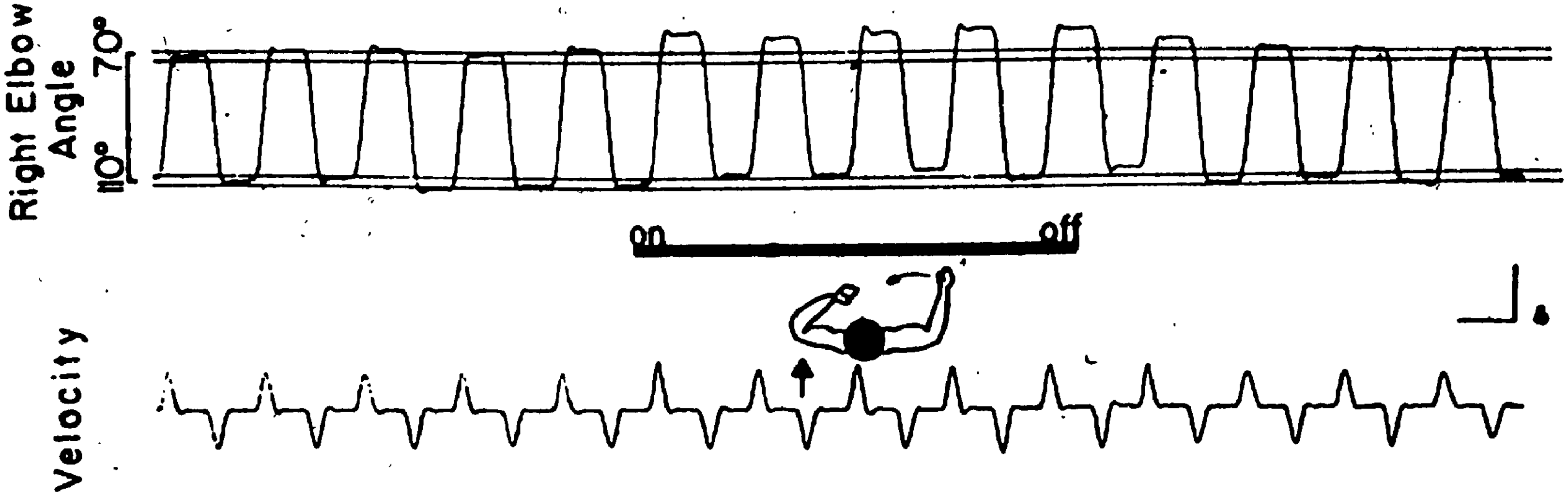

VELOCITY
POSITION
EXT.
FLX.
Elbow Angle
110°
70°

non-moving arm was vibrated during the next three flexion movements. No vibration was applied for the following two flexion movements (lower set of traces). Vibration was again applied during the last three flexion movements. In each case when vibration was applied to the non-moving arm the flexion movements of the moving arm markedly overshot the intended end-position (upper stippled bar). The movements that were accompanied by the vibration were also made at a greater peak velocity in this subject. These effects of vibration were rapidly reversed. Thus, the subject slightly overshot the target in the first flexion movement following cessation of vibration (first movement in lower traces). By the second post-vibration flexion, however, the effects of vibration had largely disappeared. This short post-vibratory effect was not uncommon in some of the subjects studied and could mean that there was an after-effect of the vibratory stimulus that lasted for a short time following cessation of vibration.

In other experiments tendon-vibration was continuously applied to the stationary arm during flexion/extension movements of the opposite arm. Figure 20 shows an example of one such experiment. The subject started by performing the usual flexion/extension movements with the right arm without visual feedback. Vibration of the left triceps tendon was then applied continuously for 30 sec (solid bar). The effect

Figure 20

Effect of continuous muscle-tendon vibration on movement performed by the opposite arm. Position and velocity records for movements of the right arm are shown. The two pairs of lines around the position record represent flexion (upper lines) and extension (lower lines) intended positions. Movements were made without visual feedback. The left triceps brachii muscle of the stationary arm was vibrated continuously (solid horizontal line) while the right arm was being moved. Vertical calibration line represents 150 degrees/sec for velocity. Horizontal calibration line represents 1.5 sec. (VN).


CONTINUOUS VIBRATION

of this continuous vibration of the left triceps tendon was an overshooting of the flexion end position by the subject's right arm. Note, in this figure, that vibration of the left triceps affected flexion end position of movements made by the right arm but did not influence the extension end position of these movements. In other experiments, vibration of the biceps tendon of the stationary arm led to overshooting of the extension end position of movements made with the opposite arm. Thus, tendon vibration of either of the two muscles of the elbow joint influenced movements of the opposite arm associated with stretching of the muscle synonymous to the one vibrated. Note that movement velocities were also affected by vibration. As seen in Figures 19 and 20 peak velocity associated with the vibration was of a greater magnitude.

In the experiments described thus far, the vibrated (left) arm was restrained in a fixed position by mechanically immobilising the left manipulandum. In other experiments in which the vibrated arm was left unrestrained, continuous vibration produced a tonic vibration reflex. Whether or not the vibrated arm was restrained did not alter the effects on the opposite moving arm. In some subjects, continuous vibration was also applied with the vibrated arm restrained and positioned at different elbow joint angles to test whether the degree of stretch of the vibrated muscle would change the effects of vibration on the opposite arm. Figure 21 shows representative data from one subject. The vibrated arm was fixed at different angles (A-D). With elbow angles of 45, 90 and 135 degrees (A-C), vibration of the triceps muscle of the non-moving arm produced an overshoot of flexion end-position in the moving arm as described previously. However, with the arm in full extension (D - 180 degrees), vibration produced no effect on movements by the non-vibrated arm.

In each subject (n=7), 10 flexion movements of the right arm made without vibration were compared with 10 flexion movements of the same (right) arm made during vibration of the triceps muscle of the stationary (left) arm. Table 6 shows the means and S.D. of the differences between actual and intended flexion end positions for movements made with and without vibration. Positive values indicate overshooting of the intended target. A two-way ANOVA on the effect of vibration showed a highly significant effect of vibration on movement end position of the non-vibrated arm. ($F=45$, $df=1,6$, $p<0.01$).

B. Tendon-vibration during simultaneous arm movements :

The experiments just described showed that kinesthetic information from the non-moving arm can affect movements made with the other arm. Are similar crossed

Figure 21

Effect of the static angular position of the vibrated arm on movements of the opposite arm. Each set of traces represents averaged position (top) and velocity (bottom) records obtained from 5 flexion movements made with the right arm. All movements were performed without visual feedback. Solid and dashed traces represent averaged records from movements of the right arm made before and during continuous vibration of the left triceps brachii respectively. In A,B,C and D the vibration was applied to the left triceps tendon with the elbow joint of that muscle at 45, 90, 135 and 180 degrees respectively. Vertical calibration line represents 15 degrees for position and 150 degrees/sec for velocity. Horizontal calibration line represents 500 ms. (AS).

