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The Effect of Visual Transformation on Implicitly and Explicitly Timed Bimanual Drawing Tasks

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**The Effect of Visual Transformation on Implicitly and
Explicitly Timed Bimanual Drawing Tasks**

Nadine Guerrette

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
In partial fulfillment of the requirements
For the MSc in Human Kinetics

School of Human Kinetics
Faculty of Health Sciences
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Abstract

Mirror drawing is a challenging task because appropriate hand actions must be planned and directed despite receiving visual feedback that is reversed by the mirror. The purpose of this study was to investigate whether visual transformation impacts the timing and spatial variability of explicitly and implicitly timed bimanual drawing tasks differently. To examine these issues, ten healthy participants bimanually drew various template shapes (circles, lines, vertical triangles and horizontal triangles) under normal (untransformed) and mirror-reflected vision conditions. Drawing movements were paced by a metronome and all templates were drawn in both symmetrical and asymmetrical coordination modes. Our results show that mirror feedback increased timing errors on implicit timing tasks but not explicit timing tasks. Mirror feedback also resulted in greater spatial variability and decreased interlimb coordination. These results provide insight into the role of visual information in the timing and performance of different types of bimanual drawing tasks.

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CHAPTER I

Introduction

Coordination involves bringing any two moving parts of the body into a functional relationship to execute a movement. In particular, bimanual coordination involves the interaction of hand movements. Patterns of bimanual action can be relatively simple, involving identical or cyclical actions of the hands, or such patterns can be relatively complex, requiring differential activity of the limbs. As such, human beings are capable of performing a variety of intermanual tasks including clapping, opening a bottle, tying ones' shoelaces, and playing a musical instrument. The apparent ease with which we achieve many daily tasks involving both our hands may disguise the true complexity of bimanual action.

A so-called coalition of constraints governs interlimb coordination and influences the execution of bimanual movements. These constraints are neural, musculoskeletal, and perceptual in nature. Many, or all, of these factors may affect performance on bimanual tasks; however, it is not clear to what extent each constraint limits or organizes bimanual movements. Though it is evident that perception and action are tightly coupled (Bogaerts, Buekers, Zaal & Swinnen, 2003), the specific role of perceptual information, including vision, is not fully understood.

It is known that visual information plays an important role in the planning and guidance of hand movements. Under conditions of perturbed visual feedback, the association between visual and proprioceptive information is affected, causing a disturbance in sensory convergence. Planning movements under these circumstances is confounded because there is conflict between motor intention and sensory feedback.

Visual transformation is an example of such a condition because it provides distorted visual feedback regarding movement execution (Cardoso de Oliveira, 2004). These transformations have been used in bimanual coordination research to dissociate the perceptual consequences of an action from the action itself (Li, Levin, Carson & Swinnen, 2004).

Some studies have shown that manipulations of visual feedback can improve performance on manual tasks (Swinnen, Dounskaia, Walter & Serrien, 1997; Mechsner, Kerzel, Knoblich & Prinz, 2001; Bogaerts et al., 2003), whereas other studies have shown that it can also make tasks more difficult (Lajoie et al., 1992; Miall & Cole, 2007). For instance, prism goggles optically displace the visual field, and when worn, the normal calibration of sensory information breaks down such that an adaptive process is required to reconcile proprioceptive and visual maps (Redding, Rossetti & Wallace, 2005). Similarly, mirror drawing is another situation in which there is discordance between sources of sensory information and performance is impaired (Lajoie et al., 1992).

Although the effect of visual transformation has been studied before, it is not yet known whether such transformations affect movement timing nor if they have a differential effect on continuous and discontinuous hand movement tasks. The purpose of this study was to address this issue by looking at the effect of mirror reflection on explicitly and implicitly timed bimanual drawing tasks.

The topic of movement timing has been an important focus in bimanual coordination research. Notably, timed movements have been divided into two classes, explicit and implicit (Zelaznik, Spencer & Ivry, 2002). Discontinuous hand movements, such as finger tapping, are marked by salient events and timing requires an explicit

temporal representation of the target interval. In contrast, interval duration for smooth and continuous hand movements, such as circle drawing, is not directly specified because they lack an event structure. Rather, it is believed that temporal regularities under such conditions emerge from the dynamics of trajectory control. In this way, timing is implicit for continuous tasks and explicit for discontinuous tasks.

The current study tested subjects on several rhythmic bimanual drawing tasks including circle drawing, line drawing and triangle drawing, while monitoring their hand movements in a mirror. This experiment allowed for the assessment of a differential effect of transformed visual feedback on continuous tasks (circle drawing and line drawing) and discontinuous tasks (horizontal and vertical triangle drawing). We were interested in determining whether mirror transformation would affect movement timing, spatial variability and hand coordination. To evaluate movement accuracy and consistency under different task conditions, timing errors, spatial deviations, peak speed and relative phase were examined. Relevant research in the fields of bimanual coordination and timing will be presented, including information regarding the different approaches to the study of interlimb coordination, constraints on coordination, and current knowledge in motor timing. More generally, the results of the present experiment provide significant insight into the role of vision in bimanual coordination and movement timing.

CHAPTER II

Review of Literature

2.1 Theoretical frameworks for the study of bimanual coordination

Research into the principles of bimanual coordination has been dominated by two frameworks: the dynamical systems approach and the information processing approach. The dynamical systems approach to interlimb coordination is centered on the concept that coordination is self-organized, whereas the information processing framework approaches coordination from a computational neuroscience perspective. Although these two research approaches are different, what they share is their common search for the principles that underlie bimanual coordination.

2.1.1 Dynamical systems approach. The human body is a highly dimensional system, a feature that imposes an issue in motor control known as the degrees of freedom problem. In executing a goal-oriented movement there are literally billions of neurons, hundreds of joints, and infinitely many possible muscle activations that can be employed to accomplish the task (Turvey, 1990). How does the motor system control redundant degrees of freedom to give rise to coordinated action? Recognizing the significance of the degrees of freedom problem, Nikolai Bernstein (1967) put forward the idea of coordinative structures as a possible solution to the issue (Turvey, 1990). Coordinative structures, or synergies, are task-specific muscle groupings that behave as a functional unit. By assembling muscles in this manner the number of variables is reduced, and the problem for motor control is simplified (Kelso, 1995).

Consistent with Bernstein's theory of coordinative structures, Kelso, Southard, and Goodman (1979) provided evidence that the brain likely controls simultaneous

movements of the limbs by organizing muscles into functional groups, rather than controlling each limb independently. When subjects made simultaneous bimanual reaching movements to targets at different distances, the hands would reach their respective targets synchronously (Kelso et al., 1979). It was suggested that muscle groupings were constrained to act as a functional unit, resulting in tight coupling of the hands. In this sense, Bernstein's concept of synergies has been integrated into the dynamical systems approach to coordinated action which suggests that rhythmic movements emerge from the coupling of non-linear oscillators. Dynamic pattern theory attempts to determine principles of pattern generation that will explain the behaviour of a system independent of the structures producing it (Scholz, 1990).

A discussion on coordination would be incomplete without mention of the work of Erich von Holst. Relative coordination of movements was first observed by von Holst in the fin movements of the *Labrus*, a species of fish that swims by oscillating its fins while keeping its main body axis immobile (von Holst, 1939/1973). Von Holst called the tendency for the fins to oscillate at their intrinsic frequency 'maintenance tendency', and the observed phenomenon whereby the rhythm of one fin imposes its inherent frequency on the rhythm of another the 'magnet effect' (von Holst, 1939/1973). The principles of coordination identified in the fish were found to be consistent across other animal species and von Holst's account of oscillatory fin movements paved the way for the study of coordination as a dynamical process (Amazeen, Schmidt & Turvey, 1995).

The principles of relative coordination established by von Holst later converged with subsequent work on interlimb coordination in humans. In 1984, Scott Kelso published a landmark paper on the nature of cyclical bimanual movements. This

experimental work demonstrated that there are only two stable patterns of coordination between the hands: in-phase (0°), involving simultaneous activation of homologous muscles and anti-phase (180°), involving alternating activation of homologous muscles (Kelso, 1984). When subjects make anti-phase movements with the two index fingers while increasing cycling frequency, abrupt phase transitions to the more stable mirror-symmetrical mode are observed (Figure 1.1). Beyond the transition point, in-phase movements become the only stable coordination mode and spontaneous switches from the in-phase pattern to the anti-phase pattern do not occur (Kelso, 1984). This has also been demonstrated with bimanual circle drawing in the horizontal plane, where the symmetrical drawing mode (one hand moving clockwise and the other counterclockwise) is preferred over the asymmetrical mode (both hands moving clockwise or counterclockwise). During fast asymmetrical movements, transitions to symmetrical movements were shown to occur (Semjen, Summers & Cattaert, 1995).



Figure 1.1. A spontaneous switch to in-phase during anti-phase finger tapping at increasing cycling frequency. Adapted from Kelso, 1984.

Building upon this work, Haken, Kelso, and Bunz (1985) proposed a mathematical formulation of phase transitions in human hand movements. The Haken-Kelso-Bunz (HKB) model describes the stability of movement patterns in terms of a potential function: $V(\phi) = -a\cos(\phi) - b\cos(2\phi)$, where ϕ is the relative phase, and a and b

are coupling parameters (Haken et al, 1985). Relative phase was found to be the most appropriate order parameter because it reflects the cooperativity between the two interacting components and captures all the spatiotemporal properties of the system (Kelso, 1995). Frequency was identified as a critical control parameter because of its ability to induce changes in relative phase (Swinnen & Wenderoth, 2004).

Each dynamical system has a collection of attractors that constitutes a theoretical potential landscape. Stable interlimb coordination patterns can be mapped onto point attractors at $\phi = 0^\circ$ and at $\phi = 180^\circ$ (Swinnen, 2002). The in-phase (0°) point attractor has the deepest basin of attraction, making it very resistant to perturbations and the most stable coordination pattern. By varying the cycling frequency of the hands or fingers, the potential landscape is altered. Accordingly, when tapping the index fingers in anti-phase (180°), the system will become unstable at a critical frequency and enter the deeper basin of attraction at 0° . Spontaneous transitions to the in-phase coordination mode occur when the energy landscape evolves such that the anti-phase attractor disappears and in-phase movements become the only stable mode. The HKB model was monumental to the dynamical systems approach to interlimb coordination and was able to account for several behavioral phenomena associated with bimanual movements, including bistability and pattern switching.

To put it briefly, the dynamical systems approach describes biological systems in terms of their time-dependent changes, and attempts to determine principles of pattern generation that will explain their emergent behaviour (Swinnen & Wenderoth, 2004). This theory transcends the organization of neural structures by suggesting that the components of a system are able to self-organize into a coherent pattern through

cooperation, rather than the pattern being specified by some higher command (Swinnen & Wenderoth, 2004).

2.1.2 Information processing approach. The computational study of motor control looks at the relationship between motor commands originating in the central nervous system (CNS) and their sensory consequences (Wolpert & Ghahramani, 2000). The information processing framework approaches the study of bimanual coordination in this manner, and searches for the neural mechanisms underlying motor behaviour.

Unlike the dynamical systems approach, the information processing perspective to motor control draws on the concept of internal models in the central nervous system (Whitney, 2004). An internal model is a representation of a sensorimotor transformation that can be used to predict or model the behavior of the motor system. When an internal model estimates the sensory consequences of a motor command, it is called a forward model. In contrast, an inverse model is a solution-based model that carries out transformations from desired consequences to actions (Wolpert & Ghahramani, 2000). It is believed that the complexity of our motor behaviour is largely due to a coupling of these transformations (Wolpert & Ghahramani, 2000).

Under the generalized motor program (GMP) model it has been proposed that the observed spatiotemporal coupling of the limbs is the consequence of a common motor plan for both hands (Cardoso de Oliveira, 2002). A GMP is a set of motor commands representing a class of movements in the CNS, and by varying the parameters of the GMP, different movements within a class can be realized (Schmidt, 1975). Bimanual related activity in the motor cortex lends support to the idea of a common motor plan (Donchin et al., 2001; Steinberg et al., 2002); however, the model fails to explain certain

behavioral phenomena related to bimanual coordination. Although a common motor program for both hands would simplify control, the GMP model is unable to explain the assimilation of movements and how the level of coupling between the hands is regulated (Cardoso de Oliveira, 2002).

Also central to the information processing framework is the issue of neural crosstalk, which assumes that limitations in task performance result from neural interference (Swinnen et al., 2004). When each hand is performing a different task, neural crosstalk can occur between the two hemispheres and cause mutual interference between limb movements. Individuals with callosal agenesis, or who have had their corpus callosum resected for medical reasons, do not exhibit spatial interference. Callosotomy patients are capable of simultaneously drawing a circle with one hand, and a square with the other (Franz, Eliassen, Ivry & Gazzaniga, 1996). This task would be quite challenging to a healthy subject, suggesting that interhemispheric transmission via the corpus callosum conveys information regarding spatial aspects of limb movements.

2.2 Constraints on bimanual coordination

There is a natural tendency to synchronize interlimb movements due to a coalition of constraints on bimanual coordination (Swinnen, 2002). These constraints are likely a reflection of the inherent limitations of the motor system as a result of its effort to control the multiple degrees of freedom of the human body. Consequently, there is a preference for bimanual movements with simple frequency ratios and specific phase relationships, namely in-phase and anti-phase. Patterns of coordination are most stable when these constraints converge to enhance each other (Swinnen & Wenderoth, 2004). Researchers

have taken different perspectives on this matter; in particular, some believe coordination to be primarily perceptual in nature, while others have taken a motoric view. We will come back to this issue after first addressing spatiotemporal constraints in bimanual coordination and the concept of coordinate reference frames.

2.2.1 Temporal and spatial constraints. Many constraints on bimanual coordination favor synchronization of the hands and when it comes to the temporal properties of bimanual movements, there is a general preference for a 1:1 frequency ratio of hand movements. Simple rhythms (e.g. 1:1, 2:1) are produced more successfully than polyrhythms. Polyrhythms are non-harmonic frequency ratios (e.g. 3:2, 4:3) and require complex phasing of the hands. With extensive practice, for instance with musical training, performance improves and more difficult coordination patterns can be achieved. Although some have purported that a separate sequence of responses may be produced for each hand (Shaffer, 1981), evidence has shown that independence of the hands is unlikely. Research on polyrhythmic tapping indicates that the two response streams are interleaved into a common time base (Deutsch, 1983; Jagacinski, Marshburn, Klapp & Jones, 1988; Klapp, Nelson & Jagacinski, 1998). Through integration of the two rhythms, the task becomes a single sequence produced with two hands (Summers, 2002).

Tight temporal coupling of the limbs is also accompanied by a synchronization of movements in the spatial domain. If an obstacle is placed in the movement path of one arm, and a bimanual movement is made, both arms will produce similar trajectories (Kelso, Putnam & Goodman, 1983). Franz, Zelaznik, and McCabe (1991) investigated spatial constraints using a bimanual drawing task. It was found that when subjects produced a circle with one hand and a line with the other, circles became more line-like

and lines became more circle-like. This spatial assimilation effect demonstrated that spatial constraints also play a role in the control of bimanual actions. As previously mentioned, callosotomy patients are capable of producing movements with different spatial demands, but maintain temporal coupling (Franz, Eliassen et al., 1996). The corpus callosum is a commissure that provides a pathway between the two hemispheres of the brain. Thus, spatial interference and coupling appears to occur at the level of the corpus callosum as a result of the interaction of spatial representations and directional plans (Franz, 1997).

2.2.2 Coordinate reference frames. Movements can be planned and controlled within two different reference frames: intrinsic and extrinsic. It has been suggested that the dynamics of motor tasks might be represented in an intrinsic joint- or muscle-based coordinate system (Shadmehr & Mussa-Ivaldi, 1994). Early on it was recognized that the tendency to move the limbs in-phase in a symmetrical fashion involves coactivation of homologous muscles (Kelso, 1984). This muscle grouping principle of interlimb coordination has been termed the egocentric constraint and is often emphasized in the literature (Swinnen, 2002). More specifically, movements of homologous effectors are made with respect to intrinsic body-centered coordinates, emerging as a preference for mirror-symmetric movements across the body midline (Meesen, Wenderoth, Temprado, Summers & Swinnen, 2006).

The allocentric spatial constraint refers to the preference to move limbs or limb segments in the same direction in extrinsic space, and is particularly significant with respect to movements of non-homologous effectors. This was first demonstrated by Baldissera and colleagues (1982) who observed cyclical movements of the ipsilateral

wrist and foot. Results showed that the more stable pattern of coordination involved moving the wrist and foot in the same direction (both up or down) (Baldissera, Cavallari & Civaschi, 1982).

It is believed that these constraints are the behavioral consequences of neural limitations in the organization of coordinated action (Swinnen et al., 1998). This framework allows us to make predictions regarding the level of stability and accuracy of specific coordination patterns. For example, in-phase hand movements produced in the median plane would be expected to be particularly stable. Under such task conditions, the egocentric and allocentric constraints reinforce each other, demonstrating that extrinsic and intrinsic reference frames are not mutually exclusive.

2.2.3 Motoric and perceptual views of bimanual action. Along these lines, there exists a motoric and a perceptual view concerning the locus of the symmetry tendency in bimanual action and the level at which movement interference occurs. Kelso (1984) marked that symmetrical interlimb movements require co-activation of homologous muscles. In this sense, the symmetry tendency might reflect crosstalk at the level of neural structures encoding motor commands. Mechsner and colleagues (2001) have taken the provocative position that coordinated movements are organized purely with respect to their perceptual consequences and irrespective of motor commands. This viewpoint is in sharp contrast with the widely held belief that the symmetry tendency emerges from a bias toward co-activation of homologous muscles and departs from the basic premise in motor control that it is the motor system that translates intentions into motor commands (Cardoso de Oliveira, 2004).

Results from several bimanual finger adduction-abduction experiments under different postural manipulations of the hands and a bimanual circling experiment were used to support this claim (Mecshner et al., 2001; Mecshner & Knoblich, 2004). During the finger adduction-abduction task in the congruent position, with both palms facing either up or down (Figure 1.2 A and B), mirror symmetrical movements involving contractions of homologous muscles were most stable. Notably, in the incongruent position with one palm facing down and the other palm facing up (Figure 1.2 C and D), symmetrical movements were again more stable than asymmetric movements. However, under this condition, visually symmetric movements can only be achieved by contracting non-homologous muscles. This was taken to be an indication that perceptual symmetry has a greater influence on performance than muscle symmetry.

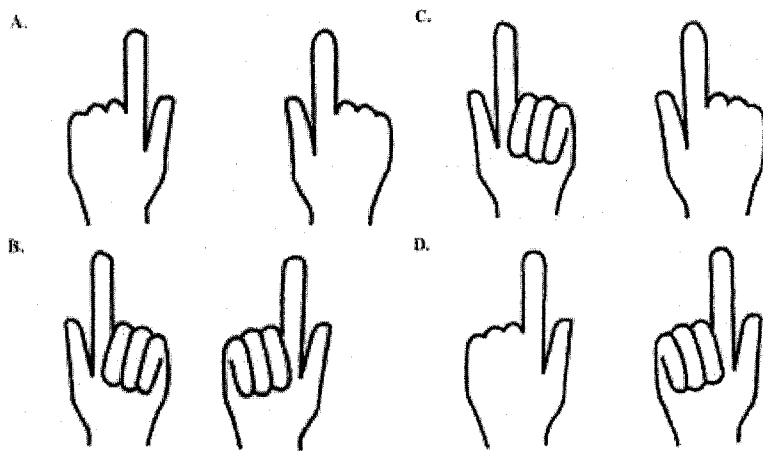


Figure 1.2. Palm positions in experiment by Mecshner et al. (2001). Congruous positions with both palms up or down (A and B). Incongruous positions with one palm up and one palm down (C and D). Adapted from Mecshner and Knoblich (2004).

In another task of particular interest, subjects were asked to circle two flags inwards in mirror symmetry or in anti-phase, using cranks hidden below a table (Figure

1.3). In this experiment it was found that participants were able to turn the cranks in a virtually impossible 4:3 circling ratio when the visual circling pattern of the flags moved with a 1:1 frequency ratio due to a gear system (Mechsner et al., 2001). Under these conditions, muscle activation patterns would not have translated into the observed perceptual pattern. This again suggested that the symmetry tendency may be perceptual in nature and not originating at the level of motor commands. Mechsner contends that if this were the case, there would be no need for internal models and voluntary movements would likely be organized using simple representations of perceptual goals (Mechsner et al., 2001).

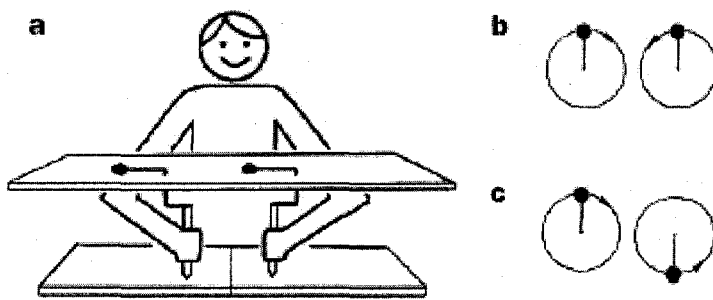


Figure 1.3. Apparatus used in experiment by Mechsner et al. (2001). (a) Subjects were instructed to generate in-phase (b) and anti-phase (c) circling patterns of the flags using their hidden hands. Adapted from Mechsner et al. (2001).

