Movement Asymmetry in a Sensorimotor Synchronization Task

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Abstract

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Sensorimotor synchronization is the process by which we are able to synchronize a motor response with a sensory stimulus that occurs at predictable intervals over time. A common experimental paradigm for studying this process is finger tapping to a metronome. It has been found that finger trajectory is asymmetric and this asymmetry increases with timing accuracy, suggesting that the relatively high velocity of the finger flexion phase compared to the extension phase may provide proprioceptive feedback that aids in synchronization. In this study, we examined how the kinematics of the motor response varies in relation to changes in the frequency of occurrence of the stimulus and to changes in the degree of sensory feedback during the motor response. Participants were asked to tap on three different surfaces offering varying degrees of tactile feedback while synchronizing to a virtual metronome playing at one of two different rates. Motion capture equipment recorded their finger movement. It was expected that the greater the amount of sensory feedback from the tapping surface, the more symmetric the finger trajectory would become, as dependence on a high velocity phase could decrease and movement could more resemble the symmetric sinusoidal motion that models of motor control would predict for the repetitive to and fro movement of finger tapping in the absence of a synchronization constraint. We provide evidence showing that the degree of tactile feedback from the tapping surface does influence trajectory and velocity.

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I would like to thank the members of the Li and Penhune Labs, especially my co-supervisors Karen Li and Virginia Penhune. I would particularly like to acknowledge Alejandro Endo for his determination and patience in breaking through the black box of motion capture and for his always helpful insights into data analysis, Chris Steele and Kevin Trewartha for invaluable discussions on data analysis and interpretation, Laura Fontil, Joannie Huberdeau, and Anthony Hopley for their help in data collection, and Ramesh Balasubramaniam and the members of his Sensorimotor Neuroscience Lab at the University of Ottawa for their generous help with experimental design and data analysis. Finally, I would like to give a special thank you to Virginia Penhune for her knowledge, experience, always sage advice, and unwavering encouragement, all of which did much to push this research forward.

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Introduction

Sensorimotor synchronization is the process by which we are able to synchronize a motor response with a sensory stimulus that occurs at predictable intervals over time. This process occurs in many contexts, ranging from the mundane event of stepping onto an escalator to the remarkable achievement of an ensemble musical performance. In seeking to understand the synchronization process, much previous research has focused on modeling the temporal accuracy of the motor response. More recent research has sought to characterize the motion, or kinematics, of the response and understand how it contributes to synchronization. In the research that is the subject of this thesis, we have focused on deconstructing the synchronized motor response into distinct phases of movement so that each can be examined individually in terms of the underlying motor control processes, with the long term goal of understanding how different brain regions are involved in each phase. We have also investigated how sensory feedback can influence the kinematics of specific phases of the motor response.

A sensorimotor synchronization task that has been well studied is finger tapping to a regular auditory stimulus such as a metronome beat. The task's behavioural simplicity makes it amenable to controlled laboratory study even as it belies the complex nature of the timing and motor processes that underlie it. Indeed, synchronized finger tapping has a long history in the scientific literature, beginning with Stevens (1886) who asked seven "gentlemen" to tap to a regularly occurring auditory stimulus that was then stopped while the subjects continued to tap at the same tempo as best they could without the aid of any external stimulus serving as a timing cue. He found that subjects could continue to reliably time a finger tap if the frequency of stimulus presentation fell within the range of 1.89 Hz to 1.15 Hz (that is, an inter-stimulus interval, or ISI, ranging from 530 ms to 870 ms). Stevens further found that faster frequencies led to negative asynchrony, such that the tap anticipated the stimulus onset, and slower frequencies were associated with a positive asynchrony such that the motor response was late.