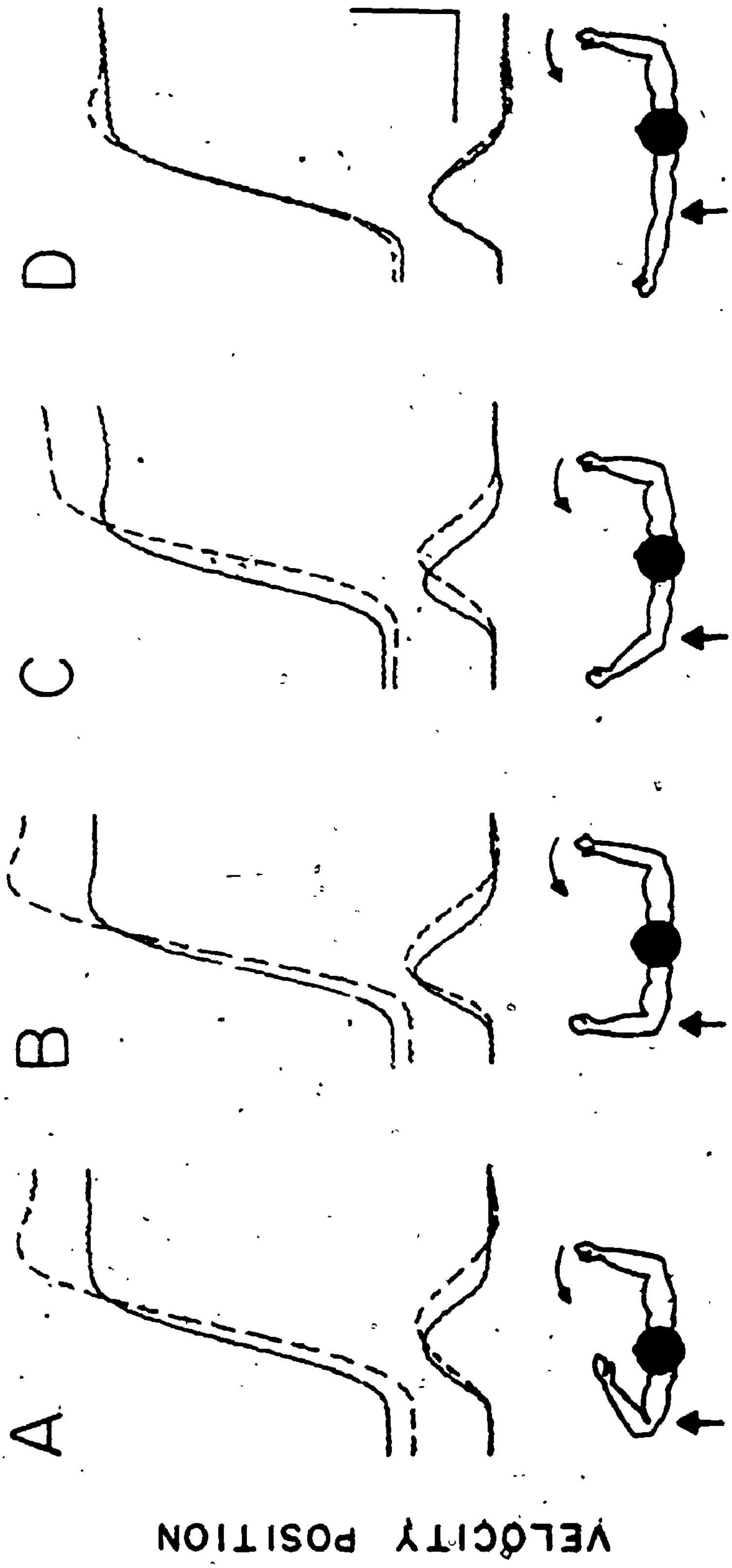

VELOCITY
POSITION
A
B
C
D

Table 6

Each number represents the mean difference and S.D. in degrees between the intended and the actual flexion end positions for movements of the right arm when the left (stationary) arm was vibrated at the triceps tendon and in the absence of tendon vibration.

Subjects	Without Vibration	With Vibration
BR	.2 (4.1)	10.3 (4.4)
KW	- 1.2 (1.7)	5.1 (2.2)
MY	.5 (1.4)	4.0 (1.5)
PZ	1.6 (1.8)	5.5 (3.3)
RJ	- 2.6 (3.7)	6.2 (4.4)
ST	- 3.9 (1.6)	1.2 (1.0)
VX	- .7 (2.5)	9.1 (4.3)

- Undershooting end-position.

effects present during bilateral movements? As described in METHODS, subjects could after practice, make the same movements with the two arms simultaneously without visual feedback. When subjects were found ready to perform consistently such bilateral arm movements without visual feedback as shown in Figure 22, the effects of tendon vibration of the biceps or triceps brachii muscles were then studied. Note in this figure the consistency with which the subject matched the movement kinematics for the two arms in addition to the consistency of moving between the required target positions. Figure 23 shows records of bilateral arm movements with brief bursts of tendon vibration applied to the right triceps muscle during three trials of the flexion movements. The subject undershot the flexion end-position with the right (vibrated) arm and overshot the flexion end-position with left (non-vibrated) arm. Similarly data from another subject is shown in Figure 24. In this experiment the left biceps tendon was vibrated (solid vertical bars) during seven successive extension movements. During vibration the subject undershot extension end-position with the left (vibrated) arm and overshot extension end-position with the right (non-vibrated) arm. It should be noted in these two examples that the degree of overshoot by the non-vibrated arm was modest compared to that seen on the vibrated arm. It was also less than that seen when the vibrated arm was stationary (cf. Figures 19,

Figure 22

<u>Movements of the two arms made at the same time without visual feedback.</u> The traces show successive flexion extension movements of the right (upper set) and left (lower set) arms. In each set of traces the upper trace represents arm position and the lower represents velocity. The pairs of horizontal lines around the positions represent flexion (upper pair) and extension (lower pair) intended target positions. Movements were performed without visual feedback. Vertical calibration line represents 20 degrees for position and 150 degrees/sec for velocity. Horizontal calibration represents 1.5 sec. (RJ)

BILATERAL ARM MOVEMENT

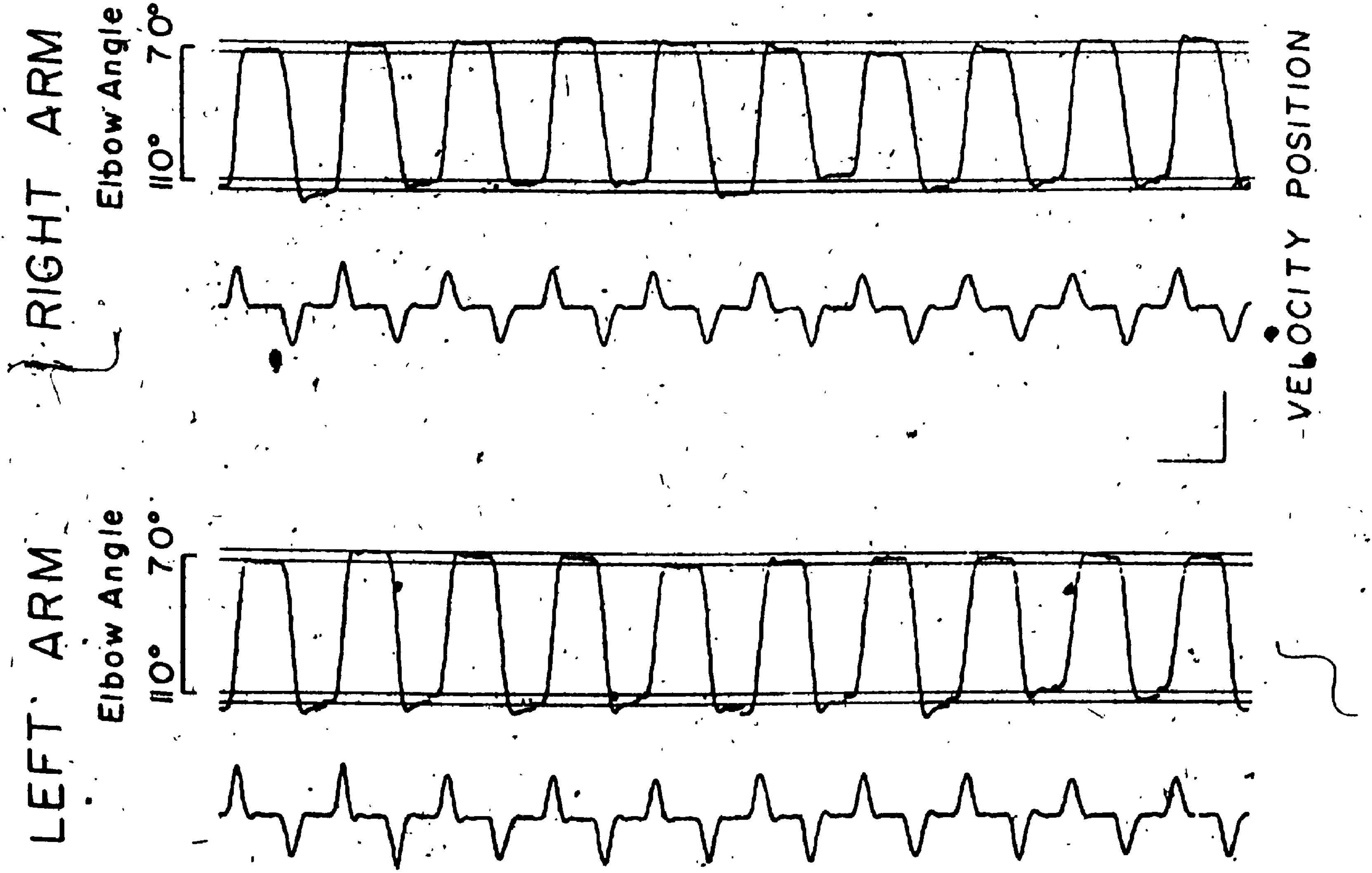


Figure 23

Responses to tendon vibration of the right arm during simultaneous bilateral arm movements. Traces represent position and velocity records from movements made at the same time by the right (upper traces) and left (lower traces) arms. The stippled bars on the position records for each arm represent target positions (flexion target is upper bar and extension target is the lower). The right triceps barchii muscle was vibrated at its tendon during these movements indicated by the small vertical bars below the lower velocity record. Vibration was applied during flexion movements. All movements were performed without visual feedback. Vertical calibration represents 100 degrees/sec for velocity and horizontal calibration represents 2 sec. (PZ).