Amazeen and colleagues (2004) suggested that Mechsner's analysis would have been more complete had he taken into consideration the details of symmetry group theory and had his conclusions not been based solely on spontaneous phase transitions, which constitute only one aspect of a changing coordination landscape (Amazeen, Amazeen & Turvey, 2004). Symmetry groups are "rules that connect different configurations of a

given set of components” (Mulvey, Amazeen & Riley, 2005) and the theory behind it enables predictions to be made regarding the behavioral effects of a given transformation. The reflectional symmetry group is of particular importance in bimanual coordination and reflectional symmetry across the body midline can be broken both temporally and spatially. When the two hands move at different frequencies (i.e. a bimanual 1:2 task) or when the effectors assume different spatial orientations (i.e. one hand up, one hand down) symmetry breaking occurs (Amazeen, Amazeen & Turvey, 1998).

2.3 Movement timing

Although the passage of time is salient, we do not have sensors for detecting time (Ivry & Spencer, 2004). So how is it that we can maintain temporal regularity in our movements? Two different models have been used to characterize an abstract neural mechanism for the representation of time: the clock-counter model and the interval model (Ivry & Richardson, 2002). In the clock-counter model, an oscillatory process, such as a pacemaker, is linked to a counting device and interval duration is determined by the frequency of pacemaker outputs to the counter. In the interval timer model, different intervals are represented by distinct elements; this can be conceptualized as multiple hourglasses containing different amounts of sand. To begin measuring time these elements must be triggered to reset, unlike in the oscillatory pacemaker model (Ivry & Richardson, 2002).

2.3.1 The Wing-Kristofferson model. The Wing-Kristofferson model of voluntary timing (as cited in Wing, 2002) utilizes the clock-counter model and examines the nature

of variation in timing. Wing and Kristofferson suggested a two-process model involving a central timer or timekeeper and a subsequent motor implementation delay (Figure 1.4).

A synchronization-continuation paradigm was used to explore timing variability in rhythmic finger tapping. Subjects were instructed to synchronize single-handed finger taps to a metronome beat and to continue to tap at the same interval following removal of the auditory cue. It was discovered that successive interresponse intervals are negatively correlated between zero and negative one-half, meaning that consecutive intervals alternate short and long (Wing, 2002). Timekeeper and motor implementation processes are assumed to be independent, and as such, variability in timing behavior can be attributed to either central (timer) or peripheral (motor) factors. Many individuals with motor disorders have impaired movement timing, and this model can be applied to locate the source of additional timing variability, be it central or peripheral.

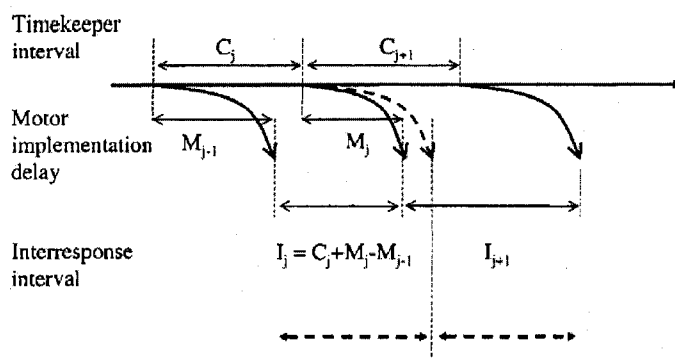


Figure 1.4. The Wing-Kristofferson hierarchical timing model. A timekeeper generates a clocking output that is subject to a motor implementation delay. Variation in the interresponse interval (I) represents variation in both the timekeeper interval (C) and in motor implementation (M). Adapted from Wing (2002).

2.3.2 The bimanual advantage. To extend our understanding of movement timing from unimanual to bimanual rhythmic movements, we must also look at the phenomenon that has come to be known as the multiple effector advantage. Helmuth and Ivry (1996) discovered that within-hand timing variability is reduced when tapping with both hands in comparison to single-handed tapping. A reduction in timing variability was also observed for movements produced with non-homologous effectors, such as a finger and a forearm. The authors evaluated the bimanual advantage by employing the Wing-Kristofferson model and attributed the effect to a reduction in central clock variability.

There is much evidence to suggest that the cerebellum plays a role in the timing of muscular activations. The cerebellum is a sub-cortical structure that is divided into two hemispheres that project ipsilaterally. Cerebellar patients have been shown to exhibit deficits on a variety of temporal tasks, such as eyeblink conditioning and finger tapping (Woodruff-Pak, 1997; Franz, Ivry & Helmuth, 1996). Subjects with unilateral cerebellar lesions exhibit greater timing variability when tapping with the ipsilesional hand than the contralesional hand. However, an analysis of timing error in the impaired hand during bimanual tapping demonstrated yet again that timing variability is greatly reduced in the bimanual condition (Franz, Ivry & Helmuth, 1996). In this manner, the reduction in within-hand timing variability during bimanual tapping was attributed to a reduction in timer variance, rather than motor variance.

2.3.3 The multiple timer model. Despite a lack of communication between the two cerebral hemispheres, callosotomy patients still show temporal coupling of the hands on discrete movement tasks and exhibit the bimanual advantage when performing repetitive bimanual movements (Ivry & Hazeltine, 1999). These findings confirmed the notion that

the locus of temporal coupling is subcortical, and it was suggested that the cerebellar cortex contained an array of timing elements (Ivry & Hazeltine, 1999). Ivry and Richardson (2002) proposed the multiple timer model to account for the presence of a multiple effector advantage. This is a form of the coupled oscillator model of timing, where timing of rhythmic movements emerges from properties of coupled oscillators. A separate clocking signal and a representation of the desired target interval is generated for each effector. To generate a signal for each effector, the model makes necessary the existence of multiple effector-specific timing elements. Secondly, these signals are integrated at a central gate that links the clock with the motor periphery. By gating the timing signals for each effector, each output represents an average of two independent signals, and over many trials the interresponse variability is significantly reduced (Ivry & Richardson, 2002). Within the context of the multiple timer model, it is the gating process that gives rise to temporal coupling and ensures that hand actions remain coordinated.

Lastly, this model assumes that an external stimulus initiates the timing process, but that once set in motion, outputs are triggered by the previous output from the gate. In this manner, timing is open-loop, and feedback from the actual responses is not used to make corrections.

2.3.4 Implicit and explicit timing. Two classes of timed movements have been identified, namely implicit and explicit. Zelaznik, Spencer & Ivry (2002) made an important distinction between the timing mechanisms involved in discontinuous tasks, such as repetitive finger tapping, and continuous tasks, such as circle drawing. It was hypothesized that movements marked by salient events require a clear representation of

the temporal goal and involve an explicit timing process. In contrast, timing is implicit for smooth and continuous movements which lack an event structure and temporal regularities likely emerge from the control of other task parameters. For instance, cycle duration may not be directly specified when circle drawing, but a consistent rate can be achieved by maintaining a constant angular velocity (Zelaznik et al, 2002).

It was discovered that patients with cerebellar lesions show greater variability on discontinuous tasks; however, performance on continuous tasks remains unperturbed (Spencer, Zelaznik, Diedrichsen & Ivry, 2003). This dissociation likely stems from differences in the temporal properties of discontinuous and continuous movements. It appears that the role of the cerebellum is to provide a representation of the temporal goal, and as such, cerebellar patients are not impaired at tasks involving implicit timing.

2.4 Drawing

There has been much research into the nature of timing and many studies have used drawing tasks to determine whether a common control process is used for the timing of all rhythmic movements. It is believed, that if two tasks share common control processes, there will be a positive correlation for timing variability across the tasks (Zelaznik, Spencer & Ivry, 2002). It has been shown that there is no correlation between timing consistency during tapping and circle drawing (Robertson et al., 1999), and Weber slope analyses of timing variability also revealed significant differences between tapping, line drawing and circle drawing (Spencer & Zelaznik, 2003). These findings provided evidence that not all timing tasks share the same temporal process and that there exists a high degree of specificity in timing processes. It seems reasonable that drawing tasks

with different spatiotemporal properties and varying degrees of complexity would require unique timing processes. When the demands of circle drawing and line drawing are considered, we see that whereas line drawing movements are timed in only one dimension, circle drawing movements are timed in two dimensions (Spencer & Zelaznik, 2003).

Based on this work, a distinction has been made between tapping and drawing tasks. Whereas finger tapping appears to have salient points in a cycle to attract timing behaviour, drawing tasks do not (Spencer & Zelaznik, 2003). Thus, tapping was categorized as an explicit timing task and line drawing and circle drawing were categorized as implicit timing tasks. Zelaznik and colleagues (2002) also investigated timing on an intermittent circle drawing task; for this experiment, subjects had to pause between each drawing cycle. Results showed that temporal consistency on intermittent circle drawing and tapping were related, suggesting that explicit timing is not only used for discrete tasks, but for any task that is not smooth and continuous. The pause during this form of circle drawing makes the use of an explicit temporal process necessary because movement initiation between cycles must be timed (Zelaznik et al., 2002).

Triangle drawing is another drawing task which has been investigated, although to a lesser extent than circle drawing. Bogaerts and Swinnen (2001) studied bimanual triangle drawing because it allowed for the assessment of dynamic aspects of the task, particularly interlimb coordination, as well as the impact of static images, on drawing performance. Triangles in vertical orientations were drawn more successfully than triangles in horizontal orientations, demonstrating that static features of a template can have an influence on movement dynamics. A static spatial plan for horizontal triangles

may be less salient because there tends to be a perceptual bias in favor of vertical triangles (Bogaerts & Swinnen, 2001). This research focused on the role of spatial constraints during triangle drawing, and to date, the role of timing in bimanual triangle drawing has yet to be studied.

2.5 Mirror Drawing

To produce an accurate hand movement, we require knowledge of our current hand position and of the motion of our arm as it moves to an intended location (Miall & Cole, 2007). Mirror drawing is a particularly difficult task because it causes a conflict between the senses. Discordance between visual and proprioceptive signals (a visuo-proprioceptive conflict) makes it a challenge to guide hand movements (Lajoie et al., 1992). Additionally, there is a conflict between motor outputs and the visually perceived consequences of movement (a visuomotor conflict) that makes it difficult to plan hand movements.

Under normal conditions, a state estimate of hand position is generated based on the integration of information from multiple sensory modalities (van Beers, Wolpert & Haggard, 2002). When making a goal-directed movement it is important that the expected sensorimotor state corresponds with the realized state. The congruency of intended actions and sensory experience is normally monitored implicitly and automatically; however, when there is a mismatch, as is the case during mirror drawing, monitoring becomes a conscious process (Fink et al., 1999). Appropriate hand actions must be planned and directed despite receiving visual cues that are reversed by the mirror (Miall & Cole, 2007).

Experiments on deafferented subjects have demonstrated that accuracy in mirror drawing tasks is improved when proprioception is lacking. Deafferented patient GL demonstrated better performance than normal subjects when tracing a star-shaped template in a mirror (Lajoie et al., 1992). This was attributed to a lack of proprioception, eliminating the visuo-proprioceptive conflict, and rendering the task a simple visual tracking task. GL showed consistent performance across all trials, whereas normal subjects demonstrated a learning effect as they recalibrated their proprioceptive map. These findings were supported by a later study in which proprioceptive deafferentation was induced in healthy subjects using repetitive transcranial magnetic stimulation (rTMS) (Balslev et al., 2004). Again, it was shown that motor control benefits from a reduction (or absence) of proprioception when there is a visuo-proprioceptive conflict.

Miall and Cole (2007) argued that there is also a visuomotor conflict that would make it difficult to plan movements, regardless of an absence of proprioception (such as in deafferented subjects). They suggested that planning conflicts in mirror drawing would be most marked at corners. Under the instruction to move as fast and as accurately as possible, subjects traced a curved template and various other templates with different degrees of complexity (different number of corners). It was found that there was a linear relationship between the number of corners in a template and tracing time. Furthermore, deviations from the template were smaller when tracing the curved pattern.

In this experiment, deafferented patient IW showed patterns of tracing performance that were similar to the controls and all subjects demonstrated a rapid improvement with practice (Miall & Cole, 2007). The finding that IW did suffer a conflict during mirror drawing, despite the absence of proprioception, implied that a

visuomotor conflict must have been impeding his performance. This discovery was in contradiction with the results of Lajoie and colleagues (1992), in which patient GL did not show a learning curve. It was proposed that GL made use of online visual feedback to guide movements, whereas IW showed evidence of forward motor planning, making him more similar to controls (Miall & Cole, 2007).

2.6 The present study

This study was designed to investigate the effect of visual transformation on the timing of repetitive bimanual movements. Based on unimanual studies of mirror drawing experiments (Lajoie et al, 1992; Balslev et al., 2004; Miall & Cole, 2007) it was expected that subjects would experience performance difficulties due to discordance between movement direction and sensory information. Circular, triangular and linear templates were used, and drawing movements were paced by an external auditory metronome. These template shapes were selected because the timing process required when rhythmically drawing a circle or a line differs from that required when drawing a triangle. Circle drawing and line drawing involve continuous hand movements and an implicit timing process, whereas triangle drawing involves discontinuous hand movements and an explicit timing process.

To date, no mirror drawing experiments have employed a procedure where both hands drew figures simultaneously. Furthermore, most bimanual experiments involving a perceptual transformation have made use of transformed visual feedback that does not allow the subjects to see their hands. For instance, graphic representations presented on a computer screen (Bogaerts et al., 2003; Weigelt & Cardoso de Oliveira, 2003) and flags

(Mecshner et al., 2001) have been used to provide the participant with transformed information regarding their hand trajectory. By utilizing a mirror drawing protocol, this study allowed subjects to maintain vision of their hands; however, this visual information was available to them by means of a mirror reflection. It was a goal of the study to clarify the role of visual information in aspects of bimanual coordination, including the timing of repetitive movements.

Each subject performed bimanual drawing tasks under two different vision conditions (normal visual feedback and mirror-reflected visual feedback) and with two different phase relationships (symmetrical and asymmetrical). An external auditory metronome was used to provide a pacing signal that specified movement frequency. The metronome was either kept on for the entire duration of the trial (synchronization condition), or it was shut off after movements were synchronized with the beat and the subject had to continue to draw at the same pace (continuation condition).

The *overall objective* of this experiment was to look at the effect of visual transformation on explicitly and implicitly timed bimanual drawing tasks to clarify the role of visual information in movement timing.

The *specific objectives* were:

1. To test *Hypothesis 1*: Mirror-reflected visual information of the hands would decrease temporal accuracy and consistency on explicit timing tasks but not implicit timing tasks.

2. To test *Hypothesis 2*: Mirror-reflected visual information of the hands would increase spatial deviations and spatial variability on discontinuous drawing tasks but not continuous drawing tasks.
3. To test *Hypothesis 3*: All drawing tasks would be more stable when performed in the symmetrical mode than the asymmetrical mode, regardless of whether visual information was untransformed or mirror-reflected.
4. To test *Hypothesis 4*: An external auditory metronome would improve timing accuracy and consistency on all bimanual drawing tasks.

CHAPTER III

Methods

The primary purpose of this study was to examine the effect of visual transformation on implicitly and explicitly timed bimanual drawing tasks. This was accomplished by assessing movement accuracy and consistency during different drawing tasks and conditions.

3.1 Participants

Ten healthy right-handed volunteers were recruited from the student population at the University of Ottawa (mean age 23 years, range 19-25 years). All participants were given an informed consent document to read before participating in the study and any concerns regarding the experiment were addressed. Once the participant had signed the informed consent document, testing began.

3.2 Procedure

Participants were seated with a mirror drawing apparatus on the table in front of them. This apparatus consisted of a shield, which could be lowered to prevent vision of the hands, and a mirror, which provided an image of the subjects' hands beneath the shield.

A template with two identical shapes was then affixed to the apparatus and subjects were instructed to concurrently trace one shape with the left hand and the other shape with the right hand, in a rhythmic manner. Direct visual feedback regarding hand movements was prevented by the shield on the mirror drawing apparatus. In the mirror

condition, participants had to rely exclusively on the mirror reflection to execute the pattern (Figure 2.1A), whereas in the normal drawing condition, the shield was flipped up so that subjects were looking directly at their hands (Figure 2.1B). Unlike the mirror condition, the normal drawing condition did not impose a sensorimotor conflict on the participant and therefore, served as a control.

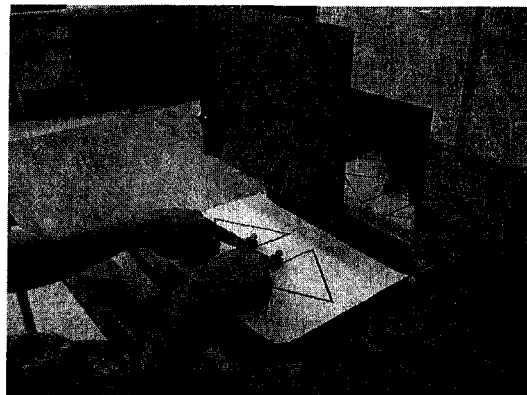
A**B**

Figure 2.1. Mirror drawing apparatus shown with the horizontal triangle template. **A**, the mirror drawing condition with the shield covering the hands. **B**, the normal drawing condition where subjects looked directly at their hands.

Four templates were used in the experiment: two circles, two equilateral triangles in a vertical orientation, two equilateral triangles in a horizontal orientation, and two vertical lines. The circles were 10 cm in diameter, the vertical lines were 10.5 cm long and all triangles had a side length of 10.5 cm (Figure 2.2). This ensured that circle circumference was approximately equal to the perimeter of a triangle and that line length was consistent across triangle and vertical line templates.

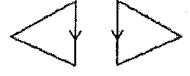
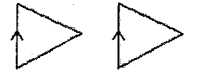
TEMPLATE	COORDINATION MODE	
	Symmetrical	Asymmetrical
Circles		
Vertical triangles		
Horizontal triangles		
Vertical lines		

Figure 2.2. The four geometric templates used in the experiment and a depiction of how each were drawn using the symmetrical mode and the asymmetrical mode.

A coordination mode, either symmetrical or asymmetrical, was specified at the start of each trial. When drawing triangles or circles in the symmetrical mode, the hands made mirror symmetrical movements by moving the left hand clockwise and the right hand counterclockwise. For this condition, subjects were always instructed to “move both hands in towards you”. In the asymmetrical mode, both hands moved in a clockwise direction. In this case, subjects were always instructed to “move both hands towards the right”. For vertical line drawing, the symmetrical mode was analogous to in-phase movements, and the asymmetrical mode corresponds with anti-phase movements. Hence, the given instructions were to “move both hands in the same direction” or to “move your hands in opposite directions”, respectively. Before beginning a given trial, the participant would place his/her left and right fingers at the top of the shapes on the template. This

was the starting position for every trial. The only exception was when drawing the vertical lines in the asymmetrical coordination mode; one finger would start at the top of a line and the other finger would start at the bottom of a line. The various templates and coordination patterns are shown in Figure 2.2.

The current study employed a synchronization-continuation paradigm to study timing in the different drawing tasks. A pacing signal was provided by a computer-controlled electronic metronome which specified the required movement frequency. When drawing the circle template, subjects had to complete one cycle of a circle per beat (0.67 Hz). When drawing triangles however, subjects drew one side of the triangle with each beat of the metronome (1.0 Hz). During the vertical line drawing condition, subjects again drew one line per metronome beat (1.0 Hz).

During synchronization trials, the pacing signal was presented for the entire duration of the trial. In the continuation condition, the metronome was only presented at the beginning of the trial and was turned off a third of the way through. For this condition, subjects were instructed to synchronize their movements with the metronome and to then continue to draw at the same frequency following removal of the signal.

The total number of conditions per subject was 32 (4 templates x 2 types of visual feedback x 2 coordination modes x 2 forms of pacing). There were five trials per condition, and all trials lasted 30 seconds. The entire experiment was divided up into five blocks of the 32 conditions each. To avoid confusion regarding the pacing signal during testing, the first 16 trials within a block were performed in the synchronization condition (paced) and the following 16 were performed in the continuation condition (unpaced). All other factors were entirely randomized.

3.3 Apparatus

The experiment was performed at the University of Ottawa in the Sensorimotor Neuroscience Laboratory. Mirror tracers (Lafayette Instrument Co., Lafayette, IN) were used for the experiment and kinematic data was acquired using the VICONTM MX-40 camera system. The VICONTM system captured the position of reflective markers placed on the index fingers at a rate of 200 Hz. The movement frequency was indicated by a computer-controlled electronic metronome that produced a 1 kHz tone for 20 ms.

3.4 Data Analysis

Kinematic data from the horizontal plane of motion and corresponding metronome data was analyzed using MATLAB and SPSS 12.0 statistical software. Our first dependent variable was timing error; this is the asynchrony between the metronome signal and the time at which the movement goal was achieved. A timing error of zero would indicate that the movement goal occurred coincident with the metronome beat. In this definition of timing error, there is no correction for drift.

