Upper Limb Asymmetries in the Utilization of Movement-related Sensory Feedback

by

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“Consciousness knows no more of the physiological process by which its sensations reach it than of that by which its intentions are executed.” – R.S. Woodworth (1899)

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Chapter 1

Introduction

The ability to perform skilled movements of the upper limbs is a defining feature of modern day humans, and has been since the time of their upright standing ancestors some 2.5 million years ago (Bradshaw and Rogers 1996). Despite sharing a large degree of biomechanical similarity, however, the left and right arms did not evolve with similar degrees of dexterity and, rather, demonstrate large differences in sensorimotor ability. This movement asymmetry, more commonly known as handedness, has been the subject of intense study within the realms of psychology, neurophysiology and others. The aim of the present chapter, therefore, is to review this scientific literature with a particular emphasis placed on upper limb asymmetries in sensorimotor behaviour. For reasons that will become more apparent in the section to follow, most research in this area has been biased towards the study of individuals with right arm preference and, thus, it will generally be beyond the scope of this review to discuss studies involving left-handed individuals. Briefly, however, it should be noted that individuals with a left-arm preference appear less lateralized and more variable than their right-handed counterparts, and are, therefore, not their simple genetic (McManus 1995) or behavioural inverse (Perelle and Ehrman 2005).

Right Arm Biases for Movement

While limb asymmetries in motor behaviour are evident to some extent in most animal species (Ward and Hopkins 1993; Vallortigara and Rogers 2005; Hopkins 2006), humans show a strong population level bias for using one arm versus the other. Based largely on self-report questionnaires, it has been estimated that 9 out of 10 individuals are right-handed such that the right arm is preferred over the left when carrying out tasks such as reaching for a target or manipulating an object (Oldfield 1971; Annett 1985; Gilbert and Wysocki 1992). Remarkably, this proportion of right-handed individuals appears stable across geographical locations/cultures (Hatta and Nakatsuka 1976; Marchant et al. 1995; Bryden et al. 1996; Ida and Bryden 1996) and has persisted over the course of time. With respect to this latter point, Coren and Porac (1977) showed a greater number of right versus left arm depictions of motor activity in various artworks spanning the past 5000 years. In addition, archaeological evidence has indicated that hominids, on earth some 1.5 to 2 million years ago, were likely right-handed with respect to weapon and stone tool use (Dart 1949; Semenov 1964; Toth 1985).

The Genetic Basis of Right Arm Preference

Despite the enduring nature of right arm preference, no consensus has been reached regarding its particular origin. One controversial point of view that been has advocated by several researchers suggests that right-handedness is a genetically fixed trait and, therefore, left-handedness represents a pathological or diseased state (Bakan et al. 1973; Coren 1996). Interestingly, this collateral hypothesis accounts for a number of correlational findings demonstrating a relationship between birth trauma and a higher incidence of left-handedness (Colburne et al. 1993; Dellatolas et al. 1993; Coren 1996). In addition, there has long been thought to be an association between left arm preference and cognitive disorders such as schizophrenia (Green et al. 1989; Orr et al. 1999) and autism (Fein et al. 1984; Waterhouse and Fein 1984; Soper et al. 1986).

In contrast to various fixed trait approaches to handedness, theories grounded in Mendelian genetics have represented a more promising means of explaining right arm preferences with the “right shift theory” of Annett (1972) being, perhaps, the foremost. This model postulates that one allele (RS+) leads to the development of both arm praxis and language abilities in the left cerebral hemisphere (i.e. controlling the right arm), and a second allele (RS-) allows for arm and language abilities to be randomly distributed in either hemisphere (Annett 1978; Annett 1998). However, this, and other related genetic models (e.g. McManus 1995), are often criticized for two seemingly fatal flaws. First, there has been no success to date in isolating the supposed gene or genes responsible for implementing a right arm preference (Geschwind and Miller 2001; Francks et al. 2002). Second, studies of monozygotic (identical) twins have found that only 75% of the paired offspring express the same arm preference, despite a 100% overlap in their genetic make up (Coren and Halpern 1991). While this latter phenomenon was recently accounted for in a random-recessive model of handedness and hair whorl direction by Klar (2003), a recent study by Jansen et al (2007) has refuted these results. Ultimately, until these issues can adequately be resolved the case for a genetic basis of handedness will no doubt remain highly debated.

Environmental Influences on Right Arm Preference

In lieu of a purely genetic explanation for right arm asymmetries in motor behaviour, the influence of environmental and socio-cultural factors on handedness has also been explored. One observation that has inspired a great deal of research in this area is the finding that a relatively higher percentage of right-handed individuals exists at the end of the age spectrum (Beukelaar and Kroonenberg 1986; Ellis et al. 1988; Dellatolas et al. 1991; Gilbert and Wysocki 1992). Based on this finding, it has been argued that natural left-handers are forced to adopt right-arm preference over the course of a lifetime in order to accommodate for living in a right-handed world, and/or to avoid the religious and social stigmas associated with "sinistrality" (Harris 1990; Coren 1993). While this notion has garnered anecdotal support from reports indicating that left-handed individuals are more prone to accidental death, and subsequently live, on average, 7 years fewer than their right-handed counterparts (Halpern and Coren 1988; Coren and Halpern 1991), a socio-cultural account for right arm preference is, by itself, unconvincing. Of particular concern is that even when environmental pressures are relatively harsh, and are present at an early age, arm preference is not easily changed (Porac et al. 1986). Indeed, Porac et al (1990) reported that attempts to change handedness most often fail entirely or result in skill performance that lags behind that of the originally preferred arm.

An Enhanced Role for the Left Hemisphere in Movement Control

In light of the discovery by Broca (1861), and later Wernicki (1874), that the left hemisphere is specialized for various aspects of language, Liepmann (1908) was the first to suggest that asymmetries in motor behaviour might also be subserved by differences in hemispheric processing. Specifically, it was thought that the hemisphere contralateral to the preferred arm (most often the left) played an enhanced role for both preferred and non-preferred arm movements. Liepmann (1920) later justified this view on the basis of observations made with respect to individuals having unilateral brain injury due to stoke. In this work, individuals with left, but not right, hemispheric damage were found to be unable to correctly perform the spatiotemporal aspects of skilled movement with either arm, a condition he termed "ideomotor apraxia". Further, injury to the left hemisphere resulted in an inability to make precise, independent movements of both hands (i.e. "limb kinetic apraxia"), whereas only the contralateral left hand was affected when injury was to the right hemisphere. While these findings have garnered support on a number of subsequent occasions (Wyke 1971; Haaland et al. 1977; Haaland and Delaney 1981; Hanna-Pladdy et al. 2002), it should be noted that more recent reports suggest that both hemispheres make significant contributions to the control of goal-directed movement (Fisk and Goodale 1988; Haaland and Harrington 1989a; 1989b; 1994; Winstein and Pohl 1995; Haaland et al. 2004). The results of these studies will be addressed in greater detail in a later section (see Open versus Closed Loop Model of Handedness).

Based largely on the notions put forth by Liepmann (1908; 1920), Derakhshan (2002; 2003; 2005) has published a series of commentaries advocating a "one-way callosal traffic" account of handedness. In this theory, movement plans are thought to be housed in the motor centers of the "major" (typically left) hemisphere, thus, allowing for direct execution of preferred arm movements, while trans-callosal communication is necessary for movement of the non-preferred arm. One strength of this theory lies in its compatibility with a number of clinical observations including the previously described apraxias of Liepmann (1920), as well as reports of left arm apraxia following sectioning of the corpus callosum (Watson and Heilman 1983; Graff-Radford et al. 1987). Beyond this anecdotal evidence, however, empirical support for this theory remains limited. In particular, it is concerning that even the most commonly cited evidence favouring the central tenet of the theory, that of a left arm time lag during the performance of bilateral arm movements (Stucchi and Viviani 1993; Swinnen et al. 1996; Viviani et al. 1998), has been contradicted during studies of unilateral reaching, where non-preferred arm reaction time advantages have often been reported (Carson et al. 1990; 1995; Velay and Benoit-Dubrocard 1999; Barthelemy and Boulinguez 2001; Boulinguez et al. 2001).

With the advent of various non-invasive brain mapping and cortical stimulation techniques, it is now possible to explore hemispheric differences in those individuals with normal brain function in vivo. Using functional magnetic resonance imaging (fMRI), for example, Kim and colleagues (1993) measured activation of the left and right motor cortices in response to finger/thumb opposition movements made by each hand. In this study, it was found that, similar to the previously described results for stoke patients, the left hemisphere of right-handers played an enhanced role in movement control. In this case, the right motor cortex was primarily active for movements of only the contralateral left hand, whereas left motor cortex activation was seen for movements of either hand. Transcranial magnetic stimulation (TMS) studies have also reported left hemisphere dominance for motor evoked potentials (MEPs) of the hand muscles. In these studies, TMS to the left hemisphere has been found to induce facilitation of MEPs in both the left and right hands, whereas right hemisphere stimulation elicits a response in only the contralateral left (Ziemann and Hallett 2001; Ghacibeh et al. 2007).

The particular function of left motor cortex activation during left arm movement in right-handed individuals remains uncertain. Contrary to the findings of Dassonville et al. (1997), who showed a correlation between ipsilateral activation and the strength of arm dominance, direct left hemispheric control of the left arm seems unlikely based on reports that only 10-15% of cortico-spinal projections remain uncrossed at the level of the medulla (Nyberg-Hansen and Rinvik 1963). Alternatively, it has been hypothesized that the left hemisphere might have some influence over the right hemisphere via the corpus callosum. In this case, it is thought that both hemispheres are active prior to movement initiation, at which point one hemisphere is inhibited by the other in order to execute a unilateral movement of the contralateral arm (Rossini et al. 1988; Britton et al. 1991). Based on this line of reasoning, it would seem that involvement of the left hemisphere during ipsilateral arm movements reflects a relative inability of the right hemisphere to inhibit the left (Chen et al. 1997). This notion is supported by TMS studies where paired-pulse stimulation has demonstrated greater inhibition of the right hemisphere versus left hemisphere (Netz et al. 1995; Kobayashi et al. 2003).

Anatomical Correlates of Handedness

Given the asymmetries in hemispheric function described above, exploration into a potential anatomical substrate for handedness has been undertaken at both macroscopic and microscopic levels. One gross structural component that initially received particular attention in right-handers is the planum temporale (PT) located on the posterior portion of the temporal lobe. Based on postmortem studies, a more abrupt and anterior upward curving of the PT has been reported for the right hemisphere, subsequently resulting in a longer and larger left PT (Geschwind and Levitsky 1968; Wada et al. 1975; Falzi et al. 1982). Given that the PT coincides largely with the speech region of Wernicki (1874), it was originally speculated that this asymmetry reflected left hemispheric specialization for language (Galaburda et al. 1978; Geschwind and Galaburda 1985). However, this line of thinking has been called into question by Steinmetz and colleagues (1991) and Steinmetz (1996), who demonstrated a positive correlation between left PT volume and the degree (i.e. strength) of right, but not left, handedness.

Impressions on the inner surface of the skull called “petalia” provide a negative of the brain’s surface topology revealing regional asymmetries in hemispheric shape and size. Although petalia in the right frontal and left occipital lobes are seen in nearly all individuals, they are most prominent in right-handers (Lemay and Kido 1978; Kertesz et al. 1986). This observation further corroborates evidence that gross morphology of the lobes is markedly different. Specifically, in most right-handed individuals, the occipital lobe is considerably wider in the left hemisphere, whereas the frontal lobe is wider in the right hemisphere (Galaburda et al. 1978). In addition, the left hemisphere has been found to protrude more often in the posterior direction, while an anterior protrusion is common for the right hemisphere (LeMay 1976). This arrangement, termed “Yakovlevian torque”, presents the illusion of brain rotation in the counter-clockwise direction.

The motor cortex is perhaps the most well studied area of the brain with respect to hemispheric differences, due primarily to its many projections leading to the spinal motor neurons. In an initial study measuring the postmortem length of the precentral sulcus, an anatomical marker of motor cortex size, a greater left than right extent was reported (White et al. 1994). However, a subsequent report by this same group with an increased number of observations found no asymmetry in precentral sulcal length between the two hemispheres (White et al. 1997). Not withstanding these results, Amunts et al (1996; 2000) used magnetic resonance morphometry to measure precentral sulcal depth in the right and left hemisphere in vivo. This analysis revealed that the precentral sulci of the left hemisphere appear deeper compared to the right, and that this relatively macroscopic asymmetry is accompanied by a microscopic difference in neurophil volume (Amunts et al. 1996). This latter finding was interpreted as reflecting a greater percentage of fibrous processes, and more profuse horizontal connections, in the left hemisphere, providing a potential substrate for the representation of more complex, preferred arm movements (Hammond 2002).

The threshold for eliciting a motor response in various intrinsic and extrinsic muscles of the preferred and non-preferred arm via TMS of the motor cortex has also been studied. In general, this work has shown that preferred arm musculature is activated at a lower threshold of contralateral brain stimulation (Cantello et al. 1991; Macdonell et al. 1991; Triggs et al. 1994), although later studies have failed to reveal arm differences (Cicinelli et al. 1997; Civardi et al. 2000). In addition, TMS has been used as a means of mapping the extent of various hand and arm representations in the motor cortex. One particularly influential study in this area was conducted by Triggs and colleagues (1999) who quantified the number of cortical sites eliciting a motor response in the abductor pollicis brevis and flexor carpi radialis muscles of the left and right hands. In this case, right-handed subjects had a larger cortical area in the left hemisphere devoted to the targeted muscles than that seen in the right hemisphere, a finding that is consistent with comparable studies using magneto-encephalography (Volkmann et al. 1998) and fMRI (Dassonville et al. 1997; Krings et al. 1997) techniques.

In association with these motor cortical asymmetries, left versus right side differences have been shown in the pattern of corticospinal fiber tract decussation. In an early study involving human neonates, for example, Flechsig (1876) noted a distinct asymmetry in the distribution of corticospinal projections at birth with the left medullary pyramid being larger, and showing greater decussation, than the right. Nearly a century later, this same asymmetric pattern of fiber decussation was also shown for more than 70% of adult specimens tested postmortem (Kertesz and Geschwind 1971), a finding that was recently corroborated by Nathan and colleagues (1990). Given that the crossed fibers from both pyramids largely innervate motor units corresponding to the hand in the spinal cord (Brinkman et al. 1970), and that use-dependent pruning of the coricospinal tract occurs early during development (Friel and Martin 2005; Friel et al. 2007; Martin et al. 2007), an additional aim of these studies was to correlate the degree of decussation to subject handedness. However, due possibly to the small number of left-handed subjects available for study, no significant association between arm preference and corticospinal organization was found.

Arm differences appear to be also prevalent in the motor periphery. In a study assessing motor unit firing behaviour of the first dorsal interosseous muscle, Adam and colleagues (1998) found strong evidence of a preferred arm advantage for recruitment threshold, initial firing rate, average firing rate at target force and discharge variability. These results agree with those showing greater Hoffmann reflex responses for the preferred versus non-preferred arm (Tan 1989a; b), although no arm difference in this measure of motoneuronal excitability were more recently reported (Aimonetti et al. 1999). Further, evidence suggests that the synchronization of motor units within the extensor muscles of the preferred arm is greater during isometric contractions (Schmied et al. 1994) and that the tendon tap reflex responses of the preferred versus non-preferred arm are greater in magnitude (Aimonetti et al. 1999). To what extent these asymmetries reflect a shift in muscle fiber composition due to repetitive, low-intensity use of preferred versus non preferred arm is not yet clear. However, at least one study has demonstrated an increased percentage of slow twitch fibers in the extensor carpi radialis brevis muscle of the preferred wrist, an important muscle during the production and maintenance of grip postures (Fugl-Meyer et al. 1982).

Arm Asymmetries in Motor Output

In line with functional and anatomical differences, one of the most traditional approaches to the study of handedness has been the quantification of arm differences in the generation of motor output. A clear demonstration of this can be seen in the classic studies of Woodworth (1899) who assessed the ability of subjects to accurately draw lines of equivalent length with either the preferred or non-preferred arm. In this case, it was found that movements of the preferred right arm were substantially more accurate than those of the non-preferred left, and that this asymmetry was enhanced in conditions where subjects were forced to move at fast velocities. Combined with the observation that the presence or absence of visual feedback did not alter the observed arm differences, these results led Woodworth (1899) to conclude that “the seat of superiority of the right hand is probably in the motor centers" (p.34) demonstrating his personal bias towards an efferent locus of upper limb asymmetries.

Subsequent to Woodworth (1899), motor behavioural research has revealed numerous preferred arm advantages in the generation of motor output including increases in the strength, speed and consistency of movement. When comparing maximum grip forces in healthy subjects, for example, it has been well accepted that the preferred arm can produce forces that are approximately 10% larger than those of the non-preferred arm (Petersen et al. 1989; Crosby et al. 1994; Armstrong and Oldham 1999; Incel et al. 2002). In addition, finger tapping experiments have demonstrated preferred arm advantages in the speed and consistency of repetitive finger flexion and extension movements (Provins 1956; Peters 1976; Peters and Durding 1979; Todor and Kyprie 1980; Todor et al. 1982). Indeed, a link between these behavioural findings and the force generating characteristics of the preferred versus non-preferred arm was made by Toder and Smiley-Oyen (1987), who directly measured the finger forces associated with tapping. In this case, a positive relationship between preferred arm tapping ability and the generation of mean force levels with decreased variability was found.

Beyond studies of finger tapping, arm asymmetries in motor output have also been revealed though various targeted reaching experiments. In an influential study by Annett and colleagues (1979), the amount of time necessary to place pegs in relatively small holes was found to be significantly shorter for the preferred right arm of right-handed individuals. Further, increased movement time for the non-preferred arm did not appear to be due to subjects making longer duration corrective movements but, rather, having to make more of them. In this case, it was argued that non-preferred arm motor output was subject to increased variability and, thus, necessitated a greater number of corrective movements. This interpretation has been utilized on at least two subsequent occasions for results indicating a preferred arm advantage in the speed of reaching and pointing to a visual target (Roy and Elliott 1989; Carson et al. 1993).

The Dynamic Dominance Hypothesis of Handedness

Sainburg (2002) first proposed the dynamic dominance hypothesis of handedness based on fundamental differences in movement strategy that were observed between the preferred and non-preferred arms of right-handed individuals. Unlike other behavioural approaches to handedness research, where motor performance of the non-preferred arm was thought to be inferior for most aspects of movement, this hypothesis proposed that each arm is specialized for a different aspect of movement control.

Preferred Arm Specialization for Trajectory Control

Evidence of preferred arm specialization for the control of movement trajectory was initially revealed in a study comparing the coordination patterns employed by the preferred and non-preferred arms during targeted reaching (Sainburg and Kalakanis 2000). In this work, it was demonstrated that movements made by the preferred right arm in right-handed subjects showed a distinctly different pattern of joint torques than those produced by the non-preferred arm. Specifically, when reaches were made to targets where the amount of elbow displacement was held constant (20 deg), but where the amount of shoulder excursion was systematically varied (5, 10 and 15 deg), significantly different coordination patterns emerged. For preferred arm reaching, straight-line hand path trajectories were achieved through a more efficient inter-limb torque pattern, as movements of both the proximal and distal arm segments were controlled with forces generated primarily at the shoulder. In contrast, the hand paths produced by the non-preferred arm had greater overall curvatures, which were associated with increased shoulder excursion due to a movement strategy that did not make efficient use of inter-segmental interaction forces.

The findings of Sainburg and Kalakanis (2000) were later expanded by Sainburg (2002) in the initial formalization of the dynamic-dominance hypothesis of handedness. In this study, subjects performed reaching to eight targets in a virtual environment that allowed for visual feedback regarding only target position and endpoint location of the index finger. This procedure was completed under two experimental conditions that attempted to determine the influence of visuomotor transformations versus novel inter-segmental dynamics on arm performance. To assess visuomotor transformations, a visuomotor rotation task was utilized where subjects were required to adapt to a feedback display of finger position rotated 30 deg relative to the start position. On the other hand, novel inter-segmental dynamics were assessed using a mass adaptation paradigm where subjects had to adapt to an unseen 1 kg mass attached to the arm. In comparing these two tasks, clear differences were seen between visuomotor and mass adaptation, such that arm performance asymmetries were evident only during mass adaptation. This asymmetry mirrored that demonstrated by Sainburg and Kalakanis (2000) in that the preferred arm used significantly less muscle torque than the non-preferred arm. It was, therefore, concluded that “manual asymmetries arise, downstream in the motor control sequence to visuomotor transformations, when the trajectory plan is transformed into dynamic properties" (Sainburg, 2002, p. 253).

The extent of right arm dominance for trajectory control has been the focus of subsequent studies by Sainburg and colleagues (Bagesteiro and Sainburg 2002; Sainburg and Wang 2002; Wang and Sainburg 2003). For example, in a reaching task that varied with respect to the amount of inter-segmental torque necessary to obtain a target position, Bagesteiro and Sainburg (2002) showed more efficient torque strategies were utilized by the preferred arm/hemisphere system independent of arm kinematics. In addition, a series of studies Sainburg and Wang (2002) and Wang and Sainburg (2003; 2004b) have shown an asymmetric transfer of learning for visuomotor rotations. In these studies, opposite arm training of rotated visual feedback resulted in an enhanced ability of the preferred arm to specify the initial direction of targeted movement trajectory. Taken together, these results provide strong support for a preferred arm advantage in the specification and control of arm trajectory.

Non-preferred Arm Specialization for Positional Control

In light of the advantages ascribed to the preferred arm in the control of limb trajectory dynamics, a role for the non-preferred arm in the control of static posture has also been suggested. Support for this hypothesis was first provided by Bagesteiro and Sainburg (2003) in an assessment of inter-limb differences in load compensation. In this study, a virtual cursor representing endpoint location of the finger was moved to a target position of 20 deg elbow flexion. On random trials a 2 kg mass was attached to the subject's forearm such that the subject had no knowledge of the added load. When faced with this mass perturbation only the non-preferred arm was able to achieve a level of endpoint accuracy similar to that found in the non-loaded condition, while the preferred arm showed consistent overshooting of the target. Based on electromyographic and kinematic analyses, the non-preferred arm was found to compensate for the unknown load through changes in muscle activation occurring post peak tangential velocity. These observations were interpreted as reflecting a specialized role for the non-preferred arm in sensory feedback-mediated error correction.

Additional support for a non-preferred arm advantage in the control of static position comes from studies regarding the inter-limb transfer of movement strategy (Sainburg and Wang 2002; Wang and Sainburg 2003). In these studies, arm asymmetries were assessed in the transfer of movement-related information following adaptation to a visuomotor rotation. In this case, following training with the opposite arm, enhancement in endpoint accuracy compared to naïve performance was reported, but only for the non-preferred arm. While this finding was not supported in a study involving visuomotor adaptation to single versus multiple targets (Wang and Sainburg 2004b), subsequent studies have found similar non-preferred arm advantages in the transfer of limb position information including tasks involving inertial dynamics (Wang and Sainburg 2004b) and load compensation (Bagesteiro and Sainburg 2003).

Open Versus Closed Loop Model of Handedness

In contrast to studies of individuals with unilateral brain injury indicating greater arm deficits for left versus right hemisphere damage (Liepmann 1908; 1920; Wyke 1971; Haaland et al. 1977; Haaland and Delaney 1981), studies by Haaland and Harrington

(1989a; 1989b; 1994), and Winstein and Pohl (1995) have supported the notion that each hemisphere may be specialized for different aspects of motor control. In these studies, comparisons were made between the visually-guided reaching movements of healthy individuals and those of individuals with right or left hemispheric damage. Overall, left hemisphere damage resulted in deficits in the early stages of movement most commonly associated with open loop (i.e. relatively feedback independent) control. These deficits included increased reaction times (Haaland and Harrington 1989b; 1994) and a slower initial movement component (Winstein and Pohl 1995). Alternatively, individuals with damage to the right hemisphere showed poorer closed loop (i.e. feedback dependent) control, as would be necessary for accurately achieving a final target position (Haaland and Harrington 1989b; Winstein and Pohl 1995).

Although this open versus closed loop hypothesis of hemispheric specialization for movement was founded on the basis of clinical observations, the results of Sainburg and Schaefer (2004) suggest this framework may also be applicable to studies of healthy individuals. In this study, the acceleratory characteristics associated with single joint reaching to targets of increasing amplitude showed that preferred arm movements were accomplished by peak acceleration scaling (i.e. pulse height control), a phenomenon associated with open loop or planning mechanisms. In contrast, reaches made by the non-preferred left arm were found to scale peak velocity duration (i.e. pulse width), which is thought to reflect more closed loop or feedback mediated processes. Interestingly, while these results favour an interpretation based on arm/hemisphere differences in open versus closed loop control mechanisms, the authors argued that they are also consistent with the dynamic dominance hypothesis of handedness. In line with this assertion, the results of

Haaland et al. (2004) also suggested that previous studies of arm reaching in individuals with unilateral brain damage may be best described in terms of the dynamic dominance theory. This conclusion was based on the finding that right hemisphere damage failed to produce deficits during the corrective phase of movement when visual target feedback was available throughout reaching. This finding highlights the relative importance of sensory information during the planning and execution of goal-directed movement, a topic that will be addressed in the following section.