RESPONSE TO VIBRATING RIGHT TRICEPS

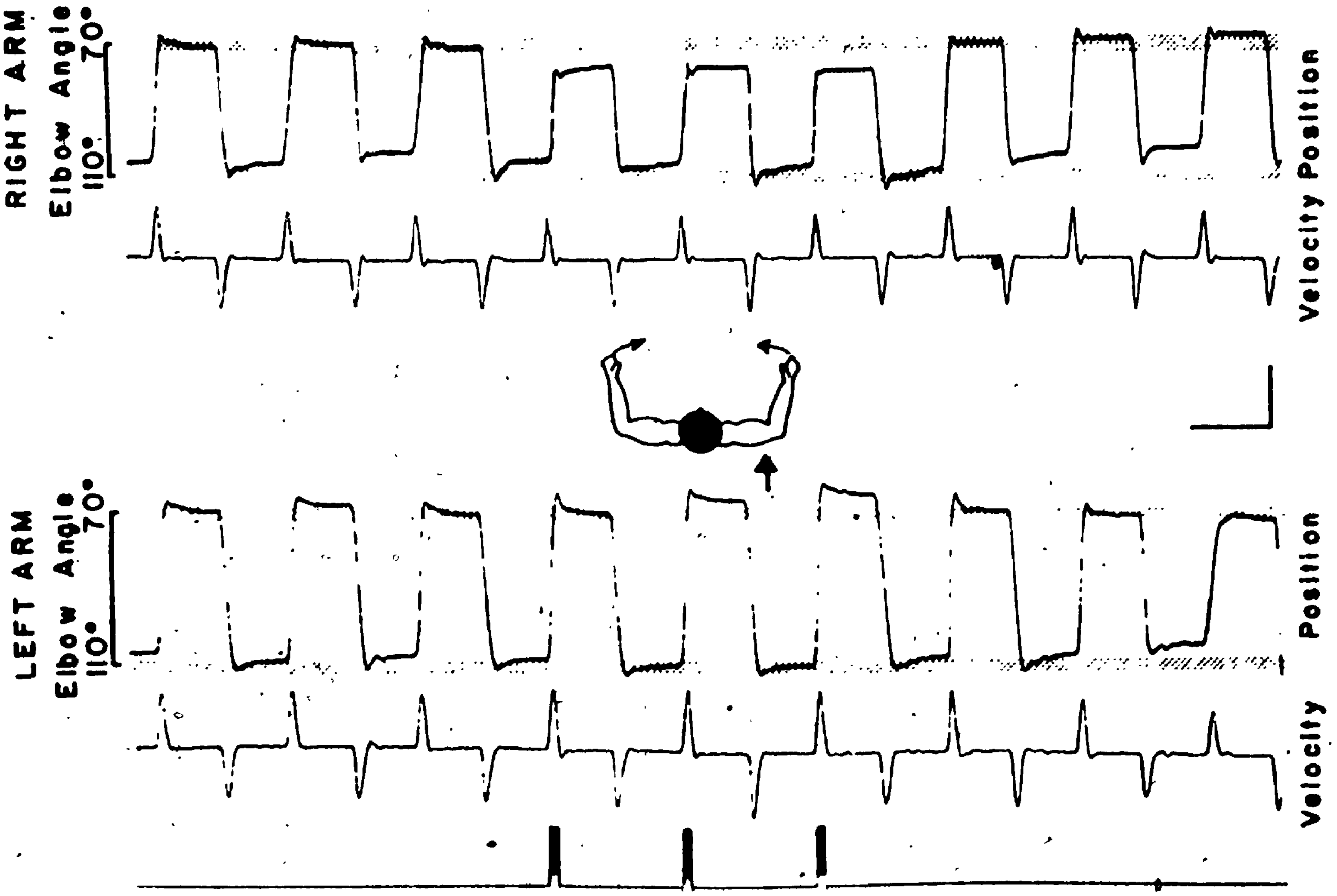
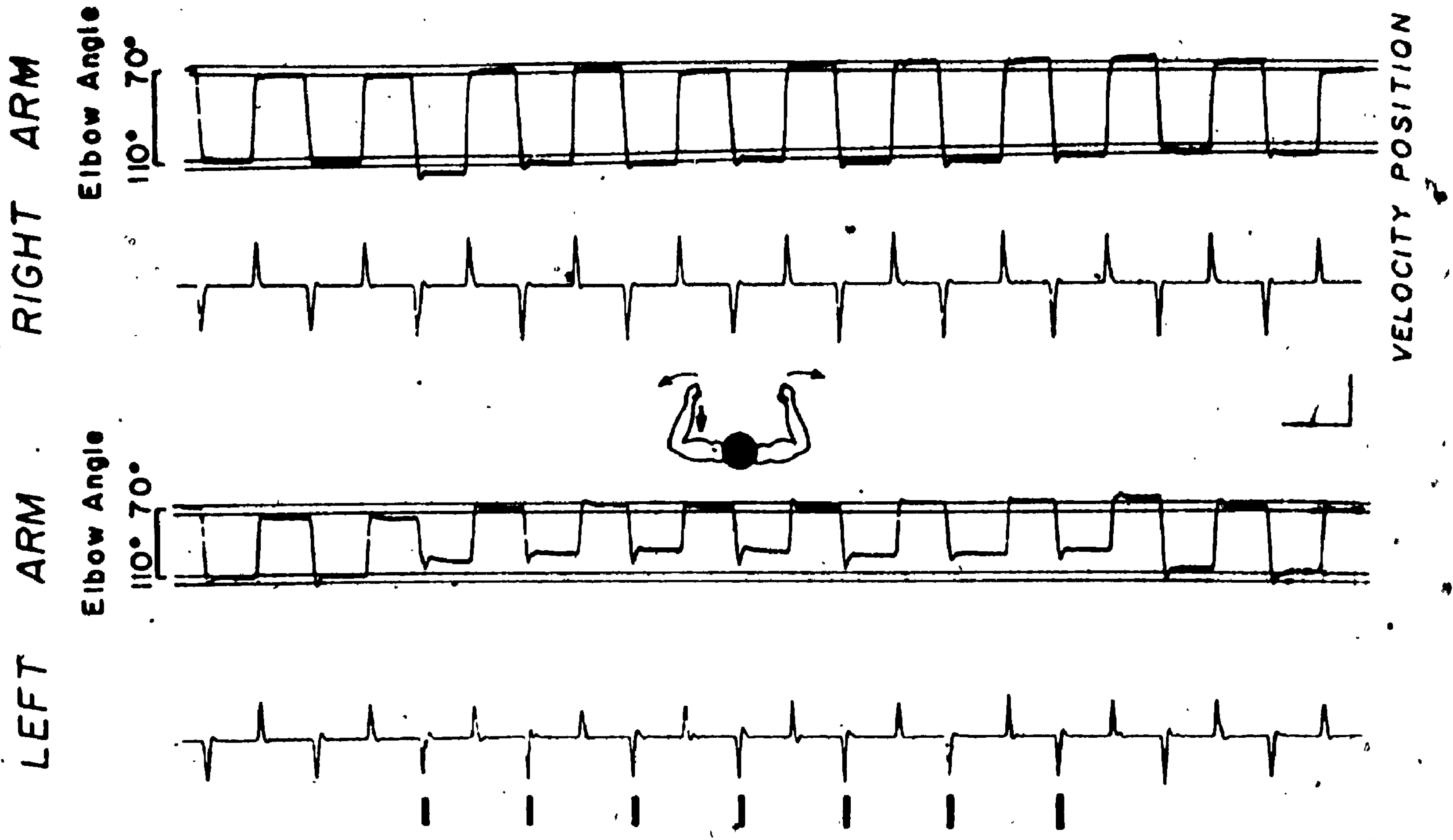


Figure 24

<u>Responses to tendon vibration of the left arm during simultaneous arm movements.</u> Traces from top to bottom represent: right arm position, right arm velocity, left arm position and left arm velocity. The pairs of horizontal lines around each of the position traces represent flexion (upper pair) and extension (lower pair) intended target position. Movements were made without visual feedback. The left biceps brachii muscle was vibrated through its tendon during those extension movements as indicated by the solid vertical bars at the bottom of the figure. Vertical calibration line represents 100 degrees/sec for velocity. Horizontal calibration represents 2 sec. (RJ).