For circle drawing, timing error was calculated by determining the asynchrony between the metronome signal and the point of maximum displacement in the *y* dimension. This point was defined as the start of a cycle for circle drawing. For line drawing, a synchronization interval was defined as a movement from the top of a line to the bottom, or vice versa. For this reason, timing error during line drawing was computed by comparing all maxima and minima in the *y* dimension to the occurrence of each metronome signal.

Triangle drawing was more complex because timing goals occurred in both the x and y dimensions. For vertical triangle drawing, the metronome was compared with the time of arrival at three different points around the triangle: the maximum in the y direction, the maximum in the x direction and the minimum in the x direction. These points correspond with the three vertices on a vertically-oriented triangle and subjects had been instructed to arrive at these target points in synchrony with each metronome beat.

Similarly, for horizontal triangle drawing, the metronome was compared with the time of arrival at the following three points on the triangle: maximum in the y direction, maximum in the x direction and lastly, the minimum in the y direction. For the continuation condition, in which the metronome was disengaged a third of the way into the trial, only data collected after metronome disengagement were analyzed for all four drawing tasks. In this case, movement goals were compared with the time at which the metronome signal would have occurred. Lastly, we calculated the means and standard deviations (SDs) of the computed timing errors across cycles and trials of the same condition for each subject separately.

To assess spatial deviations, we had to calculate different measures for each geometric shape. For circle drawing, tangential angle was selected because it provided an indication regarding the circularity of the drawn shape. Tangential angle is the angle subtended between the radius and a tangent to the circle; a constant value of 90° is required to draw a perfect circle. For circle drawing trials, this was calculated by repeatedly measuring the tangential angle between the radius and a tangent drawn from one instantaneous point to the next, then taking the mean.. The absolute difference

between the mean tangential angle and the target tangential angle of 90° was calculated to assess spatial deviations.

With respect to line drawing, line length was used as the measure of spatial deviation because it allowed us to assess whether subjects were deviating from the 10.5 cm line template. This was calculated by measuring the distance between successive maxima and minima in the y dimension. Then, the absolute difference between the mean drawn line length and target line length of 10.5 cm was computed. For triangle drawing trials, vertex angles were calculated by measuring the angles between successive line segments on the triangle. The absolute difference between the mean vertex angle and the intended angle of 60° was calculated; any deviations from 60° demonstrated a deviation from the equilateral triangle template. For all measures of spatial deviation, the average of all cycles within a trial was calculated, and then a mean and SD of all trials of the same condition was calculated for each subject separately.

For the calculation of peak speed, data were filtered using a second-order Savitzky-Golay filter with a frame size of 201 samples. Peak speeds for the line drawing trials were calculated by finding all the peaks on the speed profiles of the y component and taking the average. Peak speeds for circle and triangle trials were calculated by first calculating the x and y component speeds, then entering them into Equation 1.

$$v = \sqrt{v_x^2 + v_y^2} \quad (1)$$

Speed was plotted and the average of all peaks was calculated to determine mean peak speed for all circle and triangle drawing trials. Again, the mean and SD of all trials of the same condition was calculated for each subject.

Our last dependent variable was relative phase; this variable was selected to evaluate bimanual coordination. Prior to the calculation of relative phase, data was filtered using a tenth-order bidirectional Butterworth filter with a cutoff frequency of 10 Hz. The Hilbert transform (Equation 2) was used to calculate the instantaneous phase components for each hand, where τ is the time delay integration variable and x is the time series of the signal. The relative phase between the two hands can then be computed with Equation 3.

$$H(t) = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{x(\tau)}{t - \tau} d\tau \quad (2)$$

$$f(\tau) = \arctan \frac{Hy(t)x(t) - Hx(t)y(t)}{(x(t)y(t) + Hx(t)Hy(t))} \quad (3)$$

For line drawing, the Hilbert transform was used to compute the instantaneous phase of the y components. Subsequently, the difference between the instantaneous phase of the left and right hands was calculated to obtain relative phase. The same approach was used for circle drawing and triangle drawing; however, in this case, the Hilbert transform was used to calculate the instantaneous phase of the x components. As such, we were calculating relative phase in the x dimension. The deviation of relative phase was computed by calculating the difference between the actual relative phase that was achieved and the target or intended relative phase. The means and SDs of the computed data were calculated across cycles and trials of the same condition for each subject separately.

3.5 Results and Interpretation

The experiment involved a within-subjects design to assess movement accuracy and stability by examining timing error (ms), spatial deviation, peak speed (mm/s) and relative phase (degrees). Each template was analyzed independently because not all variables were consistent across the templates; for instance, different measures of spatial deviation were required for each geometric shape. Furthermore, a separate repeated-measures ANOVA was conducted for each dependent variable. All variables, with the exception of relative phase, involved separate measures for each hand; hence we included hand as the fourth factor in each ANOVA for timing error, spatial deviation and relative phase.

The following analyses were repeated for each template geometric template individually, including circles, vertical lines, vertical triangles and horizontal triangles. Mean and SD scores of timing error were analyzed using a 2 (Feedback) x 2 (Coordination mode) x 2 (Pacing) x 2 (Hand) analysis of variance (ANOVA) with repeated measures on all factors. Feedback refers to the type of visual information that was provided, either mirror-reversed or normal (control). Coordination mode refers to either the symmetrical or asymmetrical movement pattern and pacing refers to the synchronization and continuation conditions. Finally, hand refers to the left (non-dominant) hand and right (dominant) hand. Mean deviations of the spatial measures (tangential angle, line length and vertex angle) and SD scores of spatial measures, as well as mean peak speeds and SD scores of peak speeds were subjected to the same 2x2x2x2 ANOVA with the aforementioned factors.

Deviations from intended relative phase and SD of relative phase were also analyzed separately for each template. A 2(Feedback) x 2 (Coordination mode) x 2 (Pacing) ANOVA with repeated measures on all factors was employed. Significant effects were defined as those at the $p < 0.05$ probability level for all statistical tests.

CHAPTER IV

Results

4.1 Circle drawing

Figure 4.1 depicts typical trajectory plots of circle drawing trials where normal visual feedback was provided (Figure 4.1A) and where mirror reflected visual feedback was provided (Figure 4.1B). In the normal drawing condition, the circles appear very tight and circular, whereas in the mirror drawing condition, there is greater variability in the trajectory between successive cycles around the circle, particularly for the left hand.

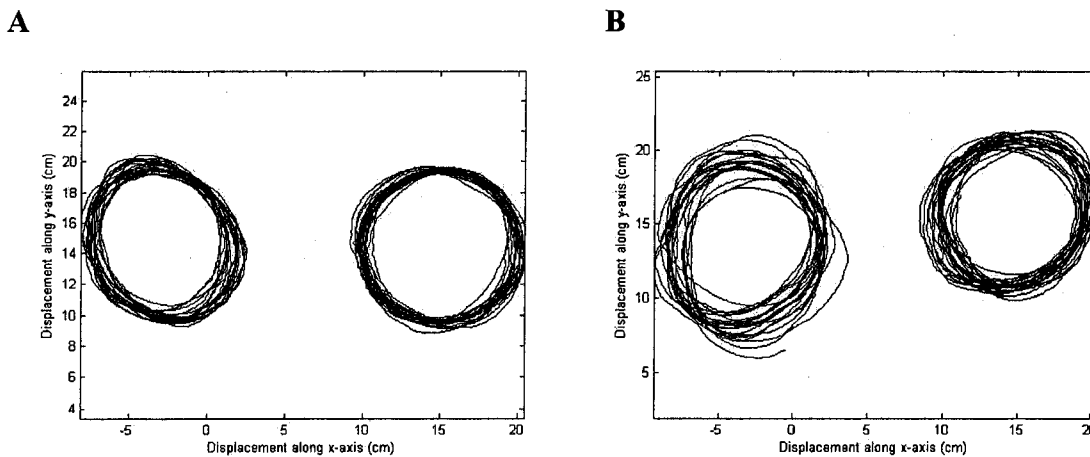


Figure 4.1. Typical trajectory plots of bimanual circle drawing trials from the first block of testing. **A**, trajectory plot of a trial with normal (untransformed) visual feedback. **B**, trajectory plot of a trial with mirror reflected visual feedback. Trajectories were produced by a subject drawing in the symmetrical mode with a metronome (0.67 Hz).

4.1.1 Timing error. Mean timing errors during circle drawing were computed and the general pattern of results showed that timing errors were greater in the unpaced phase of the continuation condition (Figure 4.2). Analysis of mean timing error revealed a significant main effect of pacing, $F(1, 9) = 35.628, p < 0.001$, which confirmed that timing

errors were greater in the continuation condition when there was no pacing signal ($M = 33.50$ ms) than in the synchronization condition ($M = 10.16$ ms).

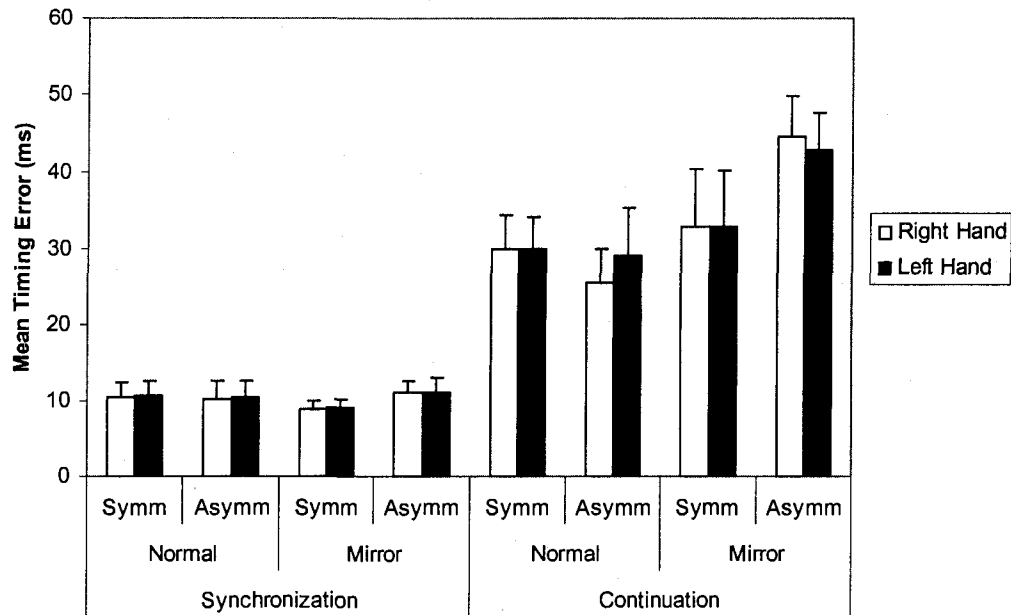


Figure 4. 2. Mean timing error (ms) during circle drawing for the right and left hands as a function of pacing, visual feedback, and coordination mode. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

A significant pacing $\times$ feedback interaction, $F(1, 9) = 5.688$, $p < 0.05$, showed that when the metronome was present, there was little difference in timing errors between the mirror drawing condition ($M = 9.96$ ms) and the normal drawing condition ($M = 10.35$ ms) (Figure 4.3). In the continuation condition however, timing errors were significantly larger for mirror drawing ($M = 38.32$ ms) than for normal drawing ($M = 28.67$ ms).

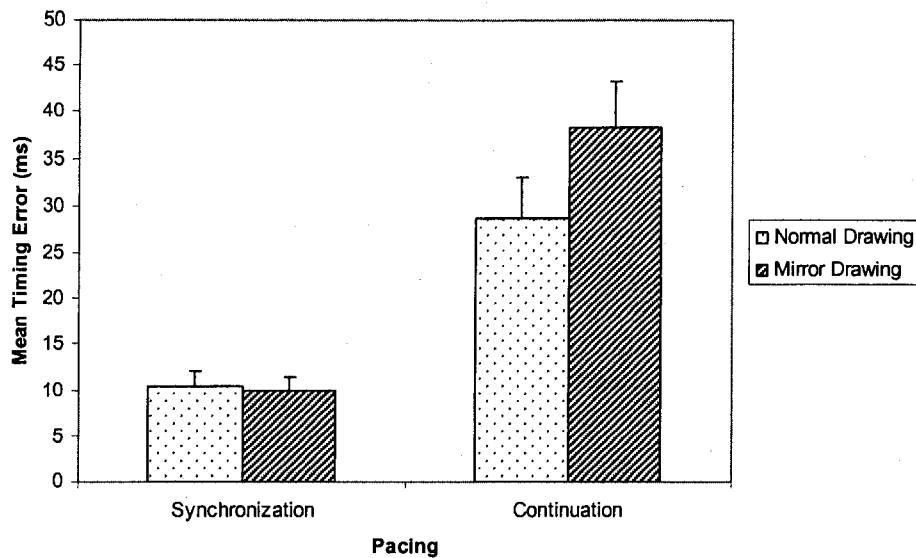


Figure 4.3. Mean timing error (ms) during normal circle drawing and mirror circle drawing as a function of pacing. Vertical lines indicate standard errors of the means.

Significant main effects of pacing, $F(1, 9) = 28.027, p < 0.001$, and hand, $F(1, 9) = 6.234, p < 0.05$, existed for the SD of timing error. Timing variability was greater in the continuation condition ($M = 20.62$ ms) than the synchronization condition ($M = 5.52$ ms) and was also greater in the right hand ($M = 13.14$ ms) than the left hand ($M = 13.00$ ms). Feedback and pacing both exhibited interactions with hand: pacing x hand, $F(1, 9) = 13.685, p < 0.05$, and feedback x hand, $F(1, 9) = 5.411, p < 0.05$.

4.1.2 Spatial deviation of tangential angle. Tangential angle was determined to evaluate spatial deviations from the circle template and to assess the spatial aspect of drawing accuracy. Mean tangential angle was influenced by coordination mode, $F(1, 9) = 6.781, p < 0.05$, such that spatial deviations were significantly greater when drawing circles in the asymmetrical mode ($M = 0.61^\circ$) than in the symmetrical mode ($M = 0.11^\circ$).

A significant interaction of pacing x hand, $F(1,9) = 6.895$, $p < 0.05$, revealed that the hands behaved differently under the two pacing conditions (Figure 4.4). Spatial deviations exhibited by the right hand were fairly similar irrespective of whether there was an external auditory metronome present ($M = 0.15^\circ$) or not ($M = 0.14^\circ$), unlike the left hand. The left hand showed smaller spatial deviations in the synchronization condition ($M = 0.10^\circ$) than the continuation condition ($M = 0.15^\circ$), and within the synchronization condition, the left hand showed greater spatial accuracy than the right hand.

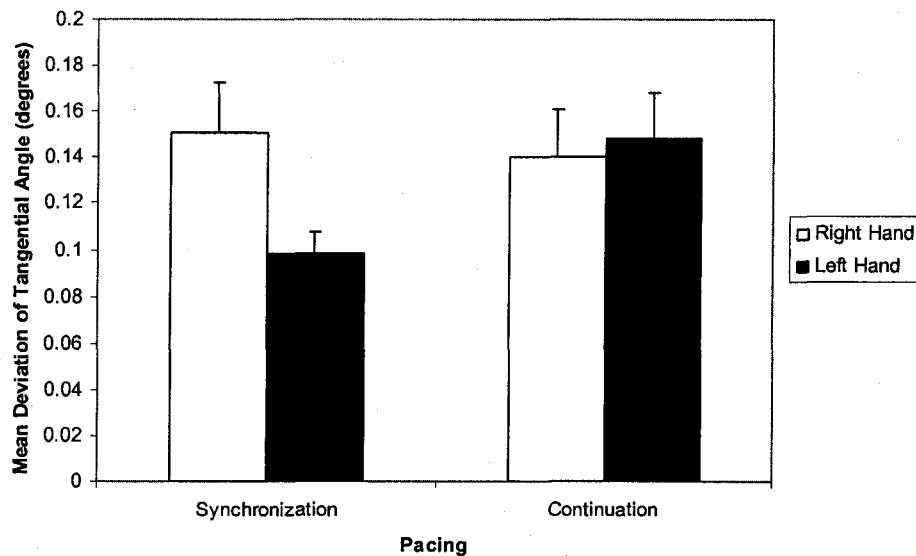


Figure 4.4. Mean deviation of tangential angle (degrees) for the right and left hands as a function of pacing. Vertical lines indicate standard errors of the means.

The SD of tangential angle was analyzed to assess whether spatial variability of the movement trajectory varied between the different experimental conditions (Figure 4.5). This analysis revealed significant main effects of visual feedback, $F(1,9) = 94.606$, $p < 0.001$ and hand, $F(1,9) = 115.515$, $p < 0.001$. The SD of tangential angle was greater

during mirror drawing ($M = 11.87^\circ$) than during control drawing ($M = 9.36^\circ$), meaning that spatial variability increased under visual transformation. Also, the left hand was found to demonstrate greater spatial variability ($M = 11.96^\circ$) than the right hand ($M = 9.27^\circ$). Recall that all subjects were right-handed.

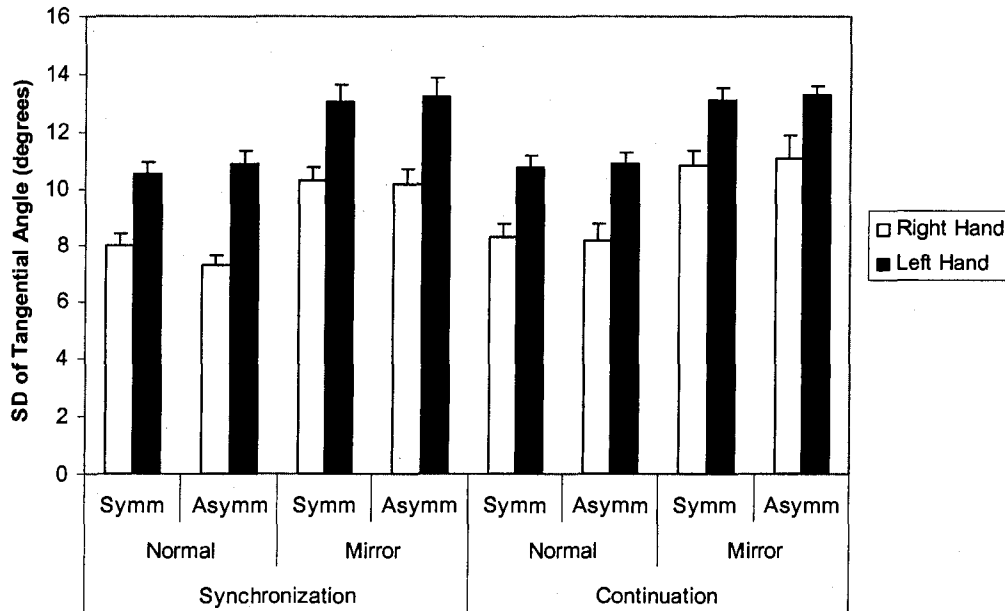


Figure 4.5. SD of tangential angle (degrees) for the right and left hands during circle drawing as a function of pacing, visual feedback, and coordination mode. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination. Vertical lines indicate standard errors of the means.

4.1.3 Peak speed. Analysis of peak speed during circle drawing revealed a significant main effect of coordination mode, $F(1,9) = 7.958$, $p < 0.05$, where mean peak speed was greater during the asymmetrical mode ($M = 209.44$ mm/s) than the symmetrical mode ($M = 207.32$ mm/s). The pacing x feedback interaction, $F(1,9) = 17.183$, $p < 0.01$, and pacing x feedback x mode interaction, $F(1,9) = 19.356$, $p < 0.01$, both

reached significance. Peak speed was higher during mirror drawing and increased dramatically during asymmetrical circle drawing in the mirror when the metronome was on ($M = 213.40$ mm/s) (Figure 4.6).

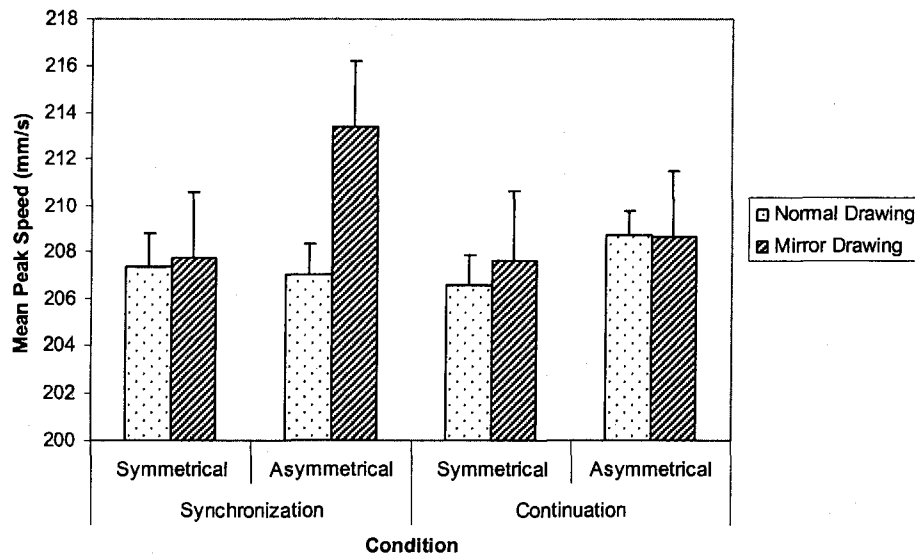


Figure 4.6. Mean peak speed (mm/s) during normal and mirror circle drawing as a function of pacing and coordination mode. Peak speed was greatly increased during mirror circle drawing in the asymmetrical mode with a pacing signal. Vertical lines indicate standard errors of the means.