Asymmetries in the Utilization of Movement-related Sensory Feedback

There has been increasing interest over the past several decades in the role that sensory feedback might play in determining arm performance asymmetries. Perhaps the most influential study in this area was conducted by Flowers (1975) who assessed arm performance during a "ballistic" (i.e. relatively feedback independent) tapping task, and a more "corrective" (i.e. relatively feedback dependent) visual aiming task. In the tapping task, subjects were asked to tap the preferred or non-preferred finger as fast as possible without aiming the movement to hit a particular point. In this case, little control of the position or force of each tap was required. In contrast, during the visual aiming task, a Fitts paradigm (Fitts 1954) was used where subjects made fast and accurate reaching movements between two targets that varied in width and movement amplitude. Overall, it was found that the preferred arm performed significantly greater than the non-preferred arm but, only in the aiming task. This led Flowers (1975) to conclude "that the essential dexterity difference between the preferred and non-preferred hands is in the sensory or feedback control of movement" (p. 39).

Following on the work of Flowers (1975), sensory feedback-based advantages for the preferred arm/hemisphere system were suggested on several other occasions based primarily on the observation that arm differences in reaching accuracy are most apparent during the latter stages of movement when sensory feedback is thought to be of particular importance. While an early description of this phenomenon was provided by Woodworth (1899), Todor and Cisernos (1985) were the first to quantify arm differences during the corrective phase of movement by having right-handed subjects perform fast and accurate reaching using an accelerometer-mounted stylus. Based on the results of this study, it was shown that longer movement durations seen for the non-preferred arm when obtaining relatively small visual targets were associated with greater time spent "homing in" the target during the deceleratory phase of movement. Taken together with ensuing studies reporting a similar preferred arm advantage in the amount of time spent the post peak velocity phase of movement (Roy et al. 1994; Elliott et al. 1995; Boulinguez et al. 2001; Mieschke et al. 2001), it seems reasonable to conclude that the preferred arm is more efficient in using online feedback to correct movement trajectory.

While the above, generalized feedback account of arm performance asymmetry represents a significant shift in thinking from classical, motor-based explanations of handedness, it is limited by its inability to address how specific modalities of sensory feedback might influence movement. In general, vision and proprioception are thought to be the most important sources of sensory feedback during the performance of voluntary movement. Vision, for example, provides an external frame of reference for movement including information regarding objects size, orientation and three dimensional position (Jeannerod et al. 1998; Goodale et al. 2004). Alternatively, proprioceptive information from skin, muscle and joint receptors plays an important role in the control of interaction torques (Sainburg et al. 1993; 1995), limb segment timing (Cordo et al. 1994; 1995b) and the acquisition of internal models of skilled movement (Kawato and Wolpert 1998; Kawato 1999). The extent to which these primary sources of movement-related sensory feedback are, therefore, lateralized to the preferred versus non-preferred arm is the focus of the following section.

Arm Asymmetries in Visual Feedback Processing for Movement

In two related studies by Honda (1982; 1984), an initial indication that visual information might have a differential influence on movements of the preferred versus non-preferred arms was provided. In these studies, eye and arm displacements were recorded during a bilateral reaching task where coupled arm movements were made to symmetrical visual targets. Based on this paradigm, it was found that subjects spent a greater amount of time visually monitoring the preferred arm and that this behaviour was related to increased target accuracy. Further, in a condition where subjects were required to only monitor the movements of only one arm versus the other, it was shown that the preferred arm was more affected by a lack of visual feedback. Taken together, these results support the notion that the preferred arm is more reliant on the use of visual information during the production of targeted movements.

In light of the findings of Honda (1982; 1984), several experiments have been conducted in which the amount of visual information available to subjects was altered during targeted reaching. In the first of two studies, Roy and Elliott (1986) asked subjects to reach to visual targets with the preferred or non-preferred arm under “full vision” or "no vision" conditions. In the full vision condition, the lights in the testing room were on throughout the reaching task, whereas in the no vision condition the lights were turned off at the time of movement initiation. Although the no vision condition had a profound effect on the subjects' overall movement accuracy, the results of this study showed a similar right arm advantage regardless of visual feedback availability. In contrast to this result, however, Roy and Elliott (1989) showed enhanced right arm accuracy in a third light availability condition where the lights were turned off 10 s prior to movement. This subsequent finding is in agreement with the findings of Honda (1982; 1984) and suggests that the preferred arm is more reliant on visual feedback during reaching.

Perhaps a more appropriate means of determining arm asymmetries in the utilization of movement-related visual feedback is the manipulation of visual target size. In this case, when targets are relatively small, and movement speed is emphasized, it has been reported on numerous occasions that movements of the preferred arm both faster and more accurate than those of the non-preferred (Woodworth 1899; Flowers 1975; Todor and Doane 1978; Todor and Cisneros 1985; Carson et al. 1993; Roy et al. 1994; Elliott et al. 1995; Mieschke et al. 2001). One clear example of this was provided in a study by Todor and Doane (1978) using a Fitts tapping paradigm. In this study, target width and movement amplitude were altered in such a way as to preserve task difficulty (i.e. the index of difficulty was held constant) while allowing the manipulation of visual feedback constraints (i.e. target size). Indeed, the results of this study showed that arm asymmetries were related to the visual demands of the task, as an increasing preferred arm advantage was seen with decreasing target size, but not with increases in target amplitude. It was, therefore, concluded that visual feedback is of greater importance to the control of preferred arm reaching movements.

Arm Asymmetries in Proprioceptive Feedback Processing for Movement

The term proprioception was originally coined by Sherrington (1906) to describe a group of sensations related to one's own movement. It is now well accepted that proprioceptive feedback from muscle spindles (Goodwin et al. 1972a; Goodwin et al. 1972b; McCloskey 1978; Burgess et al. 1982), joint receptors (Skoglund 1956) and cutaneous mechanoreceptors (Lynn 1975; Edin and Abbs 1991) provides detailed information about the position and velocity of body segments, while Golgi tendon organs are a primary sources of feedback regarding tension within the muscles (Houk and Henneman 1967; Jami 1992). Despite these observations, however, the role of proprioceptive information in determining arm performance asymmetries has been largely underappreciated. Specifically, most studies have focused solely on preferred right arm proprioceptive acuity (Paillard and Brouchon 1968; 1974; Rothwell et al. 1982; Darling 1991; Adamovich et al. 1998; Baud-Bovy and Viviani 1998; Adamovich et al. 1999; Lonn et al. 2000; 2001).

Whereas studies assessing the role of visual information on targeted movement have largely found asymmetries favouring the preferred arm, the preponderance of evidence to date suggests a non-preferred arm advantage in the ability to utilize feedback that is proprioceptive in nature. The first evidence in support of this notion was provided by Roy and MacKenzie (1978) who examined arm differences in the ability to match thumb and multi-joint arm positions in the absence of vision. While in this study no asymmetries in multi-joint arm position matching were found, a non-preferred left thumb accuracy advantage was seen. Based on these preliminary results, Colley (1984) and Riolo-Quinn (1991) also reported greater accuracy for proprioceptively-guided matches made by non-preferred thumb and Kurian and colleagues (1989) demonstrated non-preferred arm dominance for accurately reproducing elbow angles. Although Chapman et al. (2001), and Carson et al. (1990), did not show arm differences in an assessment of multi-joint position matches made in two and three dimensional space, recent studies by Goble et al. (2005; 2006), and Goble and Brown (2007), have also shown greater non-preferred arm matching accuracy during a task requiring memory and interhemispheric transfer of proprioceptive target positions.

In the Goble and Brown (2007) study the extent to which task difficulty might explain the somewhat equivocal results outlined above was explored by utilizing a variety of matching tasks that varied with respect to proprioceptive processing demands. In the first task, ipsilateral remembered matching, a similar method to that previously employed was used where subjects performed memory-based matching of previously experienced elbow positions with the same arm. In contrast, the contralateral concurrent matching task eliminated the need for memory, as the target arm remained in the target position while subjects performed matching with the opposite arm. In this case, interhemispheric transfer was necessary in order to accurately achieve the target position. Lastly, in the contralateral remembered condition, the demands of the first two tasks were combined as subjects were asked to perform memory-based matching of a previously experienced arm position with the contralateral arm. Interestingly, it was in this most difficult condition requiring both memory and interhemispheric transfer of proprioceptive target information where the greatest non-preferred arm advantage was found. This result emphasized the need to maximize proprioceptive feedback processing demands when attempting to elicit arm asymmetries.

Further support for a non-preferred arm advantage in the utilization of proprioceptive feedback comes from recent neuro-imaging studies where greater right hemisphere (i.e. non-preferred left arm) activation has been shown in association with tasks requiring enhanced proprioceptive feedback processing. For example, in a study of right-handed volunteers, Butler et al. (2004) used positron emission tomography to assess the neural correlates related to memory-based reaches made to targets that were either visual or proprioceptive in nature. Despite the fact that all matching movements in this study were made with the preferred right arm, it was found that proprioceptively-guided movements had increased activation in the temporo-parietal area of the ipsilateral right hemisphere. Similarly, a study Naito et al. (2005) explored hemispheric differences in the perception of movement illusions. In this study, greater right hemisphere activation was seen in a task where vibration of the hand extensor muscles was used to produce the illusion of wrist flexion.

While measures of end-point accuracy are common in assessments of position matching performance, the kinematics of the matching movements themselves are rarely quantified despite their potential value in determining arm differences in movement strategy (Brown and Cooke 1990; Cooke and Brown 1994). Goble and colleagues (2005; 2006) and Goble and Brown (2007) provided evidence that proprioceptively-guided matching movements are substantially different from those typically associated with well learned visually-guided movements. In particular, velocity profiles were asymmetric and multi-peaked, in contrast to the well known bell shaped velocity profiles associated with visually-guided movement (Brown and Cooke 1981a; Soechting and Lacquaniti 1981; Flash and Hogan 1985; Brown and Cooke 1990). These results suggest a movement strategy that is highly dependent on proprioceptive feedback utilization during the movement in order to make multiple “online” corrections prior to achieving the desired arm position (Woodworth 1899; Lee et al. 1997; Novak et al. 2002).

Summary

The goal of this chapter was to review relevant literature regarding asymmetries in neurophysiology and behavior of the upper limbs. It was shown that, for the majority of individuals, the right arm is preferred over the left when performing many activities of daily living, and that this arm bias likely reflects structural/anatomical differences in the neuromotor system. Despite right arm motor dominance, however, more recent theories in the area of motor control have purported that the two arm/hemisphere systems may, in turn, be specialized for different aspects of sensorimotor control (Serrien et al. 2006). In this case, the dynamic dominance theory and the open versus closed loop hypotheses of handedness have received particular attention, although there is now evidence to suggest that arm differences exist in the utilization of different sensory feedback sources such as vision and proprioception. With respect to this latter view the purpose of this dissertation will be to explore the relative contribution of sensory feedback to upper limb asymmetries in motor performance.

Dissertation Aims

The overall aim of this dissertation was to further elucidate the role of sensory feedback in determining arm performance asymmetries. In the first experiment (Chapter 2), arm differences in the utilization of visual versus proprioceptive feedback were explored by comparing preferred and non-preferred arm matching of targets that were proprioceptive versus visual in nature. In this case, both visual and proprioceptive target tasks shared a common motor output component allowing for an assessment of arm differences in the utilization of these sources of sensory feedback. It was hypothesized that the non-preferred arm would be more accurate for proprioceptive target matching, while the preferred arm would be more adept in matching visual targets. This "sensory modality specific" hypothesis of handedness provides a basis for greater understanding of arm function based on each arm's reliance on a vision versus proprioception during the performance of goal-directed activities. For example, during many bimanual activities it is common for the preferred arm to manipulate or guide an object using visual feedback, while the non-preferred arm performs stabilization of the object without visual feedback, thus, relying primarily on proprioception.

The goal of the second study (Chapter 3) was to assess arm differences in the ability to match movement dynamics on the basis of proprioceptive information. Previous studies of asymmetric proprioceptive feedback utilization have focused solely on static arm position matching with no attention paid to dynamic proprioception. In this study, blindfolded subjects experienced passive displacement of the preferred or non-preferred arm following a predetermined triangular velocity profile. Subjects then attempted to match this velocity profile through active arm movement in the absence of vision. Based on previous matching studies showing non-preferred arm advantages in proprioceptively-guided target position matching, it was hypothesized that the non-preferred arm would also show a greater ability to replicated target movement speeds. Alternatively, based on the dynamic dominance theory of handedness, a preferred arm advantage for velocity matching might have been expected due to its proposed advantage in the specification movement dynamics.

Using a paradigm similar to that previously described by Cordo et al (1994; 1995b), the third and final experiment (Chapter 4) quantified inter-arm differences in the ability to combine static and dynamic proprioceptive information. In this case, “dynamic position” matching was performed where subjects memorized a target position of the arm (i.e. static component) and then identified this position during subsequent movement of the arm through a range of motion including the target position (i.e. dynamic component). Given the relative demands of this task in terms of proprioceptive feedback processing, and recent findings suggesting greater involvement of the right hemisphere (i.e. non-preferred left arm) during tasks that rely heavily on proprioceptive feedback (Butler et al. 2004; Naito et al. 2005), it was hypothesized that the non-preferred arm would be more adept at this task than the preferred arm.

Chapter 2

Upper Limb Asymmetries in the Accuracy of Proprioceptive Versus Visually-guided Target Matching

Introduction

Arm differences in upper limb motor behaviour, more commonly known as handedness, are evident in many activities of daily living where approximately nine out of ten individuals prefer using the right versus left arm (Coren and Porac 1977; Gilbert and Wysocki 1992). In this case, asymmetries in arm selection have traditionally been associated with an enhanced ability of the preferred right arm, and presumably the contralateral left cerebral hemisphere, to generate motor output. Indeed, well documented preferred arm performance advantages exist with respect to the peak speed (Woodworth 1899; Annett et al. 1979; Todor and Cisneros 1985; Heath and Roy 2000; Boulinguez et al. 2001), strength (Provins 1967; Petersen et al. 1989; Brouwer et al. 2001; Farthing et al. 2005) and consistency (Peters 1976; Peters and Durding 1979; Todor and Kyprie 1980; Elliott et al. 1999b) of voluntary movements. Based on these observations, it is perhaps not surprising that the preferred and non-preferred arms have been referred to as being “dominant” and “non-dominant” respectively.

Although the idea of motor dominance has persisted in the handedness literature for some time, recent evidence in the area of motor control has provided an alternative view of upper limb asymmetries. Specifically, it has been suggested that neither arm is entirely dominant compared to the other but, rather, the two arms are specialized for different aspects of sensorimotor performance. On the basis of several studies assessing goal-directed reaching characteristics of individuals with left versus right hemisphere damage, Haaland and Harrington (1989a; 1989b; 1994), and Winstein and Pohl (1995), provided evidence in support of an open versus closed loop model of handedness. In these studies, subjects made ipsilesional arm movements towards visual targets in a fast and accurate manner. In general, it was found that individuals with damage to the left hemisphere were deficient in the early, open loop (i.e. feedback independent) portion of reaching, whereas right hemisphere impairment led to difficulties in the later, closed loop (i.e. feedback dependent) phase of movement. These findings remain limited, however, due to inconsistencies with other studies of reaching in individuals with unilateral brain injury (see Haaland and Harrington 1996 for review). In light of this limitation, therefore, Haaland et al (2004) reinterpreted many of these previous clinical findings in favour of another theory – the dynamic dominance hypothesis of handedness.

The dynamic dominance hypothesis of handedness, first proposed by Sainburg (2002), also supports the notion that the preferred and non-preferred arms are dominant for different aspects of sensorimotor performance. The basic tenets of this hypothesis are that the preferred arm/hemisphere system is specialized for the control of movement trajectory, whereas the non-preferred arm/hemisphere has an enhanced ability to obtain static arm positions or postures. With respect to the control of movement trajectory, preferred arm advantages during reaching tasks in a virtual environment have been demonstrated for both the production of efficient joint torques (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002; Sainburg 2002) and the specification of initial movement direction (Sainburg and Wang 2002; Wang and Sainburg 2003; 2004b). In contrast, the non-preferred arm has been found on several occasions (Sainburg and Wang 2002; Bagesteiro and Sainburg 2003; Wang and Sainburg 2004a), but not all (Wang and Sainburg 2004b), to exhibit greater end-point accuracy. Perhaps the greatest strength of the dynamic dominance hypothesis lies in its ability to relate arm differences to the functional aspects of many two-handed activities of daily living. In this case, individuals often use the preferred arm to perform trajectory-dependent movements (e.g. swinging a hammer), while the non-preferred arm is used to stabilize objects (e.g. holding a nail) in a particular position using a particular posture.

Beyond the open versus closed loop and dynamic dominance hypotheses, a third distinction between the preferred and non-preferred arms can be made on the basis of studies highlighting the role of two key sources of movement-related sensory feedback – vision and proprioception. Indeed, several studies have suggested that the preferred arm is more reliant on visual feedback during the control of movement, as might be necessary for interacting with objects in the external environment, whereas the non-preferred arm is enhanced for proprioceptive feedback processing in order to maintain postures and/or stabilize objects outside of visual attention. One of the first studies to assess asymmetries in sensory feedback utilization during movement was conducted by Flowers (1975), who compared two movement tasks that differed in sensory feedback processing demands. While no arm asymmetries were found in a relatively feedback independent (i.e. ballistic) finger tapping paradigm, the preferred arm of right-handed individuals was faster and more accurate for a sequential aiming task. Given that this latter type of task has been shown to rely heavily on visual information (Todor and Kyprie 1980), these results suggest an advantage of the preferred right arm for the utilization of visual feedback. In support of this conclusion, arm differences have been demonstrated in the kinematics of visually-guided aiming where that deceleration duration, a period of time during which online corrections in movement trajectory based on visual feedback may occur (Carlton 1981; Elliott et al. 1999a; Ma-Wyatt and McKee 2007), was longer for the non-preferred arm (Todor and Cisneros 1985; Roy et al. 1994; Elliott et al. 1995; Boulinguez et al. 2001; Mieschke et al. 2001). Based on this observation, it was argued that the preferred arm/hemisphere is more effective in its ability to process visual feedback, allowing for fewer and faster corrective movements to be made by the subject.

Honda (1982; 1984) provided further evidence in support of a preferred arm bias for utilizing visual feedback during bilateral reaching. Based on eye and arm movement recordings, these studies found that subjects spent a significantly longer amount of time monitoring movements of the preferred arm during reaching, and that when vision of one arm was eliminated, greater decrements in performance were seen for the preferred arm. In addition, unilateral reaching studies have indicated a significant relationship between visual target size and asymmetries in reaching performance. Specifically, when the visual demands of the task have been increased by reducing target size, a greater preferred arm advantage has been seen in terms of movement speed and/or target accuracy (Flowers 1975; Todor and Doane 1978; Todor and Cisneros 1985; Carson et al. 1993; Roy et al. 1994; Elliott et al. 1995; Mieschke et al. 2001).

In contrast to studies indicating a preferred arm advantage in the control of visually-guided movement, studies of arm differences in the utilization of movement-related proprioceptive feedback have, alternatively, reported asymmetries in favour of the non-preferred arm. Perhaps the earliest evidence of this phenomenon was reported by

Roy and MacKenzie (1978) who asked right-handed subjects to replicate previously experienced arm and thumb target positions in the absence of vision. While the results of this study showed no asymmetry in the accuracy of arm position matching, the non-preferred thumb was found to be significantly more accurate than the preferred thumb. This non-preferred thumb advantage for proprioceptive matching was subsequently confirmed by both Colley (1984) and Riolo-Quinn (1991), although Nishizawa (1991) failed to show any thumb matching differences.

More recently, studies by Goble et al (2005; 2006) and Goble and Brown (2007) have expanded on earlier studies of proprioceptively-guided matching by comparing three types of elbow matching tasks. These tasks were utilized in order to manipulate the difficulty of position matching and, thus, increased the need for proprioceptive feedback processing. In particular, during the ipsilateral remembered task subjects performed matching of a previously specified the target elbow angle with the same arm. The major demands of this task were the storage and retrieval of proprioceptive information from memory. In the second task, termed contralateral concurrent matching, the need for proprioceptive memory was eliminated by allowing subjects to match an elbow angle held at the target position with the contralateral arm. In this case, however, the task required interhemispheric transfer in order to perform accurate matching. Lastly, in the contralateral remembered task, both memory and interhemispheric transfer demands were combined as subjects were asked to match a previously-determined elbow angle with the contralateral arm. Importantly, it was in this most difficult task condition where the greatest asymmetries in matching accuracy were evident, with the accuracy of non-preferred arm matching being on average twice as great compared to matches made by the preferred arm.

Although the above findings are intriguing, it is important to note that a formal examination of upper limb sensorimotor asymmetries due to the differential use of visual versus proprioceptive feedback has not yet been conducted. The purpose of the present study, therefore, was to test this sensory modality specific theory of handedness. In this case, subjects in this study were asked to complete two memory-based target matching tasks where either visual or proprioceptive targets were matched using the preferred or non-preferred arm. Based on the previous literature, it was hypothesized that each arm would exhibit a different form of "sensory handedness", with the accuracy of preferred arm matching enhanced during the visually-guided task, and with non-preferred arm accuracy increased with respect to proprioceptively-guided matching. Overall, this new approach to determining arm asymmetries represents a potentially powerful means of exploring inter-arm differences in the performance of sensorimotor activities.

Methods

Subjects

Thirteen healthy, young adults (mean age 20.1 ± 1.5 years; 6 males, 7 females) participated in the study. The total number of subjects was determined based on a power analysis using data from previous position matching studies conducted in this laboratory (Goble et al. 2006; Goble and Brown 2007). At the time of testing all subjects were free of upper limb neuromuscular impairment, had normal or corrected to normal vision and showed strong right arm preference as evidenced by scores of +100 on a modified version of the Edinburgh Handedness Inventory (Oldfield 1971, see appendix). In addition, the preferred arm was also associated with significantly greater performance on several standard tests of motor ability including maximum grip strength obtained from a hand force dynamometer, the number of pegs placed per 60 s in a Purdue pegboard and the ability to maintain a 1 mm probe within a 2 mm hole for 10 s without touching the sides (i.e. hand steadiness). A summary of these performance characteristics is provided in Table 2.1 below.

Task	**Preferred Arm**	**Non-preferred Arm**
Max Grip Strength (N)	314.6 ± 24.2	290.1 ± 26.3
Motor Dexterity (# of Pegs in 60 s)	31.8 ± 0.9	29.0 ± 0.7
Hand Steadiness (# of probe touches)	8.3 ± 2.8	18.4 ± 5.0

Table 2.1 – Average (± SEM) arm performance on tests of motor ability.

Experimental Setup

Subjects performed two memory-based matching tasks with similar motor output requirements (i.e. elbow extension of 15 or 30 deg), but that varied with respect to type of sensory feedback used to represent and/or achieve the target position. In the first task, proprioceptive matching (Fig 2.1 upper panel), subjects were blindfolded and seated with their forearms resting comfortably on two height-adjustable instrumented manipulanda designed for measuring angular displacement of the elbow joint in the horizontal plane.

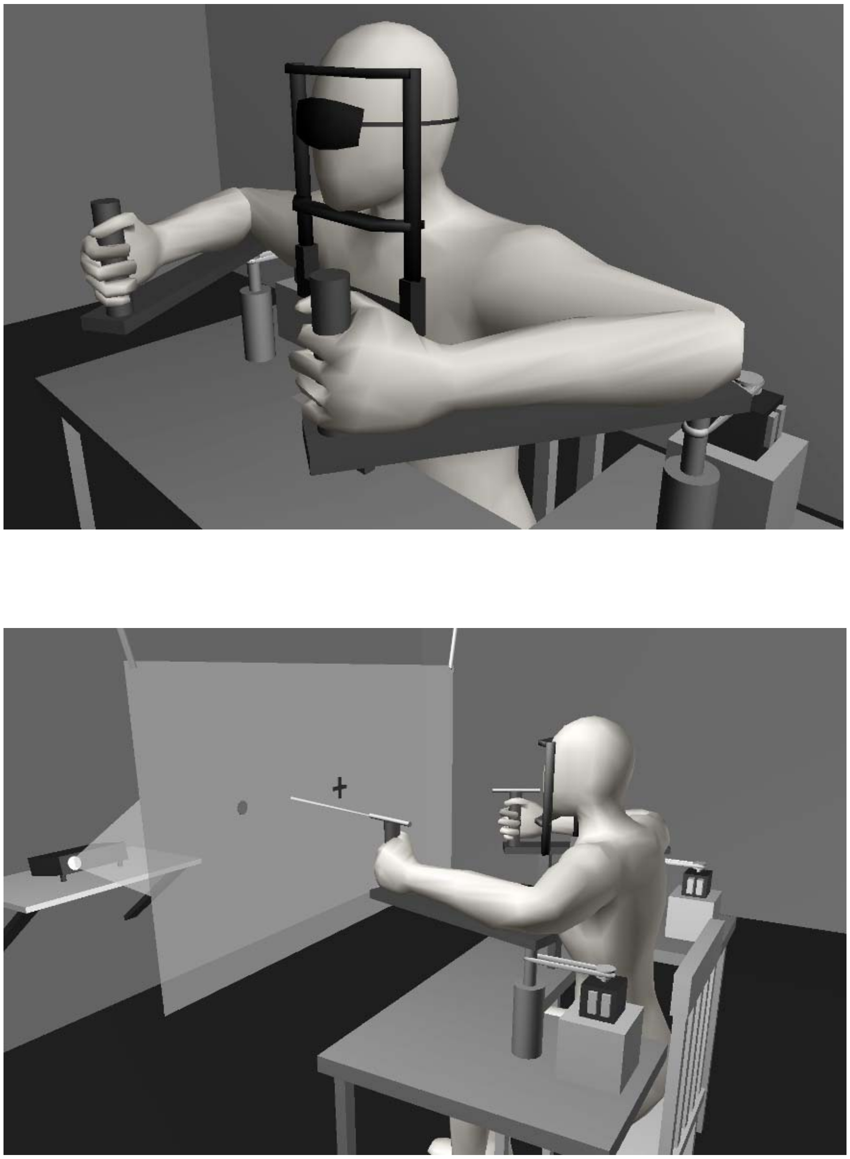


Fig 2.1 – Experimental setup for proprioceptive (upper panel) and visual (lower panel) target matching tasks.