RESPONSE TO VIBRATING LEFT BICEPS



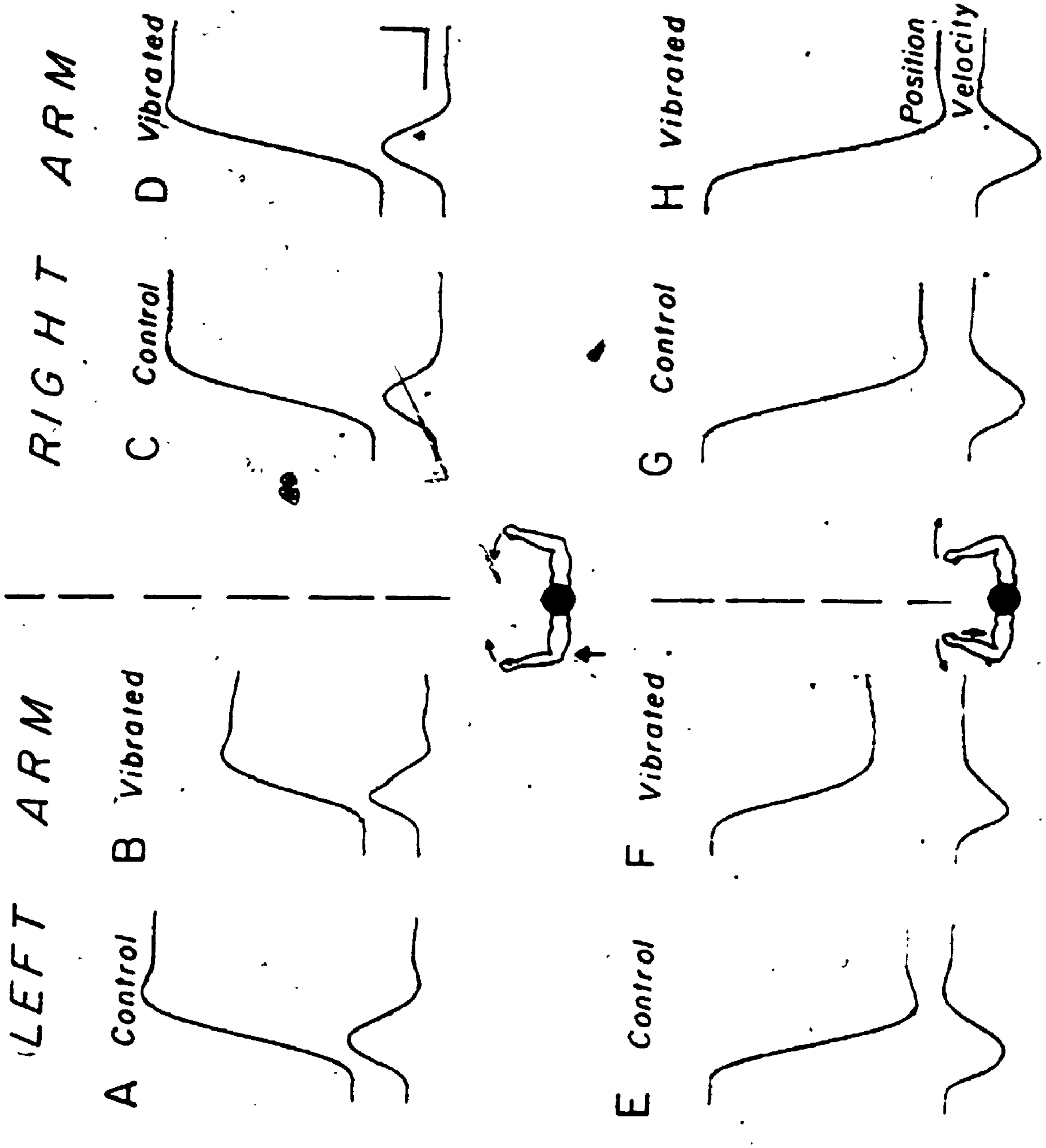
20). The direction of change, though small, was the same for those bilateral movements as for the unilateral movements.

Similar results were seen when continuous tendon vibration was applied. Figure 25 shows averaged records from movements with continuous tendon vibration applied to either the left triceps (B,D) or the left biceps tendon (F,H). Each set of traces shows average position and velocity records from 5 movements, the subject making simultaneous movements with the two arms. Control (non-vibrated) movements are shown in A,C and E,G. Continuous vibration of the left triceps tendon produced marked undershooting of the flexion end-position (B) of the vibrated arm. Peak velocity of movements by the vibrated arm also decreased. Movements of the non-vibrated (right) arm showed a modest overshooting of the intended flexion end-position (D) compared to control movements (C). The peak velocity of movements with the right arm also increased during vibration of the left triceps tendon.

Similar data from extension movements are shown in E-H. Vibration was applied continuously to the left biceps tendon (F,H). There was marked undershooting of the extension end-position and decreased peak velocity for the vibrated arm (F) as compared to control movements (E). During vibration, the non-vibrated (right) arm overshot the

Figure 25

Effect of tendon vibration on simultaneous bilateral arm movements. Each set of traces represents averages of position and velocity records. A-D represent bilateral flexion and E-H bilateral extension movements made by the two arms at the same time. The dotted lines around the averaged records represent standard deviations. Averages of 5 movements are shown in each set of records. In A-D a continuous vibration of the left triceps brachii tendon was applied for the movements made at the same time in B & D. In E-H a continuous vibration of the left biceps brachii tendon was applied for the movements made at the same time in F & H. Vertical calibration in D represents 8 degrees for position and 60 degrees/sec for velocity. Horizontal calibration represents 400 ms. (VN).


LEFT ARM
RIGHT ARM
A Control
B Vibrated
C Control
D Vibrated
E Control
F Vibrated
G Control
H Vibrated
Position
Velocity

intended end-position (H) and had a greater peak velocity.

Statistical analysis indicated a small but significant overshoot by the non-vibrated arm during simultaneous movements. Table 7 shows means and standard deviations of the differences between the actual and intended flexion end-position for movements made with the right arm before and during vibration of the left triceps muscle. Data from seven subjects is given, each mean derived from 10 movements. Over- and undershooting of intended flexion end-position are indicated by (+) and (-) signs respectively. A two-way ANOVA on the effect of vibration showed a significant effect of vibration on movement end position of the non-vibrated arm (F= 8, df=1,6 , p<0.05).

C. Summary :

Mechanical vibration applied to the muscle tendon of either the biceps or triceps brachii muscles in man has been used to study the role of kinesthetic information in the organization and control of two-arm movements. The study was conducted on movements performed without visual guidance and included two main groups of experiments. In the first group, vibration of the muscle in a stationary arm was used, i.e. applying vibration to the muscle of a stationary arm during unilateral movement of the opposite arm. In the second

Table 7

Each number represents the mean difference and S.D. in degrees between the intended and the actual flexion end positions for movements of the right arm when the left arm was vibrated at the triceps tendon and in the absence of vibration during simultaneous movements of the two arms.