There was also a significant feedback $\times$ hand interaction, $F(1,9) = 5.467$, $p < 0.05$.

Within feedback conditions, the hands showed an opposite pattern of results. In the normal drawing condition, the right hand demonstrated higher peak speed ($M = 208.69$ mm/s) than the left hand ($M = 206.11$ mm/s), whereas in the mirror condition, it was the left hand which exhibited greater peak speed ($M = 210.92$ mm/s) than the right ($M = 207.80$ mm/s) (Figure 4.7).

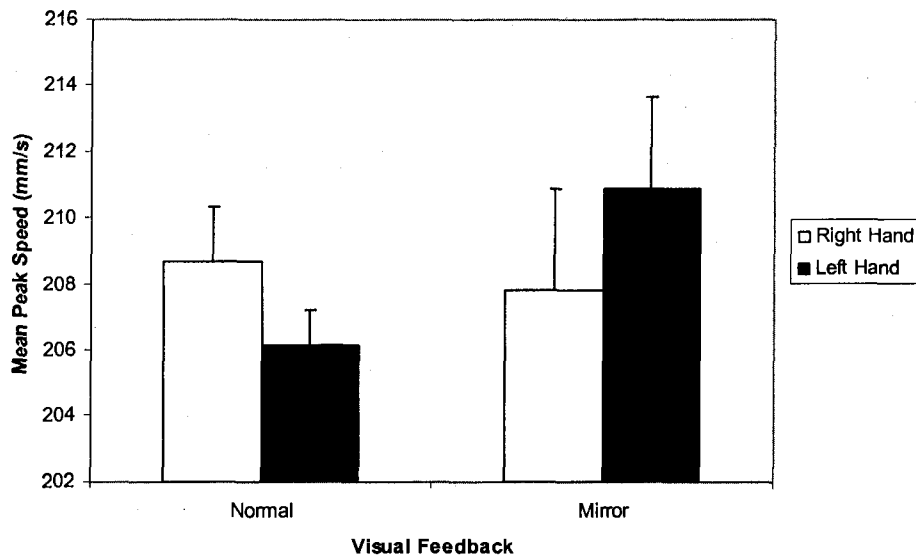


Figure 4.7. Mean peak speed (mm/s) for the right and left hands during circle drawing in the normal and mirror feedback conditions. Vertical lines indicate standard errors of the means.

With respect to the variability of peak speed, a significant main effect of feedback, $F(1,9) = 27.044, p < 0.01$, and mode, $F(1,9) = 7.503, p < 0.05$, were observed. As expected, mirror feedback resulted in greater peak speed variability ($M = 12.06$ mm/s) in comparison to normal feedback ($M = 10.42$ mm/s), and the asymmetrical coordination mode resulted in greater peak speed variability ($M = 11.67$ mm/s) than the symmetrical mode ($M = 10.81$ mm/s).

4.1.4 Relative phase. Relative phase in the x dimension was analyzed as a measure of accuracy and stability of coordination patterns. Analysis of deviations from intended relative phase revealed a main effect of feedback, $F(1, 9) = 10.130, p < 0.05$. Relative phase was less accurate during mirror drawing ($M = 10.29^\circ$) than normal

drawing ($M = 6.66^\circ$), meaning that the coupling between the hands decreased under conditions of altered visual feedback in comparison to normal drawing.

Feedback was again observed as a main effect when the SD scores of relative phase were analyzed, $F(1, 9) = 8.820, p < 0.05$. Not only did mirror drawing decrease the accuracy of relative phase, it also increased relative phase variability ($M = 10.77^\circ$) in comparison to normal drawing ($M = 9.54^\circ$). There was also a reliable effect of coordination mode, $F(1, 9) = 52.221, p < 0.001$, where relative phase was more variable when drawing circles in the asymmetrical mode ($M = 11.55^\circ$) than the symmetrical mode ($M = 8.76^\circ$).

4.2 Line drawing

Figure 4.8 shows typical trajectory plots from vertical line drawing trials where movements were monitored through direct vision of the hands (Figure 4.8A) and where movements were monitored in the mirror (Figure 4.8B). Qualitatively, the normal vision and mirror vision trials appear very similar, with the left hand showing greater variability in the horizontal direction than the right hand for both visual feedback conditions.

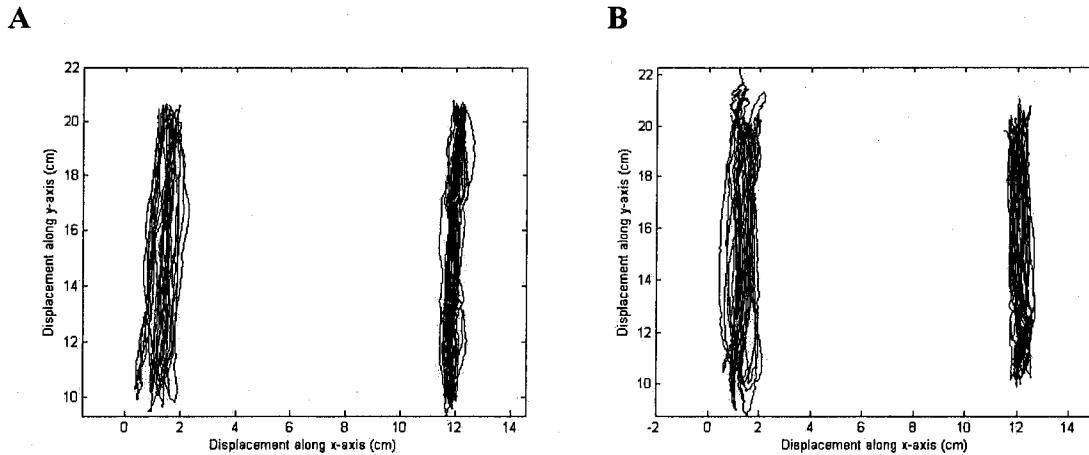


Figure 4.8. Typical trajectory plots of bimanual line drawing trials from the first block of testing. **A**, trajectory plot of a trial with normal (untransformed) visual feedback. **B**, trajectory plot of a trial with mirror reflected visual feedback. Trajectories were produced by a subject drawing in the symmetrical mode with a pacing signal (1.0 Hz).

4.2.1 Timing error. Analysis of mean timing error showed a highly significant effect of pacing $F(1, 9) = 56.926, p < 0.001$, where mean timing error was greater when there was no pacing signal ($M = 23.19$ ms) than when a signal was provided ($M = 7.26$ ms). This effect can be seen when looking at the overall pattern of results for all conditions (Figure 4.9). A three-way interaction of feedback $\times$ mode $\times$ hand was significant, $F(1, 9) = 6.153, p < 0.05$. During normal drawing, timing was more accurate in the asymmetrical mode ($M = 12.63$ ms) than the symmetrical mode ($M = 16.85$ ms), whereas the opposite pattern of results was seen for mirror drawing (Figure 4.10). Additionally, timing error for symmetrical drawing actually improved during mirror drawing ($M = 14.27$ ms), whereas timing error for asymmetrical drawing worsened when mirror drawing ($M = 17.15$ ms).

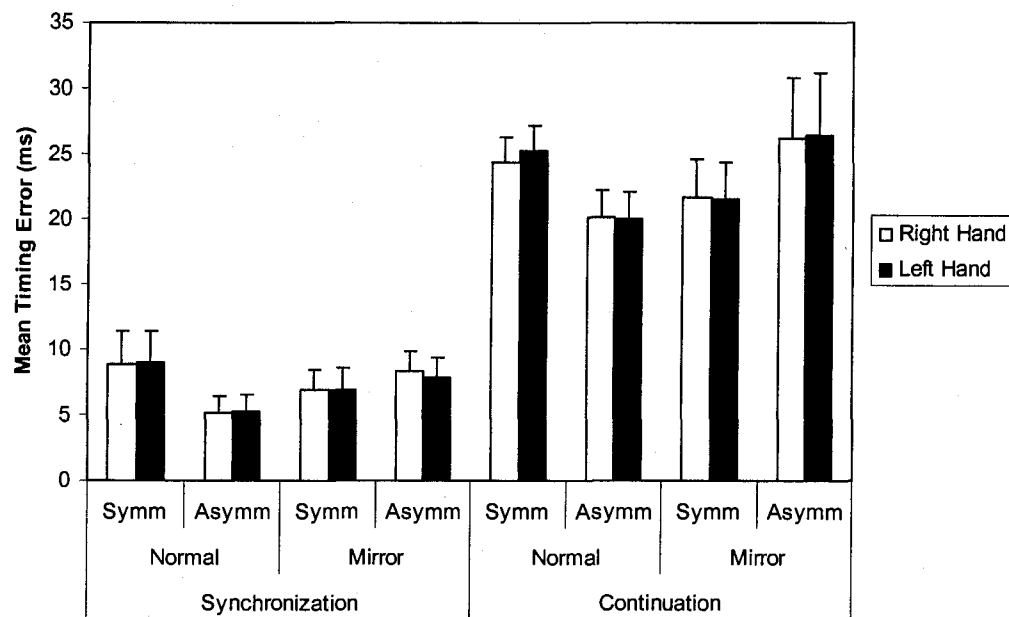


Figure 4.9. Mean timing error (ms) for the right and left hands during vertical line drawing as a function of pacing, visual feedback, and coordination mode. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination. Vertical lines indicate standard errors of the means.

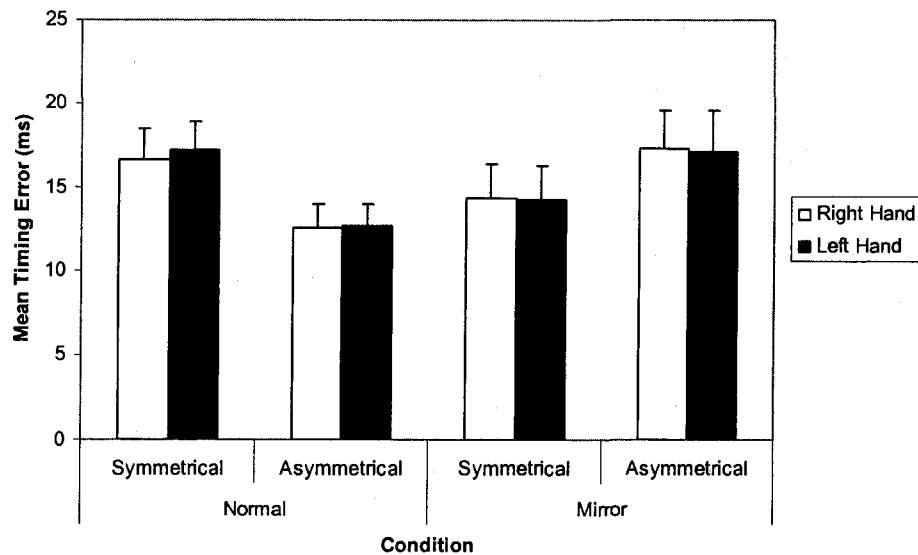


Figure 4.10. Mean timing error (ms) for the left and right hands during vertical line drawing as a function of type of visual feedback and coordination mode. Vertical lines indicate standard errors of the means.

Analysis of the SD of timing error also revealed a significant main effect of pacing, $F(1, 9) = 29.416, p < 0.001$. Again, timing variability was higher in the continuation condition ($M = 12.05$ ms) than in the synchronization condition ($M = 2.91$ ms). Timing variability was also significantly higher in the non-dominant hand ($M = 7.50$ ms) than in the dominant hand ($M = 7.46$ ms), $F(1, 9) = 6.860, p < 0.05$.

4.2.2 Spatial deviation of line length. To assess the spatial aspect of drawing accuracy, spatial deviations from the vertical line template were analyzed. Spatial deviations were significantly affected by hand alone, $F(1, 9) = 12.723, p < 0.01$. The left hand showed greater spatial deviations ($M = 8.88$ mm) than the right hand ($M = 6.87$ mm). Feedback, pacing and mode had no effect on spatial accuracy. This lack of an effect

of feedback demonstrates that during mirror drawing, subjects were capable of drawing the lines as accurately as when they were looking directly at their hands.

Although subjects were able to accurately trace the lines on average, it is possible that this was accomplished with considerable variation between iterations and trials. The SD of drawn line length across all conditions was analyzed (Figure 4.11). A linear increase of line length variability was evident in the progression from simpler drawing tasks, involving either the symmetrical coordination or normal visual feedback (or both), to more complex drawing tasks, involving either the asymmetrical coordination mode or mirror reflected visual feedback (or both). This analysis revealed significant main effects of feedback, $F(1, 9) = 33.210, p < 0.001$, mode, $F(1, 9) = 77.030, p < 0.001$, and hand, $F(1, 9) = 25.184, p < 0.01$.

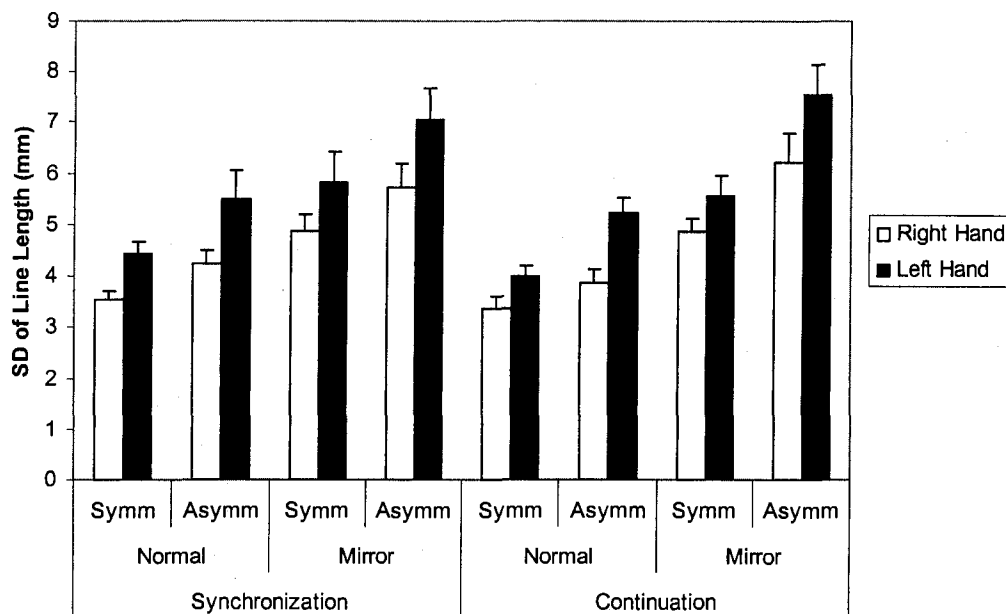


Figure 4.11. SD of drawn line length (mm) across all drawing conditions. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

Feedback and hand both exhibited interactions with coordination mode: feedback x mode, $F(1, 9) = 6.532$, $p < 0.05$, and hand x mode, $F(1, 9) = 11.335$, $p < 0.01$. As expected, spatial variability was greater during mirror drawing ($M = 5.96$ mm) than under normal drawing conditions ($M = 4.27$ mm). Furthermore, the asymmetrical coordination mode ($M = 5.67$ mm) also resulted in greater variability than the symmetrical mode ($M = 4.55$ mm) (Figure 4.12). This is consistent with the predictions of the HKB model where anti-phase movements are predicted to be less stable than in-phase movement patterns. Similar to the analysis of variability of tangential angle for circle drawing, the left hand ($M = 5.64$ mm) again showed greater spatial variability than the right hand ($M = 4.59$ mm) during line drawing. Both hands also showed increased variability when drawing in the asymmetrical mode (Figure 4.13).

Feedback and hand both exhibited interactions with coordination mode: feedback x mode, $F(1, 9) = 6.532$, $p < 0.05$, and hand x mode, $F(1, 9) = 11.335$, $p < 0.01$. As expected, spatial variability was greater during mirror drawing than under normal drawing conditions and was more variable when drawing in the asymmetrical mode than the symmetrical mode, regardless of the type of visual feedback (Figure 4.12). This is consistent with the predictions of the HKB model where anti-phase movements are predicted to be less stable than in-phase movement patterns. Similar to the analysis of tangential angle variability for circle drawing, the left hand again showed greater spatial variability than the right hand (Figure 4.13). Furthermore, both hands also showed increased variability when drawing in the asymmetrical mode.

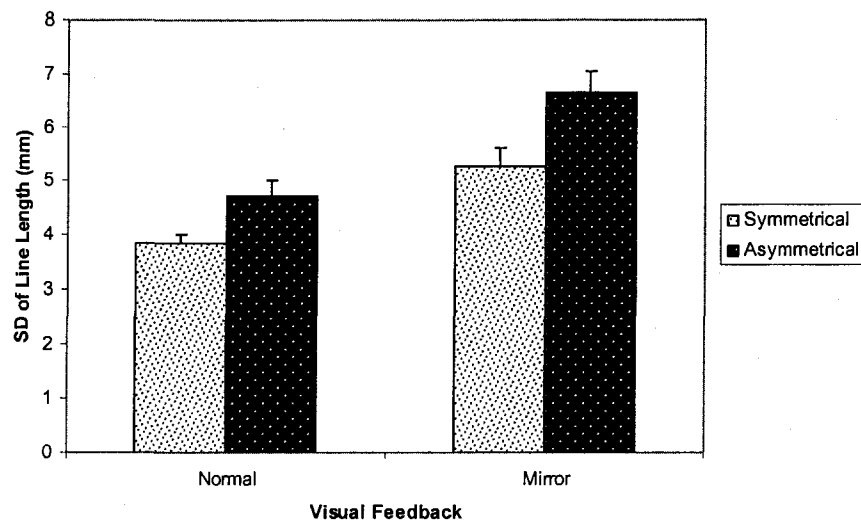


Figure 4.12. SD of drawn line length (mm) for the symmetrical and asymmetrical modes in normal and mirror feedback conditions. Vertical lines indicate standard errors of the means.

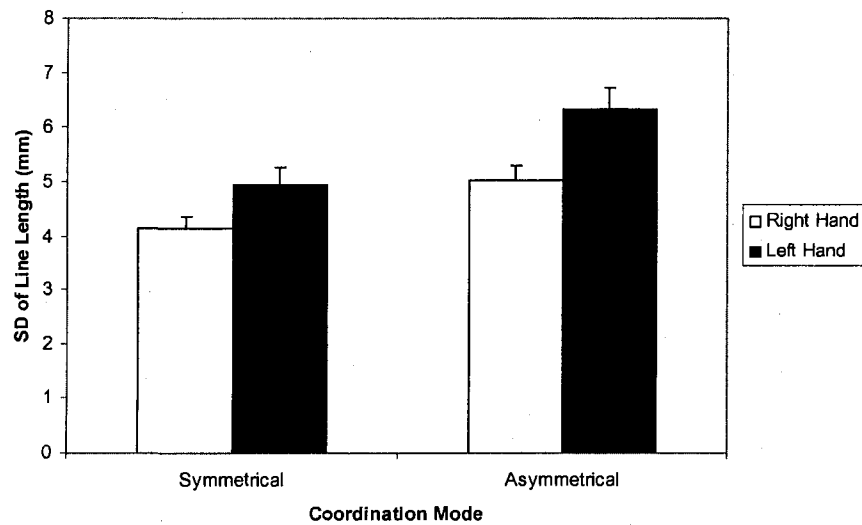


Figure 4.13. SD of drawn line length (mm) for the right and left hands as a function of coordination mode. Vertical lines indicate standard errors of the means.

4.2.3 *Peak speed.* Mean and SD of peak speed were analyzed to gain insight into aspects of the actual execution of the drawing movements. This analysis revealed significant main effects of pacing, $F(1, 9) = 16.282, p < 0.05$, feedback, $F(1, 9) = 6.860, p < 0.05$, and hand, $F(1, 9) = 9.041, p < 0.05$, on peak speed during vertical line drawing. Mean peak speed was higher when there was no pacing signal ($M = 175.57$ mm/s) than when the metronome was provided ($M = 172.79$ mm/s). Furthermore, peak speed was lower during mirror drawing ($M = 169.63$ mm/s) than control drawing (178.74 mm/s) and was also lower in the right hand ($M = 172.18$ mm/s) than in the left hand ($M = 176.19$ mm/s).

A significant feedback x mode interaction, $F(1, 9) = 7.031, p < 0.05$, showed that for the normal vision condition, peak speed was greater when drawing in the asymmetrical mode ($M = 181.60$ mm/s) than the symmetrical mode ($M = 175.89$ mm/s). During mirror drawing however, there was an overall decrease in peak speed and little difference between the peak speed of symmetrical ($M = 170.52$ mm/s) and asymmetrical coordination modes ($M = 168.74$ mm/s) (Figure 4.14). Lastly, there was a significant pacing x feedback x mode x hand interaction, $F(1, 9) = 5.917, p < 0.05$.