Each manipulandum consisted of a servomotor-driven horizontal metal support adjusted to the length of the subject's forearm and mounted on a frictionless pivot beneath the elbow joint. Standardized starting positions for the shoulder (80 deg abduction, 15 deg flexion), elbow (75 deg extension) and wrist (neutral) were maintained across subjects. In addition, the effects of altered head position were minimized by means of a steel chin rest and support frame surrounding the lateral aspects of the head.

For the second task, visual target matching (Fig 2.1 lower panel), the same set-up was implemented as outlined above, with the exception that subjects were not blindfolded and a back projection system was used to present visual targets. This system consisted of a flat, translucent screen suspended directly in the front of the subject upon which small (1 cm diameter) circular targets were projected from behind the screen. The screen was sufficiently large so as to limit the use of visual background information during matching (Krigolson and Heath 2004; Lemay et al. 2004). The position of the targets and fixation point were software adjusted to be along the sightline of a laser pointer fixed to the distal end of the manipulandum just below eye level.

Experimental Procedures

Subjects performed the two matching tasks (proprioceptive versus visual target matching) in a sequential fashion with approximately half (n = 7) of the subject pool starting with the proprioceptive task, while the remaining subjects (n = 6) began with visual target matching. Prior to data collection for each task, subjects were given a full description of the experimental procedures and as many practice trials as necessary to ensure full understanding of the instructions provided. On average, each task lasted half an hour with a 10 min rest break provided in between tasks.

Proprioceptive Target Matching Task

In this task, subjects performed matching of a previously-determined static arm position in the absence of vision. In this case, each trial consisted of two components – target determination and target matching. In the target determination phase, the preferred or non-preferred forearm was passively displaced by the torque motor system at a constant velocity of 15 deg/s to a predetermined elbow angle (15 or 30 deg of elbow extension from start position). The subject was then given 3 s to memorize the target position based on static proprioceptive feedback. It was assumed that feedback was first presented to the contralateral hemisphere based on the anatomical arrangement of the ascending proprioceptive fiber tracts. Lastly, the forearm was displaced back to the start position by the motor at a constant speed of 15 deg/s.

Following a 2 s delay, the target matching phase was initiated where subjects responded to an auditory tone by actively extending the elbow at a self-selected pace to the memorized target position. This was done with either the same forearm as that used to determine the target (ipsilateral remembered condition), or with the opposite forearm in a mirror symmetric fashion (contralateral remembered condition). The demands associated with the ipsilateral remembered condition were, thus, largely comprised of the storage, and retrieval of proprioceptive target information, whereas the contralateral remembered condition required both memory and interhemispheric transfer of proprioceptive target information. Upon completing the target matching phase, subjects held their forearm steady for a minimum of 2 s prior to the forearm being passively returned to the start position in preparation for the next trial.

Visual Target Matching Task

Similar to the proprioceptive target matching task, the visual target matching task was also comprised of two phases. In the target determination phase, subjects focused on a fixation point that appeared in the center of the screen directly to the front of them. This point remained on the screen for 3 to 5 s and then disappeared in accordance with the presentation of a visual target displayed for 75 ms to the right or left of the fixation point. Since subjects did not have time to foveate the target, this method was used to channel visual information to either the left or right hemisphere (for reviews of this technique see Hellige 1983; Efron 1990). Specifically, targets presented in the left hemifield were initially "seen" by the right hemisphere, while right hemifield target information was first available to the left hemisphere.

In the next phase of the task, *target matching*, subjects responded to an auditory tone by directing the endpoint of the laser attached to the manipulandum toward the memorized target position on the screen. As was the case in the proprioceptive task, this targeted movement required 15 or 30 deg of elbow extension. Matching movements were made with either the forearm on the same side as the visual target (ipsilateral remembered condition) or to a mirror image of the target using the contralateral forearm (contralateral remembered condition). Once again, matching in the ipsilateral condition was thought to be less difficult than that in the contralateral condition, as the former required primarily memory, while the latter involved both memory and interhemispheric transfer of visual target information. Subjects moved at self-selected speed with an emphasis on directing the pointer to the center of the visual target presented.

Data Collection and Analysis

In both proprioceptive and visual matching conditions, 5 trials were collected for each combination of task (ipsilateral remembered versus contralateral remembered), arm (preferred versus non-preferred) and target amplitude (15 versus 30) in a random block design. Elbow joint rotations were recorded by a laptop computer as the voltage output of precision potentiometers mounted beneath the pivot points of the manipulanda. The analog signal was then digitized at 100 Hz, filtered (4th order Butterworth, zero phase lag, 8 Hz) and multiplied by a displacement calibration coefficient prior to data analysis. The following dependent measures were obtained from the data:

1. *Absolute Error* – The absolute value of the difference between the end target and matching movement positions was used to assess the overall ability to match target position. Target and matching positions were determined by differentiating the displacement signals into velocity and then using a threshold detection algorithm of +/- 2 SD from the baseline (zero) signal.
2. *Constant Error* – The signed difference between the target and matching positions was used as an estimate of matching bias in terms of target undershooting versus overshooting. Target and matching positions were determined as described for absolute error.

3. *Variable Error* – The standard deviation of errors across a series of trials was used as measure of matching movement variability.
4. *Peak Movement Velocity* – The self-selected maximum speed of movement, as determined by the highest value in the differentiated position (i.e. velocity) signal associated with the target matching phase.
5. *Percent time to Peak Velocity* – The symmetry of velocity profiles during target matching was assessed as the time to maximum peak velocity from movement onset, determined as above, divided by total movement time. Total movement time was calculated using a threshold detection algorithm indicating the point in time where velocity deviated beyond +/- 2 SD from baseline.
6. *Average Movement Smoothness* – Relative matching movement smoothness was based on the following jerk score calculation:

   $$\text{Jerk Score} = \text{sqrt}(1/2 \cdot \int j^2(t)\,dt \cdot d^5/a^2)$$

   where j is the third derivative of position (i.e. jerk), d is the movement duration, and a is the movement amplitude (Ketcham et al. 2002; Seidler et al. 2002).

Statistical Analyses

For each of the visual and proprioceptive target matching conditions, mean measures of accuracy (absolute, variable and constant error) and movement kinematics (peak velocity; percent time to peak velocity and movement smoothness) were subjected to repeated measures analyses of variance. Where significant main effects and/or interactions were found, data were subsequently collapsed across non-significant factors and tested post-hoc for simple effects using Tukey's honestly significant differences test. For all analyses statistical significance was set at the level of $p<.05$.

Results

Absolute Errors

The absolute accuracy of proprioceptive and visual target matching is shown in Fig 2.2 for the preferred and non-preferred arms in each matching task (ipsilateral remembered versus contralateral remembered) and amplitude (15 deg versus 30 deg) condition. With respect to proprioceptive target matching, absolute errors were smaller across all task and amplitude conditions when matching was performed by the non-preferred versus preferred arm ($F_{1,12}=13.6$; $p<.01$). This asymmetry, although significant when 15 and 30 deg data were combined in the ipsilateral remembered task (Tukey's method), was most apparent during contralateral remembered matching where both memory and interhemispheric transfer of target information were required (Tukey's method). Indeed, preferred arm errors in this condition were approximately twice as large as those seen for the non-preferred arm, due largely to an increase in preferred arm error when matches were made in the ipsilateral remembered versus contralateral remembered task condition (Tukey's method). No significant differences in absolute error were seen as a function of target amplitude.

In contrast to proprioceptive matching, subjects were significantly more accurate in terms of absolute error when matching visually-determined targets with the preferred arm ($F_{1,12}=13.3$; $p<.01$). The magnitude of this arm asymmetry, however, was similar

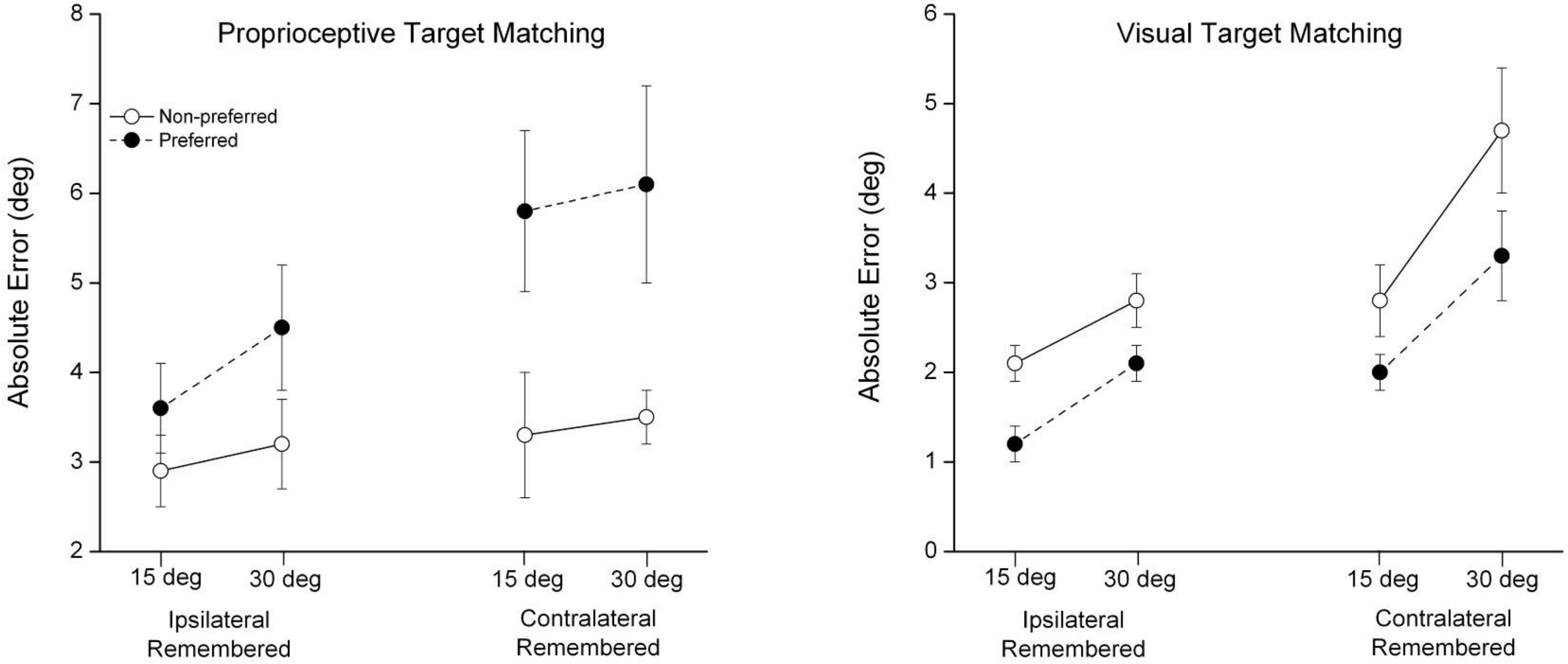


Fig 2.2 – Mean (+/- SEM) group differences in absolute error for proprioceptive (left panel) and visual (right panel) target matching tasks.

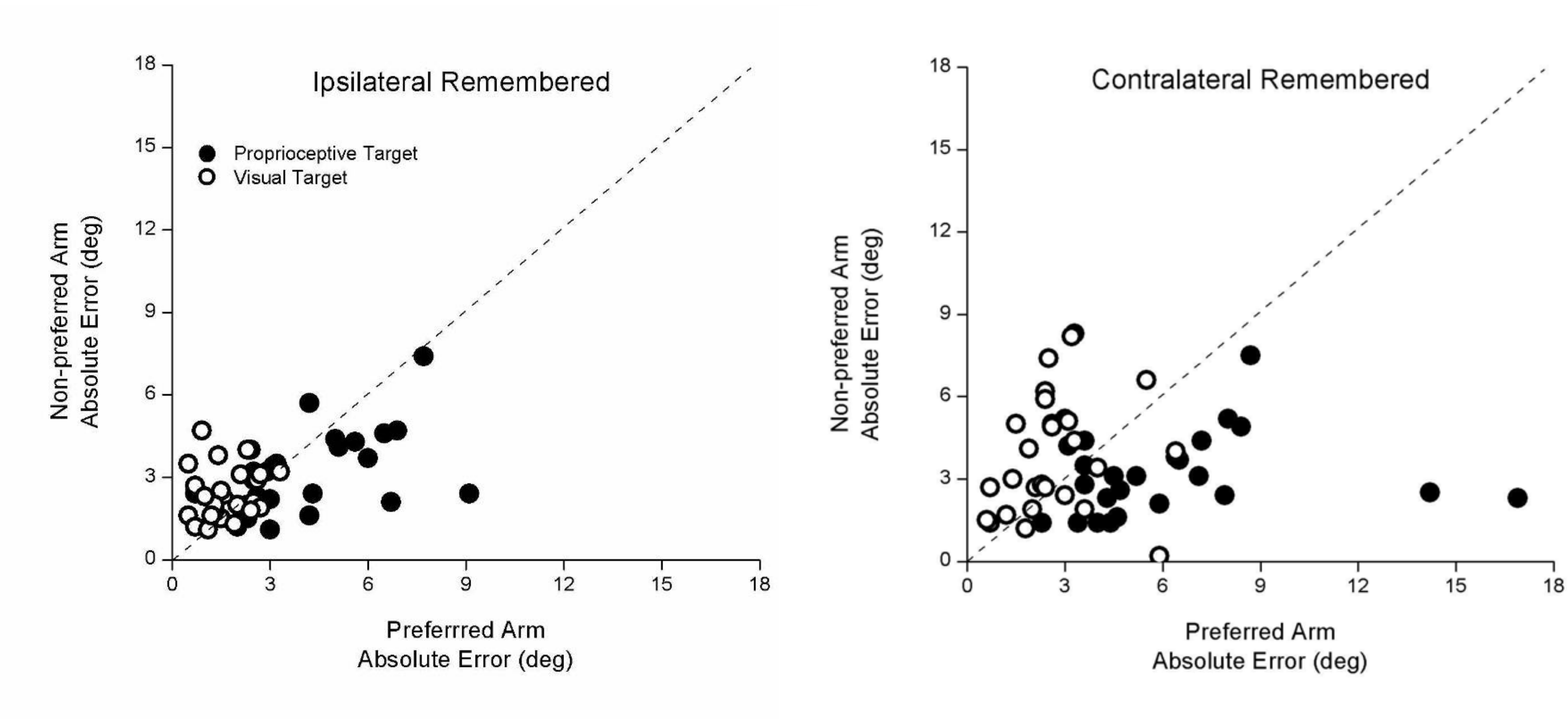


Fig 2.3 – Individual subject arm comparison of mean absolute error generated in the visual and proprioceptive matching conditions. Data shown for the ipsilateral remembered (left panel) and contralateral remembered (right panel) tasks.

across task and amplitude conditions despite significant increases in absolute error for matches made by either arm during the more difficult contralateral remembered task ($F_{1,12}$=18.0; p<.001) and when matching the 30 deg compared to 15 deg target amplitude ($F_{1,12}$=24.4; p<.001). Although not statistically significant, the magnitude of absolute errors in the visual task were on average greater in the contralateral remembered, as opposed to ipsilateral remembered condition.

The extent to which the group asymmetries in matching performance described above were also evident at the individual subject level is demonstrated in Fig 2.3. In this figure, average preferred and non-preferred arm errors within a particular task and target amplitude condition were cross-plotted and a line of symmetry drawn along the diagonal. In the ipsilateral remembered task, 73% of arm comparisons for proprioceptive target matching fell below the line of symmetry, reflecting poorer matching performance (i.e. greater errors) by the preferred arm. In contrast, when the two arms were compared in the visual target matching task, the same percentage of comparisons (i.e. 73%) were located above the line of symmetry indicating larger errors for the non-preferred arm. Indeed, these trends for proprioceptive and visual target matching were even more pronounced in the contralateral remembered task. In this case, 85% of subjects showed poorer matching of proprioceptive targets with the preferred arm, while 77% were less effective matching visual targets with the non-preferred arm.

Variable Errors

The consistency of subject matching, as determined by variable error, is shown in Fig 2.4. Similar to the absolute error findings, variable errors in the proprioceptive task

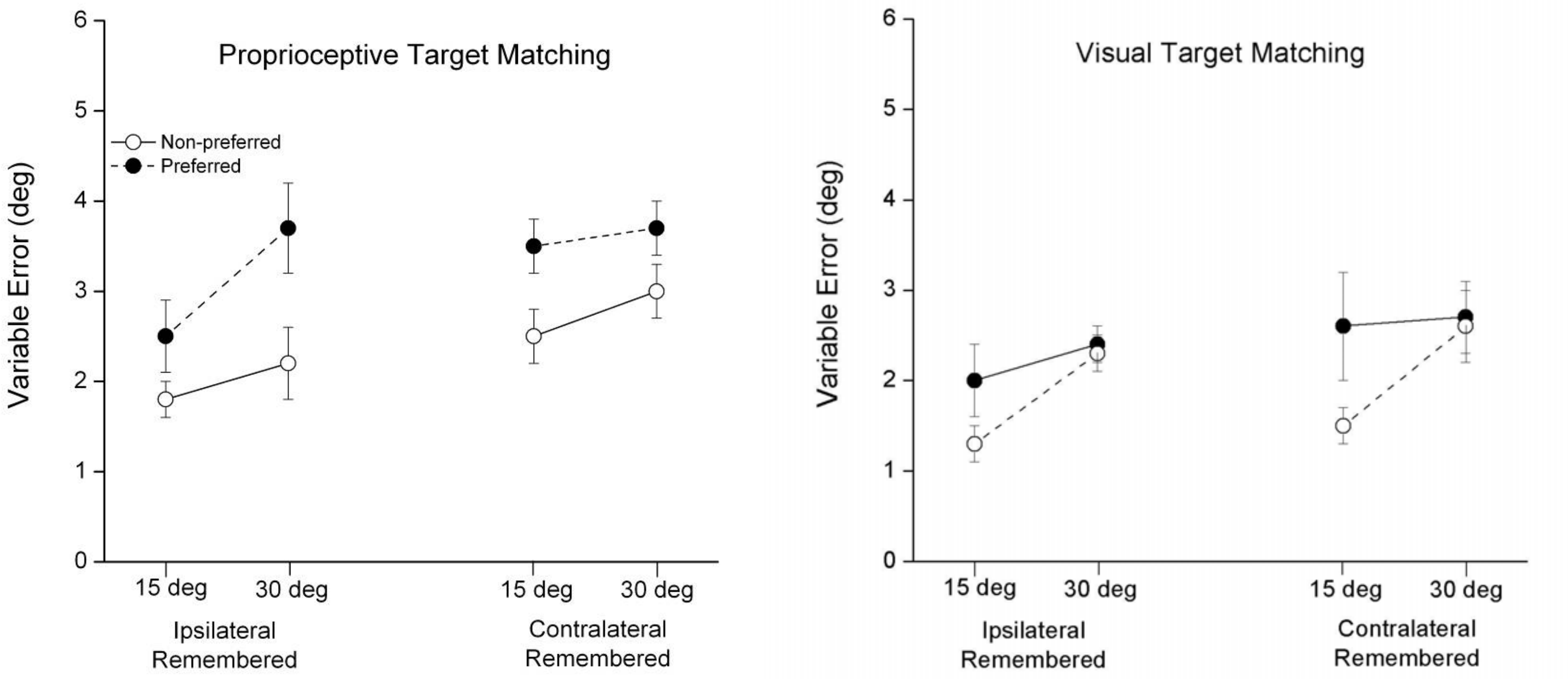


Fig 2.4 – Mean (+/- SEM) group differences in variable error for proprioceptive (left panel) and visual (right panel) target matching tasks.

were significantly smaller across all conditions for matches made by the non-preferred arm compared to the preferred arm ($F_{1,12}$= 48.7; $p<0.001$). However, this arm asymmetry was not influenced by the type of matching task, as similar magnitude arm differences were seen in the both ipsilateral remembered and contralateral remembered conditions. While variable errors were greater for 30 versus 15 deg target matching when data were collapsed across all arm and task conditions ($F_{1,12}$= 5.3; $p<.05$), post hoc comparisons of this effect revealed a significant difference for only the preferred arm during ipsilateral remembered matching (Tukey's method).

In the visual target matching task, the pattern of variable errors was different than that observed during proprioceptively-guided matching. Overall, preferred arm variable errors were significantly smaller than those seen for the non-preferred arm ($\mathrm{F}_{1,12}$; $p<.05$), however, this effect was mediated by target amplitude. In this case, a significant decrease in variable error was seen for the preferred arm during 15 deg target matching compared to the non-preferred arm, which led to greater preferred arm matching performance in only this condition (Tukey's method). These results were consistent for both ipsilateral remembered and contralateral remembered tasks.

Constant Errors

Constant errors in the direction of target matching are provided in Fig 2.5 where positive errors represent target overshooting and negative errors indicate undershooting. In the proprioceptive task, where subjects' responses were largely biased towards overshooting, arm asymmetries were only seen in the contralateral remembered condition ($F_{1,12}$=9.5; $p<.05$). In this case, preferred arm matches showed significantly greater

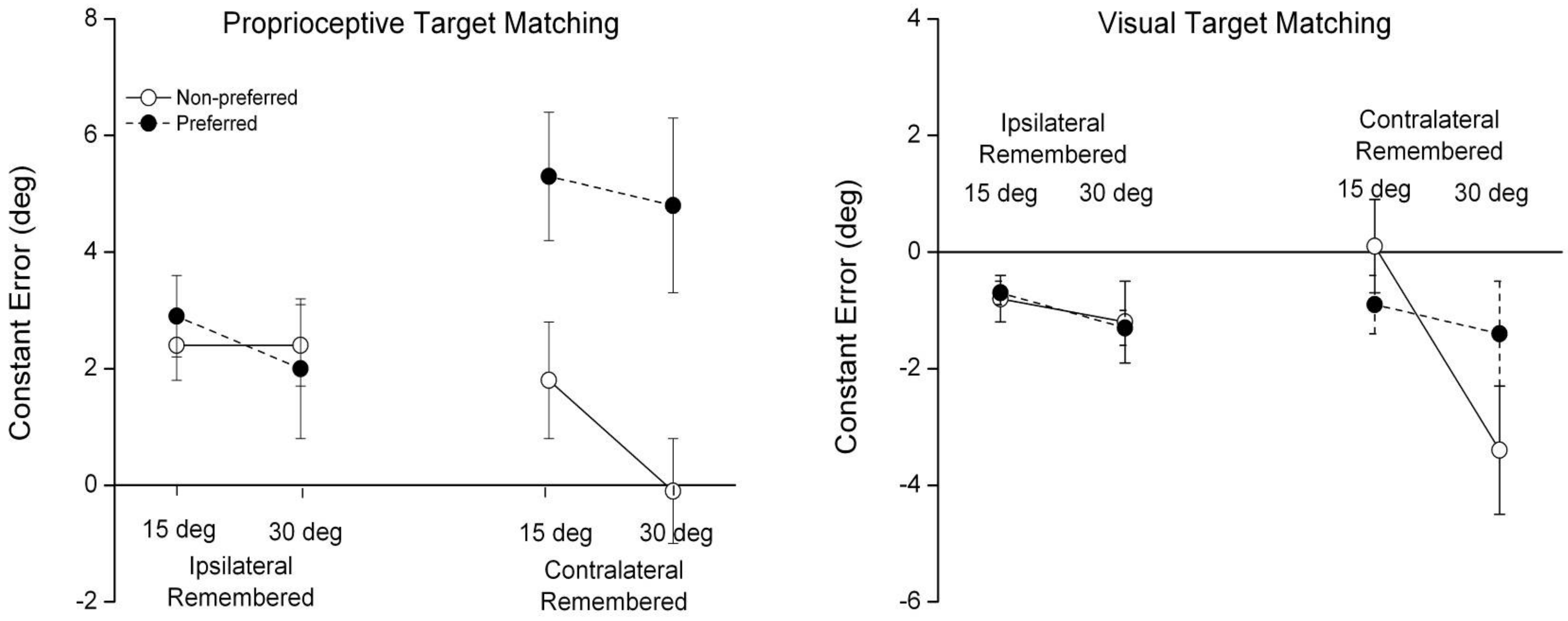


Fig 2.5 – Mean (+/- SEM) group differences in constant error for proprioceptive (left panel) and visual (right panel) target matching tasks.

overshooting compared to the non-preferred arm (Tukey's method), and compared to either arm in the ipsilateral remembered task condition (Tukey's method). While no effect of target amplitude on constant errors was found across conditions for the proprioceptive task, there was a non-significant trend towards greater overshooting in the 15 deg condition of the contralateral remembered task.