Subjects	Without Vibration	With Vibration
BR	1.1 (2.7)	4.2 (4.3)
KW	- .7 (3.8)	2.9 (1.1)
MY	.7 (1.5)	1.4 (1.6)
PZ	- .8 (2.2)	.6 (2.7)
RJ	- 2.3 (1.9)	- .7 (1.5)
ST	- 1.8 (1.7)	- 1.4 (2.7)
VN	- .1 (2.2)	2.1 (1.4)

- Undershooting end-position.

group, vibration of the muscle was used during bilateral simultaneous arm movements. In either situation, it was found that vibration of a muscle tendon of one arm altered movement made with the other arm. This change can be hyperflexion or hyperextension depending on the muscle vibrated. Vibration applied to a muscle that was inactive (i.e. in a stationary arm) was more effective in modifying a voluntary movement made by the opposite non-vibrated arm, than if the vibrated arm was also moving.

DISCUSSION

I. Movement Peak Velocity-Amplitude Relations

The present study focussed on movements made simultaneously or independently by the two arms, in normal humans. The movements used were self-terminated and thus may have involved strategies or central organization different from those used in mechanically terminated movements. These latter movements have been extensively studied, often in relation to the finding by Fitts (1954) of a trade-off between movement speed and movement accuracy or, more exactly, movement difficulty. In self-terminated movements, speed is related to movement amplitude. This is true of single-joint movements (Bouisset & Lestienne,1974; Cooke, 1980), reaching movements (Jeannerod, 1984), movements in the speech system (Ostry & Cooke, in press; Ostry, Keller and Parush, 1983) and multi-joint movements in a pointing task (Soechting, 1984). As in other studies (Bouisset and Lestienne, 1974; Cooke, 1980), the present data shows that the peak velocity-amplitude relation is linear. In addition, the relation is the same for the two arms, at least within the range of movement amplitudes studied here. Thus, for a given movement amplitude, the preferred peak velocity is the same for the two limbs. In addition, overall movement speed as indicated by movement duration, is also the same for the two arms. Moreover, matching of movements made independently by the two arms is stable and invariant over a long period of time lasting months.

Certain theories on motor control, in the last two decades, have focussed on the mechanical properties of the moving system; its mass, viscosity, stiffness and the equilibrium position in performing voluntary movements in man and in animals (Astrayan and Fel'dman, 1965; Cooke, 1980; Kelso, 1977; Kelso and Holt, 1980; Polit and Bizzi, 1978; Schmidt, 1980). These studies presented evidence that whole limbs behave similarly to a mass-spring system whose parameters of stiffness and equilibrium position can be set by the nervous system. Theoretical studies (Cooke, 1980) showed that a second order system (damped oscillator) displays many of the properties of simple arm movements of the type studied in the present work. As an example of the operation of Cooke's model, if the initial or starting stiffness of the opposing sets or springs is increased proportionately, no change in initial position occurs. This is similar to contracting both agonist and antagonist muscles (cocontraction) across a joint with the result that no net movement is produced in that joint. Movement occurs only if a step increase in stiffness of the agonist or if a disproportionate change in the stiffness of agonist/antagonist is produced. Thus, limb final position can be specified in terms of a balance (or equilibrium point) between the length-tension properties of agonist and antagonist muscles. Movements generated by simple changes in mechanical properties of this model were found to have a linear peak velocity-amplitude relation. The slope of this velocity-amplitude relation was related to the overall stiffness of the system. Thus the linear velocity-amplitude relation seen in normal subjects may be considered as indicative of an oscillatory process operating in the generation of movement. Stiffness (as indicated by the slope of the peak velocity-amplitude relation) may be looked at, therefore, as a means by which the subject tunes the motor act to the behavioural requirement of the task. The present result of consistently high correlation between movement amplitude and velocity in all simultaneously and independently made arm movements and during unilateral limb loading as well as with unilateral visual guidance is a strong evidence that the prediction of a mass spring model is met.

If the peak velocity-amplitude relation is indicative of the operation of an oscillatory process in the generation of movements, the present results show, that the process is closely linked for the two arms. Thus, when the movement of one limb was artificially modified by loading, movement of the opposite (unloaded) limb followed the same pattern of changes occurring for the loaded limb. The results of this study are thus similar to those of Kelso, et al. (1981) who interpreted their results in terms of linked oscillators. In their study, rhythmic cyclical movements were phase locked and both simultaneous and independent movements of the right and left index fingers were closely similar in amplitudes and periods.

II. Simultaneously Made Movements:

In 1903, Woodworth observed that "it is common knowledge that movements with the left and right hands are easy to execute simultaneously, we need hardly try at all for them to be nearly the same" (Woodworth, 1903, p. 97 in Schmidt et al, 1979). The present study shows that there is a close matching in the performance between movements of the two arms made at the same time: There is a moment-to-moment matching of positions and velocities, matching of movement kinematics and movement durations as well as equality of the slopes of the peak velocity-amplitude relation for the two arms. How is this matching of movement of the two arms achieved by the central nervous system? Analyses of various tasks such as walking, reaching, posture control and speech suggest that one way such co-ordination is achieved is by recruitment of the muscle groups involved as a single functional synergy rather than as independent muscles (Bernstein, 1967; Grillner, 1973; Kelso et al, 1979; Nashner, 1977; Saltzman, 1979; Shik & Orlovsky, 1976). According to Bernstein and those who have followed his point of view, the nervous system solves the problem of movements with multi-degrees of freedom by linking together the participating muscles into units and thereby reducing the number of these individual muscles to a minimum number of muscle groups. These muscle groups are called: "coordinative structures" (Kugler, Kelso and Turvey, 1980) and defined as: "a group of muscles often spanning a number of joints that is constrained to act as a single functional unit" (Kelso et al, 1983). Such functional linkage may span several joints or limbs, and even muscle groups quite distant from the moving segment may participate (Belen'kii, Gurfinkel & Pal'tsev, 1967; Marsden, Merton and Morton, 1983). For example, in normal locomotion, nearly all the segments of the body work as an ensemble. Cerebellar stimulation during cat locomotion affects only the magnitude of muscle contraction, and not the timing among muscles relative to the step cycle (cf. Shik and Orlovskii, 1976). In bimanual reaching, the time-space behaviour of both arms is tightly linked, even when the movement of one arm is perturbed by an obstacle (Kelso, et al., 1979a,b). There are important consequences of encompassing the many participating elements (the musculature of the two arms, in this case) in a movement as a single functional unit or synergy. For example, the number of control decisions is greatly reduced, lessening the demands on the computational and storage capacities of the brain.