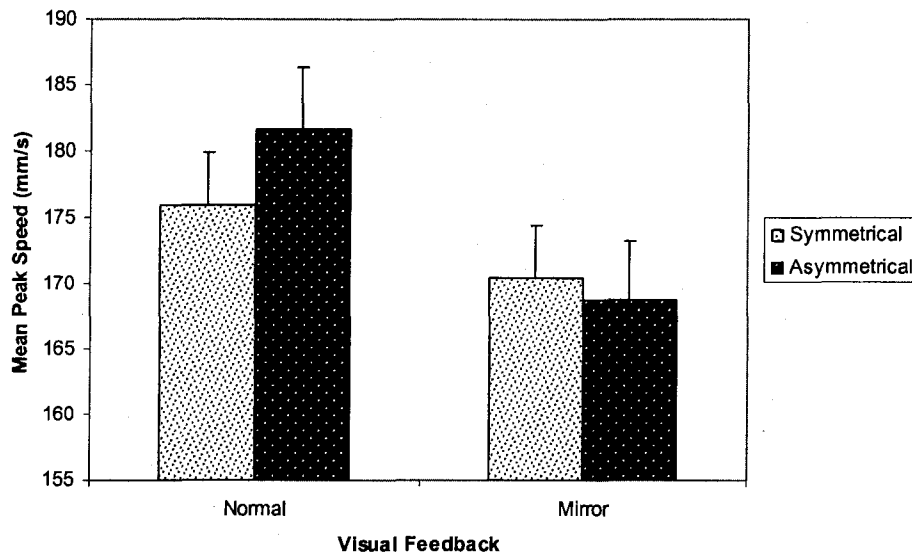


Figure 4.14. Mean peak speed (mm/s) during vertical line drawing for the symmetrical and asymmetrical coordination modes as a function of visual feedback condition. Vertical lines indicate standard errors of the means.

The SD of peak speed during line drawing was significantly affected by feedback, $F(1, 9) = 13.995$, $p < 0.01$, mode, $F(1, 9) = 104.942$, $p < 0.001$, and hand, $F(1, 9) = 24.022$, $p < 0.01$. Peak speed was less consistent when drawing with mirror feedback ($M = 11.17$ mm/s) in comparison to normal vision ($M = 9.72$ mm/s). The asymmetrical coordination mode ($M = 11.13$ mm/s) yielded more variable peak velocities than the symmetrical coordination mode ($M = 9.75$ mm/s) and peak speed variability was also greater in the left hand ($M = 11.36$ mm/s) than the right hand (9.52 mm/s).

Feedback and hand both interacted with pacing: pacing x feedback, $F(1, 9) = 9.182$, $p < 0.05$ and pacing x hand $F(1, 9) = 12.517$, $p < 0.01$. The three-way interaction of pacing x feedback x hand, $F(1, 9) = 5.817$, $p < 0.05$, also reached significance (Figure 4.15). In the normal drawing condition, peak speed variability was greater when there

was no pacing signal, whereas in the mirror feedback condition, variability was actually greater when the metronome was present. However, this effect was more pronounced in the left hand than the right hand. For the right hand, peak speed variability was similar across the pacing conditions.

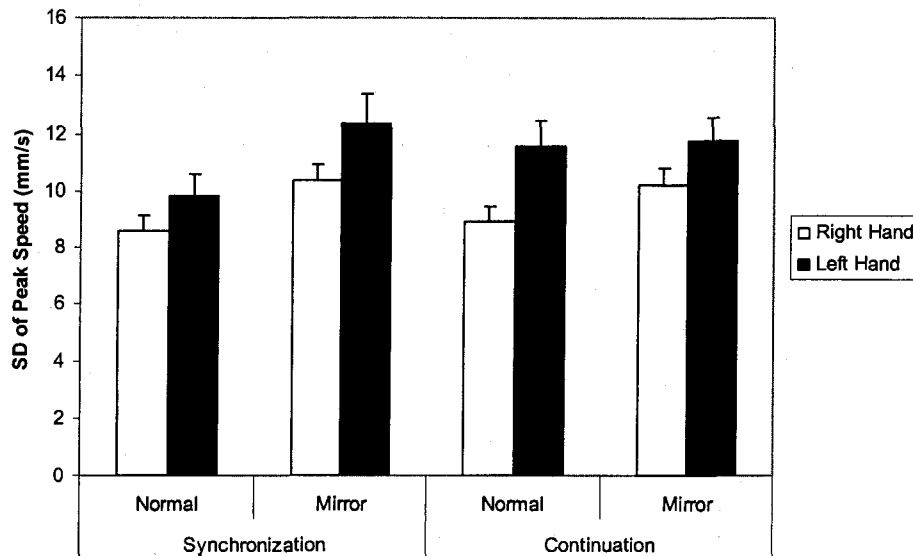


Figure 4.15. SD of peak speed (mm/s) for the right and left hands during vertical line drawing as a function of pacing and type of visual feedback. Vertical lines indicate standard errors of the means.

Analysis of peak speed variability scores also revealed a reliable interaction of mode x hand interaction, $F(1, 9) = 23.263, p < 0.01$, and pacing x mode x hand, $F(1, 9) = 5.547, p < 0.05$. These interactions showed that peak speed variability of both hands increased during asymmetrical line drawing, but the increase in variability of the left hand was more pronounced. Peak speed variability was similar across pacing conditions for symmetrical coordination whereas asymmetrical coordination showed greater variability in the unpaced condition (Figure 4.16).

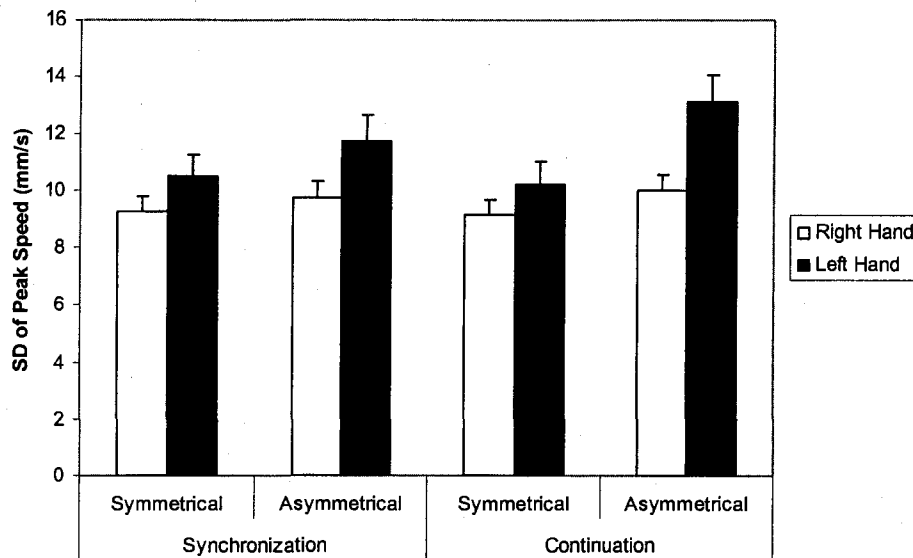


Figure 4.16. SD of peak speed (mm/s) for the right and left hands during vertical line drawing as a function of pacing and coordination mode. Vertical lines indicate standard errors of the means.

4.2.4 *Relative phase.* Deviations from the intended relative phase during vertical line drawing were evaluated and a significant main effect of mode, $F(1, 9) = 6.267$, $p < 0.05$, and a pacing x mode interaction, $F(1, 9) = 9.634$, $p < 0.05$, were observed. Relative phase during symmetrical line drawing seems unaffected by the pacing signal; mean deviation of relative phase in the synchronization condition ($M = 1.59^\circ$) was similar to that in the continuation condition ($M = 1.60^\circ$). In the asymmetrical condition however, relative phase accuracy was reduced overall and was worse when the pacing signal was present ($M = 3.01^\circ$) in comparison to the unpaced condition ($M = 2.55^\circ$) (Figure 4.17).

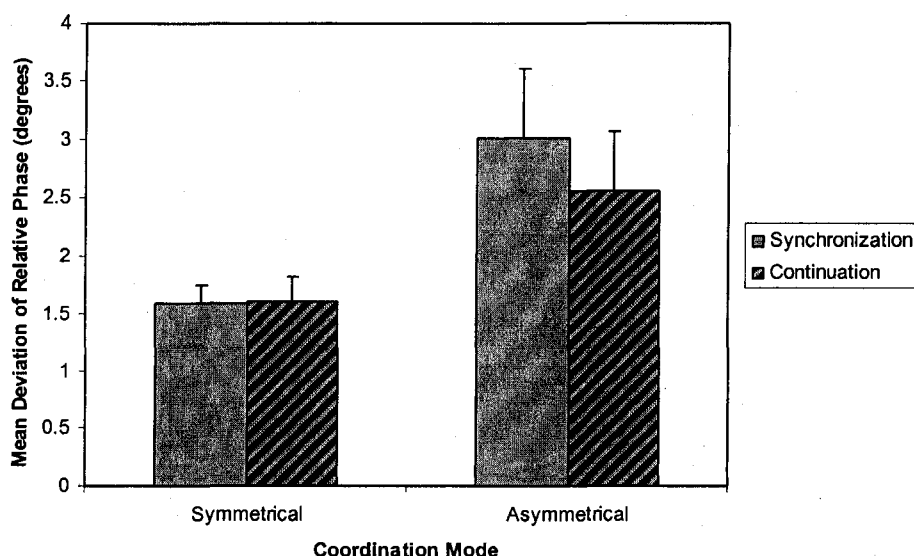


Figure 4.17. Mean deviation of relative phase (degrees) during vertical line drawing for the synchronization and continuation conditions as a function of coordination mode.

Vertical lines indicate standard errors of the means.

With respect to relative phase variability, analysis of the SD scores of relative phase revealed significant main effects of pacing, $F(1, 9) = 6.608, p < 0.05$, feedback, $F(1, 9) = 8.092, p < 0.05$, and mode, $F(1, 9) = 88.574, p < 0.001$. Relative phase variability was greater during line drawing with a metronome ($M = 7.11^\circ$) than during the unpaced phase of continuation drawing ($M = 6.68^\circ$). Furthermore, variability was higher under conditions of transformed visual feedback ($M = 7.46^\circ$) than normal vision ($M = 6.34^\circ$) and was significantly greater for asymmetrical coordination ($M = 9.20^\circ$) than for symmetrical coordination ($M = 4.60^\circ$).

4.3 Vertical triangle drawing

Figure 4.18 depicts typical movement trajectory plots of vertical triangle drawing trials for the different vision conditions. The trajectory plot for the normal vision condition (Figure 4.18A) shows greater accuracy and far less spatial variability than the trajectory plot for the mirror vision condition (Figure 4.18B). During mirror drawing, triangle vertices appear more rounded and line segments are less linear. This effect is especially apparent in the trajectory made by the left hand.

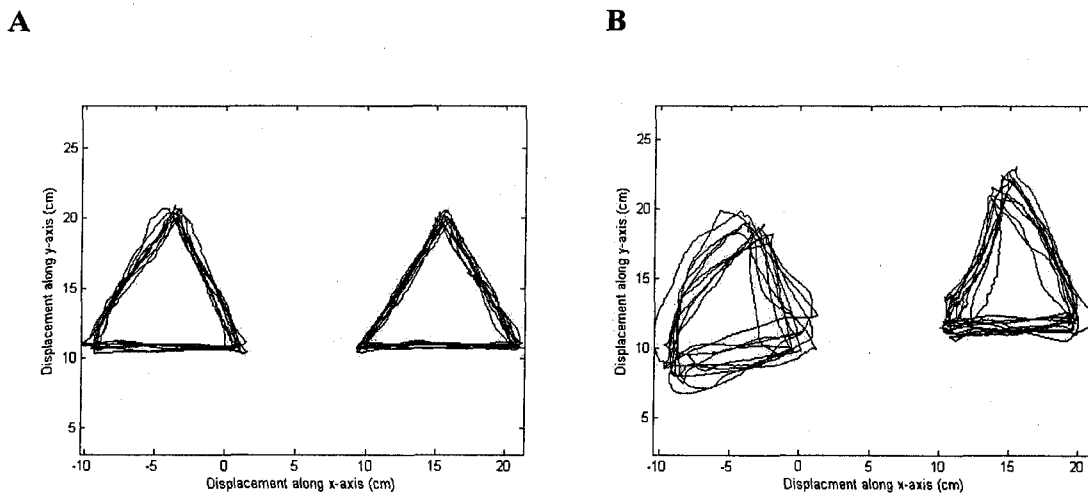


Figure 4.18. Typical trajectory plots of bimanual vertical triangle drawing trials from the first block of testing. **A**, trajectory plot of a trial with normal (untransformed) visual feedback. **B**, trajectory plot of a trial with mirror reflected visual feedback. Trajectories were produced by a subject drawing in the symmetrical mode with a pacing signal (1.0 Hz).

4.3.1 Timing error. Mean timing error per cycle during vertical triangle drawing was affected reliably by pacing alone, $F(1, 9) = 25.773$, $p < 0.05$. As expected, timing errors were reduced by the presence of a pacing signal across all conditions ($M = 10.01$

ms) and consequently increased when the metronome was removed ($M = 26.84$ ms) (Figure 4.19). Likewise, there was a significant effect of pacing on the SD of timing error, $F(1, 9) = 22.554$, $p < 0.05$; this indicates that timing variability is greater in the continuation condition ($M = 14.28$ ms) than the synchronization condition ($M = 3.94$ ms).

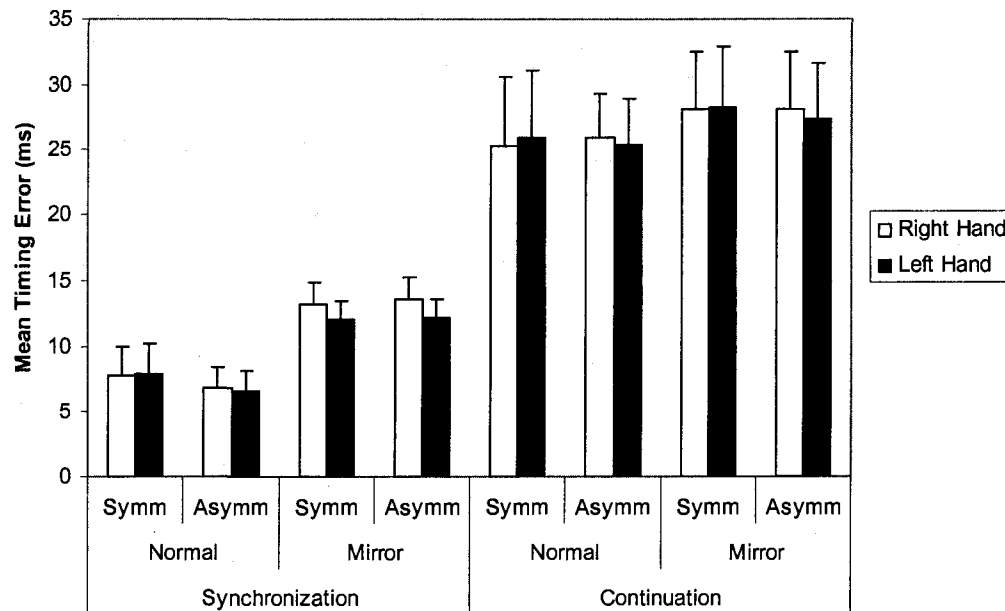


Figure 4.19. Mean timing error (ms) for the right and left hands during vertical triangle drawing across all conditions. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

4.3.2 Spatial deviation of vertex angles. Pacing, feedback, mode and hand did not affect the accuracy of vertex angles. The lack of any main effects or interactions suggests that participants were able to accurately achieve vertex angles of 60° under all conditions.

The analysis of SD scores of vertex angles showed a main effect of feedback, $F(1, 9) = 33.642, p < 0.001$, where vertex angle variability increased when drawing with mirror reflected visual information ($M = 8.23^\circ$), in comparison to normal visual feedback ($M = 5.17^\circ$) (Figure 4.20). Pacing and feedback both interacted with mode and hand: pacing $\times$ mode $\times$ hand, $F(1, 9) = 5.608, p < 0.05$, and feedback $\times$ mode $\times$ hand, $F(1, 9) = 8.904, p < 0.05$. This first interaction (Figure 4.21) revealed that within pacing conditions, the right hand appeared to be less affected by coordination mode and thus, stayed more consistent between the symmetrical and asymmetrical coordination patterns. The overall variability of both hands was consistently greater in the synchronization condition than the continuation condition.

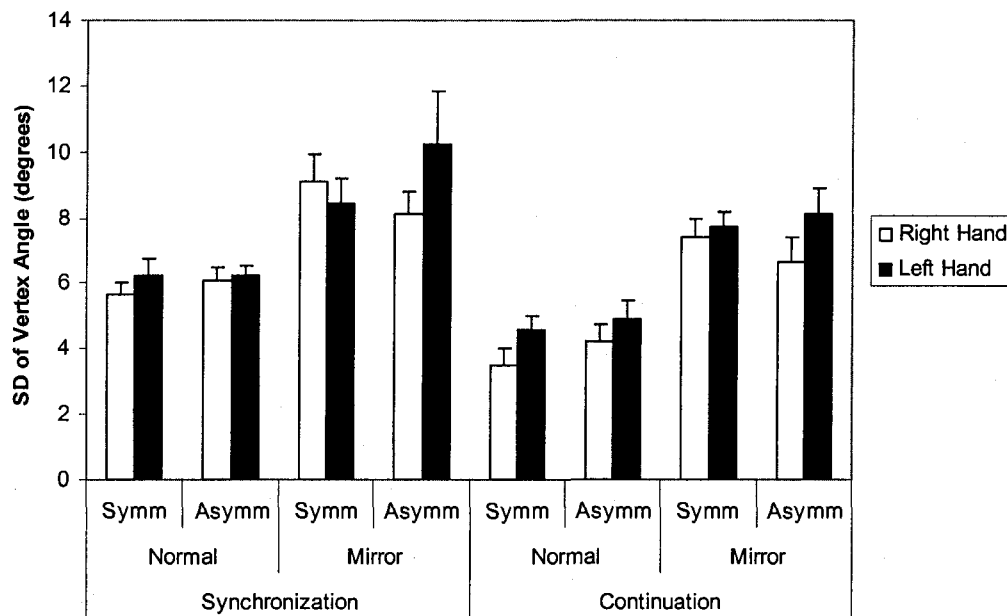


Figure 4.20. SD of vertex angle (degrees) for the right and left hands during vertical triangle drawing across all conditions. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

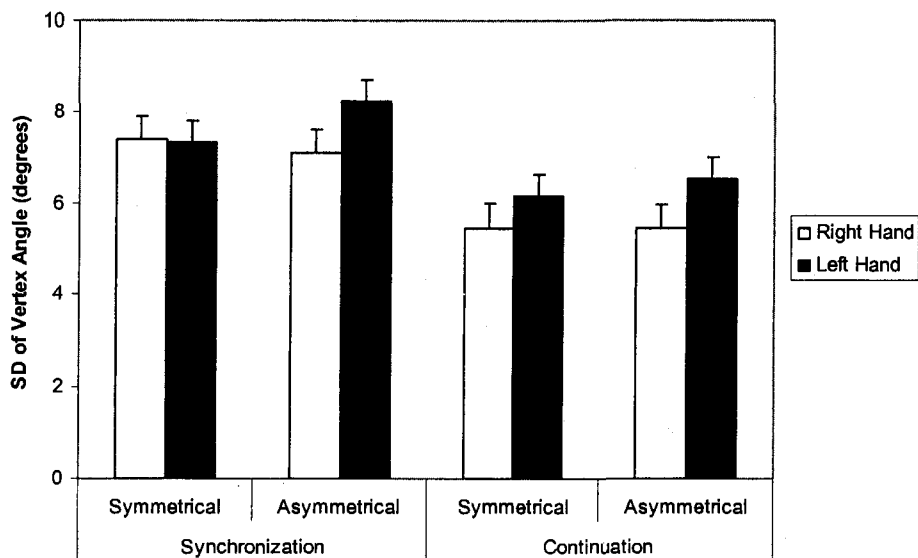


Figure 4.21. SD of vertex angle (degrees) drawn by the right and left hands during vertical triangle drawing as a function of pacing and coordination mode. Vertical lines indicate standard errors of the means.

With respect to the feedback $\times$ mode $\times$ hand interaction (Figure 4.22), an overall increase in variability of both hands was observed during mirror drawing and generally, there was also an increase in variability during asymmetrical drawing. However, the right hand appears to have behaved differently than the left hand during mirror drawing; vertex angles were actually more variable for symmetrical triangle drawing than asymmetrical triangle drawing. This finding is contrary to expectations since it was hypothesized that the symmetrical coordination mode would be more stable for all drawing tasks.