In contrast to the results for proprioceptively-guided target matching, subjects exhibited target undershooting in the visual task. During ipsilateral remembered matching, the degree of target undershooting was, on average, 1 deg for both the preferred and non-preferred arms. While the preferred arm maintained this level of undershooting for the contralateral remembered task, non-preferred arm errors were dependent on the target amplitude ($F_{1,12}$=13.7; p<.01). In this case, matching the 15 deg target amplitude showed essentially no directional bias, whereas 30 deg target matching was characterized by undershooting of approximately 3 deg.

Movement Kinematics

Ensemble averaged velocity profiles from a representative subject during proprioceptive and visual target matching are presented in Fig 2.6 for each experimental condition. Further, group data quantifying various features of the matching movements is provided in Fig 2.7-2.9. Overall, few differences were found with respect to movement strategy regardless of whether subjects were matching proprioceptive or visual targets. In all cases, peak movement velocity scaled with target amplitude. Specifically, as can be seen in both Fig 2.6 and 2.7, proprioceptive ($F_{1,12}$=37.6, p<.001) and visual ($F_{1,12}$=26.5; p<.001) target matches exhibited higher maximum speed in the 30 deg versus 15 deg

Proprioceptive Target Matching Visual Target Matching

Ipsilateral Remembered – Preferred Arm

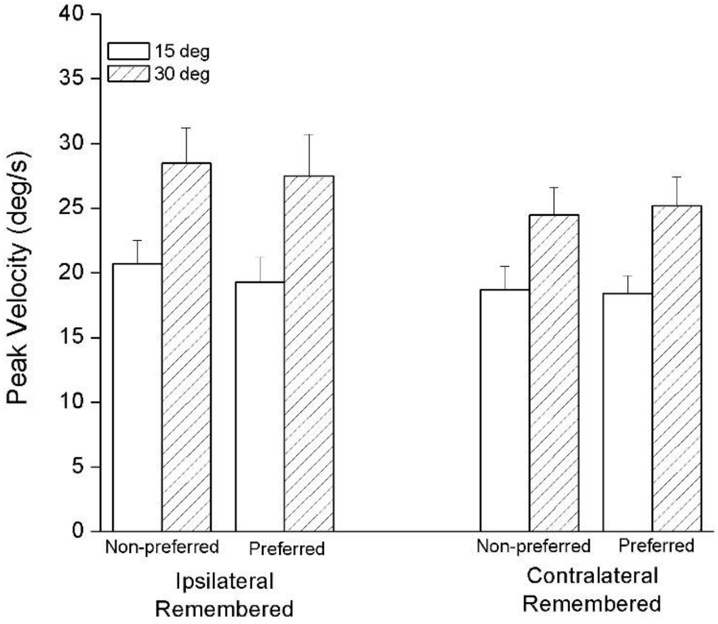
Ipsilateral Remembered – Non-preferred Arm

Contralateral Remembered – Preferred Arm

Contralateral Remembered – Non-Preferred Arm

Fig 2.6 – Ensemble averaged velocity profiles during target matching for a representative subject in each experimental condition.

Proprioceptive Target Matching



Visual Target Matching

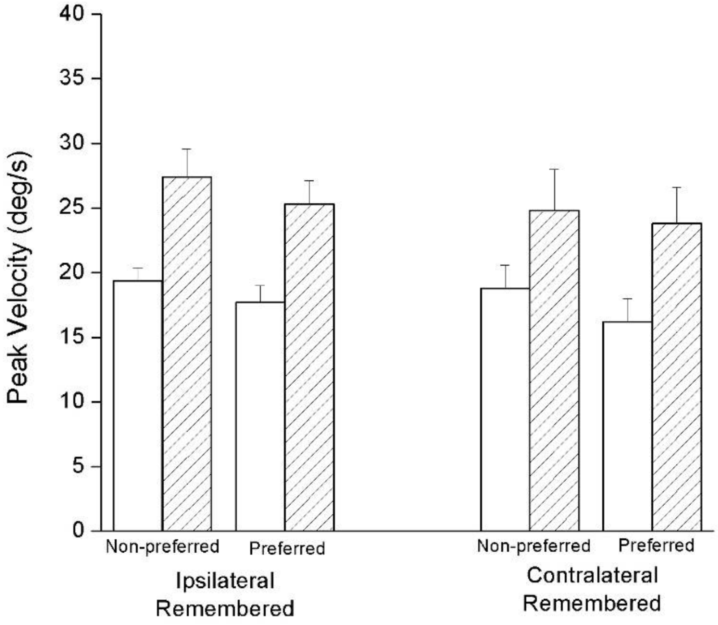
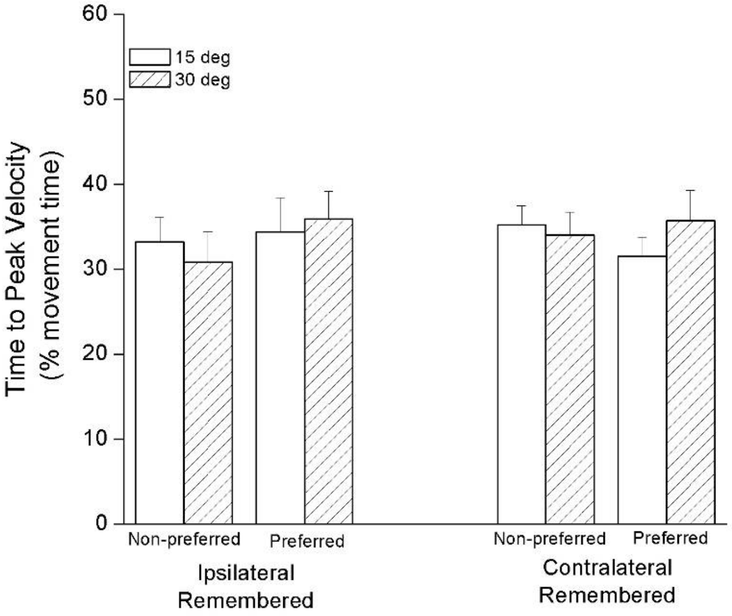


Fig 2.7 – Mean (+/- SEM) group differences in the peak velocity of matching movements made to proprioceptive (top panel) and visual (bottom panel) targets.

Proprioceptive Target Matching



Visual Target Matching

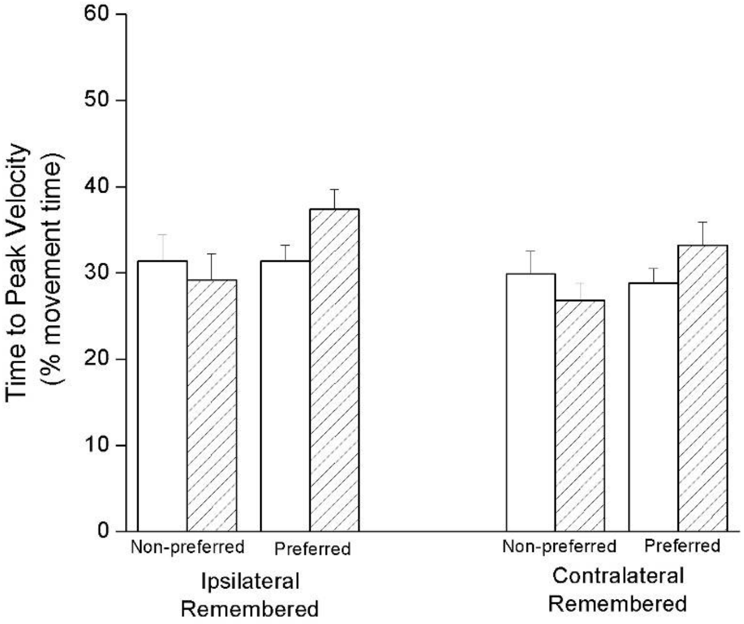


Fig 2.8 – Mean (+/- SEM) group differences in the percent time to peak velocity of matching movements made to proprioceptive (top panel) and visual (bottom panel) targets.

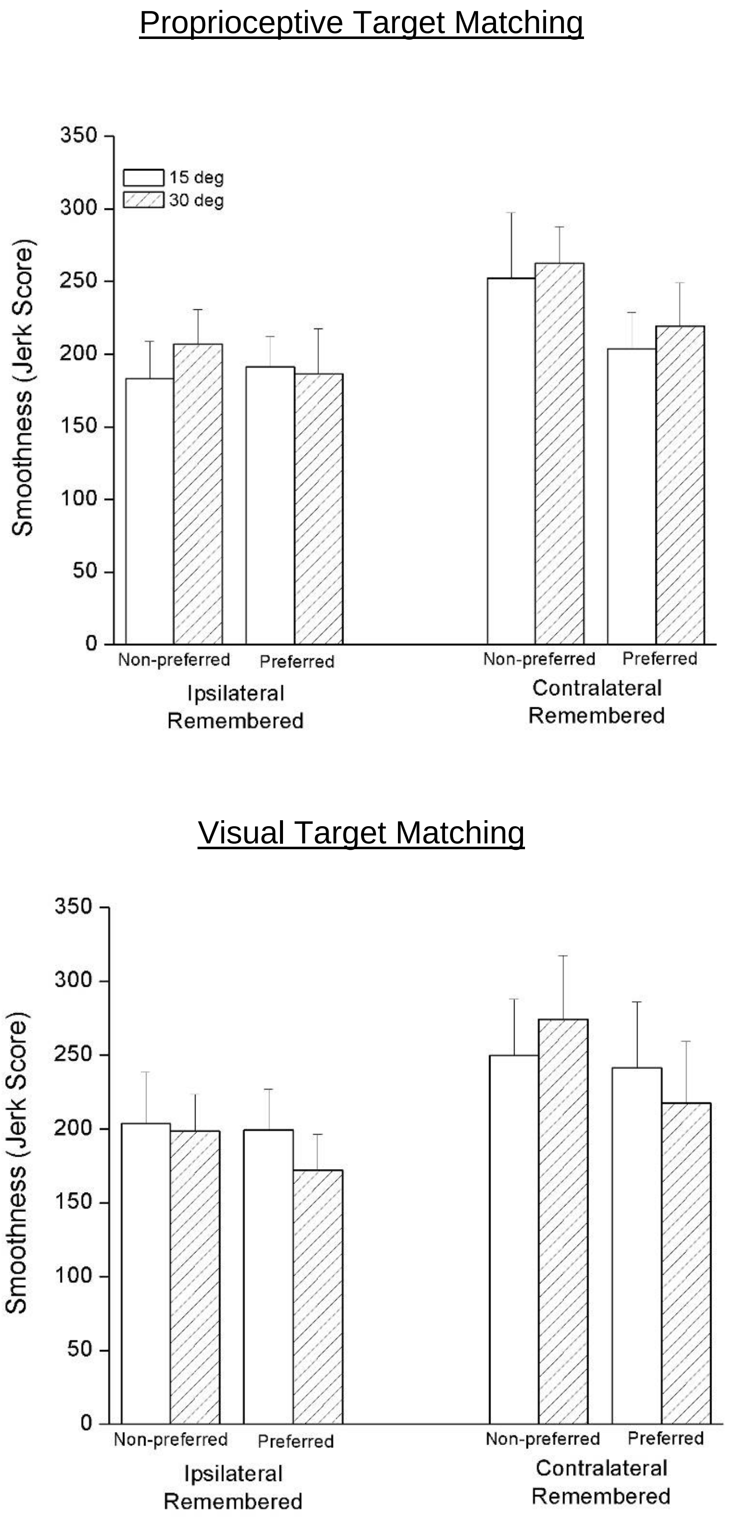


Fig 2.9 – Mean (+/- SEM) group differences in the smoothness of matching movements made to proprioceptive (top panel) and visual (bottom panel) targets.

condition. This scaling effect was not influenced by the type of matching condition (i.e. ipsilateral versus contralateral remembered), despite an overall decrease in peak speed during contralateral remembered matching ($F_{1,12}$=4.9; p<.05).

In contrast to the time-symmetric bell-shaped velocity profiles associated with well learned arm movements (Brown and Cooke 1981a; Soechting and Lacquaniti 1981; Flash and Hogan 1985; Brown and Cooke 1990), matching movements in the present study were time-asymmetric with time to peak velocity occurring earlier in the movement (Fig 2.6; 2.8). In the proprioceptive task, peak speed occurred approximately one third (33.9%) into the movement regardless of arm, task or target amplitude condition. The percent time to peak velocity in the visual target matching task was also on average approximately one third (31.0%) of the way into the movement regardless of matching condition. In the visual case, however, a small but significant increase in the percent time to peak velocity was seen for 30 deg target matches made with the preferred versus non-preferred arm ($F_{1,12}$=14.8; p<.01; Tukey's method).

Whereas the velocity profiles in this study were relatively smooth and stereotyped during the acceleratory phase, movement deceleration was far more irregular in nature with several secondary peaks in the velocity profile evident. Using normalized jerk score as a measure of movement smoothness (Fig 2.9), it was found that these irregularities were not significantly different between arms in either the visual or proprioceptive target matching task. When collapsed across matching arm and amplitude conditions, ipsilateral remembered matching was smoother than contralateral remembered matching, however, regardless of whether subjects were matching targets that were proprioceptive ($F_{1,12}$=9.0; p<.05) or visual ($F_{1,12}$=7.0; p<.05) in nature.

Discussion

Upper limb asymmetries in motor behaviour have traditionally been viewed from the standpoint of preferred arm dominance for generating absolute motor output. More recently, however, the open versus closed loop and dynamic dominance hypotheses of handedness have suggested that the preferred and non-preferred arm/hemispheres are specialized for different aspects of sensorimotor performance. In line with this thinking, the aim of the present study was to elucidate arm asymmetries that may exist in the utilization of different types of sensory feedback. In this case, the preponderance of evidence showed that the preferred arm of right-handed individuals was more adept at obtaining visual targets, whereas the non-preferred arm was enhanced for matching targets on the basis of proprioception. These arm differences were mediated to some extent by the demands of the matching task, but were largely independent of arm differences in movement strategy. As such, a sensory modality-based hypothesis of handedness is proposed whereby the non-preferred and preferred arms differ on the bases of their relative reliance on proprioceptive versus visual information in the control of targeted arm movements.

With respect to arm asymmetries in the utilization of proprioceptive feedback, mounting evidence from position matching studies indicates that the non-preferred left arm is more accurate when making targeted movements in the absence of vision. One of the first examples of this was provided by Roy and MacKenzie (1978) who found a non-preferred left arm advantage for the matching of previously experienced thumb, but not arm, positions. Subsequent to this finding, a non-preferred thumb advantage was also shown in studies by Colley (1984) and Riolo-Quinn (1991), although Nishisawa (1991) was unable to show any difference between preferred and non-preferred thumb matching. In addition, while no arm differences were found in the matching of proprioceptively-determined endpoints in two and three dimensional space (Carson et al. 1990; Chapman et al. 2001), a recent study from this laboratory attempted to explain these equivocal results on the basis proprioceptive processing demands (Goble and Brown 2007). In this case, a greater non-preferred arm advantage was seen during a contralateral remembered task requiring memory and interhemispheric transfer of proprioceptive target information versus tasks where only memory (ipsilateral remembered) or interhemispheric transfer (contralateral concurrent) was required.

Given the preferential role of the contralateral hemisphere in the control of arm movements, a non-preferred left arm advantage for proprioceptive target matching may reflect specialization of the right hemisphere for the processing proprioceptive feedback. Support for this hypothesis comes from two lines of research. First, studies of individuals with unilateral brain injury have shown that patients with right versus left frontal and/or medial temporal damage have a greater difficulty reproducing the extent of passively-determined kinesthetic targets (Leonard and Milner 1991a; Leonard and Milner 1991b; Rains and Milner 1994). Specifically, large right hemisphere excisions affected subjects' ability to monitor proprioceptive feedback during both the presentation of proprioceptive targets and the planning/execution of proprioceptively-guided matching movements. Further, support for hemispheric differences in the processing of proprioceptive feedback comes from studies of healthy adults using functional brain imaging techniques. In a study of goal-directed reaching, for example, Butler and colleagues (2004) compared activation of the left versus right hemisphere during both visual and proprioceptively-guided reaching to remembered targets. In the proprioceptive matching task it was found that subjects showed preferential activation of a subset of areas in the temporo-parietal cortex of the right hemisphere. In agreement with this finding, Naito et al. (2005) also found increased activation in a number of right hemisphere areas, including the primary somatosensory cortex, during the perception of movement illusions at the wrist. Taken together, these results provide strong support of greater right hemisphere involvement for the processing of movement-related proprioceptive feedback.

While preferred arm accuracy advantages for visually-guided tasks have been described since the time of Woodworth (1899), it is only during the past three decades that attempts to describe the specific role of vision in determining handedness have been undertaken. Based, in part, on the work of Flowers (1975), preferred arm advantages for accurately obtaining visual targets of progressively smaller size have most often been attributed to arm differences in the ability to utilize visual feedback for making small corrective movements during the latter stage of reaching (Todor and Doane 1978; Todor and Kyprie 1980; Todor and Cisneros 1985; Carson et al. 1993; Roy et al. 1994; Elliott et al. 1995; Mieschke et al. 2001). Indeed, this asymmetry in visual feedback processing has also been inferred from the kinematics of visual-guided reaching movements where the amount of time spent post peak velocity, a period of time thought to rely heavily on the use of visual feedback to monitor and correct movement (Carlton 1981; Elliott et al. 1999a), has been shown to be shorter for preferred arm movements (Todor and Cisneros 1985; Roy et al. 1994; Elliott et al. 1995; Boulinguez et al. 2001; Mieschke et al. 2001). Interestingly, in the 30 deg visual target condition of the current study, a similar result was found where a greater proportion of time spent post peak velocity was seen for movements of the non-preferred arm. However, given the overall magnitude of these arm differences, it remains unclear whether an advantage in visual feedback processing can, in fact, be inferred from this result.

Although it is appealing to attribute the preferred right arm advantages for accurately obtaining visual targets to specialization of the contralateral left-hemisphere for visual feedback processing, evidence in support of this notion has, to date, been limited. One interesting observation that lends support to a left hemisphere advantage for the processing of visual information is the proportion of individuals who demonstrate right eye dominance. In this case, it has been shown that 65% of the population prefers the right eye for monocular tasks (Porac and Coren 1976; 1978), and that information from the nasal (i.e. crossed) fibers of this eye, leading to the left hemisphere, exhibit processing dominance over the temporal (i.e. uncrossed) fibers traversing to the right hemisphere (Hubel and Wiesel 1959; 1962; Crovitz 1964). In addition, beyond this somewhat anecdotal evidence, studies of visual acuity have also shown a left hemisphere advantage in terms of temporal resolution (see Okubo and Nicholls 2005 for review). In a study by Nicholls (1994), for example, the threshold for detecting fusion of two light flashes presented in quick succession was examined in a group of healthy, right handed adults. Based on this paradigm, it was found that subjects were, indeed, most accurate for stimuli presented in the right visual field (i.e. left hemisphere). Lastly, it is worthy of note that anatomical differences exist between the left and right visual cortices. Specifically, the left occipital lobe extends further anteriorly and is wider than the right, leading to a greater volume of neural substrate available to the left visual cortex (Galaburda et al. 1978; Geschwind and Galaburda 1985).

In accordance with previous proprioceptive matching studies conducted by this laboratory (Goble et al. 2006; Goble and Brown 2007), asymmetries in absolute matching errors favouring the non-preferred arm were particularly pronounced in the contralateral remembered condition. Given that this task is largely dependent on the interhemispheric transfer of memorized proprioceptive feedback prior to making an accurate matching movement (Sperry et al. 1969; Fabri et al. 2001), it therefore seems logical to conclude that subjects more readily transferred this information from the left to right hemisphere. Support in favour of this directional bias with respect to the interhemispheric transfer of positional information has previously been provided in studies assessing the transfer of learning following opposite arm training in a visuomotor rotation task. Specifically, it has been shown that previous experience with the unseen preferred arm (i.e. left hemisphere) under rotated feedback conditions enhances the final position accuracy of the unseen non-preferred arm (i.e. right hemisphere), and not vice versa (Sainburg and Wang 2002; Wang and Sainburg 2003). To what extent this effect may be workspace dependent (Wang and Sainburg 2006), however, remains unclear.

Somewhat surprisingly, a comparable increase in matching asymmetry was not seen in the contralateral remembered condition of the visual target matching task. Rather, both arms showed increased errors in this more difficult condition, with the magnitude of the preferred arm advantage remaining relatively constant. This finding further contrasts those studies that have employed the method of Poffenberger (1912), where asymmetric transfer of visuomotor information has been shown favouring the right to left hemisphere direction (see Marzi et al. 1991 for review). In this case, however, Poffenberger-type studies only require subjects to make ballistic tapping movements in response to the appearance of visual target. In the present study, a goal-directed reaching task was used where sensory feedback was of particular importance, and where the movements were made at a self-selected pace.

On a number of occasions, errors in the present study were found to increase for movements made to the larger, 30 deg amplitude target position. This “distance effect” was recently explored in some detail by Lemay and Proteau (2001) in an examination of three hypotheses. First, in the motor output hypothesis, increases in error with target distance that might be due signal dependent noise (Schmidt et al. 1979; Harris and Wolpert 1998) were assessed by asking subjects to make slower reaching movements to the farther of two targets. In this case, however, despite a reduction in the motor output signal, reaches made to the far target remained less accurate than those to the close target. Next, the role of sensory acuity, such that more distant targets might be less accurately perceived by the visual system (Ma-Wyatt and McKee 2006), was assessed by comparing reaching errors to a more distant target when movements were made at either a slow or fast speed. It was found that, even though the target distance to the eye was constant for all movements, greater errors existed for slower movements. This result argued in favour of a third hypothesis of the distance effect, which is a movement duration account. In this case, it has been suggested that an increased length of time for completing a matching movement results in memory decay and/or interference with the encoding process. Since, in the present study, 30 deg movements were of also of longer duration, it is possible that the greater endpoint errors demonstrated in the 30 deg condition were, at least in part, due to a similar memory decay/encoding interference effect.

In the present study, the constant errors observed were biased in the direction of overshooting for proprioceptive targets and undershooting for visual targets. This result is comparable to that reported by Adamovich and colleagues (1998) who demonstrated a similar tendency for subjects to reach beyond proprioceptively-determined targets, while falling short of targets that were obtained under visual guidance. Although the neuro-physiological basis for this pattern of errors remains unclear, Adamovich and colleagues (1998) suggested that these results likely reflect a modality specific difference in the representation of space. In this case, the perception of kinesthetic space was thought to be subject to a relative “stretching” along the lateral direction, whereas there may have been a comparable “contraction” in visual space.

While absolute errors in this study provided the clearest indication of subject’s overall ability to match the target position, it should be noted that this measure of performance is complex combination of variable and constant errors (Shultz and Roy 1973). In this case, variable errors represent the consistency of matching performance, and have been associated with noise in the sensorimotor system, while constant errors are more reflective of the central representation of target position (McIntyre et al. 2000). Compared to absolute errors, variable errors in this study showed a similar pattern of arm differences related to the type of target feedback (i.e. vision versus proprioception) with enhanced non-preferred arm performance in the proprioceptive task, and greater preferred arm accuracy during15 deg visual target matching. In contrast, the constant error results in this study showed an asymmetry in only the contralateral remembered condition of the proprioceptive target task. These constant error findings might provide some insight into the modulation of proprioceptive gain in the preferred and non-preferred arms (personal communication - B. Martin and D. Adamo). In particular, it is possible that enhanced non-preferred arm matching in the contralateral remembered condition was due, in part, to a more adequate representation of the target arm position by the preferred arm. Indeed, it has been shown that the central representation of hand/arm in the sensorimotor cortex is larger in the left hemisphere (i.e. preferred arm) of right handed individuals (White et al. 1994; Amunts et al. 1996; Amunts et al. 2000). In addition, arm differences in h-reflex amplitude (i.e. gain) have shown greater responses for the preferred versus non-preferred arm (Tan 1989a; 1989b; Aimonetti et al. 1999).