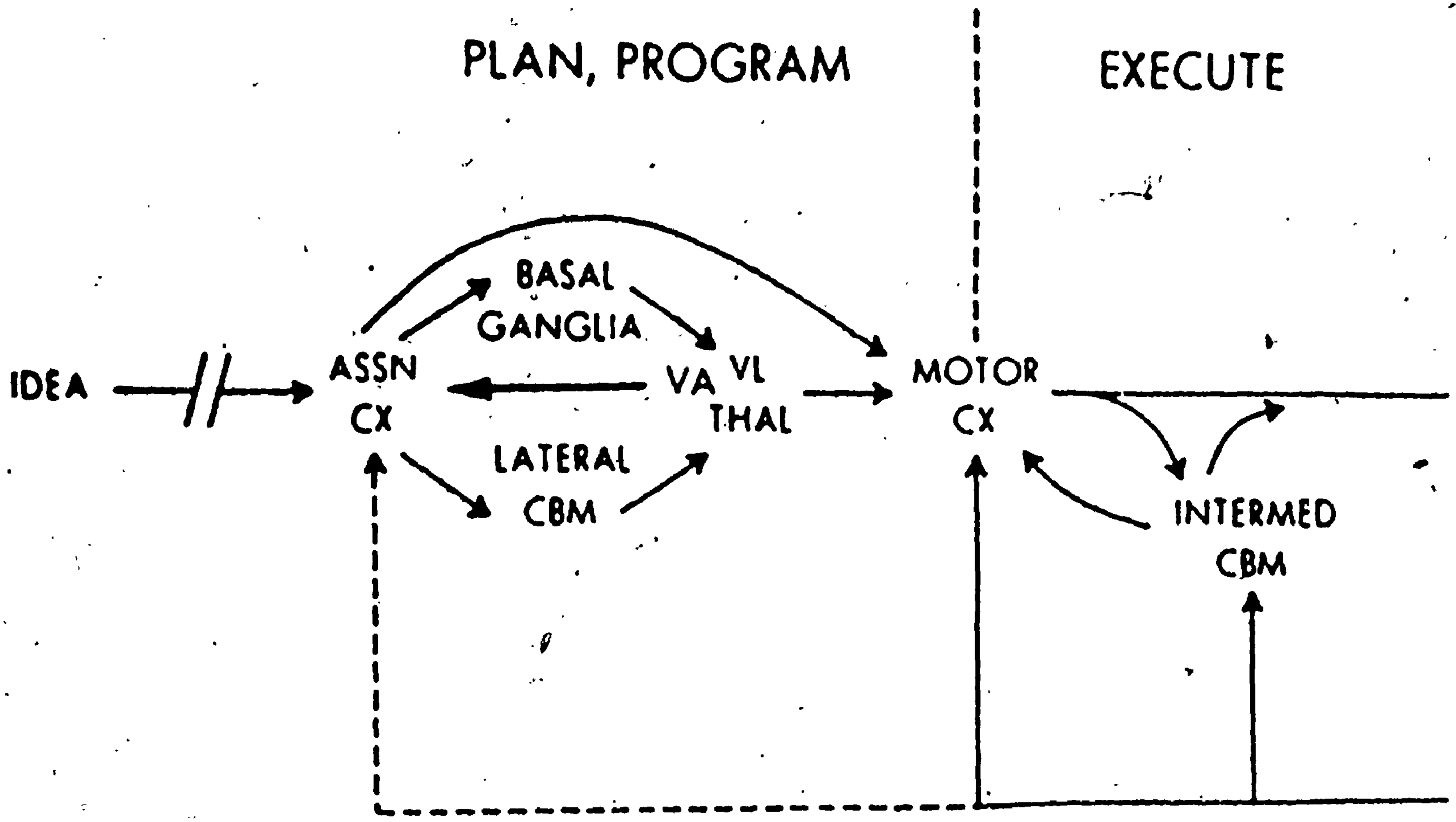
III. Matching of Movements Made Independently

The present study has also shown matching made independently "at the subject's own speed" with the two arms. This matching, as indicated by similarity of the slopes of the velocity-amplitude relation for the two arms, is very stable and was unchanged over periods of months in the same subject. As mentioned earlier, the results presented here are consistent with a model for limb movement in which the nervous system operates on a second order mechanical system. What is of particular interest is that even in the case of non-rhythmic movements the results of this operation are the same for both limbs. It is perfectly clear that, under appropriate circumstances, differences in movement performance can be seen between the two limbs (e.g. Flowers, 1975; Peters and Durding, 1978; Wyke, 1967, 1968, 1969). How can this be reconciled with the evidence that motor performance is linked between the two limbs even when movements are not simultaneous? Peters (1981) suggested two models for co-ordination of movements. In the one model, there would be independent control of the two limbs. That is, there would be two, separate, central control systems. In the other model, there would be a single central system which acts on both limbs. Thus, in the one case there would be two, independently controllable command systems for movement of the two limbs whereas in the other there would be a single command that would be distributed to both limbs. The present finding that movements which are made independently are closely matched suggests a single control system. This is of course at the very abstract level of motor control. The two models suggested by Peters can be incorporated in the model proposed by Schmidt et al, (1979) (Figure 1, see INTRODUCTION).

The common motor command may operate at a rather abstract level. It is thus possible that such areas as the association cortex (particularly the premotor association area) together with the lateral cerebellum and basal ganglia that are engaged in preprogramming of voluntary movements (Allen and Tsukahara, 1974) represent this common control system (see Figure 26). At this level common parameters may be allocated to the movements of the two arms as well as the specified pattern of movement. In the subsequent path/of the command, parameters specific to either limb may be added before the commands reach the motoneurones of the spinal cord. As the command proceeds to the muscles of the two

Figure 26

Diagram showing pathways concerned in planning, execution and control of voluntary movement. Assn Cx, association cortex; lateral CBM, cerebellar hemisphere; intermed CBM, pars intermedia; VA, VL nuclei in thalamus (from Brooks, 1984, based on Allen and Tsukahara, 1974).


PLAN, PROGRAM
EXECUTE
IDEA
ASSN
CX
BASAL
GANGLIA
LATERAL
CBM
VA VL
THAL
MOTOR
CX
INTERMED
CBM

sides, it passes through many centres where the right and left sides are functionally and anatomically linked starting with the corpus callosum that links the two cerebral hemispheres and ending at the level of the spinal cord where the motoneurones of the two sides are connected as shown by many physiological studies. Preilowski (1972) presented some evidence from experiments on split brain patients suggesting that direct inter-hemispheric interaction of motor corollary outflow is essential for co-ordination of bilateral motor activity. He found that patients performed at a consistently inferior level for speed and quality and were forced to rely on slower visual and proprioceptive feedback systems during bilateral movement following a partial commissurotomy and concluded that direct hemispheric interaction appears to be important for the fine regulation of lower motor system from within each hemisphere.

Feedback systems are essential for the CNS to monitor and update the information about the limb during movement. Overall limb position results from the angle at which the different joints of the limb are held. In order to control limb position, the CNS must therefore monitor and control joint angles both when the limbs are stationary and during movements.

Awareness of changes in joint angle is fairly accurate in humans. Limb movements at very low velocities (0.5 deg./min.) producing changes in knee joint angle of only 2-4 degrees can be sensed (Clark and Burgess, 1975). This suggested the existence of slowly adapting receptors providing an afferent signal proportional to knee joint angle.

The receptors that are involved in the perception of limb position are still unknown (cf. Burgess, Clark and Simon, 1982). The knee joint of the cat has been studied most extensively. Articular receptors signal mainly whenever the knee is at or near the end of its range (Skoglund, 1956; Burgess and Clark, 1969; Clark and Burgess, 1975; Grigg, 1975; Ferrell, 1980). Direct recordings from the posterior articular nerves showed that there were always receptors tonically active at all intermediate joint positions (Ferrell, 1980). Specifying the receptors that signal joint motion in the articular nerve in animals, does not necessarily mean that information for the conscious perception of joint position is provided through this channel. Some of the receptors that signal joint position may actually be spindle receptors from muscles surrounding the joint (Burgess and Clark, 1969). Even if the firing from the muscle spindle receptors was to be considered affected by joint angle position the problem of how movement is perceived remains incompletely solved. Muscle spindles, like any other receptors whose activity is modulated by efferent input, are affected by external change in muscle length as well as by the fusimotor discharge which changes the spindle tension. The problem becomes even more complicated when muscle spindle activity is considered since this activity has been found to increase during isometric contraction (Vallbo, 1971, 1974). Rymer and D'Almeida (1980) reported an interesting experiment where they examined the ability of subjects to match the static positions of the proximal interphalangeal joints of the left and right index fingers during continuous loading of the right finger. They found that movement of the loaded finger was a crucial factor in determining whether the position of the loaded joint was correctly sensed or not. That is, when the subject was allowed to flex the loaded right joint he correctly matched the joint angle with the left finger. Mis-matching occurred whenever the subject applied isometric flexion force with the loaded finger. Rymer and D'Almeida suggested that the joint position sense may be, "a `derived' quantity, computed from length and force-related muscle afferent signals".

In summary, there is no conclusive evidence at present that articular receptors around the knee joint are important for the conscious awareness of joint position. The existing evidence suggests that the signals generated by muscle receptos (spindle primary and secondary endings and

Golgi tendon organs) need to be processed in a complicated circuitry in the central nervous system before awareness of joint position and kinesthesia are extracted. Very little is known about such integrated circuitry at the present time.

Kinesthesis and position sense may be served by the so called, "motor outflow." Efferent control signals go not only to the muscles but also via an internally derived "corollary discharge" to some comparator or correlator structure inside the CNS. Sperry (1950) first used the term "corollary discharge" and later von Holst (1954) spoke of "efference copy" to describe this mechanism. This postulated, internally monitored signal may also be responsible for the "sense of effort" described even ealier by Helmholtz (1925), and re-used by Merton (1964) to account for the ability of surgically deafferented monkeys to perform accurate reaching movement even without visual control. Following a series of interesting experiments by McCloskey and colleagues (McCloskey, 1973; McCloskey, Ebeling and Goodwin, 1974; see also review by McCloskey, 1981), it was concluded that corollary discharges participate in kinesthetic sensibility by generating sensations of muscular force but not sensations of movement.