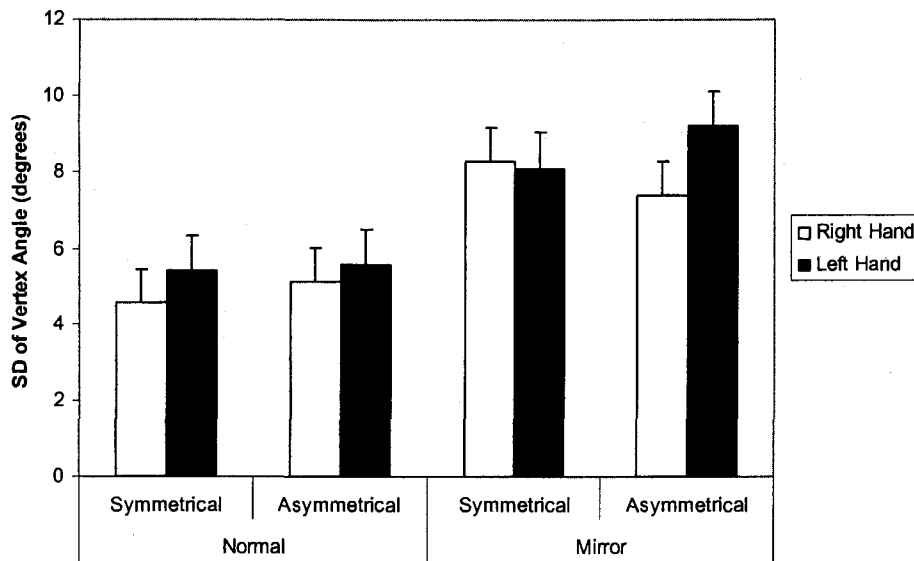


Figure 4.22. SD of vertex angle (degrees) drawn by the right and left hands during vertical triangle drawing as a function of the type of visual feedback and coordination mode. Vertical lines indicate standard errors of the means.

4.3.3 Peak speed. Analysis of mean peak speed during vertical triangle drawing revealed significant main effects of pacing, $F(1,9) = 5.669, p < 0.05$, and feedback, $F(1,9) = 103.097, p < 0.001$. Peak speed was greater when there was no metronome to pace drawing movements ($M = 171.40$ mm/s) in comparison to the paced condition ($M = 168.22$ mm/s). Visual feedback also affected peak speed such that movements were significantly slower when drawing in the mirror ($M = 163.14$ mm/s) than during normal drawing with unaltered visual feedback ($M = 176.47$ mm/s).

The effect of visual feedback differed between the left and right hands resulting in a significant feedback $\times$ hand interaction, $F(1,9) = 6.491, p < 0.05$. The interaction of feedback $\times$ mode $\times$ hand also reached significance, $F(1,9) = 7.245, p < 0.05$. Under the normal vision condition, peak speed of the left hand was lower for symmetrical

coordination ($M = 174.75$ mm/s) than asymmetrical coordination ($M = 177.31$ mm/s), whereas during mirror drawing, the peak speed was similar across both coordination modes (Figure 4.23). The opposite was seen in the right hand, where peak speed was similar across both coordination modes in the normal vision condition and it was in the mirror condition that a lower peak speed was observed for symmetrical triangle ($M = 160.07$ mm/s) drawing than asymmetrical drawing ($M = 162.93$ mm/s).

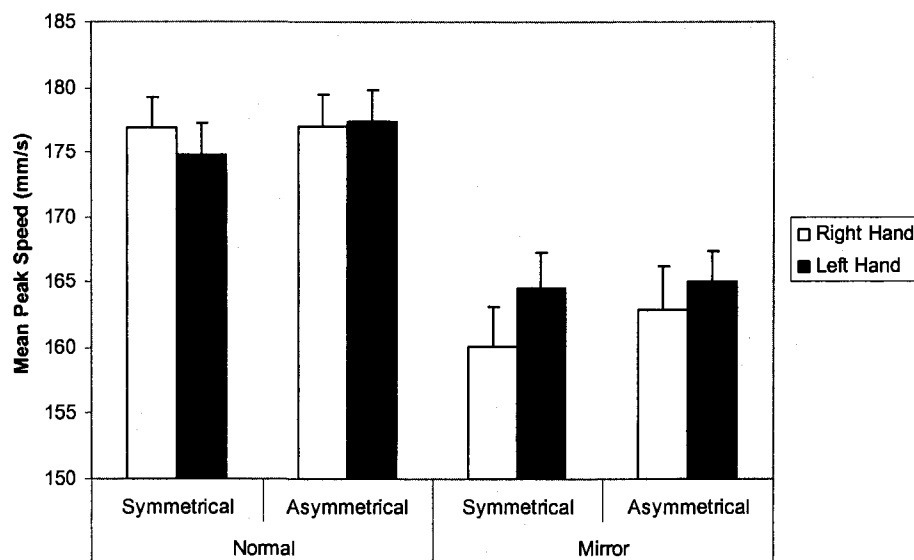


Figure 4.23. Mean peak speed (mm/s) for the right and left hands during vertical triangle drawing as a function of visual feedback and coordination mode. Vertical lines indicate standard errors of the means.

Analysis of the peak speed variability scores revealed significant main effects of feedback, $F(1,9) = 27.530$, $p < 0.05$, and hand, $F(1,9) = 5.447$, $p < 0.05$. As was the case with line drawing, peak speed of limb movements became less consistent during mirror drawing ($M = 13.74$ mm/s) than normal drawing ($M = 11.75$ mm/s). Also, the left hand ($M = 13.30$ mm/s) showed greater peak speed variability than the right hand ($M = 12.19$

mm/s). There were three significant interactions: pacing x mode, $F(1,9) = 6.996$, $p < 0.05$, pacing x hand $F(1,9) = 11.075$, $p < 0.01$, and feedback x mode x hand $F(1,9) = 10.542$, $p < 0.05$. Overall, peak speed variability was greater in the left hand than the right hand (Figure 4.24). Furthermore, variability of the left hand did not appear to be affected by the pacing, whereas the right hand exhibited less peak speed variability when the metronome was turned off.

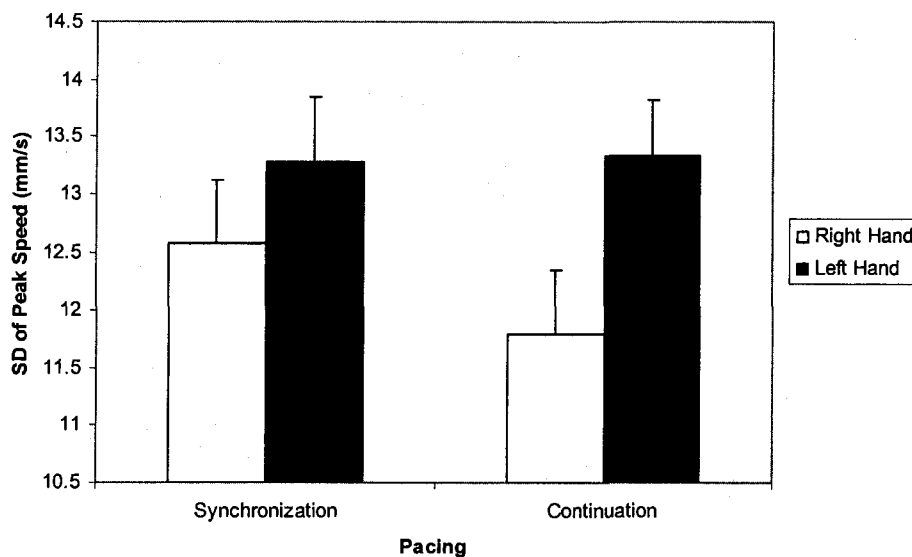


Figure 24. SD of peak speed (mm/s) for the right and left hands during vertical triangle drawing in the synchronization and continuation conditions. Vertical lines indicate standard errors of the means.

During symmetrical triangle drawing, the paced ($M = 12.42$ mm/s) and unpaced ($M = 12.48$ mm/s) conditions both yielded similar scores of peak speed variability (Figure 4.25). In the asymmetrical mode however, the presence of the metronome resulted in significantly greater peak speed variability ($M = 13.43$ mm/s) than the unpaced continuation condition ($M = 12.65$ mm/s).

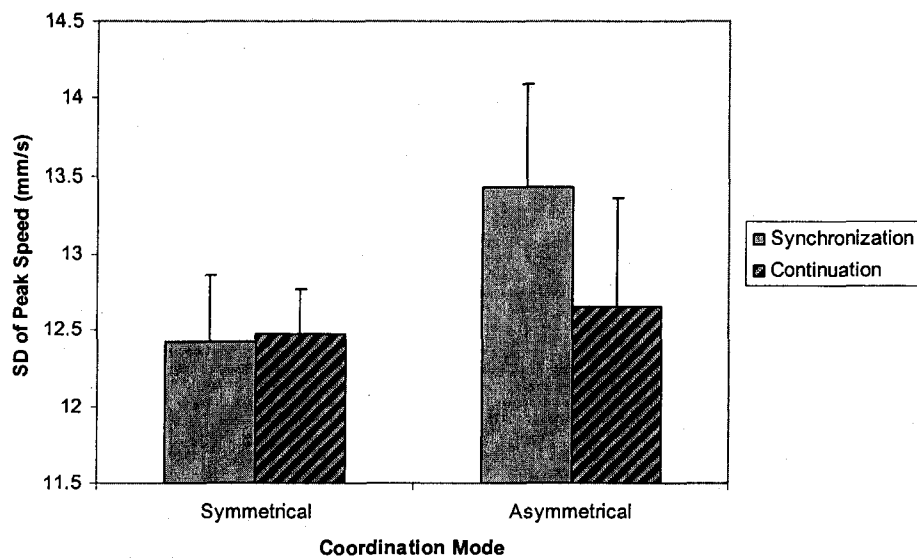


Figure 4.25. SD of peak speed (mm/s) for the synchronization and continuation conditions during vertical triangle drawing as a function of coordination mode. Vertical lines indicate standard errors of the means.

4.3.4 Relative phase. Analysis of mean deviation of relative phase showed no significant effects, implying that the target relative phase was achieved. SD scores of relative phase were analyzed to assess the consistency of the coordination pattern. Significant effects of feedback, $F(1,9) = 15.391, p < 0.01$, and mode, $F(1,9) = 28.878, p < 0.001$, were observed. In the mirror vision condition relative phase variability was greater ($M = 9.54^\circ$) than in the normal vision condition ($M = 6.95^\circ$). The asymmetrical coordination mode also displayed less consistent relative phase values ($M = 9.33^\circ$) than the symmetrical mode ($M = 7.16^\circ$). The interaction of pacing x feedback reached significance, $F(1,9) = 5.582, p < 0.05$. Performance during the normal vision condition was similar whether or not a pacing signal was provided, however, relative phase

variability increased during mirror drawing and to an even greater extent when a pacing signal was present (Figure 4.26).

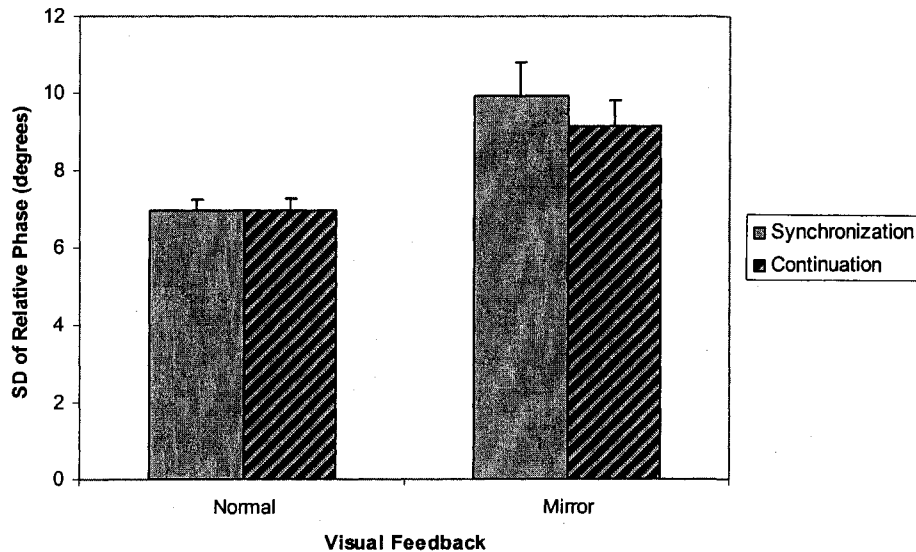


Figure 4.26. SD of relative phase (degrees) for the synchronization and continuation conditions during vertical triangle drawing as a function of the type of visual feedback provided. Vertical lines indicate standard errors of the means.

4.4 Horizontal triangle drawing

Figure 4.27 depicts typical trajectory plots of horizontal triangle drawing trials for the different vision conditions. Much like the vertical triangle drawing plots (Figure 4.18), horizontal triangle drawing in the normal vision condition (Figure 4.27A) showed greater accuracy and consistency than in the mirror vision condition (Figure 4.27B). Again, triangle vertices took on a more rounded appearance during mirror drawing and line segments were less linear. Spatial deviations appeared greater for oblique line segments than for vertical line segments, a finding which is consistent with those of Lajoie and colleagues (1992).

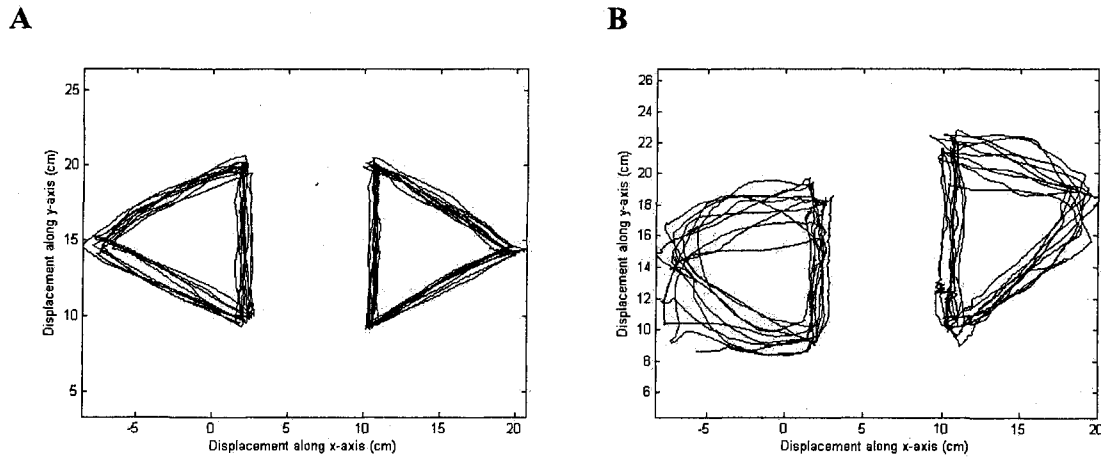


Figure 4.27. Typical trajectory plots of bimanual horizontal triangle drawing trials from the first block of testing. **A**, trajectory plot of a trial with normal (untransformed) visual feedback. **B**, trajectory plot of a trial with mirror reflected visual feedback. Trajectories were produced by a subject drawing in the symmetrical mode with a pacing signal (1.0 Hz).

4.4.1 Timing error. With respect to analyses of timing error, horizontal triangles showed a similar pattern of results to vertical triangles (Figure 4.28). Again, timing errors in the synchronization condition ($M = 10.13$ ms) were significantly smaller than in the continuation condition ($M = 28.74$ ms), $F(1,9) = 27.795$, $p < 0.05$. There was also a main effect of pacing on timing variability during horizontal triangle drawing, as revealed by analysis of SD of timing error, $F(1,9) = 27.756$, $p < 0.05$. Timing variability was lower during the synchronization condition ($M = 4.00$ ms) than the continuation condition ($M = 15.93$ ms).

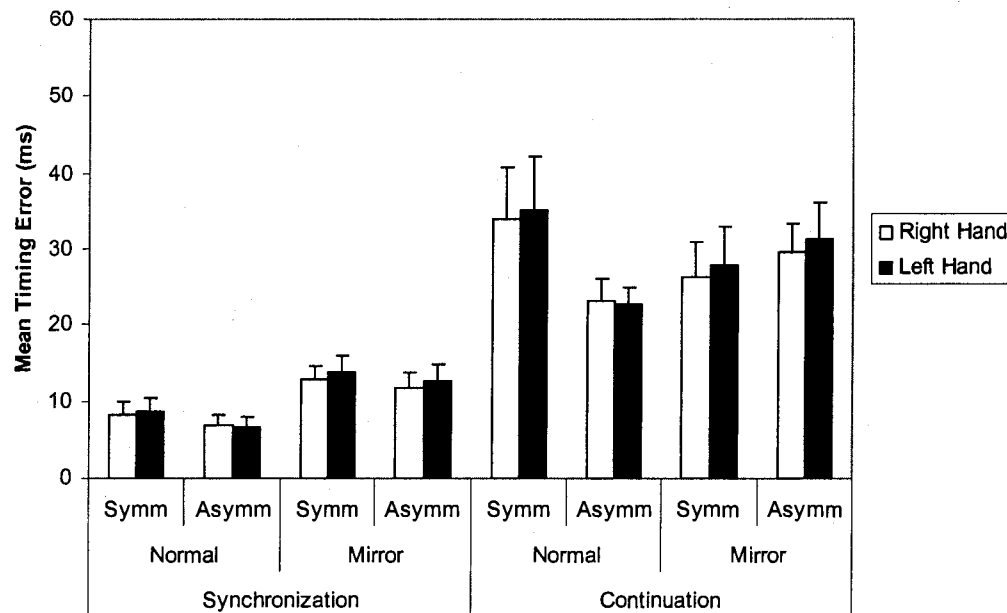


Figure 4.28. Mean timing error (ms) for the right and left hands during horizontal triangle drawing across all conditions. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

4.4.2 *Spatial deviation of vertex angles.* Deviations from a target angle of 60° were evaluated and, like vertical triangle drawing, pacing, feedback, mode and hand did not affect the accuracy of the vertex angles. Again, this suggests that participants were able to accurately achieve vertex angles of 60° under all conditions.

Vertex angle variability was also analyzed and showed a similar pattern of results to that of vertical triangles (Figure 4.29). Vertex angle variability was influenced by feedback, $F(1,9) = 13.165$, $p < 0.01$, and the interaction of pacing x feedback, $F(1,9) = 10.305$, $p < 0.05$. Vertex angles were drawn less consistently when the subject received mirror reflected visual feedback ($M = 8.42^\circ$) than when they received normal visual

feedback ($M = 4.87^\circ$). Furthermore, the presence of a pacing signal actually increased spatial variability; this effect was stronger when drawing with normal visual feedback (Figure 4.30).

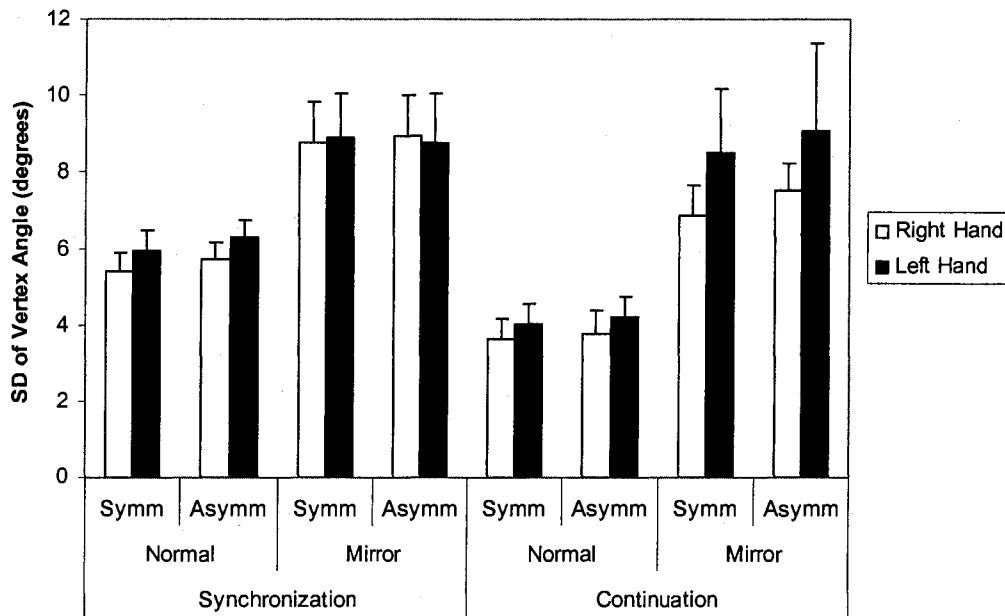


Figure 4.29. SD of vertex angle (degrees) for the right and left hands during horizontal triangle drawing across all conditions. *Symm* refers to the symmetrical coordination mode, and *Asymm* refers to the asymmetrical coordination mode. Vertical lines indicate standard errors of the means.