One limitation of this study was that during the visual target matching task proprioceptive feedback was available for use during the matching phase of each trial. It might, therefore, be argued that any asymmetry in matching performance might be due to a preferred arm advantage for the utilization of vision and/or proprioceptive feedback, rather than only vision itself. While the specific contribution of each source of feedback was not determined in the present study, previous research in this area would suggest that subjects were heavily reliant on visual feedback during both the target presentation and target matching phases of the visual task. In particular, visuo-proprioceptive mismatch paradigms have shown that the planning of movement direction (Lateiner and Sainburg 2003; Sober and Sabes 2003; Bagesteiro et al. 2006) and movement extent (Sarlegna and Sainburg 2006) are highly dependent on visual information with weighting estimates as high as 90% for vision compared to only 10% for proprioception (Sober and Sabes 2005). This strategy is thought to represent an effective means of minimizing the number of transformations necessary between frames of reference allowing for the minimization of metabolic costs due to greater neural computations and/or undue noise resulting from the coordinate transformations (Soechting and Flanders 1989b; 1989a).

The matching movements made in this study were typical of those that have been reported for targeted movements made in the absence of speed constraints and where an emphasis on accuracy has been placed (Fisk and Goodale 1985; Milner and Ijaz 1990; Milner 1992; Goble et al. 2005; 2006). Specifically, velocity profiles consisted of a primary movement component, characterized by a gradual rise to peak velocity, and a prolonged deceleration phase with multiple sub-peaks post peak velocity (Soechting 1984; Novak et al. 2002). In addition, peak velocity was found to scale with movement amplitude in both the ipsilateral remembered and contralateral remembered tasks, as has been shown to be an invariant characteristic of goal-directed reaching (e.g. Brown and Cooke 1981a; 1984; 1990; Gottlieb et al. 1990; Gottlieb 1998; Pfann et al. 1998). With respect to movement smoothness, greater irregularity in the velocity profile was seen during contralateral remembered matching in both the visual and proprioceptive target matching task. This finding likely reflects the greater need for subjects to make a greater number of feedback-based corrections in the online movement trajectory in order to achieve a more uncertain target end position (Milner and Ijaz 1990; Rohrer et al. 2002; Fishbach et al. 2007).

To what extent subjects in the present study may have utilized amplitude versus position matching strategies is not certain, however, it seems fair to assume that the final arm position was the primary basis for planning matching movements. This assumption is based on both the instruction given to subjects (i.e. focus on the final arm position and try to replicate it) and on previous research examining errors in the proprioceptively-guided matching of movement extent versus target location. Specifically, it has been shown that when subjects are required to utilize a strategy based on movement, increased errors (Marteniuk et al. 1972; Marteniuk 1973) and directional biases (Imanaka and Abernethy 1992a; 1992b) are seen with respect to the target position.

Overall, the results of the present study provide strong evidence supporting a sensory modality specific hypothesis of asymmetries in motor behaviour. It has been shown that the non-preferred left arm of right-handed individuals was more accurate when matching targets that are proprioceptive in nature, whereas the preferred arm is more accurate for visual target matching. To what extent these results reflect different roles for the preferred and non-preferred arms during the performance of many activities of daily living remains unclear. However, given the use-dependent neural plasticity that is now known to exist within the sensorimotor system (see Monfils et al. 2005 for review), it seems plausible that neural networks within the left and right hemisphere may have evolved to more adequately deal with proprioceptive versus visual feedback, respectively. In this case, left hemisphere specialization for visual feedback processing would allow for greater interactions between the preferred arm and objects in the external environment (e.g. reaching out for a glass of water). In contrast specialization of the right hemisphere for proprioceptive feedback would be important for maintaining objects in a particular location outside of visual attention (e.g. holding a piece of bread) prior to them being manipulated by the preferred arm (e.g. buttering it with a knife).

Chapter 3

Upper Limb Asymmetries during the Proprioceptively-guided Matching of Movement Dynamics

Introduction

The term proprioception was first coined by Sherrington (1906) to describe the group of sensations elicited by stimulation of receptors within the body during one's own movement. While these sensations are thought to include such information as the force of muscle contraction and the relative timing of motor commands (see Gandevia et al. 1992; 2002 for reviews), it is the ability to detect body segment positions and movement that has received the most attention to date. This bias is likely due to the vital role this type of sensory information plays during the planning and execution of goal-directed movements (McCloskey 1978; Matthews 1982; Cordo et al. 1994; Grill and Hallett 1995; Prochazka and Hulliger 1998).

From a neurophysiological standpoint, it is generally well accepted that the muscle spindle afferents are of primary importance in the conscious perception of limb position and velocity (see Matthews 1982 for review), with smaller contributions made by skin (Moberg 1983; Ferrell and Smith 1988), joint (Ferrell et al. 1987; Ferrell and Craske 1992) and Golgi tendon organ receptors (Jami 1992). The enhanced role of the muscle spindle in signaling changes in limb position was perhaps best demonstrated by Goodwin et al (1972a; 1972b) in their classic series of studies using muscle tendon vibration. In these studies, high frequency, low amplitude vibration was applied to the biceps or triceps tendons of the preferred arm, as a means of increasing the firing rate of, primarily, group 1a muscle spindles (Bianconi and van der Meulen 1963; Burke et al. 1976a). Over the course of stimulation, subjects were then asked to use the opposite arm to indicate either the position, or speed and direction, of the vibrated arm. Based on this paradigm, illusory effects in both the perception of elbow joint position and velocity were shown, consistent with a perceived lengthening of the vibrated muscle.

Further evidence that limb position and velocity information are distinctly represented in the nervous system comes from studies that have used microneurography to directly record from the sensory afferents of cats (Jansen and Matthews 1962b; 1962a; Matthews 1964; Merton 1964) and humans (Hagbarth and Vallbo 1968; Vallbo 1970; 1974; Roll and Vedel 1982). Based on these studies, neural firing patterns have been identified consisting of both static and dynamic components, which correspond to changes in muscle length (i.e. limb position) and the rate of change of muscle length (i.e. joint movement velocity) respectively (see McCloskey et al 1978 for review). In this case, however, it is the primary muscle spindle afferents (1a) that show the greatest sensitivity to the rate of change of muscle length, while both primary and secondary (II) spindle afferents show altered neural firing in response to changes in muscle length (Burke et al. 1976b; 1976a; Edin and Vallbo 1988; 1990).

In the realm of motor behaviour, the ability to perceive and replicate joint position based on proprioceptive feedback has been extensively studied with errors of less than 5 deg typically reported (Marteniuk et al. 1972; Worringham and Stelmach 1985; Darling 1991; Adamovich et al. 1998; 1999; Lonn et al. 2000). In addition, there is now mounting evidence to suggest that the accuracy of proprioceptively-guided position matching is enhanced for movements made by the non-preferred arm. While early position matching studies were rather equivocal showing either a non-preferred arm advantage (Roy and MacKenzie 1978; Colley 1984; Kurian et al. 1989; Riolo-Quinn 1991) or no arm differences (Nishizawa 1991; Chapman et al. 2001), recent studies from this lab have shown a non-preferred arm advantage for tasks requiring increased proprioceptive processing demands (Goble et al. 2006; Goble and Brown 2007). Specifically, it has been found that, in a task requiring both memory and interhemispheric transfer of elbow position information, preferred arm errors were approximately twice as large as those of the non-preferred arm.

In contrast to studies of position matching, the ability to match the dynamics of upper limb movements in the absence of vision has largely been ignored in the motor behaviour literature. This is perhaps surprising, given what is now known from studies involving individuals with proprioceptive deficits due to large fiber neuropathy where movement-related proprioceptive feedback has been shown to be critical for the control of intersegmental dynamics during goal-directed movements. In a study by Sainburg et al. (1993), for example, two deafferented subjects were asked to perform a movement sequence similar to that associated with slicing a loaf of bread. For both subjects, it was found that movement performance was significantly impaired with gross curvatures seen in wristpath trajectory, and a severe temporal decoupling between the shoulder and elbow joints. Similar deficits have subsequently been reported for tasks involving the tracing of lines oriented in different directions (Sainburg et al. 1995) and target matching in three dimensional space (Messier et al. 2003).

Of the few studies that have attempted to quantify subjects' ability to perceive arm speed/dynamics in the absence of vision, most have utilized a velocity-discrimination paradigm where a speed comparison is made between two successive movements (Lonn et al. 2001; Kerr and Worringham 2002; Djupsjobacka and Domkin 2005). Based on these studies, conducted solely using the preferred arm of right-handed individuals, the primary finding to emerge has been that of a speed effect where subjects were more accurate when discriminating against a slower criterion target speed. In addition, one known report exists regarding the ability to perceive and replicate movements of the upper limb (Lonn et al. 2001). In this study, right handed subjects were asked to match the speed of both self-generated are passively-experienced target movements. Overall, it was shown that subjects were also more accurate when matching self-generated target movements with slower peak velocities. In this case, however, subject performance was assessed with respect to errors in peak and average speed and not for other aspects of the target movement such as acceleration and/or deceleration.

The purpose of the present study, therefore, was to further explore the extent to which healthy individuals can perceive and replicate the dynamics of a proprioceptively-determined target arm movement, with a particular emphasis place on arm differences in matching performance. This was accomplished using an elbow matching paradigm where subjects were asked to match the speed of a previously-experienced target arm movement with either the same (ipsilateral remembered) or opposite (contralateral remembered) arm in the absence of vision. It was hypothesized that, based on position matching studies conducted by this laboratory (Goble et al. 2006; Goble and Brown 2007), accuracy would be greatest for the non-preferred arm in the less difficult ipsilateral remembered matching task. In addition, greater matching errors were expected for the preferred arm during the more difficult contralateral remembered task where matching required both memory and interhemispheric transfer of target information.

Methods

Subjects

Eleven healthy, young adults (mean age 20.5 ± 2.7 years; 4 males, 7 females) participated in the study. All procedures were approved by the research ethics review board of the University of Michigan. Subjects were free of upper limb neuromuscular impairment at the time of testing and showed a strong right arm preference, as evidenced by scores of +100 on the modified Edinburgh Handedness Inventory (Oldfield 1971) provided in the appendix. In addition, subjects showed significant right arm performance advantages on several common tests of motor ability. These measures, summarized in Table 3.1, included maximum grip strength, the number of pegs placed in a Purdue pegboard (i.e. manual dexterity) in 60 s and the ability to maintain a 1 mm probe within a 2 mm hole without touching the sides (i.e. hand steadiness) for 10 s.

Task	Preferred Arm	Non-preferred Arm
Max Grip strength (N)	304.8 ± 11.8	282.2 ± 12.7
Manual Dexterity (# of Pegs in 60 s)	30.3 ± 1.0	27.1 ± 0.7
Hand Steadiness (# of side touches)	11.0 ± 3.1	21.9 ± 8.5

Table 3.1 – Average (± SEM) arm performance on tests of motor ability.

Experimental Setup

The setup for this experiment, depicted in Fig 3.1, consisted of servo-motor driven manipulanda devices designed for elbow displacement in the horizontal plane. Blindfolded subjects were seated with forearms resting comfortably on separate length and height-adjustable aluminum levers. Rotation of the levers about the elbow joint occurred by either active movement of the subject, or via the programmable servo-motor system. Standardized start positions were maintained for the shoulder (80 deg abduction, 15 deg flexion), elbow (75 deg extension) and wrist (neutral) across subjects. The effects of altered head position were minimized by means of a steel chin rest and support frame surrounding the lateral aspects of the head.

Experimental Procedures

Subjects in this study were asked to complete a series of proprioceptively-guided matching tasks consisting of two phases. In the first phase, target determination, the subject's elbow was passively extended by the servomotor system following one of two target triangular velocity profiles. In the 30 deg/s peak speed condition, the forearm was accelerated for 1 s at 30 deg/s/s to a peak speed of 30 deg/s, and then decelerated at –30 deg/s/s for 1 s back to rest. Conversely, in the faster, 60 deg/s peak speed condition, the forearm was accelerated for 1 s at either 60 deg/s/s to a peak speed of 60 deg/s, and then decelerated at –60 deg/s/s for 1 s bask to rest. In both conditions, the elbow position was subsequently returned to the start configuration along the same speed trajectory but in the opposite direction.

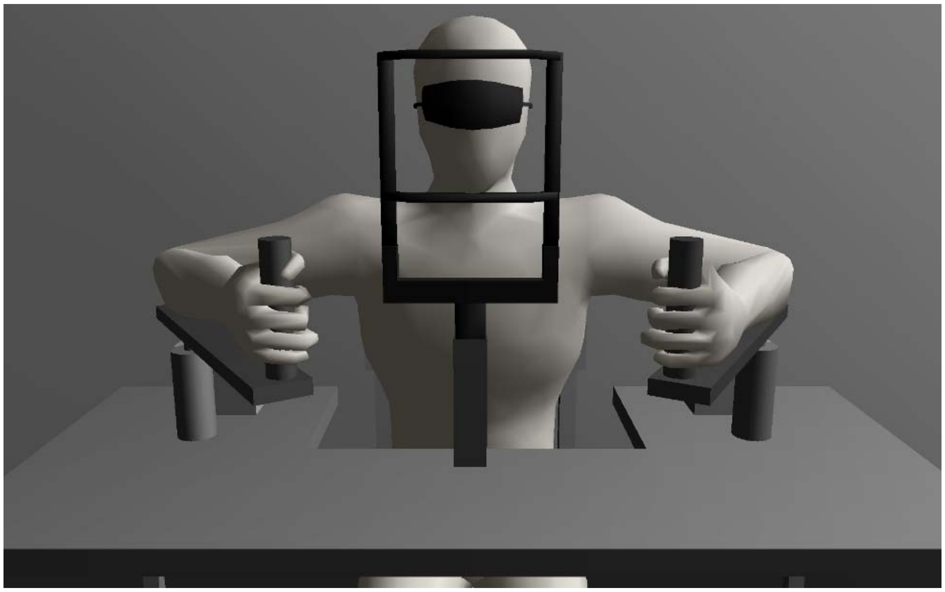


Fig 3.1 – Experimental setup for velocity matching task.

In the second phase of the procedure, target matching, subjects were given an auditory signal that coincided with disengagement of the motors. At this point, subjects were free to match the previously-experienced target velocity profile through active extension of either the same (ipsilateral remembered condition) or opposite (contralateral remembered condition) elbow. Based on this procedure, matches made in the ipsilateral remembered condition were thought to consist largely of the memory-based storage and retrieval of dynamic proprioceptive information. In contrast, contralateral remembered matching required both memory and interhemispheric transfer of dynamic proprioceptive feedback, given the anatomical arrangement of the ascending afferent pathways. Once matching was completed, the subject’s arm was returned to the start position at a constant speed of 15 deg/s in preparation for the next trial.

Data Collection and Analysis

Five trials of each task (ipsilateral remembered vs. contralateral remembered), arm (preferred vs. non-preferred) and peak target speed (30 deg/s vs. 60 deg/s) condition were completed in a random block design. In particular, each combination of arm and task was blocked and presented in a random order, while peak target speeds were fully randomized within each block. Elbow rotation was recorded from the voltage output of precision potentiometers mounted beneath the pivot point of each manipulandum. This analog signal was digitized at 100 Hz, filtered (4th order Butterworth, zero phase lag, 8 Hz) and multiplied by a calibration coefficient prior to data analysis to convert the signal from volts to degrees. The following dependent measures were obtained from the data to characterize the accuracy of subject matching performance:

1. *Average Acceleration Error* – The ability of subjects to replicate the acceleratory portion of the target velocity profile was assessed as the absolute difference between the target (i.e. 30 or 60 deg/s/s) and matching movement average accelerations from movement onset to peak velocity. Movement onset was determined as occurring when the corresponding velocity signal exceeded +/- 2 SD of a 200 ms baseline value. The maximum value in the velocity record was taken as representing peak velocity.
2. *Peak Velocity Error* – The overall ability to match the peak speed of the target movement was calculated as the absolute difference between the maximum target (i.e. 30 or 60 deg/s) and matching peak speeds.
3. *Average Deceleration Error* – The ability of subjects to replicate the deceleratory portion of the target velocity profile was determined as the absolute difference between the average deceleration of the target profile (i.e. -30 or -60 deg/s/s) and the average deceleration of the subject's matching movement from peak velocity to the end of the matching movement. Movement offset was determined using similar criteria to that previously specified for movement onset.
4. *Area under the Curve (i.e. Final Position) Error* – The overall ability of subjects to match the entire target movement was assessed by calculating the absolute difference between the area under the target (i.e. 30 or 60 deg) and the matching movement velocity profiles. This was accomplished by integrating the velocity signal from movement onset to offset. This measure is equivalent to calculating final position error.

Statistical Analyses

The mean group values for each measure of velocity matching error (i.e. average acceleration, peak velocity, average deceleration, area under the curve) were subjected to a repeated measures analysis of variance. Where significant main effects or interactions were discovered, the data were subsequently collapsed across non-significant factors and tested for simple effects post-hoc using Tukey's honestly significant differences test. Statistical significance was set at the level of $p<.05$ for all analyses.

Results

Representative ensemble averaged target and matching movements from one subject have been overplotted in Fig 3.2 for each experimental condition. With respect to the servo-motor generated target movements (dashed lines) a time symmetric triangular velocity profile was achieved with equal periods of constant acceleration and constant deceleration over the course of 2 s. In comparison, matches made by the subject (thick lines) were most often characterized by time asymmetric velocity profiles with a greater time spent decelerating, rather than accelerating, the arm. Further, a number of movement irregularities, or secondary peaks were evident during matching movements, particularly during the deceleratory phase.

Average Acceleration Error

Absolute differences in the ability of subjects to match the target average acceleration specified by the servomotor are shown in Fig 3.3. For matches made in the ipsilateral remembered condition, significantly smaller errors were seen when matching

Ipsilateral Remembered – 30 deg/s

Ipsilateral Remembered – 60 deg/s

Contralateral Remembered – 30 deg/s

Contralateral Remembered – 60 deg/s

Fig 3.2 – Ensemble averaged velocity profiles for a representative subject in each experimental condition. Traces represent the mean of 5 target (dashed line) and matching (solid line) movements.

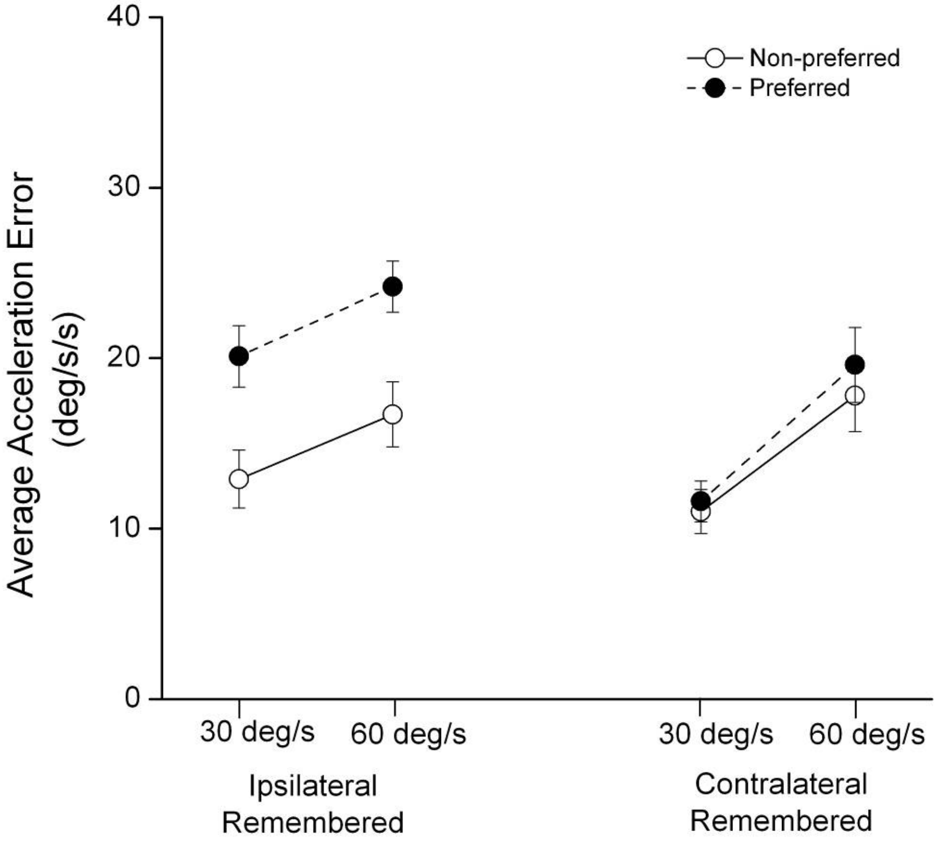


Fig 3.3 – Mean (+/- SEM) average acceleration errors.

was performed by the non-preferred, versus preferred, arm ($F_{1,12}$= 5.9; *p*<.05; Tukey's method). In contrast, no arm differences were seen for the contralateral remembered task where both memory and interhemispheric transfer of target information were required. This lack of asymmetry during contralateral remembered matching was largely due to a decrease in preferred arm error compared to the ipsilateral remembered task, whereas no task differences were seen for the non-preferred arm (Tukey's method). Regardless of arm or matching task, average acceleration errors were significantly greater in the faster (i.e. 60 deg/s) versus slower (30 deg/s) peak speed condition ($F_{1,12}$= 12.2; *p*<.01). This effect of target speed was significantly greater during contralateral remembered versus ipsilateral remembered matching ($F_{1,12}$= 5.9; *p*<.05).

The extent to which the group asymmetry in matching performance described above for the ipsilateral remembered task was also evident at the individual subject level is demonstrated in Fig 3.4. In this figure, average acceleration errors from the 5 preferred and non-preferred arm trials in each of the 30 (filled circles) and 60 (open circles) deg/s peak speed conditions were cross-plotted for each subject with respect to a line of unity. In this case, the large majority of arm comparisons (19 out of 22) fell below the line of unity. This result is consistent with greater matching performance (i.e. smaller errors) by the non-preferred arm.

Peak Velocity Error

The ability of subjects to match the peak speed of target movements based on proprioceptive feedback is shown in Fig 3.5 for each experimental condition tested. For this measure of matching ability, no arm asymmetries were seen for either the ipsilateral

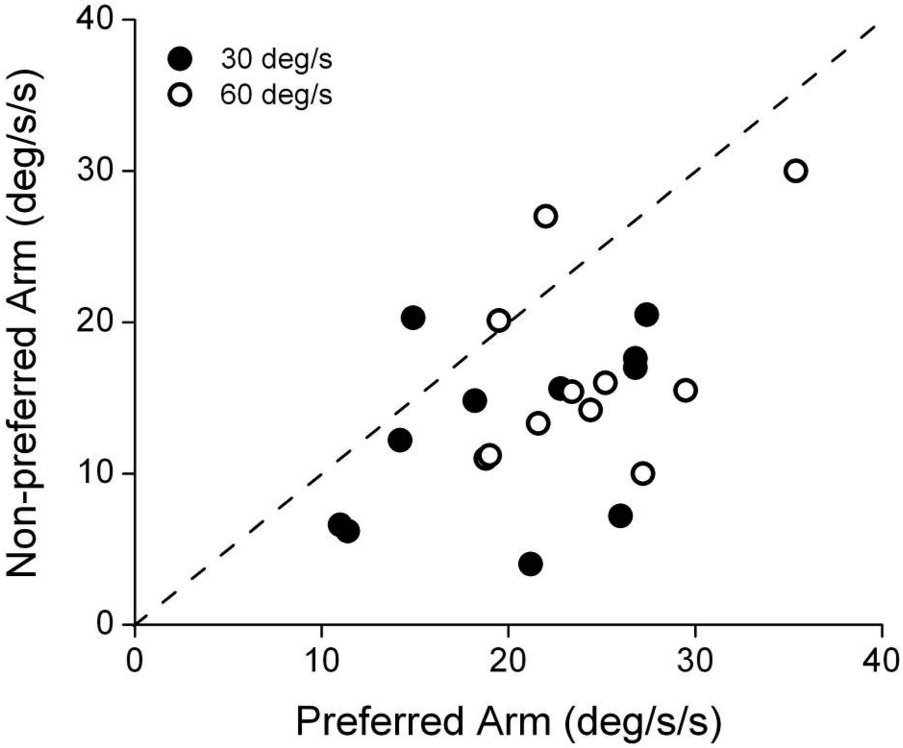


Fig 3.4 – Comparison of average acceleration matching error for the preferred versus non-preferred arm in the ipsilateral remembered task.