IV Compensation for Unilateral Loading:

Subjects altered the movements of their two arms and showed similar changes for both limbs when faced with an added load on one arm. Loading changed the relation between the kinematic variables of peak velocity and movement amplitude. In the case of the simultaneous arm movements with short-term loading, the 12 lb weight used affected the loaded as well as the unloaded arm by decreasing the velocity at all amplitudes examined and therefore decreased the value of the slope of peak velocity-amplitude relation. The decrease in the slope due to the loading has also been shown by Cooke (1980) to occur in the case of the mass spring model.

In the chronic loading (one week period for the normal subjects and several weeks for the two patients with orthopaedic casts), the 1 lb weight used also changed the velocity-amplitude relation with the pattern of changes varying from subject to subject. The most consistent finding in the chronic loading study was that the same change occurred in the loaded and the unloaded arms. It might therefore be useful to know that the motor performance with the intact arm, in a patient wearing a cast on the opposite (fractured) arm, would not necessarily be normal. This observation might be of some interest to physiotherapists and workers on rehabilitation.

The receptors that might be stimulated by the load include cutaneous, joint, tendon and muscle receptors. Cutaneous receptors have been shown to fire in response to pressure and deformations of the skin (Adrian, Cattell and Hoagland, 1931) so that they could serve to indicate the weight applied to the forearm in the chronic loading process. There are some reports (Lee and Ring, 1954) that interference with skin sensation around a joint does not affect position sense for movement of that joint. It does not seem, however, that this source of information could be a determining factor in the observed effects of the load application. Golgi tendon organs (GTO) respond to active tension in the muscle (Houk and Henneman, 1967). It is possible that movements with the arm loaded may cause the GTOs to fire more than under normal conditions as stronger force needs to be generated by the muscles to move a loaded arm.

V. Simultaneous Movements and Visual Guidance:

The results of this study show that movements of the two arms are matched in peak velocity-amplitude relation irrespective of the presence or absence of visual guidance. The results also show that when simultaneous movements of the two arms were performed, mis-matching in the positions and velocities between movements of the two arms could occur depending on the visual information presented. This mis-matching was not dependent on handedness. The data showed that movements of the two arms are matched in movement durations in the absence of visual guidance. When visual guidance for one arm or the other was provided, the data showed an effect related to handedness. Thus, movement durations were the same for movements of the two arms when visual guidance was provided for the right arm. There was, however, significant prolongation in movement duration of the right arm when the visual guidance was provided for the left arm. There were therefore two kinds of asymmetries observed during these simultaneous bilateral arm movements. First, whenever visual attention was directed at one arm, asymmetries in movement kinematics (amplitude and velocity) occurred. Second, when visual attention was directed at the left arm, asymmetry in movement duration occurred in addition to the asymmetries in movement kinematics. The effects of visual information on bilateral simultaneous arm movements, observed in this study, were unexpected and there is no ready explanation to be offered to this phenomenon at the present time. Attention to one arm during a bimanual task has been shown to affect the motor performance. Peters (1981) reported that right-handed subjects could follow the beat of a metronome with the left hand while tapping as quickly as they could with the right hand much better than they could with the converse arrangement. He suggested that the preferred hand, because of its involvement in skilled activities, demands more attention than the non-preferred hand. However, since all the subjects used in the present study were right-handed, it is rather early to attribute this effect totally to handedness. Further experiments are needed to examine the phenomenon in left-handed subjects.

VI. Effect of Kinesthetic Information:

The present experiments on the effects of mechanical vibration were designed to define the influence of kinesthetic information from one limb on movements made with the opposite limb. The effects of vibration on movements of the non-vibrated arm were significant, whether or not the vibrated arm was moving. It must be emphasized, however, that vibration applied to a muscle in a stationary (non-moving) arm was found to be more effective than that applied to a moving arm. This was shown to be true, in the same subject, whether the vibration applied to a stationary arm was tested first or following the test of vibration on a moving arm.

These results showed that tendon vibration of the biceps or triceps brachii muscles of one side of the body, produced effects on the voluntary movements of the opposite non-vibrated arm. These effects were shown to be exactly opposite to the effects of vibration on movements made by the vibrated arm. As was seen previously (Capaday and Cooke, 1981,1983) movements of the vibrated arm undershot the intended final end-position when the muscle antagonistic to the movement was vibrated. In contrast, movement of the opposite (non-vibrated) arm overshot the intended final end-position during vibration. The effect of vibration of a particular muscle was not bidirectional i.e. affecting both flexion and extension movements of the opposite arm. Thus, vibration of the triceps muscle affected only flexion movements of the opposite arm and did not affect extension movements (cf. Figure 20). Similarly, vibration of the left biceps muscle affected only extension movements of the right (opposite) arm and did not affect flexion movements. This unidirectional effect of tendon vibration was also found on the vibrated side (Capaday and Cooke, 1981,1983). The lack of effect of agonist vibration on movement trajectory on the same side may be due to a decreased sensitivity of spindle receptors during rapid muscle shortening (spindle afferents were silenced during muscle shortening, see e.g. Vallbo, 1973).

What mechanisms underly the effects of vibration on the contralateral limb? Mechanical vibration applied to the muscle tendon through the skin can stimulate various receptors. Mechano-receptors in the skin are sensitive to vibration (Mountcastle, 1980). Pacinian corpuscles located deeply in the border region between the dermal and subcutaneous tissue are responsive to high frequency vibration. The effects of vibration on arm movements in this study was not due to stimulation of these cutaneous receptors since no effect was obtained by vibrating tendons of fully slackened muscles, e.g. triceps tendon with fully extended elbow (cf. Figure 21). Data presented by Capaday and Cooke (1983) showed that stimulation of cutaneous receptors, by loosely placing the vibrator on the skin of the moving arm during movement, was also ineffective in modifying movement end position.

The receptors stimulated by mechanical vibration in the present work, that affected movement performance, are assumed to be the primary endings of the muscle spindle. The primary spindle endings are highly sensitive to low amplitude, high frequency vibration and can be selectively activated by such stimulation (Matthews, 1966; Brown, Engberg and Matthews, 1967). The frequency of the vibration used in the present study was high (120 Hz) and therefore, was optimal for activating the primary endings. Vibration might have activated the force sensitive receptors located in the muscle tendon, the Golgi tendon organs. These receptors produce discharge in Ib afferents which inhibit the agonist and excite the antagonist motoneurones of the same side. They produce the opposite effects on the contralateral side in the decerebrate cats (Baxendale and Rosenberg, 1977). Although it is unlikely that the ipsilateral effects of vibration would be attributed to Ib firing, the effect of such firing on the contralateral responses to vibration cannot be ruled out.

Goodwin et al.(1972a,b) found that muscle-tendon vibration produced disruption of normal accuracy of joint angle perception in human. Vibration with the limb restrained produced the sensation of an apparent movement of the limb with the subject feeling the limb moving in the direction of stretch of the vibrated muscle. Eklund and Hagbarth (1965) reported that vibration activates primary endings of muscle spindles and can produce a reflex contraction of the vibrated muscle called the tonic vibration reflex. There is also anatomical evidence that muscle afferents [illegible]oject to the cerebral cortex in the cat, monkey and baboon ([illegible]nderson, Landgren and Wolsk, 1966; Oscarsson, Rosen and Sulg, 1966; Phillips, Powell and Wiesendanger, 1971). Therefore, when vibration is applied during rest the subject experiences an illusory motion of the limb or the limb moves (TVR) depending on whether the limb is restrained or not. If vibration is applied during limb movement, the subject may perceive the limb position incorrectly and stop the limb short of its intended end position when the antagonist is vibrated. The other possibility is that mechanisms acting at the segmental spinal level could contribute to this undershooting. No effect is produced on the movement if the agonist is vibrated because of the silencing of the Ia afferents during rapid shortening.