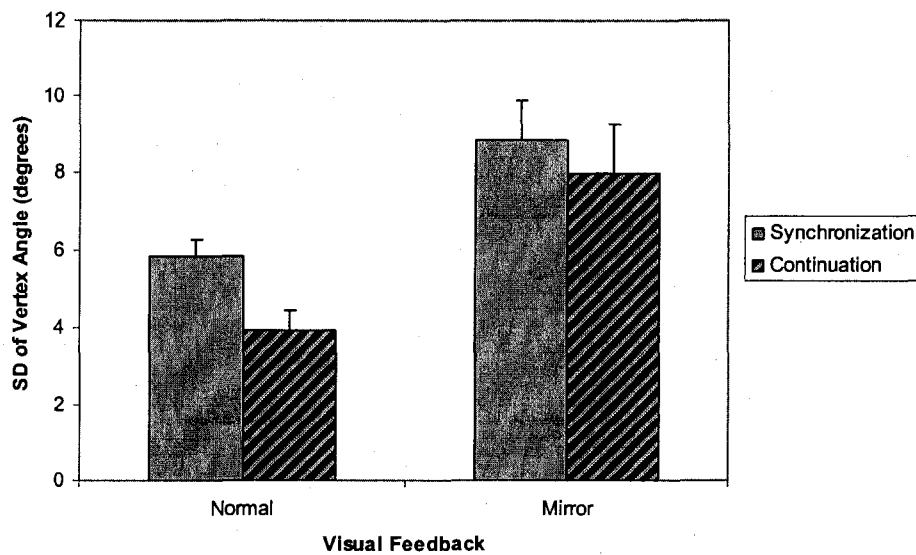


Figure 4.30. SD of vertex angle (degrees) for the synchronization and continuation conditions during horizontal triangle drawing as a function of the type of visual feedback provided. Vertical lines indicate standard errors of the means.

4.4.3 Peak speed. Significant main effects of feedback, $F(1,9) = 29.105$, $p < 0.001$, mode, $F(1,9) = 6.551$, $p < 0.05$, and hand, $F(1,9) = 11.482$, $p < 0.01$, were observed for mean peak speed during horizontal triangle drawing. Drawing movements were slower when the hands were being monitored in the mirror ($M = 168.22$ mm/s) than when direct vision of the hands was allowed ($M = 177.55$ mm/s). The asymmetrical condition also yielded a lower mean peak speed ($M = 172.01$ mm/s) than the symmetrical condition (173.76 mm/s). The interaction of feedback x hand reached significance, $F(1,9) = 6.011$, $p < 0.05$. This effect showed that in the normal drawing condition, both hands approached similar values of peak speed and these values were much higher than in the mirror drawing condition. Although peak speed of both hands decreased when monitoring hand movements in the mirror, this effect was greater in the right hand (Figure 4.31).

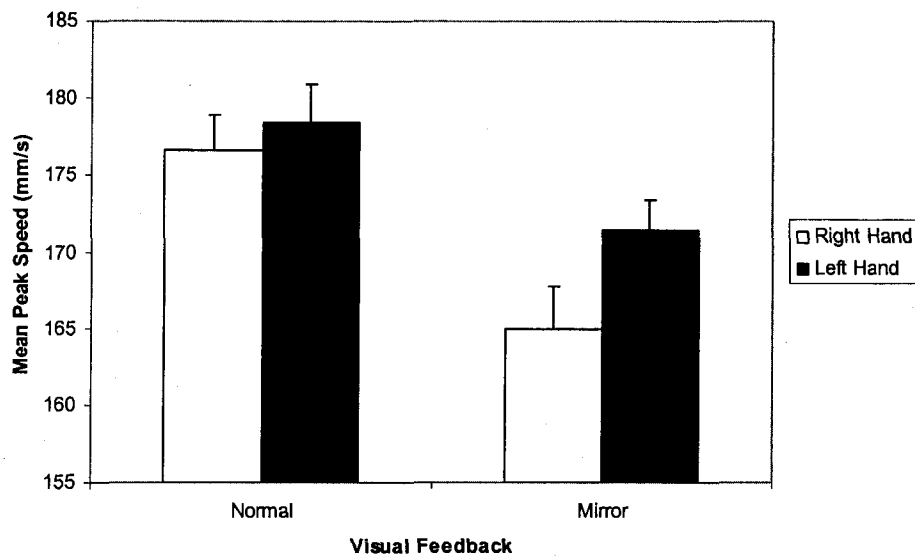


Figure 4.31. Mean peak speed during (mm/s) for the right and left hands during horizontal triangle drawing as a function of the type of visual feedback provided. Vertical lines indicate standard errors of the means.

Like the analysis of mean peak speed, analysis of SD scores also revealed significant main effects of feedback, $F(1,9) = 27.459, p < 0.01$, and hand, $F(1,9) = 7.967, p < 0.05$. Peak speed was not only lower in the mirror condition, but was also more variable ($M = 14.11$ mm/s) than in the normal vision condition ($M = 10.99$ mm/s). Secondly, whereas it was the right hand which demonstrated a smaller peak speed, it was the left hand which exhibited greater peak speed variability. Finally, a significant main effect of pacing was observed, $F(1,9) = 7.039, p < 0.05$, where the presence of a metronome caused an increase in peak speed variability ($M = 12.87$ mm/s) in comparison to unpaced drawing ($M = 12.22$ mm/s).

4.4.4 Relative phase. Mean deviation of relative phase was significantly affected by mode, $F(1,9) = 6.711, p < 0.05$. Deviations from the target relative phase were greater when drawing in the asymmetrical mode ($M = 3.91^\circ$) than the symmetrical mode ($M = 2.63^\circ$). A significant effect of mode, $F(1,9) = 9.420, p < 0.05$, was also observed for SD scores of relative phase. Relative phase during horizontal triangle drawing in the asymmetrical mode was not only less accurate, but was also more variable ($M = 9.02^\circ$) than the symmetrical mode ($M = 6.35^\circ$). Unlike vertical triangle drawing, the effect of feedback on relative phase variability did not reach significance.

CHAPTER V

Discussion

The purpose of this study was to investigate the effect of mirror reflection on various bimanual drawing tasks and to examine whether visual transformation would impact the timing and spatial properties of continuous and discontinuous drawing tasks differently. It has been shown that unimanual mirror drawing tasks are quite difficult; during mirror drawing, subjects not only exhibit reduced drawing speeds, they also show a decrease in the smoothness of movement (Lajoie et al., 1992; Miall & Cole, 2007). In these studies, subjects were not given a specific timing goal, rather they were instructed to move as quickly as possible. The present mirror drawing experiment made use of an auditory pacing signal to impose a time constraint. This research is not only the first to look at the impact of mirror-reversed visual cues on implicit and explicit timing processes, it is also the first to look at the impact of mirror drawing on bimanual coordination.

5.1 Timing Error

The current study employed a synchronization-continuation paradigm to study bimanual drawing tasks. Confirming our hypothesis, we found that timing accuracy and consistency were superior during synchronization drawing in comparison to continuation drawing when the pacing signal was terminated. We expected timing errors to be smaller in the synchronization condition because the metronome was continuously providing a cue as to where the finger position should be on the drawing template at specific times.

When the pacing signal was terminated, timing likely drifted because the metronome could no longer be used as a reference to correct for deviations from the temporal goal.

5.1.1 Effect of mirror reflection on circle drawing and triangle drawing. Our first hypothesis stated that performance on implicit timing tasks would remain unchanged during mirror drawing, whereas performance on explicit timing tasks would show greater variability. With respect to timing error, our results did not support this hypothesis. An effect of mirror feedback on timing was found for the two implicit timing tasks only: circle drawing and line drawing. When drawing circles in the synchronization condition, subjects achieved the same level of timing accuracy for both the normal vision condition and the mirror vision condition. However, in the unpaced phase of the continuation condition, mirror reflected visual information was found to have a significant effect on timing during circle drawing. Although timing errors increased in the continuation condition regardless of the type of visual feedback, these errors were significantly greater in the mirror feedback condition. This effect was not observed for either of the triangle drawing tasks, and there are two explanations as to why this might be the case.

Firstly, when drawing circles, temporal regularity is achieved by keeping the magnitude of tangential velocity constant. Given that control and smoothness of movement is reduced during mirror drawing (Miall & Cole, 2007), it is possible that it was more difficult to maintain a constant tangential velocity when circle drawing in the mirror. If this were true, then without the additional temporal information provided by the metronome, timing ability may have been compromised.

A feature of emergent timing tasks like circle drawing is that in order to produce consistent timing, the entire trajectory is crucial (Robertson et al., 1999). This feature is

not shared with discontinuous tasks like triangle drawing. Therefore, in the case of triangle drawing, to achieve consistent timing it is not of particular importance what sort of trajectory is produced in between each vertex, but simply that each triangle segment be completed at the correct time. This form of control is thought to be accomplished using a temporal representation of the interval between each event, in this case, between each vertex (Zelaznik et al., 2005). Although our results show that spatial deviations increased during mirror drawing on triangle drawing tasks, subjects were likely able to maintain a consistent pace by controlling the timing of movement onset and offset.

Lastly, the visual features of the circle template and triangle template differ substantially, which may have affected the perceptibility of timing goals. The apex of a circle is a less visually salient cycle endpoint than the vertex of a triangle. Reaching the top of a circle is also a less proprioceptively apparent event in comparison to the change in direction which occurs at a triangle vertex. Therefore, it is possible that timing during circle drawing was more susceptible to perturbations caused by the visual transformation when a pacing signal was not provided. Without the stabilizing cue of a metronome, the additional cognitive load required to resolve the mirror transformation may have impaired judgments regarding the time of arrival at the top of the circle.

5.1.2 Implicit and explicit timing aspects of vertical line drawing. Results for timing error during vertical line drawing were less straightforward than those for circle drawing and triangle drawing. During asymmetrical line drawing, timing accuracy decreased when subjects were required to monitor their hand movements in the mirror. Unexpectedly, timing during symmetrical line drawing actually improved when mirror-reversed visual feedback was provided.

One possibility is that symmetrical line drawing and asymmetrical line drawing actually employ different temporal control processes. Symmetrical line drawing might utilize a more emergent control process than asymmetrical drawing. The alternating nature of asymmetrical line drawing might result in a more event-like timing structure which could be making timing explicit. Spencer and Ivry (2007) noted that unlike in-phase (symmetrical) wrist flexion movements, anti-phase (asymmetrical) movements are composed of two events per movement cycle. The turn-around point during wrist flexion movements, much like the turn-around point during line drawing, might constitute a salient event, and whereas this event occurs simultaneously for both fingers when making symmetrical movements, it occurs 180° out of phase when making asymmetrical movements (Spencer & Ivry, 2007). This feature may contribute to an increase in explicit control during asymmetrical line drawing, as compared with its symmetrical counterpart.

Considering the nature of emergent timing tasks, a logical prediction would be that once set in motion, these tasks would require less monitoring or feedback than explicit timing tasks. Explicit timing is achieved using an event-based representation of time and greater sensory feedback may be necessary for the perception of these events. Although this would not explain the observed decrease in mean timing error during symmetrical line drawing in the mirror, it could potentially explain why timing did not deteriorate when faced with transformed visual feedback. This suggests that during asymmetrical drawing, timing errors were greater when mirror feedback was provided due to greater dependence on visual feedback.

Although we are suggesting that implicitly timed line drawing might be less compromised during mirror drawing because it is less dependent on feedback, we cannot

generalize this hypothesis to all implicit timing tasks. It is important to note that the spatiotemporal properties of line drawing and circle drawing are quite different. Whereas the vertical line template used in the current study involved movement along a single axis, the circle template required movement along two axes. The additional dimensionality and complexity of circle drawing might be sufficient to explain why identical results for timing error were not observed for the two implicit tasks. Due to this complexity, circle drawing might be more reliant on vision than line drawing, making it more difficult to keep time when circle drawing with transformed visual feedback.

Ultimately, a unified explanation of the impact of mirror feedback on implicitly and explicitly timed bimanual drawing tasks does not seem possible. Rather, the impact of mirror reflection on timing would need to be assessed on a task-specific basis; all drawing tasks have qualitatively different spatial demands and may require varying degrees of visual monitoring which could impact timed motor behaviour (Robertson et al., 1999).

5.1.3 Effect of triangle orientation on timing error. Lastly, there was no apparent effect of the static features of vertical and horizontal triangle templates on timing error. Regardless of orientation, the presence or absence of a pacing signal was the only factor which had a significant effect on timing during triangle drawing. Bogaerts and Swinnen (2001) reported that vertically oriented triangles were drawn more successfully than horizontally oriented triangle; the authors suggested that static aspects of the templates affected movement dynamics due to a perceptual bias for vertical triangles. Although vertical and horizontal triangles have different reflectional properties, it appears that in

the case of triangle drawing, the influence of orientation is limited to the spatial domain and does not translate to the temporal domain.

5.2 *Spatial Deviations*

Given that different measures of spatial deviation were required for the circle, line and triangle templates used in the current study, it was not possible to compare spatial deviations for the various drawing tasks directly. Instead, some general trends that emerged across the different tasks will be discussed.

5.2.1 Mirror reflection and spatial variability. Spatial variability increased under visual transformation for all drawing tasks. This finding does not support our hypothesis that spatial variability would increase on discontinuous drawing tasks but not continuous drawing tasks. Visual transformation creates a conflict of the senses which can only be resolved by learning the new mapping between visual and proprioceptive information. Movement planning is also complicated because motor commands do not translate into the expected visual outcome. Thus, for the current experiment, it is apparent that these conflicts made movement execution more challenging and led to increased spatial variability regardless of whether it was a continuous or discontinuous drawing task.

5.2.2 Effect of hand dominance on drawing tasks. Measures of spatial variability for circle and line drawing also revealed significant performance differences between the hands. The left hand was found to be more variable than the right hand. Since only right-handed subjects were recruited to participate in the study, the effects of right hand dominance appear to have impacted the quality of drawings made by each hand. It has been proposed that there is an attentional bias for the preferred hand during bimanual

tasks (Carson et al., 1997). If this is the case, greater attentional focus may have been placed on the right hand during the drawing tasks in our study. As a result, less attention would have been on the left hand, resulting in more frequent deviations from the template than the dominant hand.

For triangle drawing, there was no significant main effect of hand on vertex angle variability and this can possibly be explained by the nature of the task. In the case of triangle drawing, visual feedback would have been especially important at the vertices because movement direction changed at these points. Consequently, subjects may have directed their gaze at their non-dominant hand more often during triangle drawing than during circle drawing or line drawing. Subjects may have naturally attended to their preferred hand while drawing along a line segment of a triangle and then quickly alternated their gaze back and forth between both hands when changing direction at a vertex. This finding would be better investigated using an eye tracker in order to determine conclusively what is going on in terms of visual attention directed at the hands.

5.2.3 Effect of coordination mode on line drawing and triangle drawing. A significant effect of coordination mode on spatial variability was apparent for vertical line drawing. It was found that lines drawn in the symmetrical mode were less spatially variable than lines drawn in the asymmetrical mode. As previously mentioned, this finding follows the basic predictions of the HKB model; vertical line drawing in the symmetrical mode requires the simultaneous activation of homologous muscle groups across both effectors and also results in isodirectional movements. Thus, during symmetrical line drawing, the egocentric and allocentric constraints are satisfied.

Although it was hypothesized that the symmetrical coordination mode would be more stable than the asymmetrical mode for all drawing tasks, results from the current experiment reveal that this is not always true. It was found that during vertical triangle drawing, each hand was not affected by the coordination mode and mirror reflection in the same way. Whereas the left hand showed an increase in spatial variability when triangles were drawn using asymmetrical coordination, the opposite was observed for the right hand – spatial variability of triangles drawn by the right hand was smaller when they were drawn in the asymmetrical mode. The latter finding contradicts our hypothesis that drawing tasks would be more stable when performed in the symmetrical mode, regardless of the type of visual feedback.

When subjects were looking in the mirror, vertical triangle drawing was likely more stable in the asymmetrical mode because visual feedback of the two hands showed them moving in the same direction. This would not have been the case for symmetrical drawing. As previously discussed, visual attention might have been biased towards the dominant hand, which would have enabled the right hand to benefit from the stabilizing effect of isodirectional movements more than the left hand. Hence, the stability of different coordination modes is not invariant, but rather stability is dependent on the demands and perceptual aspects of the task at hand.

5.2.4 Effect of pacing on discontinuous tasks. The presence of a pacing signal only had an impact on the spatial variability of discontinuous tasks and not continuous tasks. Neither the variability of tangential angle during circle drawing nor the variability of line length during line drawing was significantly affected by the metronome. Both triangle drawing tasks on the other hand showed statistically significant interactions with

pacing. These interactions were not identical; for the horizontal triangle template, an interaction of pacing and feedback was observed, whereas in the case of the vertical triangle template, pacing interacted with mode and hand.

Common between the effects of both interactions was the increase in spatial variability during experimental conditions with a pacing signal. When the metronome was on, subjects may have compromised the quality of their triangles to keep up with the beat. Conversely, when the metronome was off, the time constraint may have seemed less salient. With the metronome disengaged, timing goals may have been less imminent and focus likely shifted from temporal aspects of the task to spatial aspects. Hence, it appears there was a tradeoff between temporal stability and spatial consistency. When the pacing signal was present, timing was better but at the expense of drawing consistency, and when there was no pacing signal, timing deteriorated and spatial ability improved.

To explain the feedback x pacing interaction observed for horizontal triangle drawing, we suggest that when subjects were mirror drawing to a metronome, it may have been very difficult to produce consistent vertex angles because they were faced not only with a visual conflict, but with a time pressure as well. Interestingly, vertical triangles showed a pacing x mode x hand interaction. In this case, variability was greatest when drawing in the asymmetrical mode with the pacing signal. Since asymmetrical drawing is typically more unstable to begin with, it is not unreasonable to assume that performing this coordination pattern with a time constraint resulted in greater spatial variability.

Although we can only speculate as to why there were differences between vertical triangle drawing and horizontal triangle drawing, the most plausible explanation would

lie in the static features of these templates. As previously discussed, it is believed that observers typically think of triangles as pointing up and that the static spatial plan for horizontal triangles may be less salient (Bogaerts et al., 2001). For this reason, subjects may have been more reliant on visual feedback when drawing triangles in the horizontal orientation, whereas other aspects of the task conditions, such as coordination mode, bore greater importance on vertical triangle drawing.

5.2.5 Effect of pacing on continuous tasks. Unlike triangle drawing, the pacing signal did not affect the spatial variability of drawing performance on continuous drawing tasks in this study. Zelaznik and colleagues (2005) have investigated how emergent timing is established when timing goals are defined externally by a metronome. A transformation hypothesis was proposed which suggests that implicit timing tasks, like circle drawing, initially use an event-based representation of time to match the movement pace to the metronome, however, within a few cycles, control processes are established that enable emergent timing to take over and a representation of cycle duration is no longer necessary.

The external auditory metronome likely did not affect the spatial variability of continuous tasks in our study for this reason. The idea behind the transformation hypothesis would suggest that during synchronization trials, the metronome was not necessarily being used for the entire trial duration. As a result, there would have been little difference between the synchronization and continuation conditions when performing an implicit timing task. Both conditions afforded the subjects with an externally specified temporal goal at the beginning of the trial and beyond that, the pacing signal was obsolete. Since the metronome may not have been attended to

continuously during the implicit timing tasks, this may explain why its presence was not detrimental to drawing performance during circle drawing and line drawing, while it was for triangle drawing.

5.3 Peak Speed

It has previously been shown that when tracing straight or curved line templates in a mirror, tracing time increases linearly with the complexity of the template (Miall & Cole, 2007). In line with this research, our data show that peak speed was consistently smaller and more variable when drawing lines or triangles in a mirror. Unlike the Miall and Cole study, we specified movement speed using an external auditory metronome. Nonetheless, subjects still achieved lower mean peak velocities during line and triangle drawing tasks when faced with the visual transformation in comparison to normal drawing. Interestingly, the opposite trend was observed for circle drawing; peak speed actually increased during mirror drawing. We will first discuss the results of peak speed for line drawing, vertical triangle drawing and horizontal triangle drawing and then we will look at circle drawing. We believe that the magnitude of peak speed was dependent on task complexity and that the variability of peak speed was related to the use of different movement strategies.

Peak speed was not only affected by the type of visual feedback, but by coordination mode as well. Peak speed was smaller and more variable during asymmetrical drawing; this was the case for both the line template and the horizontal triangle template. When the effects of visual feedback and coordination mode on peak speed are considered together, it is evident that the magnitude and stability of movement

speed decreased as a function of task difficulty. This behavior likely reflects an effort to minimize the speed/accuracy tradeoff.

For discrete tasks, such as goal-directed arm movements, it has been observed that movement variability increases with speed. This speed/accuracy tradeoff is well-known as Fitts' law (Fitts, 1954). Harris and Wolpert (1998) have proposed a theory, known as signal-dependent noise, which accounts for this behavioral phenomenon. In essence, it is believed that when planning a trajectory, considerations are made to minimize movement variability and improve endpoint accuracy. More specifically, this theory assumes that there is noise present in neural control signals. Movements of greater magnitude show increased movement variability because they require large signals which are associated with greater signal-dependent noise.

Our results show that peak speed consistently decreased during more complex task conditions. We suggest that subjects slowed down their movements to adequately meet the requirements of the task; these requirements included spatial consistency, accurate timing, and proper phasing between the hands. If subjects had attempted to move at higher speeds, the amount of noise in the motor command would have increased and resulted in greater spatial deviations (Harris & Wolpert, 1998). The observed drop in peak speed during more difficult task conditions seems to reflect a change in movement execution as a result of motor planning. These results support the argument that, in addition to a visuo-proprioceptive conflict (Lajoie et al., 1992), there is also a strong visuomotor conflict affecting movement at the planning level during mirror drawing (Miall & Cole, 2007).