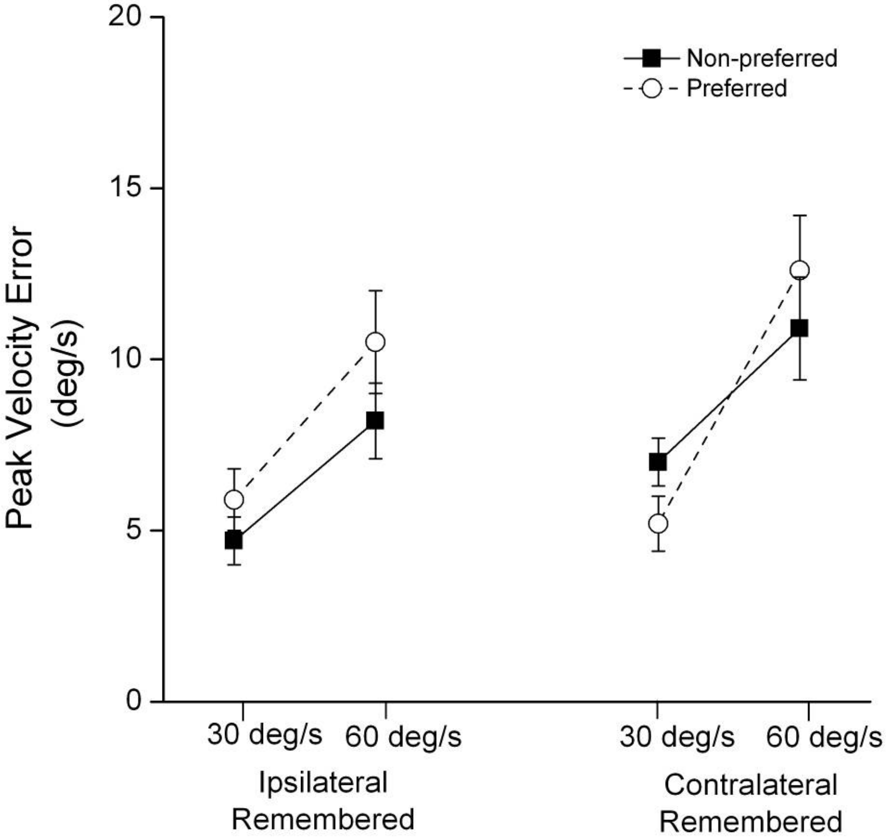


Fig 3.5 – Mean (+/- SEM) peak velocity errors.

remembered or contralateral matching task. There was, however, a significant effect of peak target speed on matching performance with an approximate doubling of errors seen in the faster, 60 deg/s target condition. Further, a non-significant trend toward greater peak speed accuracy in the ipsilateral remembered condition was seen compared to the contralateral remembered condition. In this case, a significant increase in error during contralateral remembered versus ipsilateral remembered matching was found for only the non-preferred arm across peak speed conditions (Tukey's method).

Average Deceleration Error

Mean absolute differences in the average deceleration of target and matching movements are provided in Fig 3.6. Similar to the findings for peak velocity matching, no arm asymmetries were found for this variable in either the ipsilateral remembered or contralateral remembered conditions. However, when collapsed across the preferred and non-preferred arms, average deceleration errors were found to be influenced by both the type of matching task ($F_{1,12}=6.2$; $p<.05$) and the target peak speed ($F_{1,12}=61.3$; $p<.001$). Specifically, average deceleration errors were smaller during ipsilateral remembered versus contralateral remembered matching, and when peak target speeds were slower (i.e. 30 deg/s) in magnitude (Tukey's method).

Area under the Curve Error

An estimate of overall matching performance was provided by calculating the absolute difference in area under the velocity curve for target and matching movements (Fig 3.7). This measure is equivalent to calculating an error in final position and, thus, it

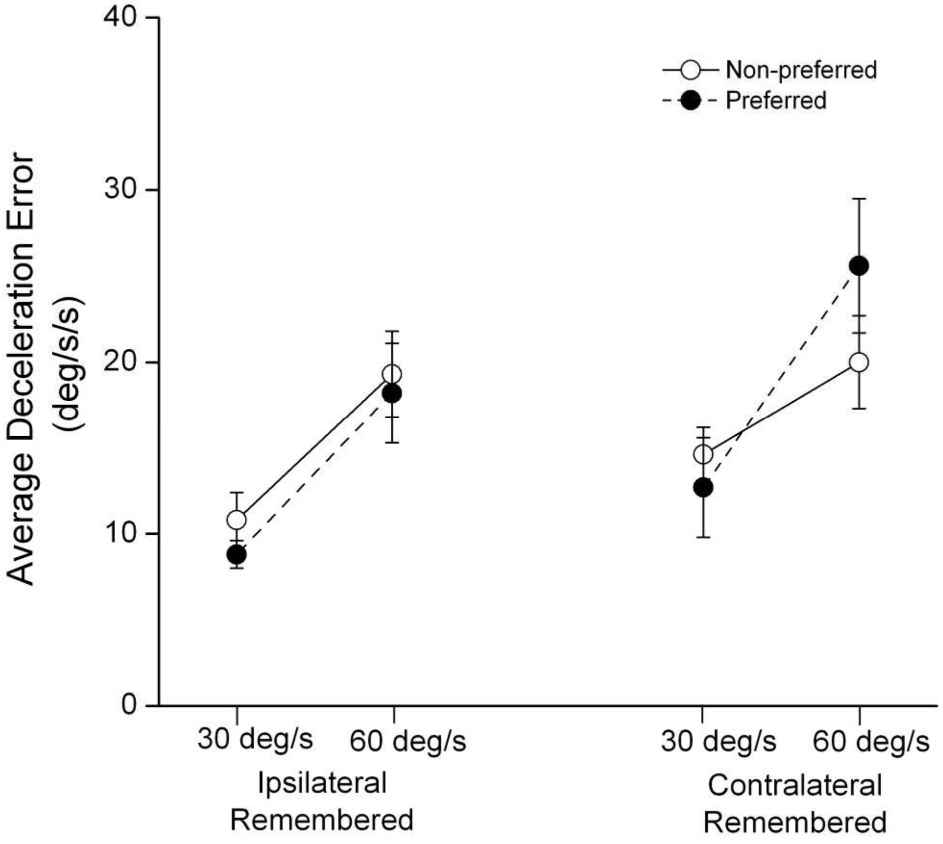


Fig 3.6 – Mean (+/- SEM) average deceleration errors.

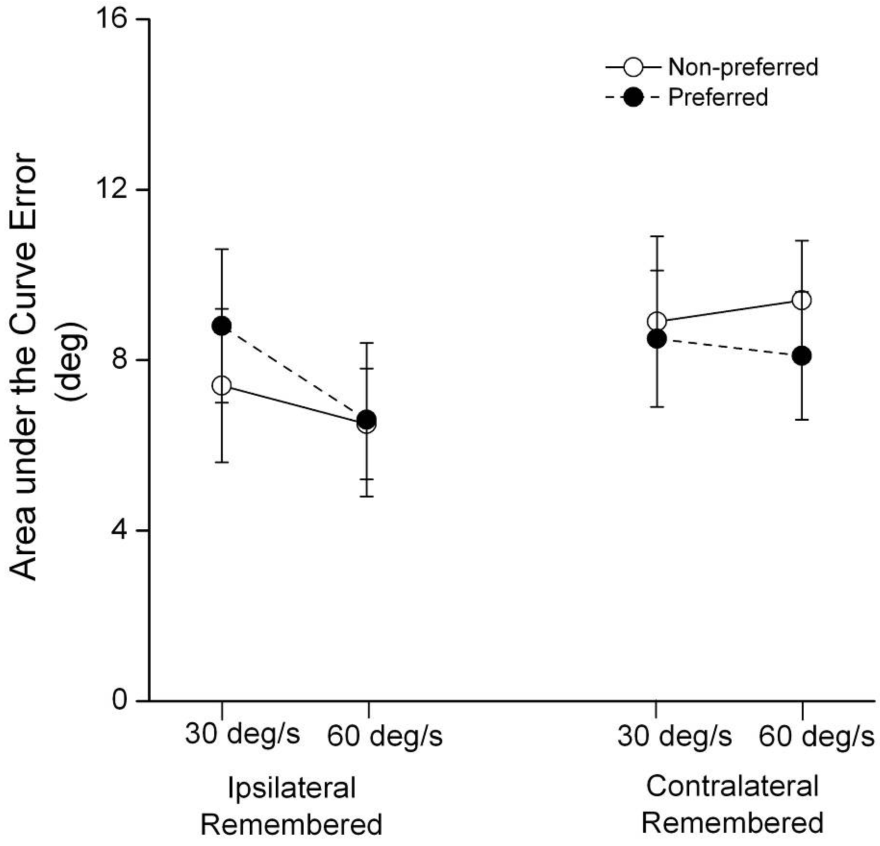


Fig 3.7 – Mean (+/- SEM) area under the curve errors.

is worthy of note that errors in this study were, on average, larger than those typically reported for studies of proprioceptively-guided position matching (i.e. greater than 5 deg). However, in contrast to position matching studies, no arm differences in the area under the curve were seen for either contralateral remembered or ipsilateral remembered matching. Further, area under the curve errors were not influenced by peak speed of the target arm movement or difficulty of the matching task.

Discussion

In contrast to those studies regarding the acuity of joint position sense, the ability to perceive and replicate joint movement speed/dynamics has been largely ignored in the motor behavioral literature. This is despite strong neurophsyiological evidence to suggest that both static and dynamic aspects of limb movement are encoded in the discharges of limb proprioceptors (Burke et al. 1976b; 1976a; Edin and Vallbo 1988; 1990), as well as reports indicating a vital role for dynamic proprioceptive feedback during the control of arm movement trajectory (Sainburg et al. 1993; 1995; Messier et al. 2003). The purpose of the present study, therefore, was to determine the extent to which healthy individuals were able to perceive and replicate dynamic aspects of a target arm movement based solely on proprioceptive information. This was accomplished by comparing the accuracy of dynamics matching for the preferred and non-preferred arms in tasks that varied in terms of proprioceptive processing demands. Overall, the accuracy of proprioceptively-guided matching was found to be largely symmetric with a non-preferred arm advantage seen during only the ipsilateral remembered task with respect to the average acceleration measure. Additionally, increases in target movement speed and, to a lesser extent, the proprioceptive processing demands associated with matching, negatively influenced subject performance.

The fact that arm asymmetries were generally not seen in the present study contrasts several previous studies of proprioceptively-guided position matching, where non-preferred arm accuracy advantages have been demonstrated (Roy and MacKenzie 1978; Colley 1984; Kurian et al. 1989; Riolo-Quinn 1991; Goble et al. 2006; Goble and Brown 2007). In particular, recent studies by this laboratory have shown that the ability to perform memory-based matching of elbow position with the contralateral arm (i.e. contralateral remembered condition) results in preferred arm errors that are twice as large as those seen for matching with the non-preferred arm (Goble et al. 2006; Goble and Brown 2007). While it was not clear from these initial studies whether this asymmetry reflected a non-preferred arm advantage in the utilization of proprioceptive feedback in general, the results of the present study suggest that arm differences in proprioceptive feedback processing are somewhat specific to arm position as compared to dynamic proprioceptive information.

Despite the overall lack of asymmetries seen in the present study, a non-preferred arm advantage was evident for the matching of average acceleration in the ipsilateral remembered task. While the acceleratory portion of movement has traditionally been ascribed to various planning and/or feedforward aspects of motor control, recent theories involving the use of forward models of arm position have suggested that feedback-based corrections are possible during the early stages of movement (see Desmurget and Grafton 2000 for review). Indeed, this notion is supported by behavioral studies where direction dependent changes in muscle electromyography have been shown almost immediately after the application of brief resistive or assistive forces during step-tracking movements (Brown and Cooke 1981b; 1986). Further, it has been argued on the basis of ipsilesional reaching studies in individuals with unilateral brain injury, that the two arms differ with respect to their relative reliance on feedforward versus feedback mechanisms during goal-directed movement (Haaland and Harrington 1989a; 1989b; 1994; Winstein and Pohl 1995). Specifically, it has been shown that damage to the left hemisphere was associated with deficits involving the early, open loop phase of movement, while right hemisphere injury affected the latter, more closed loop aspects of performance. To what extent the results of the present study, therefore, reflect a relative indifference of the left hemisphere (i.e. preferred right arm) towards the use of proprioceptive feedback during the acceleratory phase of movement remains unclear.

One possible reason for a non-preferred arm advantage in the perception and replication of the average acceleration measure, versus other measures of dynamic proprioceptive matching performance, lies in the function of the non-preferred arm during many bilateral tasks. In this case, the non-preferred arm is most often used to hold an object in a particular static position while the preferred arm is used to manipulate it (e.g. screwing the lid onto a jar). While previous studies from this laboratory have shown that the non-preferred arm is enhanced for achieving a proprioceptively-guided target position, the maintenance of this position will rely on the ability to detect movement of the arm from this location. Indeed, in order for the quickest response to a perturbation of position to occur a non-preferred arm advantage for the monitoring of the early (i.e. acceleratory) phase of movement would be of certain value.

Perhaps surprisingly, the arm differences seen for average acceleration matching in the ipsilateral remembered task were not evident during the more difficult contralateral remembered task where interhemispheric transfer of target movement information was required. In addition, preferred arm errors were actually improved during contralateral remembered versus ipsilateral remembered matching to a performance level that was equal to the non-preferred arm in both task conditions. While no immediate explanation of these results can be provided, it is worthy of note that during ipsilateral remembered matching with the preferred arm, where the largest errors were seen, involvement of the right hemisphere was seemingly minimized, since both the initial proprioceptive target information and the control centers for movement were located in the left hemisphere. In contrast, during all other matching tasks, right hemisphere involvement was inherently necessary in order to receive initial target feedback and/or execute the target movement. In this case, it may be possible that the errors in these right-hemisphere dependent tasks were reduced due to a right hemispheric specialization for the processing of movement related feedback. Support for this hypothesis comes from studies of individuals with unilateral brain injury, which have shown that patients with right versus left frontal and/or medial temporal damage have a greater difficulty reproducing the extent of passively-determined kinesthetic targets (Leonard and Milner 1991a; Leonard and Milner 1991b; Rains and Milner 1994). Further, using neuroimaging techniques, Butler et al (2004) has recently shown preferential activation of areas in the right temporo-parietal cortex during proprioceptively-guided reaching, and Naito et al. (2005) found increased activation in, especially, the right primary somatosensory cortex related to the perception of movement illusions at the wrist. Taken together, therefore, these results provide strong support of greater right hemisphere involvement for the processing of movement-related proprioceptive feedback.

One of the most consistent findings reported in previous studies of arm velocity perception has been a decrease in acuity during faster target speed conditions (Lonn et al. 2001; Kerr and Worringham 2002; Djupsjobacka and Domkin 2005). In these studies, a threshold detection method has commonly been utilized where subjects were asked to indicate whether the second of two passively-experienced arm movements was faster or slower than the first. Although the present study involved a slightly different paradigm, where active replication of a passive target was utilized, similar increases in matching error were seen for, especially, the peak speed measure. For example, peak velocity errors were approximately 5 and 9 deg/s in the 30 and 60 deg/s peak speed conditions of the present study. This is comparable to the 7 and 10 deg/s errors reported by Kerr and Worringham (2002) for the same speed conditions.

A possible explanation for the decreased ability of subjects to perceive higher velocity movements lies in the results of studies assessing attenuation of somatosensory feedback during movement. While it has been long recognized that subjects are less able to perceive cutaneous stimuli that are presented to their moving versus stationary limb (e.g. Giblin 1964; Lee and White 1974; Angel and Malenka 1982), it was only in the last decade that Collins et al (1998) demonstrated that a similar phenomenon exists for the perception of muscle afferent feedback. In this study, the extensor carpi ulnaris muscle of the preferred arm was electrically stimulated at various intensities during different phases of wrist and arm movement. It was found that the ability to sense the evoked muscle twitches was significantly reduced during movement, and that this attenuation increased with movement speed. Based on these findings, it was suggested that suppression of the afferent signal was necessary with increased movement speed in order to reduce the vast amount of afferent input during fast movements.

For most measures in this study, there was a trend towards greater errors in the contralateral remembered versus ipsilateral remembered matching task. This result likely reflects the increased difficulty associated with the contralateral remembered condition, as has been previously demonstrated on numerous occasions by this laboratory (Goble et al. 2005; Adamo et al. 2007; Goble and Brown 2007). In these studies, three position matching tasks were compared that varied with respect to the need for memory and/or interhemispheric transfer of proprioceptive information. In the ipsilateral remembered and contralateral concurrent tasks, where only memory or interhemispheric transfer of elbow position feedback was required respectively, the magnitude of matching error was similar regardless of the arm performing the task. In contrast, during the contralateral remembered condition, where both memory and interhemispheric transfer were necessary for accurate performance, errors were increased during, especially, matches made by the preferred arm. This result further underscores the need to maximize processing demands when assessing any aspect of proprioceptive ability.

The dynamic dominance hypothesis, first proposed by Sainburg (2002), has recently gained acceptance as a function-based account of arm performance asymmetries. In this theory, it is suggested that the preferred arm/hemisphere system of right-handed individuals is specialized for the control of arm dynamics such as movement trajectory, whereas the non-preferred arm/hemisphere is specialized for maintaining static arm positions/postures. Based on this hypothesis, it might have been predicted that preferred arm matching in this study would show enhanced performance, due to the emphasis that was placed on the matching of movement dynamics. However, in studies purporting the dynamic dominance theory, the two variables most commonly associated with a preferred arm trajectory advantage have been the ability to specify an initial movement direction (Sainburg and Wang 2002; Wang and Sainburg 2003; 2004a) and the control of intersegmental dynamics (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002; Sainburg 2002). In this case, use of a single joint paradigm in the present study largely precludes any comparison with the dynamic dominance hypothesis, as the direction of matching movements was limited to one dimension, and compensation for the effects of interactional joint torques was unnecessary.

In conclusion, the results of the present study extend the current knowledge regarding use of speed/dynamics information during the performance of goal-directed movements in the absence of vision. The fact that arm asymmetries were not seen for most measures of matching performance, regardless of matching task, demonstrates that non-preferred arm advantages for the utilization of proprioceptive feedback are somewhat specific to static versus dynamic information. This phenomenon may reflect preferential use of the non-preferred arm for the maintenance of static postures. Indeed, this is a role often incurred by the non-preferred arm during bimanual tasks in order to stabilize an object while preferred arm manipulates it.

Chapter 4

Upper Limb Asymmetries in the Proprioceptively-guided Matching of Dynamic Elbow Position

Introduction

The tendency for humans to prefer use of one arm versus the other when performing various activities of daily living has been cited as one of the most obvious examples of lateralized brain function (Hellige 1983). This phenomenon, commonly known as "handedness", typically favours use of the right arm (Annett 1985; Gilbert and Wysocki 1992) and, thus, has classically been explained in terms of a contralateral left hemisphere specialization for the control of motor output. Indeed, this line of thinking was first justified in the pioneering studies of Liepmann (1908; 1920) who demonstrated that individuals with unilateral brain injury to the left hemisphere exhibited greater deficits in motor performance compared to those with right hemisphere damage. Further, neuroanatomical studies conducted over the course of the past two decades have shown the existence of asymmetries favouring the left hemisphere in terms of both total surface area, and the amount of neurophil, devoted to the primary motor cortex (White et al. 1994; Amunts et al. 1996; 2000).

In contrast to this preferred arm/hemisphere "motor dominance", however, recent studies by this laboratory have suggested that a non-preferred arm/hemisphere advantage exists in the utilization of movement-related proprioceptive feedback. Specifically, it has been shown that the ability to match elbow angles in the absence of vision is enhanced for the non-preferred arm, especially when the processing demands associated with matching are increased by requiring both memory and interhemispheric transfer of proprioceptive target information (Goble et al. 2005; 2006; Goble and Brown 2007). These results, expand upon those of previous position matching studies, where use of less demanding matching tasks resulted in either a non-preferred arm accuracy advantage (Roy and MacKenzie 1978; Colley 1984; Kurian et al. 1989; Riolo-Quinn 1991) or no arm differences at all (Carson et al. 1990; Chapman et al. 2001).

Although the above findings, en masse, argue in favour of the asymmetric use position-related proprioceptive information, they offer little insight into the other, more dynamic aspects of proprioception. From a neurophysiological standpoint, it is generally well accepted that both limb position and movement velocity are represented in the nervous system, as has been shown in microneurography studies where direct neural recordings were made from the sensory afferents of cats (Jansen and Matthews 1962b; 1962a; Matthews 1964; Merton 1964) and humans (Hagbarth and Vallbo 1968; Vallbo 1970; 1974; Roll and Vedel 1982). In these studies, the neural firing patterns identified consisted of both static and dynamic components corresponding to changes in muscle length (i.e. limb position) and the rate of change of muscle length (i.e. movement velocity) respectively (see McCloskey 1978 for review). In this case, however, it was the primary muscle spindle afferents (1a) that showed the greatest sensitivity to the rate of change of muscle length, while both primary and secondary (II) spindle afferents showed altered neural firing in response to changes in muscle length (Burke et al. 1976b; 1976a; Edin and Vallbo 1988; 1990).

Additional evidence that limb position and velocity information are separately perceived by healthy individuals was provided in the classic studies of Goodwin et al (1972a; 1972b). In these studies, high frequency, low amplitude vibration was applied to the biceps or triceps tendons of the preferred arm, as a means of increasing the firing rate of, primarily, group 1a muscle spindles (Bianconi and van der Meulen 1963; Burke et al. 1976b). Over the course of stimulation, blindfolded subjects were asked to use the non-preferred arm to indicate either the perceived position, or speed and direction, of the vibrated arm. Based on this paradigm, illusory effects in both the perception of elbow joint position and velocity were shown and these illusions were consistent with a perceived lengthening of the vibrated muscle.

During the performance of most movement tasks, however, static and dynamic sources of proprioceptive feedback are rarely utilized in isolation and, rather, individuals are often required to combine information regarding both arm position and movement speed in order to perform a sequence of actions. For example, during the throwing of an object, the position of multiple rotating body segments (i.e. upper arm, forearm, hand) must be monitored in order to determine when the arm is in an appropriate position to release the object. This ability to know body segment position during movement has been termed "dynamic position sense" by Cordo et al. (1990; 1994; 1995a; 1995b), and has been extensively studied using a paradigm where subjects indicate when their unseen elbow reaches a predetermined joint angle during movement. Based on this paradigm, it has been shown that, with limited feedback regarding performance, subjects can estimate dynamic arm position within several degrees of elbow rotation. To date, however, there has been no attempt to compare asymmetries in dynamic position matching between the preferred versus non-preferred arms.

When assessing dynamic position sense in a manner similar to that described by Cordo et al (1990; 1994; 1995a; 1995b) it is important to address the possible influence of target movement duration on subject performance. Indeed, it has been noted for some time in the psychology literature that there is a strong interdependence of time and space in the estimation of movement extent (Helsen 1930; Helsen and King 1931). Specifically, when subjects experience two successive arm movements of an equal extent but, which vary in speed, the faster movement will be perceived as traveling further than the slower. In a recent study by Chieffi et al (2004), for example, subjects made reaching movements with the preferred arm to a near or far target position at a fast or slow speed. Then, based on short-term memory, reproduction of the target occurred at a speed that was equal to (i.e. congruent) or different (i.e incongruent) to that of the original target movement. The results of this study showed that subjects were, indeed, biased towards the duration of the target movement in the incongruent conditions. In this case, when matching occurred at a speed faster than that used to achieve the target originally, subjects were biased towards overshooting. In contrast, undershooting was seen when matches were performed at a speed slower than the original.

The primary aim of the present study was to determine the extent to which arm differences may exist in the proprioceptively-guided matching of dynamic position. To accomplish this, blindfolded subjects were asked to indicate the location of previously-experienced target elbow positions during constant speed movement of either the same or opposite arm. In addition, the influence of differences in target and matching speeds was addressed in a set of trials where the target determination speed was systematically altered with respect to target matching, but where target position remained the same. Based on the previous position matching findings by this laboratory (Goble et al. 2006; Goble and Brown 2007), it was expected that subjects would show enhanced dynamic position accuracy for the non-preferred versus preferred arm, especially during tasks requiring greater processing of proprioceptive information.

Methods

Subjects

Thirteen healthy, young adults (mean age 23.0 ± 3.0 years; 7 males, 6 females) participated in this study. The number of subjects was determined on the basis on a power analysis conducted using previous position matching data (Goble et al. 2006, Goble and Brown 2007). Subjects were free of upper limb neuromuscular impairment and showed strong right arm preferences as evidenced by scores of +100 on a modified version of the Edinburgh Handedness Inventory (Oldfield 1971, see appendix). In addition, subjects demonstrated right arm performance advantages on several common tests of motor output ability. These measures are summarized in Table 4.1 and include maximum grip strength, the number of pegs placed in a Purdue pegboard (i.e. manual dexterity) in 60 s and the ability to maintain a 1 mm probe within a 2 mm hole without touching the sides (i.e. hand steadiness) for 10 s. All procedures were approved by the research ethics review board of the University of Michigan prior to testing.

Task	Preferred Arm	Non-preferred Arm
Max Grip strength (N)	368.5 ± 24.5	343.0 ± 21.6
Manual Dexterity (# of Pegs in 60 s)	30.3 ± 1.1	27.4 ± 1.1
Hand Steadiness (# of side touches)	10.4 ± 5.1	19.0 ± 3.4

Table 4.1 – Average (± SEM) arm performance on tests of motor ability.

Experimental Setup

The setup for this experiment, depicted in Fig 4.1, consisted of servo-motor driven manipulandum devices designed for elbow displacement in the horizontal plane. Blindfolded subjects were seated at the device with forearms resting comfortably on separate length and height-adjustable aluminum levers. Standardized start positions for the shoulder (80 deg abduction, 15 deg flexion), elbow (75 deg extension) and wrist (neutral) were maintained across subjects. The effects of altered head position were minimized by means of a steel chin rest and support frame surrounding the lateral aspects of the head (Knox and Hodges 2005; Knox et al. 2006). Additionally, subjects were outfitted with a uniaxial electrogoniometer along the long axis of each hand for the purpose of recording indicator movements made via extension of the index and middle fingers. The electrogoniometers were attached below the wrist joint and on the distal segments of the index and middle fingers.