What happens to the arm opposite to the vibrated side? During vibration of a non-contracting muscle with the arm restrained, the subject overshoots the intended end-position that is in the same direction as the illusory motion. There is no effect of vibration on the intended end-position that is opposite in direction to the illusory motion. This can be interpreted by considering that the effect of the vibration on reaching consiousness acts to modify the movement of the opposite arm to match the apparent position of the illusory motion. This matching manifests itself more clearly when the subject moves both arms simultaneously. In this case the vibrated side undershoots the end-position while the opposite arm reduces its overshooting of the end- position as if it were matching the apparent position of the vibrated arm. It is also possible to attribute some of the effects on the opposite arm to mechanisms acting at the segmental spinal level. In the decerebrate cat it was shown that Ia discharge which is excitatory to the muscle of origin, produces opposite effects in the symmetrical muscle on the contralateral side (Baxendale and Rosenberg, 1976) and the Ib discharge inhibits ipsilateral and excites contralateral synonymous muscles (Baxendale and Rosenberg, 1977). The overall effect of vibration on the opposite arm may, therefore, be a result of both spinal and supraspinal actions.

SUMMARY

1. A study was made of the characteristics and control of bilateral, voluntary arm movements in normal humans. The question asked was how the nervous system organizes and co-ordinates movements of the two arms.

2. A total of 25 normal human subjects were used in the various aspects of this study. In addition two patients wearing an orthopaedic cast on their left forearms were also studied. Subjects made step-tracking movements about the elbow. Movements were made at the subject's own speed. Subjects either moved their two arms simultaneously or moved each arm independently. Movements were made either with or without visual guidance.

3. In the absence of visual feedback, movements made simultaneously with the two arms were initiated at the same time and were similar in amplitude, duration and speed. These simultaneous movements were also dynamically matched throughout the movements with no phase lags or leads.

4. Visually displaying the position of one arm to the subject during simultaneous two arm movements produced a consistent disproportion between the movements of the two

arms. Movements of the non-displayed arm were always greater in amplitude and peak velocity than those of the displayed arm.

5. There was no significant difference between movement durations for the two arms when the position of the right arm was displayed to the subject during simultaneous movements. In contrast, movement duration was significantly greater for movements of the right arm when the position of the left arm was displayed.

6. Step-tracking movement speeds were characterized by a linear increase in movement peak velocity with increased movement amplitude. This linear relation was the same for flexion and extension movements and for movements made with the right and left arms. There was no significant difference between the slopes of the relation for movements of the two arms whether the movements were made simultaneously, independently or in the presence or absence of visual guidance. This matching in velocity-amplitude relation in its slope for the two arms was invariant, in the same subject, for periods of up to two months.

7. Alteration of the speed of one arm by application of unilateral limb loading (added mass) produced a significant decrease in the slope of the peak

velocity-amplitude relation for that arm. A significant decrease in the slope of the relation also occurred in the non-loaded arm during simultaneous movements.

8. Changes in the slope of the velocity-amplitude relation of movements of the left arm occurred when subjects wore a 1 lb weight on their forearm for one week. Identical changes in the slope of the velocity-amplitude relation were seen in the right (non-loaded) arm when the two arms were tested independently for movement. A similar re-matching between the slopes of the relation for movements of the two arms occurred following removal of the load. The same matching and re-matching was seen in the two patients who wore an orthopaedic cast on their left forearms.

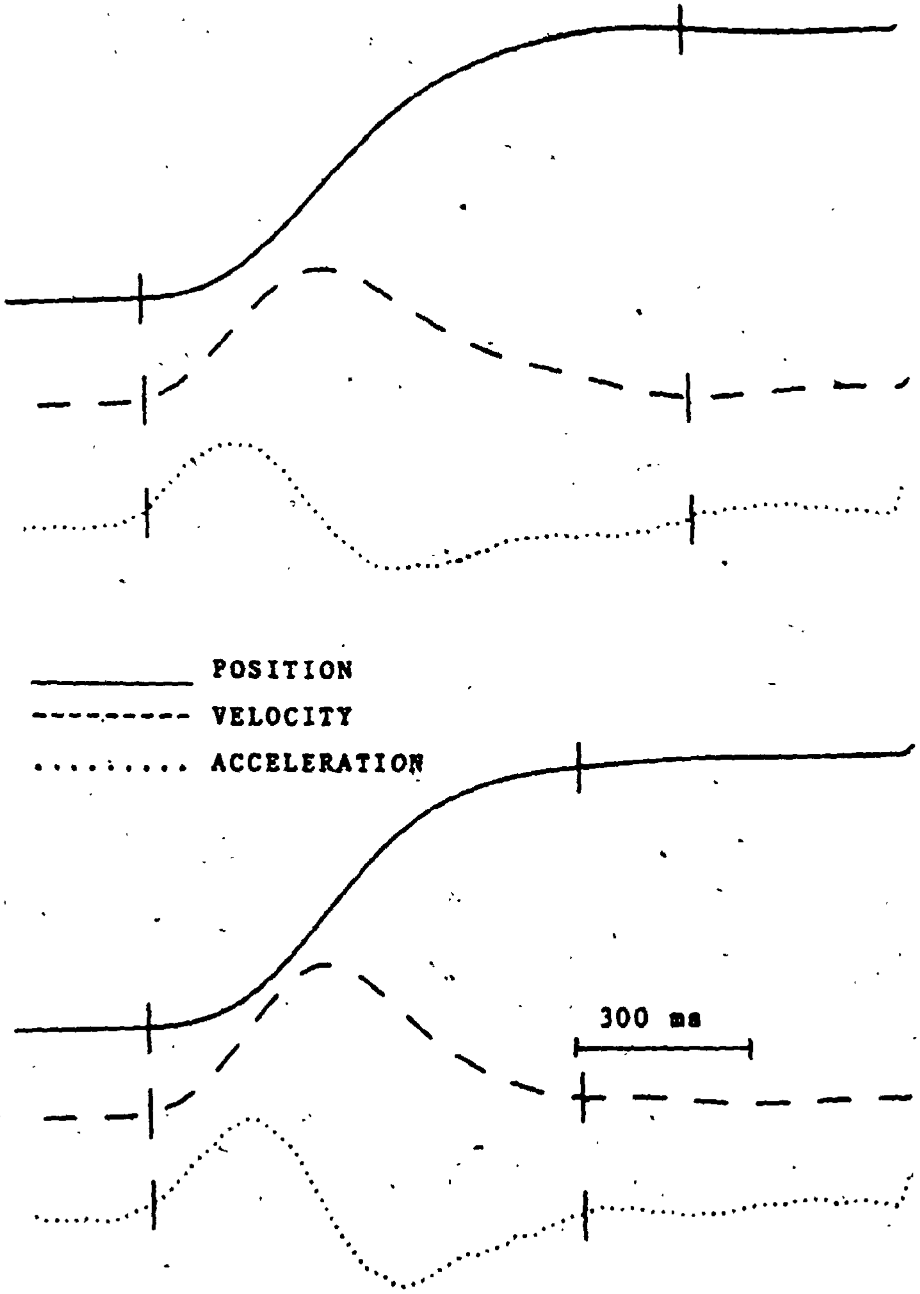
9. Using mechanical vibration of muscle tendon, limb movements were shown to be influenced by kinesthetic information arising from the opposite arm both when that arm was stationary and when it was moving. The effects of tendon vibration during simultaneous arm movements showed that vibration of the muscle antagonistic to the movement led to undershooting of the intended end-position of the movement on the vibrated side and overshooting of the intended end-position by the opposite arm. The effects of the vibration were stronger on the vibrated side than the non-vibrated side. Changes in movement produced by vibration

of muscles of the opposite arm were less pronounced during simultaneous movements.

10. It is concluded that in the symmetrical matching task studied, the two arms are treated by the central nervous system as a functional unit sharing a common "motor command". Kinesthetic information is used by the central nervous system during movement to produce a matching of the apparent positions of the two arms. The results are discussed in terms of the two arms working as a functional unit with the basic movement variable being controlled as a common parameter for the muscles of both arms.

APPENDIX 1

Movement analysis was done by determining movement acceleration by digital differentiation of the velocity signal after filtering (20 Hz. cutoff, 0 phase shift) with a differentiation interval of 12 msec. Timing points (vertical markings, see accompanying figure of two examples of single flexion movements) were determined using a threshold of 120 degrees/sec/sec in acceleration.


POSITION
VELOCITY
ACCELERATION
300 ms

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