5.3.1 Movement strategies affecting peak speed variability. On a different note, to explain the observed increase in peak speed variability during mirror drawing, we must also consider potential movement strategies. To achieve the specified timing goals, one could have moved quickly to the end of a line segment and then waited for the metronome beat (yielding high peak speed), or the full one second interval could have been used to reach the endpoint (yielding low peak speed). If subjects tried multiple movement strategies during the mirror drawing trials, this would explain why peak speed variability was greater than normal drawing trials.

5.3.2 Effect of pacing signal on peak speed. Greater peak velocities were observed during line drawing and vertical triangle drawing when there was no pacing signal. It is possible that higher peak velocities were achieved because without the impending metronome present to urge movement, more time may have been taken to plan each action. As a result, subjects likely had greater confidence in their movement trajectory and moved faster and more consistently. Furthermore, the variability of peak speed increased during paced trials which may be because subjects varied their movement speed to arrive in time with the metronome beat. Alternatively, increases in peak speed during unpaced drawing may simply reflect a preference for faster movement speeds and subjects may have drifted towards their preferred speed when the metronome was off.

5.3.3 Peak velocity during circle drawing. Finally, we must now address the aforementioned circle drawing results. These results were quite different from those for line drawing and triangle drawing in that peak speed was often higher for some of the more challenging conditions. Our data show that mean peak velocity increased significantly during asymmetrical circle drawing and was highest in one of the most

complex task conditions, asymmetrical mirror drawing with a pacing signal. It is possible that mean peak velocity increased during more difficult conditions simply because drawing movements were on average slower and quick compensatory movements were required to complete the circles on time.

It is important to note that peak speed is not an ideal measure of speed during circle drawing because velocity should remain consistent throughout movement cycles. It appears that without more information regarding speed, peak speed does not impart significant insight into movement control during circle drawing. When looking at the variability data for peak speed, we gain evidence that there is not necessarily a large discrepancy between circle drawing and the other drawing tasks. Mirror reflected visual feedback and the asymmetrical coordination mode again resulted in greater peak speed variability; this is consistent with the line drawing and triangle drawing findings.

5.4 Relative Phase

The templates used in our experiment were all drawn using a symmetrical and an asymmetrical coordination mode. These coordination patterns had a significant impact on the stability of bimanual coordination for the drawing tasks. Subjects showed more consistent phase relationships between the hands when they traced using the symmetrical pattern. Previous research has shown that deviations from target relative phase are greater in the asymmetrical mode for circle drawing (Carson et al., 1997), whereas a significant effect of mode on relative phase variability during triangle drawing was not confirmed (Bogaerts & Swinnen, 2001). In disagreement with the findings of Bogaerts and

Swinnen, we observed that asymmetrical triangle drawing (both vertical and horizontal) resulted in greater relative phase variability than the symmetrical mode.

Bimanual tasks involving movement in only one spatial dimension, such as finger tapping, tend to demonstrate greater stability when performed in the symmetrical mode (Kelso, 1984). Vertical line drawing, as performed in our experiment, is similar to bimanual finger tapping, given that it also involves maintaining a phase relationship along a single axis. Thus, with the exception of triangle drawing, our results corroborate the findings of previous research. As of now, little work has been done on triangle drawing; further investigation would be necessary to determine conclusively whether coordination mode plays a reliable role on the stability of interlimb coordination during bimanual triangle drawing.

Visual information also affected interlimb coordination on all drawing tasks, with the exception of horizontal triangle drawing. Mirror reflected visual information consistently resulted in either greater deviation from the target relative phase or increased relative phase variability during circle, line and triangle drawing. Evidently, visual information plays a significant role in establishing an accurate and stable phase relationship between the hands. When this feedback is perturbed, such as during mirror drawing, the hands show greater asynchronies and stability of the interlimb relationship is compromised.

The results of relative phase support our initial hypotheses that relative phase would be more stable when the drawing tasks were performed using a symmetrical coordination mode, and also, visual transformation, in the form of mirror reflection, again proved to be detrimental to performance.

5.5 Limitations

The main limitation of this study was that the experiment was quite long and repetitive. In a pilot study, one subject reported feeling hypnotized by the rhythmic motion of the hands. To ensure that participants did not become fatigued or lose focus, frequent breaks were encouraged and testing was split into two or more sessions.

Another potential limitation was that we did not specify where subjects should direct their gaze. Although this was done intentionally, so as not to influence where people would naturally look during the tasks, it also means that subjects may have used different visual strategies. Whereas one subject may have directed his/her gaze at the dominant hand, another subject could have focused towards the centre of each template. We have also made the assumption that subjects did pay attention to the visual information in the mirror on mirror drawing trials and did not resort to a cognitive representation of the template.

Lastly, although the mirror drawing apparatus enabled us to prevent vision of the hands, it did not block vision of the upper limbs. We cannot rule out the possibility that subjects may have gained some visual information from the arms during mirror drawing. This could have potentially aided performance because visual feedback of the upper limbs was not subjected to the visual transformation.

5.6 Conclusion

The results of our experiment demonstrate that the effect of visual transformation on explicitly and implicitly timed bimanual drawing tasks is dependent on the individual task demands. Although circle drawing and line drawing are both thought to involve

continuous movements, and vertical and horizontal triangle drawing both require discontinuous movements, we still found performance differences between tasks belonging to the same movement class. We hypothesized that continuous drawing movements are less reliant on perceptual information due to their emergent nature and that timing on these tasks would not be affected by visual transformation. Counter intuitively, when mirror reflected visual information of the hands was provided during circle drawing and line drawing, temporal accuracy decreased. These results seem to suggest that timing during continuous movements may be less “emergent” than is currently thought. Alternatively, visual feedback could be influencing the planning and control processes that act to constrain movement trajectory during continuous tasks. It has been suggested trajectory control mechanisms and the neural processes that govern them could have an effect on the temporal regularity of movement (Balasubramaniam, Wing & Daffertshofer, 2004). In contrast, timing on discontinuous tasks was not affected by visual transformation, which supports the notion that explicit timing is open-loop and not feedback-dependent (Ivry & Richardson 2002; Wing, 2002).

Our results also show that the spatial variability of movement trajectory was greater during the mirror condition for all template shapes. This again emphasizes the fact that emergent tasks are not resistant to the effects of visual transformation. Furthermore, with the exception of circle drawing, we consistently observed a decrease in peak speed for more complex task conditions, such as mirror drawing and asymmetrical drawing. Considering the fact that timing goals were externally specified by a metronome, this decrease in peak speed during mirror drawing demonstrates that visual transformation did have an effect on movement planning. Difficulties during mirror drawing cannot only be

attributed to a conflict between visual information and proprioceptive feedback, there is also a conflict between visual information and motor output which makes it difficult to plan movements. Due to this visuomotor conflict, it appears that subjects planned their movements accordingly by moving at a slower speed. This strategy was likely employed so that they could draw the templates as accurately as possible despite the visuo-proprioceptive conflict affecting movement execution.

The relative phase data also revealed a decrease in bimanual coordination during mirror drawing. This suggests that visual information regarding hand movements plays an important role in establishing a stable and meaningful relationship between the hands. This finding seems intuitive when we consider the everyday execution of bimanual tasks; for example, when tying our shoelaces we generally direct our visual attention to our hands.

Future studies should further investigate the role of visual information during implicit timing tasks. It would be of interest to determine the mechanisms by which visual feedback influences the movement control processes employed on these tasks, especially under transformed feedback conditions. Subsequent studies could also make use of more complex visual transformations and more complex geometric shapes to tease out the differences between visuo-proprioceptive conflict and motor planning effects.

References

- Amazeen, P.G., Amazeen, E.L., & Turvey, M.T. (1998). Breaking the reflectional symmetry of interlimb coordination dynamics. *Journal of Motor Behavior*, 30(3), 199-216.
- Amazeen, P.G., Amazeen, E.L., & Turvey, M.T. (2004) Symmetry and the devil. *Journal of Motor Behavior*, 36(4), 371-372.
- Amazeen, P.G., Schmidt, R.C., & Turvey, M.T. (1995). Frequency detuning of the phase entrainment dynamics of visually coupled rhythmic movements. *Biological Cybernetics*, 72, 511-518.
- Balasubramaniam, R., Wing, A.M., & Daffertshofer, A. (2004). Keeping with the beat: movement trajectories contribute to movement timing. *Experimental Brain Research*, 159, 129-134.
- Baldissera, F., Cavallari, P., & Civaschi, P. (1982). Preferential coupling between voluntary movements of ipsilateral limbs. *Neuroscience Letters*, 34(1), 95-100.
- Balslev, D., Christensen, O., Lee, J., Law, I., Paulson, O., & Miall, R.C. (2004). Enhanced accuracy in novel mirror drawing after repetitive transcranial magnetic stimulation-induced proprioceptive deafferentation. *The Journal of Neuroscience*, 24 (43), 9698-9702.
- van Beers, R.J., Wolpert, D.M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, 12(10), 834-837.
- Bogaerts, S., Buekers, M.J., Zaal, F.T., & Swinnen, S.P. (2003). When visuo-motor incongruence aids motor performance: the effect of perceiving motion structures during transformed visual feedback on bimanual coordination. *Behavioural Brain Research*, 138(1), 45-57.
- Bogaerts, H., & Swinnen, S.P. (2001). Spatial interactions during bimanual coordination patterns: The effect of directional compatibility. *Motor Control*, 2, 183-199.
- Cardoso de Oliveira, S. (2002). The neuronal basis of bimanual coordination: recent neurophysiological evidence and functional models. *Acta Psychologica*, 110, 139-159.
- Cardoso de Oliveira, S. (2004). Control is good; prediction is better? *Journal of Motor Behavior*, 36(4), 375-378.
- Deutsch, D. (1983). The generation of two isochronous sequences in parallel. *Perception & Psychophysics*, 34(4), 331-337.

- Donchin, O., Gribova, A., Steinberg, O., Bergman, H., Cardoso de Oliveira, S., & Vaadia E. (2001). Local field potentials related to bimanual movements in the primary and supplementary motor cortices. *Experimental Brain Research*, 140(1), 46-55.
- Fink, G.R., Marshall, J.C., Halligan, P.W, Frith, C.D., Driver, J., Frackowiak, R.S., et al. (1999). The neural consequences of conflict between intention and the senses. *Brain*, 122, 497-512.
- Fitts, P.M. (1954). The information capacity of the human motor system in controlling the amplitude of movements. *Journal of Experimental Psychology*, 47, 381-391.
- Franz, E.A. (1997). Spatial coupling in the coordination of complex actions. *The Quarterly Journal of Experimental Psychology*, 50(3), 684-704.
- Franz, E.A., Eliassen, J.C., Ivry, R.B., & Gazzaniga, M.S. (1996) Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science*, 7, 306-310.
- Franz, E.A., Ivry, R.B., & Helmuth, L.L. (1996). Reduced timing variability in patients with unilateral cerebellar lesions during bimanual movements. *The Journal of Cognitive Neuroscience*, 8, 107-118.
- Franz, E.A., Zelaznik, H.N., & McCabe, G. (1991). Spatial topological constraints in a bimanual task. *Acta Psychologica*, 77, 137-151.
- Haken, H., Kelso, J.A.S., & Bunz, H. (1985). A Theoretical Model of Phase Transitions in Human Hand Movements. *Biological Cybernetics*, 51, 347-356.
- Helmuth, L.L. & Ivry, R.B. (1996). When Two Hands Are Better Than One: Reduced Timing Variability During Bimanual Movements. *Journal of Experimental Psychology: Human Perception and Performance*, 22(2), 278-293.
- Jagacinski, R.J., Marshburn, E., Klapp, S.T., & Jones, M.R. (1988). Tests of parallel versus integrated structure in polyrhythmic tapping. *Journal of Motor Behavior*, 20, 416-442.
- Klapp, S.T., Nelson, J.M., & Jagacinski, R.J. (1998) Can people tap concurrent bimanual rhythms independently? *Journal of Motor Behavior*, 30, 301-322.
- Ivry, R.B., & Hazeltine, E. (1999). Subcortical locus of temporal coupling in the bimanual movements of a callosotomy patient. *Human Movement Science*, 18, 345-375.
- Ivry, R.B., & Richardson, T.C. (2002). Temporal control and coordination: The multiple timer model. *Brain and Cognition*, 48, 117-132.

- Ivry, R.B., & Spencer, R.M. (2004). The neural representation of time. *Current Opinion in Neurobiology*, 14, 225-232.
- Kelso, J.A.S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT Press.
- Kelso, J.A.S. Phase transitions and critical behaviour in human bimanual coordination. (1984). *American Journal of Physiology*, 246, 1000-1004.
- Kelso, J.A.S., Putnam, C.A., & Goodman, D. (1983). On the space-time structure of human interlimb coordination. *The Quarterly Journal of Experimental Psychology*, 35A, 347-375.
- Kelso, J.A., Southard, D.L., Goodman, D. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, 5(2), 229-38.
- Lajoie, Y., Paillard, J., Teasdale, N., Bard, C., Fleury, M., Forget, R., et al. (1992). Mirror drawing in a deafferented patient and normal subjects: Visuoproprioceptive conflict. *Neurology*, 42, 1104-1106.
- Li, Y., Levin, O., Carson, R.G., & Swinnen, S.P. (2004). Bimanual coordination: constraints imposed by the relative timing of homologous muscle activation. *Experimental Brain Research*, 156, 27-38.
- Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, 414, 69-73.
- Mechsner, F., & Knoblich, G. (2004). Do muscles matter for coordinated action? *Journal of Experimental Psychology*, 30(3), 490-503.
- Meesen, R.L., Wenderoth, N., Temprado, J.J., Summers, J.J., & Swinnen, S.P. (2006). The coalition of constraints during coordination of the ipsilateral and heterolateral limbs. *Experimental Brain Research*, 174(2), 367-75.
- Miall, R.C., & Cole, J. (2007). Evidence for stronger visuo-motor than visuo-proprioceptive conflict during mirror drawing performed by a deafferented subject and control subjects. *Experimental Brain Research*, 176, 432-439.
- Mulvey, G.M., Amazeen, P.G., & Riley, M.A. (2005). The use of (symmetry) group theory as a predictive tool for studying bimanual coordination. *Journal of Motor Behavior*, 37(4), 295-309.
- Redding, G.M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: a tutorial in theory and method. *Neuroscience and Biobehavioral Reviews*, 29, 431-444.

- Robertson, S., Zelaznik, H., Lantero, D., Gadacz, K., Spencer, R., & Doffin, J. (1999). Correlations for timing consistency among tapping and drawing tasks: Evidence against a single timing process for motor control. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1316-1330.
- Schmidt, R.A. A schema theory of discrete motor skill learning. (1975). *Psychological Review*, 82(4), 225-260.
- Semjen, A., Summers, J.J., & Cattaert, D. (1995). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology*, 21, 1139-1157.
- Scholz, J.P. (1990). Dynamic pattern theory – some implications for therapeutics. *Physical Therapy*, 70(12), 827-843.
- Shadmehr, R., & Mussa-Ivaldi, F.A. (1994). Adaptive representation of dynamics during learning of a motor task. *The Journal of Neuroscience*, 14, 3208-3224.
- Shaffer, L.H. (1981). Performances of Chopin, Bach, and Bartok: Studies in motor programming. *Cognitive Psychology*, 13, 326-376.
- Spencer, R.M., & Ivry, R. (2007). The temporal representation of in-phase and anti-phase movements. *Human Movement Science*, 26, 226-234.
- Spencer, R.M., & Zelaznik, H.N. (2003) Weber (Slope) Analyses of Timing Variability in Tapping and Drawing Tasks. *Journal of Motor Behavior*, 35(4), 371-381.
- Spencer, R.M., Zelaznik, H.N., Diedrichsen, J., & Ivry, R.B. (2003). Disrupted Timing of Discontinuous But Not Continuous Movements by Cerebellar Lesions. *Science*, 300, 1437-1439.
- Steinberg, O., Donchin, O., Gribova, A., Cardoso de Oliveira, S., Bergman, H & Vaadia, E. (2002). Neuronal populations in primary motor cortex encode bimanual arm movements. *European Journal of Neuroscience*, 15(8), 1371-1380.
- Summers, J. (2002). Practice and training in bimanual coordination tasks: strategies and constraints. *Brain and Cognition*, 48(1), 166-178.
- Swinnen, S. (2002). Intermanual coordination: From behavioural principles to neural-network interactions. *Nature*, 3, 350-361.
- Swinnen, S., Dounskaia, N., Walter, C.B., & Serrien, D.J. (1997). Preferred and induced coordination modes during the acquisition of bimanual movements with a 2:1 frequency ratio. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1087-1110.

- Swinnen, S.P., Jardin, K., Verschueren, S., Meulenbroek, R. Franz, L., Dounskaia, N., et al. (1998). Exploring interlimb constraints during bimanual graphic performance: effects of muscle grouping and direction. *Behavioural Brain Research*, 90, 79-87.
- Swinnen, S.P., Li, Y., Dounskaia, N., Byblow, W., Stinear, C., & Wagemans, J. (2004). Perception-action coupling during bimanual coordination: the role of visual perception in the coalition of constraints that govern bimanual action. *Journal of Motor Behavior*, 36(4), 394-398.
- Swinnen, S.P., & Wenderoth, N. (2004). Two hands, one brain: cognitive neuroscience of bimanual skill. *Trends in Cognitive Sciences*, 8(1), 18-25.
- Turvey, M.T. (1990). Coordination. *The American Psychologist*, 45(8) 938-953.
- von Holst, E. (1939/1973). Relative coordination as a phenomenon and as a method of analysis of central nervous function. In R. Martin (Ed. & Trans.), *The selected papers of Erich von Holst, vol 1*. Methuen, London.
- Weigelt, C., & Cardoso de Oliveira, S. (2003). Visuomotor transformations affect bimanual coupling. *Experimental Brain Research*, 148, 439-450.
- Whitney, A.G. (2004). Internal models for bi-manual tasks. *Human Movement Science*, 23, 747-770.
- Wing, A.M. (2002). Voluntary Timing and Brain Function: An information Processing Approach. *Brain and Cognition*, 48, 7-30.
- Wolpert, D.M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, Supplement 3, 1212-1217.
- Woodruff-Pak, D.S. (1997). Classical Conditioning. *International Review of Neurobiology*, 41, 341-366.
- Zelaznik, H.N., Spencer, R.M., & Ivry, R.B. (2002). Dissociation of Explicit and Implicit Timing in Repetitive Tapping and Drawing Movements. *Journal of Experimental Psychology: Human Perception and Performance*, 28(3), 575-588.
- Zelaznik, H.N., Spencer, R.M., Ivry, R.B., Baria, A., Bloom, M., Dolansky, L., et al. (2005). Timing Variability in Circle Drawing and Tapping: Probing the Relationship Between Event and Emergent Timing. *Journal of Motor Behavior*, 37(5), 395-403.

Appendix: Ethics Certificate



Université d'Ottawa University of Ottawa

Service de subventions de recherche et d'éthologie Research Grants and Ethics Services

September 11, 2007

Ramesh Balasubramaniam
School of Human Kinetics
Faculty of Health Sciences
University of Ottawa
125 University Street, Room 360
Ottawa, ON K1N 6N5

Object: Dynamics of Sensorimotor Synchronization (file H 04-05-10)

Dear Dr. Balasubramaniam,

You will find enclosed the Health Sciences and Science Research Ethics Board renewal certification for the abovementioned research project.

Please note that it is the responsibility of the researchers to:

- a) Notify the ethics office of any changes in the research project; and
- b) Fill out an annual status report to be sent to the Protocol Officer for Ethics in Research.
Such report can be found on the ethics web site at:

http://www.uottawa.ca/services/research/rge/rebs/download/rapport_annuel_projets_anglais.doc

A copy of this renewal approval will be sent to Research Services, if necessary.

Please do not hesitate to contact me at extension 5387 if you should have any questions.

Sincerely yours,

Germain Zougo
Protocol Officer for Ethics in Research
For Dr. Daniel Lagarec, Chair of the Health
Sciences and Science REB



Université d'Ottawa University of Ottawa

Service de subventions de recherche et d'éthologie Research Grants and Ethics Services

HEALTH SCIENCES AND SCIENCE RESEARCH ETHICS BOARD

CERTIFICATION OF ETHICS APPROVAL

This is to certify that the University of Ottawa Health Sciences and Science Research Ethics Board (REB) examined the application for extension of ethics approval for the research project **Dynamics of Sensorimotor Synchronization (file H 04-05-10)** submitted by Dr. Ramesh Balasubramaniam of the School of Human Kinetics. This project received initial ethics approval on June 28, 2005 by the REB as meeting appropriate ethical standards set out in the Tri-Council Policy Statement and in the Procedures of the University of Ottawa Research Ethics Boards and was renewed on July 7, 2006. The University of Ottawa REB members accordingly gave it an extension of ethics approval. This ethics renewal certification is valid for one year from the following date: July 7, 2008.

Germain Zongo
Protocol Officer for Ethics in Research
For Dr. Daniel Lagarec, Chair of the
Health Sciences and Science REB

September 11, 2007
Date