Experimental Procedures

The ability to perceive target arm positions during movement (i.e. dynamic position sense) was assessed following a two-phase procedure. In the first phase, target

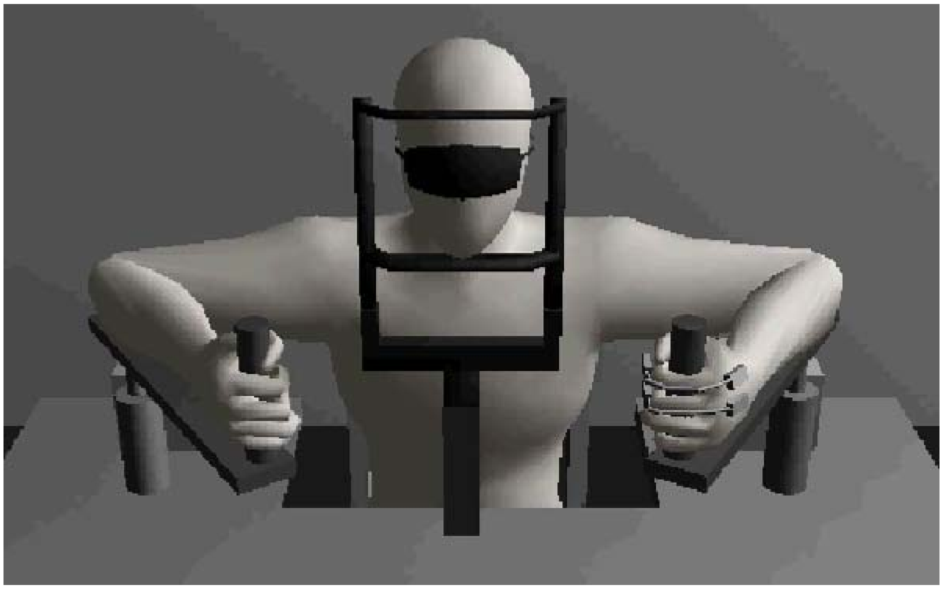


Fig 4.1 – Experimental setup for dynamic position matching. Note that in this figure a goniometer has been placed along the hand and fingers of only the non-preferred arm. In the actual experiment, goniometer placement was bilateral.

determination, the preferred or non-preferred elbow was passively extended at 10 deg/s to a target position of 10, 20 or 30 deg. The arm was then held at this location for 3 s while the subject memorized the target position, and returned passively to the start position at the same speed. In the second phase, target matching, the same (ipsilateral remembered task) or opposite (contralateral remembered task) arm as that used to establish the target was slowly extended at 5 deg/s through a range of motion that included, but went beyond, the given target position. During this phase, subjects were instructed to indicate the point in time when the moving arm matched the target elbow position by quickly extending the index and middle fingers of the moving arm. Given this paradigm, ipsilateral remembered matching was thought to represent a less difficult task as arm position and movement speed information were both provided to the same hemisphere. In contrast, contralateral remembered matching required interhemispheric transfer in order to combine static and dynamic proprioceptive feedback that was received by different hemispheres during the target and matching movement phases.

In the above experiment, different speeds were chosen for the target determination and target matching phases in an attempt to discourage subjects from using temporal cues regarding the duration of target arm movement. To further address the potential influence of target and matching speed differences on dynamic position matching, an additional set of ipsilateral remembered trials were performed. In this case, subjects were always given the same, 20 deg target position during the target determination phase. However, the target determination speed was faster (10 deg/s), slower (2.5 deg/s) or the same (5 deg/s) as the speed of elbow extension during target matching. Based on this paradigm, any bias towards matching target movement speed/duration would result in undershooting when target determination occurred at a faster speed than target matching, overshooting when target determination was slower than target matching, and no directional bias when the target and matching speeds were congruent.

Data Collection and Analysis

Five trials of each combination of experimental conditions were completed in a random block order. Blocks consisted of all trials for a particular combination of arm (preferred vs. non-preferred) and/or task (ipsilateral remembered vs. contralateral remembered) condition with either the amplitude or target determination speed fully randomized within that block. Using a laptop computer, the voltage output from precision potentiometers located below the pivot point of the elbow joint was recorded. This analog signal was subsequently digitized at 100 Hz, filtered (4th order Butterworth, zero phase lag, 8 Hz) and multiplied and converted to a measure of angular displacement (deg) by a calibration coefficient prior to data analysis. The following dependent measures were extracted from the data:

1. *Absolute Error* – The overall ability of subjects to determine dynamic elbow position was assessed as the absolute difference between the target arm position and the position of the arm when the indicator movement first occurred. In this case, it was necessary to calculate both the offset of the target movement and onset of the indicator movement using a threshold detection algorithm of +/- 2 SD from baseline (zero) velocity signal.

2. *Constant Error* – The signed difference between the target arm position and the elbow angle at the time of target indication was used as an estimate of directional bias (i.e. target undershooting or overshooting). Target and matching positions were determined as described for absolute error.
3. *Variable Error* – The standard deviation of constant errors across a series of trials was used as a measure of matching consistency.

Statistical Analyses

Mean measures of movement accuracy (absolute error, constant error and variable error) were subjected to repeated measures analyses of variance. Where significant main effects and/or interactions were revealed the data was subsequently collapsed across non-significant factors and tested for simple effects using a Tukey's honestly significant differences test. Statistical significance was set at $p<.05$.

Results

Dynamic position matching data from the 30 deg target condition is provided in Fig 4.2 for a representative subject. From this figure, it is apparent that the servo motor system was successful in displacing the preferred (solid line) and non-preferred (dashed line) arms to the desired target locations at the predetermined speeds. This was true for both the target determination (i.e. first half of trial) and matching (i.e. second half of trial) phases of the task. With respect to subject matching performance, dynamic position was generally underestimated, especially with the preferred arm, as evidenced by crosshairs showing the actual (match) and ideal (target) times of target indication.

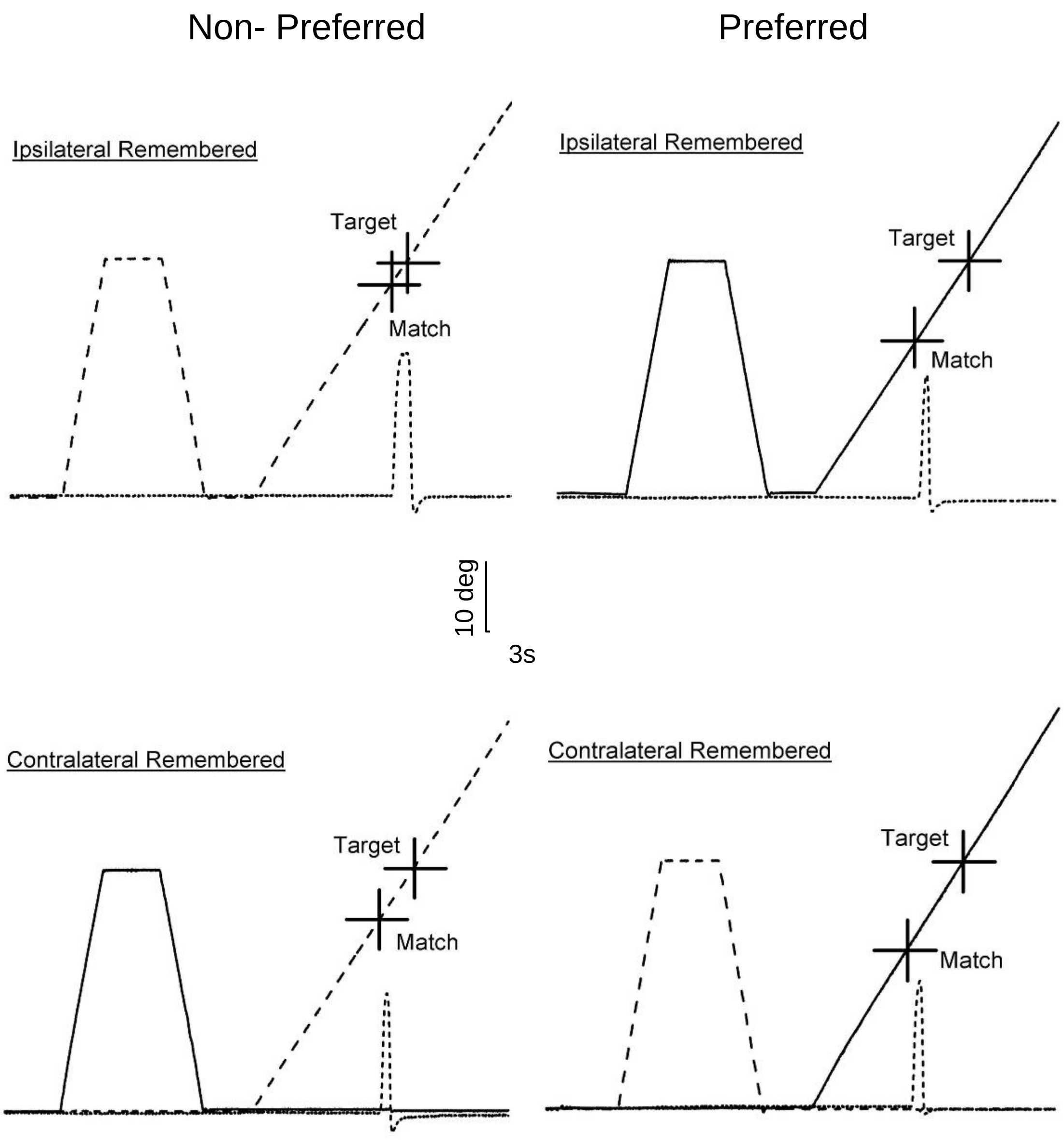


Fig 4.2 – Representative data for 30 deg dynamic position matching in the ipsilateral remembered and contralateral remembered conditions. See text for figure description.

Task and Target Amplitude Effects on Dynamic Position Matching Asymmetries

Asymmetries in the overall accuracy of dynamic position sense, as indicated by absolute error, are displayed in Fig 4.3 for each task and target amplitude condition. With respect to arm asymmetries, similar results were found as those seen in previous studies of proprioceptively-guided position matching. In this case, errors were significantly smaller across matching task and target amplitude conditions when matching involved movement of the non-preferred versus preferred arm ($F_{1,12}=10.3$; $p<.01$). This arm difference, however, was significantly influenced by target amplitude ($F_{1,12}=4.9$; $p<.05$), as preferred arm matching errors significantly decreased across all (i.e. 10, 20 and 30 deg) amplitude conditions, while the non-preferred arm showed a significant increase in error between only the 10 and 20 deg targets (Tukey's method). Due to this pattern of errors, the non-preferred arm advantage for dynamic position accuracy was, therefore, most noticable in the 30 deg condition. For both arms, the contralateral remembered task was associated with greater errors than the ipsilateral remembered task, particularly for 30 deg target matching ($F_{1,12}=6.2$; $p<.05$; Tukey's method).

Constant errors in dynamic position matching are provided in Fig 4.4, as an indication of directional biases in matching performance. As evidenced by the negative constant error values in all task conditions, a strong bias in matching error towards undershooting the target position was seen with less than ten percent of all trials in the direction of a target overshoot. Given the relationship between constant and absolute error, the pattern of constant errors seen were, thus, similar to those reported for absolute errors. Specifically, while subjects were more accurate (i.e. less likely to undershoot the target) across task and amplitude conditions when the non-preferred arm was used for the

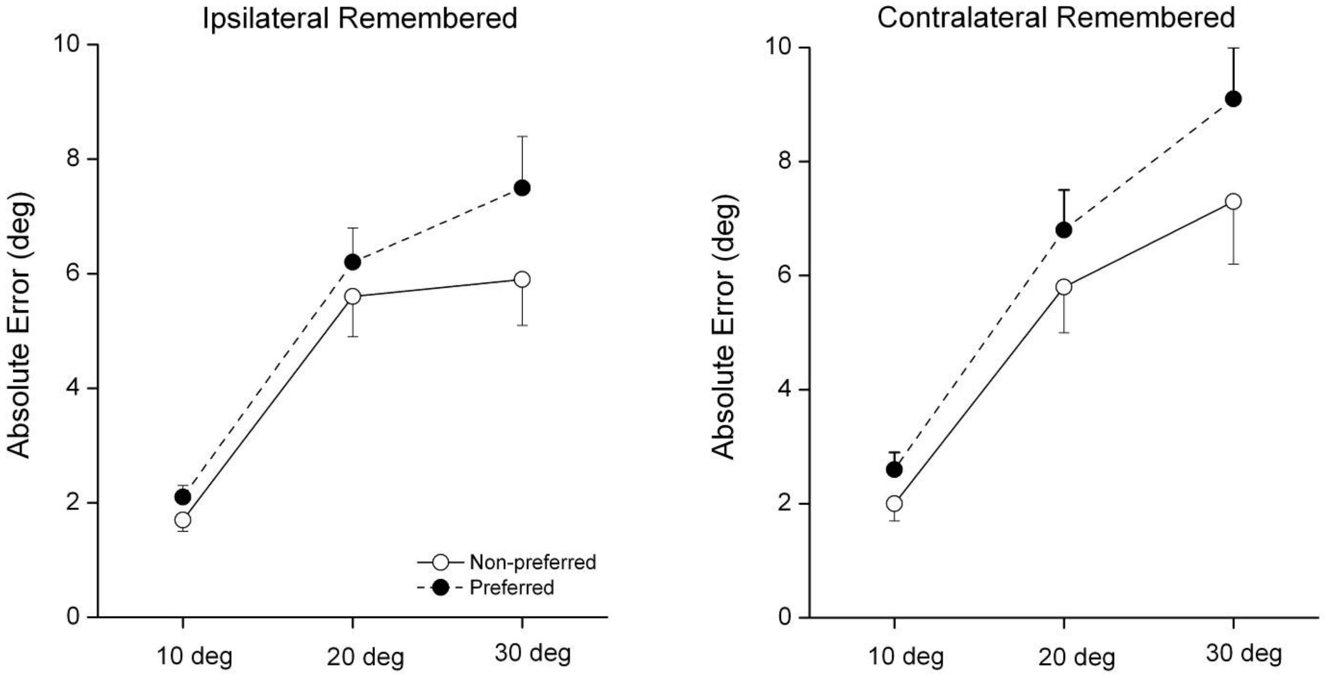


Fig 4.3 – Mean (+/- SEM) absolute errors in dynamic position matching for 10, 20 and 30 deg targets in the ipsilateral remembered (left panel) and contralateral remembered (right panel) tasks.

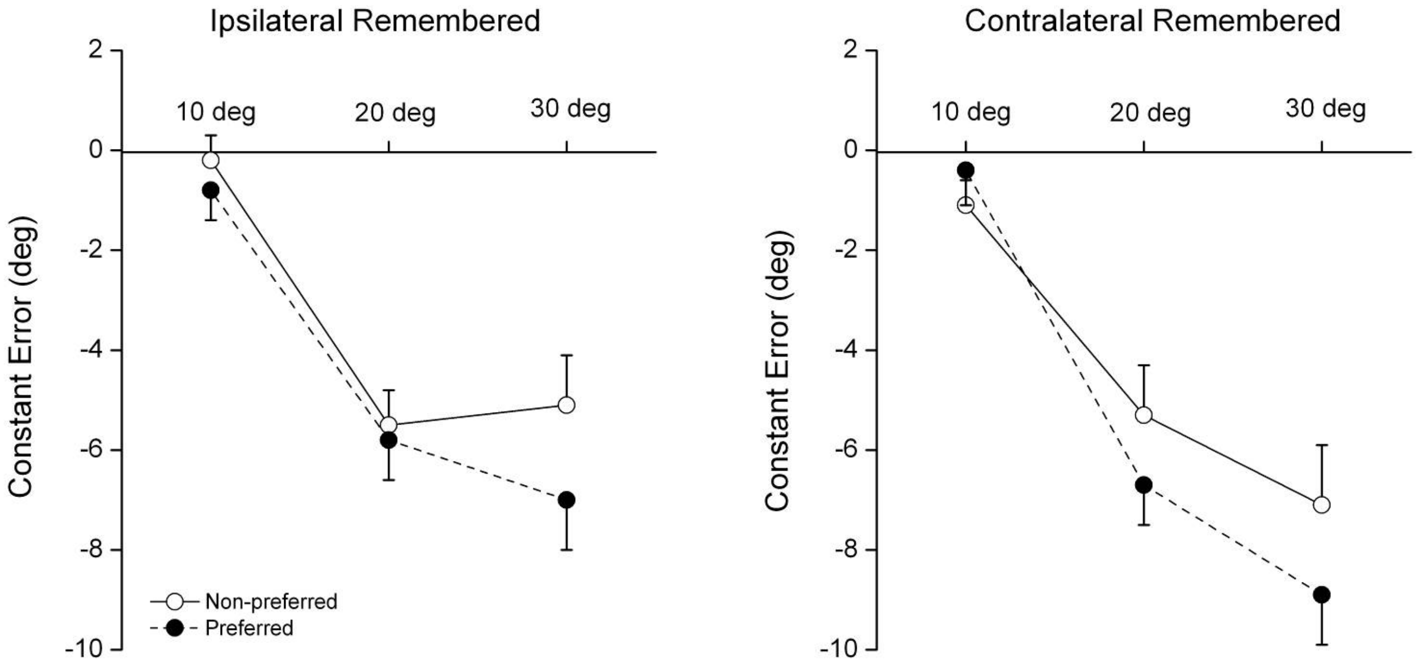


Fig 4.4 – Mean (+/- SEM) constant errors in dynamic position matching for 10, 20 and 30 deg targets in the ipsilateral remembered (left panel) and contralateral remembered (right panel) tasks.

matching phase, this arm asymmetry was mediated by target amplitude ($F_{1,12}$=15.5; p<.01). In this case, a non-preferred arm advantage was only seen in the 30 deg target condition, due largely to an increase in preferred, but not non-preferred, arm error (Tukey's method). Further, greater target undershooting was seen in the 30 deg condition of the more difficult contralateral remembered versus ipsilateral remembered task ($F_{1,12}$=5.9; p<.05; Tukey's method).

In contrast to absolute and constant error results, the consistency of dynamic position matching performance (i.e. variable error) was not significantly different for the preferred and non-preferred arms across task and amplitude conditions ($F_{1,12}$=1.2; p>.05). These results are shown in Fig 4.5 where both arms show a similar increase in variable error with increased target amplitude ($F_{1,12}$=36.6; p<.001). In addition, there was no significant difference in the consistency of ipsilateral remembered versus contralateral remembered matching performance ($F_{1,12}$=.1; p>.05).

The Effect of Target Determination Speed on Dynamic Position Matching Asymmetry

Asymmetries in dynamic position matching are shown in Fig 4.6 with respect to faster (10 deg/s), slower (2.5 deg/s) and congruent (5 deg/s) target determination speed conditions. As shown in Fig 4.6A, a non-preferred arm matching advantage in terms of absolute error was seen regardless of target determination speed ($F_{1,12}$=14.8; p<.01). This asymmetry, although greater on average in the 10 deg/s condition, was not influenced by the speed of target determination. In addition, both arms showed a significant increase of absolute error in the 10 deg/s condition where the target determination speed was faster than the target matching speed ($F_{1,12}$=5.2; p<.05; Tukeys method).

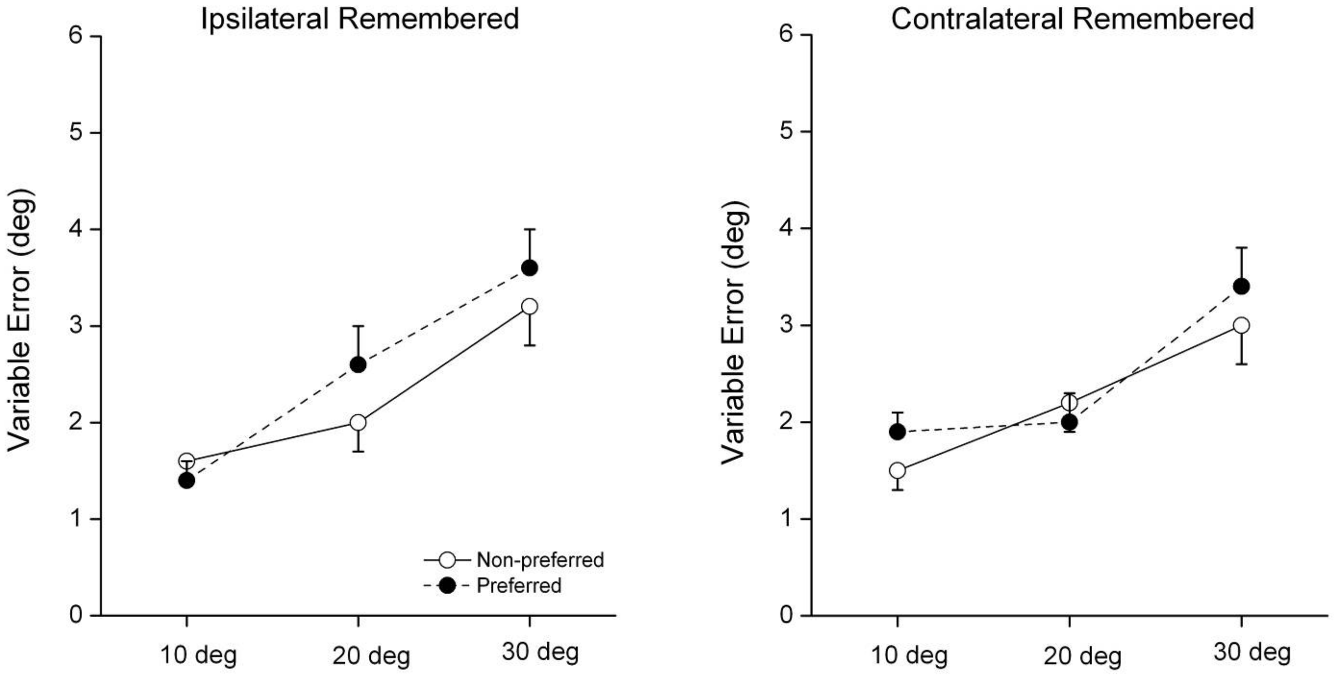


Fig 4.4 – Mean (+/- SEM) variable errors in dynamic position matching for 10, 20 and 30 deg targets in the ipsilateral remembered (left panel) and contralateral remembered (right panel) tasks.

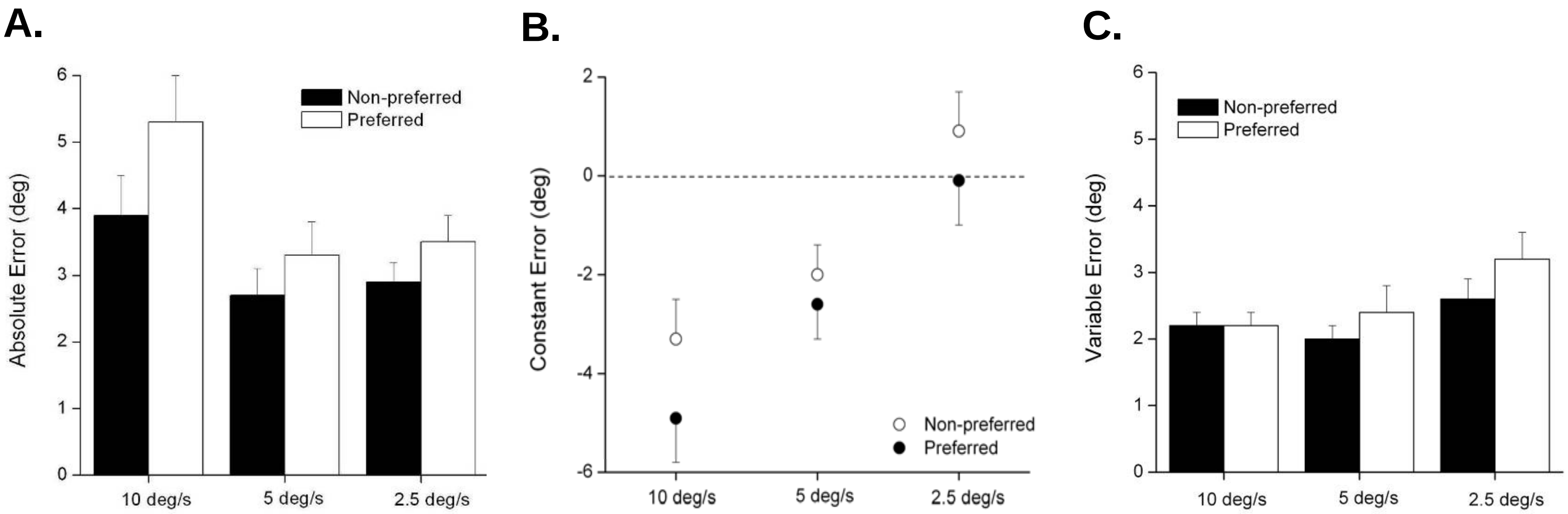


Fig 4.6 – The effect of target determination speed on dynamic position matching error. Mean (+/- SEM) absolute (A), constant (B) and variable (C) errors are presented for target determination speeds that were faster (10 deg/s), slower (2.5 deg/s) or the same (5 deg/s) as that of the target matching phase.

As evidenced by constant errors (Fig 4.6B), target determination speed had a strong influence on the direction of both preferred and non-preferred arms matching error ($F_{1,12}$=46.9; p<.001). Compared to the 5 deg/s condition, where both target and matching speeds were congruent, subjects made greater undershooting errors in the faster, 10 deg/s condition and were biased more towards overshooting in the slower 2.5 deg/s condition. While this effect was similar for both arms in the 5 and 2.5 deg/s target determination speed conditions, the non-preferred arm was less biased towards undershooting in the 10 deg/s condition where the target determination speed was faster compared to the speed of the matching movement (Tukey's method).

The influence of target and matching speed differences on variable errors in dynamic position is shown in 4.6C for each of the arm and target determination speed conditions. While there was only a tendency for greater non-preferred arm matching consistency ($F_{1,12}$=4.5; p<.10), especially in the slower, 2.5 deg/s condition (Tukey's method), there was a significant influence of speed on the magnitude of variable errors in both arms. In particular, when subjects were asked to indicate dynamic arm position based on a static target that was determined at the slowest (2.5 deg/s) speed, matching errors were significantly greater compared to the 10 deg/s and 5 deg/s conditions ($F_{1,12}$=9.1; p<.01, Tukey's method).

Discussion

The ability to combine static and dynamic proprioceptive information into an estimate of dynamic position is critical for the timing and control of many goal-directed activities of daily living. Given the previous results from this laboratory demonstrating a non-preferred arm advantage for the proprioceptively-guided matching of elbow position (Goble et al. 2006; Goble and Brown 2007), the goal of the present study was, thus, to determine arm asymmetries in dynamic position matching. To accomplish this, subjects were asked to indicate a memory-based target elbow position during movement of either the same or opposite arm. Overall, it was found that errors were typically smaller when the matching phase involved the non-preferred versus preferred arm. This effect, however, was influenced by both target amplitude and the speed of target determination. Specifically, a greater non-preferred arm advantage was seen for the matching of larger target amplitudes and when the speed of target determination was faster than that of target matching.

One appealing explanation for the asymmetries found in this study is that of a right hemisphere specialization for the processing proprioceptive feedback. Indeed, several lines of evidence support of this hypothesis including the study of individuals with unilateral brain injuries. In a series of experiments by Leonard and Milner (1991a; 1991b; 1995), for example, individuals with various cerebral cortex excisions for the relief of focal cerebral seizures, were tested on their ability to match target movement amplitudes in the absence of vision. In this case, the results showed that subjects with large excisions to the right, but not left, frontal hemisphere including motor, premotor and supplementary motor areas were less adept at matching large amplitude targets. It was, therefore, concluded that the right frontal hemisphere played an important role in the monitoring and recall of movement-related proprioceptive feedback. In accord with these findings, neuroimaging techniques have allowed for the in-vivo assessment of right versus left hemisphere differences in the proprioceptive feedback processing ability of healthy individuals. Indeed, Butler et al (2004) found increased temporal-parietal activation in the right hemisphere using positron emission tomography during the proprioceptively-guided matching of target positions in the absence of vision. Further, Naito et al (2005) showed evidence of right hemisphere dominance for the perception of vibration-induced proprioceptive illusions based on functional magnetic resonance imaging and cytoarchitectural mapping techniques. Taken together, these studies strongly suggest the existence of an enhanced role for the right hemisphere in the processing of proprioceptive feedback.

In the present study, target amplitude had a strong influence on the magnitude of dynamic position errors with greater errors seen for the matching of larger amplitude targets. In this case, it is likely that subjects were, in some way, incorporating information regarding the speed/duration of the target determination phase into their representation of the final arm position. For the tasks where target amplitude effects were assessed, the speed of target determination was twice that of target matching and, thus, any attempt to match movement duration would explain the progressively greater undershooting that was seen with increased in target amplitude. In addition, the influence of target determination speed was directly tested in the present study by assessing dynamic position matching accuracy of a single target for target determination speeds that were either faster, slower or the same as that utilized during target matching. In this case, it was found that subjects were, indeed, biased towards movement speed/duration, despite being instructed to focus only on target end position.

While the relationship between target amplitude perception and movement speed has been well established for movements associated with the preferred arm (e.g. Hollins and Goble 1988; Imanaka and Abernethy 1992a; Chieffi et al. 2004), the present study represents the first known assessment of arm differences related to this phenomenon. Interestingly, it was shown that, in the case where target determination speed was greater than that utilized during target matching, the preferred arm was influenced to a larger extent by this temporal factor than the non-preferred arm. To what extent this asymmetry in matching behavior reflects a greater preferred arm/hemisphere reliance on temporal cues during the estimation of target position, however, remains unclear. While preferred right arm advantages have been noted for the execution of movement sequences (Taylor and Heilman 1980; Edwards and Elliott 1989), and the maintenance of tapping intervals (Peters and Durding 1979; Todor and Kyprie 1980; Todor et al. 1982), studies involving individuals with unilateral brain injuries have, contrarily, indicated an enhanced role for the right hemisphere (Harrington et al. 1998; Kagerer et al. 2002; Koch et al. 2003). For example, in a study by Kagerer et al (2002), subjects were asked to reproduce standard intervals ranging from 1 to 5.5 s based on memory. It was found that patients with lesions of the right hemisphere were impaired in reproductions of stimuli longer than 2 s. Given that attention did not appear to be impaired in these subjects, it was argued that integrity of the right hemisphere is important for temporal reproduction.

Although greater matching errors were generally seen during the more difficult contralateral remembered matching task, there was no association between task difficulty and the magnitude of arm asymmetries. This result contrasts previous position matching studies conducted by this laboratory where a greater non-preferred arm advantage has been shown during contralateral remembered versus ipsilateral remembered matching, presumably due to poorer transfer of memorized arm position information (Goble et al.

2005; 2006; Goble and Brown 2007). There are two notable task differences that may account for these equivocal findings. First, while previous studies were largely specific to the processing of position-related proprioceptive feedback, the present study required the processing of both position and movement speed information. Indeed, while studies assessing the asymmetric transfer of position have shown greater transfer in the direction of the non-preferred arm/hemisphere system (Wang and Sainburg 2003; 2004b), there is no known evidence supporting the asymmetric transfer of movement velocity. Secondly, unlike previous studies of position matching, the present study did not consist of an active matching component. In this case, it is possible that the enhanced asymmetries seen previously for contralateral remembered position matching were due, at least in part, to the planning and execution of a target movement.

Cordo et al (1994) estimated that a delay of approximately 200 ms exists between the perception of dynamic position and the execution of an indicator movement. Given the speed used during the target matching phase of the present study (i.e. 5 deg/s), such a delay would result in matches that were biased approximately 1 deg towards the direction of target overshooting. Further, it should be acknowledged that slight differences are thought to exist with respect to reaction times of the preferred and non-preferred arms. Specifically, it has been shown that visuomotor reaction time is often faster for the non-preferred arm with a mean arm difference on the order of 10 ms (Carson et al. 1993; 1995; Boulinguez and Nougier 1999; Velay and Benoit-Dubrocard 1999; Barthelemy and Boulinguez 2001; 2001; 2001). In the present study, however, this difference would have had only minimal (i.e. 0.05 deg) influence on matching error.

In conclusion, the results of the present study underscore the importance of proprioceptive feedback during the control of non-preferred arm movements that rely on both static and dynamic information. Whether a similar asymmetry might exist in the dynamic position matching ability of left handed individuals, however, is not yet clear. In a recent study by Lenhard and Hoffmann (2007), the ability of left handed individuals to reach to visual targets with their unseen arm was assessed showing a non-preferred arm advantage in terms of constant but not variable error. In light of these findings, it seems possible that a non-preferred arm/hemisphere accuracy advantage might exist for the processing of proprioceptive information independent of handedness. This phenomenon may reflect a functional specialization of the non-preferred arm for obtaining/stabilizing arm postures without the aid of vision, as is necessary during the performance of many two-handed activities of daily living.

Chapter 5

Conclusion

Summary of Major Findings

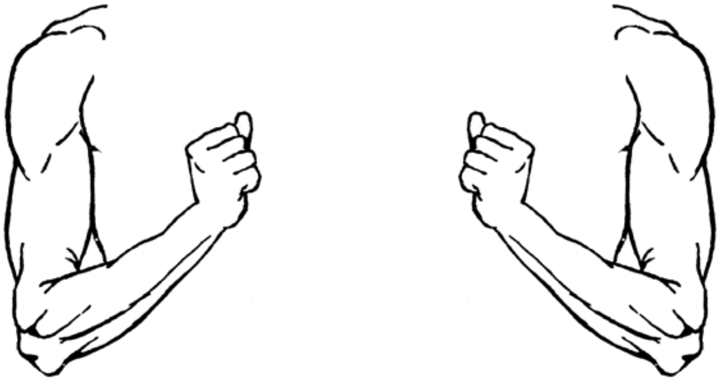
The overall purpose of the present dissertation was to explore upper limb asymmetries in the ability to utilize movement-related feedback. In Fig 5.1 a schematic outlines the major findings from this work. In the first experiment (Chapter 2), arm differences in the accuracy of matching target elbow positions was explored for both proprioceptively-guided and visually-guided matching tasks. In this case, it was shown that, similar to previous studies conducted by this laboratory (Goble et al. 2006; Goble and Brown 2007), matching of static proprioceptive targets was more accurate for the non-preferred arm, and that this asymmetry was particularly pronounced in the contralateral remembered condition where processing demands were increased by requiring both memory and interhemispheric transfer of target information. In contrast to proprioceptive matching, however, subjects were more accurate with the preferred arm when matching visual targets. This asymmetry was similar for both the ipsilateral remembered and contralateral remembered tasks, although there was a significant increase in matching error during the more difficult contralateral remembered condition. Taken together, the findings of the first experiment provide support for a sensory modality-based hypothesis of handedness, where the non-preferred and preferred

VISUAL
TARGET MATCHING
ADVANTAGE FOR:

- POSITION (Chapter 2)

PROPRIOCEPTIVE
TARGET MATCHING
ADVANTAGE FOR:

- POSITION (Chapter 2)
- AVERAGE ACCELERATION (Chapter 3)
- DYNAMIC POSITION (Chapter 4)



Preferred Arm

Non-preferred Arm

Fig 5.1 – Summary of overall arm differences demonstrated during the visual and proprioceptive target matching tasks utilized in this dissertation.

arms favour use of different sources of sensory information (i.e. proprioceptive versus visual) during the control of goal-directed movement.

Given that proprioception is not specific to joint position sense, but rather has a dynamic component as well, the focus of the second experiment (Chapter 3) in this dissertation was to determine arm asymmetries in the memory-based matching of proprioceptively-determined target arm trajectories. Specifically, subjects were asked to match previously-experienced triangular velocity profiles with either the preferred or non-preferred arm in the absence of vision. It was found that, in accordance with the proprioceptively-guided matching of position, the accuracy of speed matching was greater for the non-preferred arm during the early (i.e. acceleratory) phase of ipsilateral remembered matching movements. Conversely, other measures of dynamic matching performance (i.e. peak speed, deceleration, area under the velocity curve) showed no arm differences regardless of task condition. This led to the conclusion that non-preferred arm advantages for proprioceptive feedback processing are largely specific to the use of static position information.

In the third experiment (Chapter 4), the extent of non-preferred arm advantages for the utilization of proprioceptive feedback was further explored by assessing arm asymmetries in dynamic position sense. In this case, dynamic position was defined as the ability to perceive arm position during movement of the limb. This was tested by having subjects indicate when a memorized target position was reached during movement of the preferred or non-preferred elbow through a range of motion that included that target position. The results were in line with those seen for both the proprioceptively-guided matching of elbow position, and average movement acceleration, as the non-preferred arm was more accurate in dynamic position matching than the preferred. In this case, however, both target amplitude and target determination speed had a significant influence on matching asymmetry. Specifically, greater non-preferred arm advantages were seen with increased target amplitude and when the target speed was greater than that used during target matching.

Relation to Previous Models of Handedness

Motor Output Hypothesis

Perhaps the most traditional approach to explaining arm differences in motor behavior is one grounded in motor output (Woodworth 1899; Provins 1956; Peters 1976; Peters and Durding 1979; Todor and Kyprie 1980; Todor et al. 1982; Petersen et al. 1989; Incel et al. 2002). In this view, the fundamental difference between arms is an inherent ability of the preferred arm to generate larger muscle forces at a faster rate and with less variability than the non-preferred arm. In the experiments conducted in the present dissertation, subjects showed both a strong right arm preference and, not surprisingly, were "motor dominant" based on standard measures of motor ability. This was evidenced by preferred arm advantages in a timed peg placement task, maximum grip strength and hand steadiness.

Despite these results, however, in the two studies for which a motor output component was required, little evidence was found regarding an asymmetry in movement kinematics. In experiment 1 (Chapter 2), for example, matching movements made by both the preferred and non-preferred arm were characterized by velocity profiles that were not bell-shaped and time symmetric, but rather, consisted of prolonged deceleratory phases with multiple velocity peaks. One likely explanation for this lack of asymmetry lies in the simplistic nature of the motor response required of subjects. Specifically, it might be expected that greater asymmetry would occur if matching movements were not limited to only one joint, thus, eliminating the need to compensate for the intersegmental dynamics (Almeida et al. 1995; Gribble and Ostry 1999). Further, any asymmetries due to the effects of gravity (Virji-Babul and Cooke 1995) were minimized in this study by constraining the forearm to move on the horizontal plane.

Open Versus Closed Loop Hypothesis

The open versus closed loop model of handedness has emerged from studies of individuals with unilateral brain damage where the ability to make goal-directed reaching was differentially affected according to which cerebral hemisphere (left versus right) was injured (Haaland and Harrington 1989a; Haaland and Harrington 1989b; Haaland and Harrington 1994; Winstein and Pohl 1995; Haaland and Harrington 1996). In the case of left hemisphere damage, it has been found that reaching is most affected during the early phase of the movement related to feedforward (i.e. open loop) movement planning (Haaland and Harrington 1989b; 1994). In contrast, deficits in the latter phases of movement including final position accuracy, most often requiring closed-loop feedback-based corrections, have been observed with right hemisphere impairment (Haaland and Harrington 1989a; Winstein and Pohl 1995; Haaland and Harrington 1996).

Overall, the results of this dissertation partially support an open versus closed loop account of sensorimotor asymmetries. Indeed, in experiment 1 (Chapter 2), a non-preferred arm (right hemisphere) advantage was seen for the accuracy of matching proprioceptive targets. Given that the kinematics associated with this task suggested a closed loop strategy involving the online-correction of ongoing movement, this result fits well with the notion of an enhanced role for the right hemisphere in feedback processing. However, in this same experiment, a similar strategy was also noted during the matching of visual targets and, in this case, an accuracy advantage was seen for the preferred (i.e. left hemisphere) rather than non-preferred arm. Further, with respect to arm/hemisphere differences in the feedforward control of movement, it is worthy of note that both arms demonstrated significant scaling of peak velocity, a characteristic typically thought to reflect movement planning (e.g. Brown and Cooke 1981; 1984; Sainburg and Schaefer 2004). To what extent these inconsistencies may be related to the variability associated with the fact that open versus closed loop studies involved individuals with somewhat diffuse, brain injuries remains unclear.

Dynamic Dominance Hypothesis

Based on studies of targeted reaching in a virtual environment, the dynamic dominance hypothesis of handedness provides a functionally-based account of arm asymmetries (Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2002; Sainburg 2002; Sainburg and Wang 2002; Bagesteiro and Sainburg 2003; Wang and Sainburg 2004a; 2004b; Sainburg 2005). Whereas the preferred arm is thought to be specialized for the control of arm trajectory/limb dynamics, non-preferred arm advantages have been suggested for the control of arm position/posture. In terms of limb dynamics, the results of this dissertation initially appear to be in conflict with the dynamic dominance theory, as the matching movements made in experiments 1 (Chapter 2) and 2 (Chapter 3), which relied on dynamic proprioceptive feedback largely showed no arm differences in terms of kinematics. However, it should be noted that in the present study active movements of the subject were constrained to only the elbow joint and, thus, the need to control of inter-segmental dynamics was negated. In this case, it may not be possible to compare the present results with those favouring a dynamic dominance hypothesis, as the two best indicators to date of a preferred arm advantage for controlling arm trajectory (i.e. initial target direction and the efficiency of inter-segmental torques) were not applicable to these dissertation studies.

With respect to the accuracy of obtaining final arm positions, the results of experiment 1 (Chapter 2) contrasted those of the dynamic dominance hypothesis by suggesting a link between target accuracy and the type of feedback available during the matching movement. Specifically, when the target was visual in nature, a preferred arm advantage was seen, as has been shown in numerous other studies of visually-guided reaching (e.g. Woodworth 1899; Todor and Cisneros 1985; Roy et al. 1994). In contrast, the ability to match a target location based on proprioceptive feedback showed enhanced performance for the non-preferred arm, presumably due to a right hemisphere advantage for proprioceptive feedback processing. Based on these findings, it can be suggested that the non-preferred arm advantages previously described under the dynamic dominance hypothesis might reflect an emphasis on proprioceptive feedback for, at least, the non-preferred arm. Interestingly, in studies addressing the dynamic dominance hypothesis, visual feedback has only been provided regarding fingertip location and target position increasing subjects' reliance on proprioceptive feedback in order to monitor the otherwise unseen arm. This might explain the non-preferred arm (right hemisphere) accuracy advantages that have been reported.

Combining Theories – Current State of Handedness Thinking

While convenient, it is ultimately naïve to suggest that one theory versus another best describes the complex phenomenon that is human handedness. Rather, an integrated approach to the problem may provide the best characterization of upper limb asymmetries in sensorimotor behaviour. In this way, it would seem that right-handed humans, comprising the majority of the population, might be described as having two arms that are anatomically similar but that have evolved specialized control features to allow for enhanced bilateral motor performance. Specifically, given the increase in contralateral left hemisphere sensorimotor representation, the preferred right arm can be viewed as being more well suited for computationally challenging tasks such as those involving the manipulation of objects or interacting with the external environment. This processing advantage might, subsequently, manifest itself in movements that are faster and more efficient as has been shown in studies advocating a motor output hypothesis, as well as during the feedforward planning of multi-segmented reaching movements, as shown for the dynamic dominance and open loop theories of handedness. In addition, interacting with the external environment would also implicate vision versus proprioception as a key source of sensory feedback to locate and guide movements in external space.

In contrast to the preferred arm, the non-preferred arm/hemisphere system might alternatively be viewed as providing a support framework for the dexterous function of the preferred arm. In this case, the non-preferred arm would appear more specialized for holding objects in a steady position as a basis for subsequent manipulation of that object by the preferred arm. The ability to hold a steady position would certainly require the use of sensory feedback as suggested by the open versus closed loop hypothesis in order to monitor arm position throughout a movement task. While the dynamic dominance hypothesis has shown that the non-preferred arm is enhanced for reaching a final target position, the sensory-feedback specific hypothesis suggested in this dissertation provides strong evidence that this non-preferred arm position monitoring is likely to be biased towards the proprioceptive modality.

Limitations and Future Directions

Do these Results Reflect Hemispheric Specialization?

While it is tempting to infer hemispheric differences on the basis of the arm asymmetries seen in this dissertation, further studies employing various neuroimaging or clinical models of brain dysfunction would be of value in order to determine the particular role of the two hemispheres with respect to the processing of visual versus proprioceptive feedback. With respect to vision, it should be noted that, from an anatomical standpoint, the volume of the left occipital cortex, comprising the primary visual areas, is greater than the right occipital cortex in most right-handed individuals (Galaburda et al. 1978; Geschwind and Galaburda 1985). Further, this gross anatomical asymmetry has been associated with both an enhanced temporal resolution for the detection of visual targets (Nicholls 1994) and greater neural activation in response to light stimuli presented in the right hemifield (Hubel and Wiesel 1959; 1962; Crovitz

1964). Despite these findings, however, it has been difficult to assess the specific role of the left hemisphere regarding vision, as visual signals are most often represented in both hemispheres based on the anatomical arrangement of the nasal and temporal fibers arising from the optic nerves of the eyes.

In contrast to the study of visual feedback processing, hemispheric differences in the utilization of proprioceptive feedback have been reported on several occasions. Using positron emission tomography, for example, Butler and colleagues (2004) found greater activation in the temporal-parietal areas of the right hemisphere during the performance proprioceptively-guided target movements. In addition, a study by Naito et al (2005) identified a number of areas in the right hemisphere including, especially, the primary somatosensory cortex in response to vibration induced illusions of movement. Taken together with the results of studies involving individual with unilateral brain lesions where large excisions of the right hemisphere resulted in decreased accuracy for the matching of proprioceptively-determined movement extent (Leonard and Milner 1991a; Leonard and Milner 1991b; Leonard and Milner 1995; Naito et al. 2005), there is strong evidence to suggest an enhanced role for the right hemisphere in proprioceptive feedback processing.

Are there Single versus Multi-joint Differences?

In the present dissertation, a single joint paradigm was used where elbow movements were restricted to the horizontal plane. How well these findings relate to more “natural”, unconstrained multi-joint movements made in three-dimensional space remains to be determined. It has been shown, however, that the central nervous system can compensate for changes in interaction torques (Almeida et al 1995; Gribble and Ostry 1999; Virji-Babul and Cooke 1995), movement extent and direction (Gordon et al 1994), and changes in gravitational forces (Virji-Babul et al 1994), as evidenced by invariance of movement characteristics. It might be expected , therefore, that the arm differences demonstrated in this dissertation for the utilization of visual versus proprioceptive feedback would, indeed, translate to the multijoint level.

<u>What about Left-handed Individuals?</u>

In this dissertation only right-handed individuals were studied and, thus, the applicability of these results to left-handed individuals is unknown. In general, left-handers appear less lateralized and more variable than their right-handed counterparts, and are, therefore, not their simple genetic (McManus 1995) or behavioural inverse (Perelle and Ehrman 2005). In a recent study by Lenhard and Hoffmann (2007), the ability of left handed individuals to reach to visual targets with their unseen arm was assessed showing a non-preferred arm advantage in terms of constant but not variable error. In light of these initial findings then, it seems possible that some degree of non-preferred arm advantage exists in the proprioceptively-guided matching of position independent of subject handedness.

Implications of this Work

The most obvious implication of the results presented in this dissertation is the influence of feedback type (i.e. vision versus proprioception) on the accuracy of

Fig 5.2 – Sample tasks demonstrating a preferred right arm dependence on visual feedback and non-preferred arm reliance on proprioception. Images from http://images.google.com.

preferred versus non-preferred arm performance. When obtaining a target position, for example, visual feedback is likely to improve the accuracy of preferred arm movements, whereas propriopceptively-guided tasks may actually favour use of the non-preferred arm. In this case, the traditional view that the non-preferred arm is a less well practiced, clumsier version of the preferred arm must be called into question. Instead, both arms should be viewed as being specialized for different aspects of sensorimotor performance. To what extent this phenomenon reflects the fundamental roles of the preferred and non-preferred arms during the performance of many activities of daily living remains unclear. However, given the use-dependent neural plasticity that is known to exist within the sensorimotor system (see Monfils et al. 2005 for review), it is possible the hemispheres may have evolved to more adequately deal with proprioceptive versus visual feedback. In this case, left hemisphere specialization for vision would allow greater interactions between the preferred arm and objects in the external environment. In contrast, specialization of the right hemisphere for proprioceptive feedback would be important for maintaining objects in a particular location outside of visual attention prior to them being manipulated by the preferred arm. Examples of activities demonstrating these roles for the two arms are provided in Fig 5.2.

Lastly, the results of this dissertation may have important implications for the rehabilitation of individuals with unilateral brain injuries. Specifically, where the left cerebral hemisphere has been damaged, it might be expected that individuals will have reduced ability to control typical movements of the preferred arm that are visually-guided in nature. In contrast, where right hemisphere damage has occurred, the ability to monitor the non-preferred arm via proprioceptive feedback might be compromised. In this way, it might be possible to develop training interventions that are tailored towards the sensory modality of greatest import to the affected arm/hemisphere. This contrasts the current approach to rehabilitative therapy where arm-specific interventions are rarely utilized in the treatment of various movement disorders.

APPENDIX

Modified Edinburgh Questionnaire

Task	Right Arm	Left Arm
1. Writing		
2. Throwing		
3. Scissors		
4. Toothbrush		
5. Knife (without fork)		
6. Spoon		
7. Hammer		
8. Screwdriver		
9. Dealing Cards		
10. Racquet		

Instructions

Please indicate your preference in the use of hands for the following activities by putting + in the appropriate column. Where the preference is so strong that you would never try to use the other hand unless forced to, put ++. If any case you are really indifferent put + in both columns.

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