Since that initial series of experiments, many interesting characteristics of sensorimotor synchronization, as represented by the finger tapping task, have emerged from multiple studies. The negative mean asynchrony discovered by Stevens has also been consistently observed in paced tapping, at least when done by non-musicians, but it is still not well understood (Aschersleben, 2002; Repp, 2005). However, it clearly indicates that subjects are anticipating the stimulus onset, typically by tens of milliseconds, and that some manner of an internal timer process is at work. It is important to realize that the downward flexion of the finger tap must be initiated well before stimulus onset in order for the finger to arrive at the spatial target of synchronization at the point in time of stimulus onset. This implies that, even in the case of externally paced tapping, there is an internal timing process that allows the subject to predict when the next stimulus will occur.

Another finding is that the ISI range within which sensorimotor synchronization is most accurate is between 200 and 1800 ms but evidence suggests that we may hit our physical threshold for executing a high frequency sequence of motor responses before we reach our "threshold of synchronization", and those with musical training may have synchronization thresholds as low as 100 ms (Repp, 2005). The lower limit of 100 to 200 ms may be due to an inability to perceive a rhythmic pattern beyond this periodicity. Meanwhile, if the phenomenon of negative mean asynchrony implies a predictive process at work, then the observed upper limit of the synchronization range is perhaps more intriguing and informative as to the nature of sensorimotor synchronization than is the lower limit, hinting, as it does, at the limits of this predictive ability. Thus as periodicity of stimulus presentation lengthens, prediction becomes more difficult. In fact, when Miyake, Onishi, and Pöppel (2004) asked subjects to tap to an auditory stimulus as they memorized a list of words, they showed that, when the ISI is between 450 and 1500ms, subjects' predictive abilities were not affected by performance of the dual task as evidenced by a steady rate of negative asynchrony across this range. However as ISI increases beyond 1500ms, the rate at which subjects execute anticipatory tapping, as opposed to reactive tapping, begins to fall off and is significantly less while performing the memory task than when tapping alone. The authors interpret their results as implying that two timer processes may be present. The first, active at shorter ISI's, is characterized as automatic while the second, used for managing longer ISI's, requires more attentional resources.

A well known model of finger tap synchronization in the unpaced continuation phase is that of Wing and Kristofferson (1973), which apportions the variance of tapping performance to two sources: A central timer process and the implementation of the motor response. In other words, when we attempt to execute a series of motor responses at a regular tempo and without the aid of any external timer, the variability in our synchrony will be due to a combination of difficulties in keeping time and delays in executing the response. We can even characterize the two sources of variability such that a motor delay will have a local effect on the subsequent inter-response interval (IRI) while timer variability will have a global long-term effect resulting in drift away from the target tempo (Vorberg & Wing, 1996).

The Wing-Kristofferson model can be described by a relatively simple set of equations. If we let I_j be the jth IRI, C_j be the jth interval between successive triggers of an internal timing mechanism, and D_j be the motor delay occurring after the jth timer trigger, then:

$$I_j = C_j - D_{j-1} + D_j \qquad (1)$$

so that the jth IRI depends somewhat on the motor delay of the previous IRI, although this is not meant to imply the presence of a feedback process. Wing and Kristofferson show that if C and D are independent random variables, then the variance of the jth IRI, or lag zero covariance, is given by:

$$\mathrm{var}(I_j) = \sigma^2_C + 2\,\sigma^2_D \quad (2)$$

where σ^2_C is the variance of the internal timer and σ^2_D is the variance of the motor delay. The covariance of successive IRI's, also known as the lag one auto-covariance, can be shown to be:

$$\mathrm{cov}(I_{j-1}, I_j) = -\,\sigma^2_D \qquad (3)$$

so that the greater the (j-1)th IRI, the smaller the jth IRI and this covariance is only a function of the shared motor delay D_{j-1}. In other words, if the (j-1)th tap is late because of a relatively large motor delay on that tapping cycle, making the (j-1)th IRI large, then the next IRI will be shortened because of the lateness of that previous tap, but not because of any attempted compensation in the current tapping cycle to make up for the previous lateness via a feedback process. Rather, the relative shortness of the jth IRI is simply due to the fact that, by definition, it starts only when the previous IRI ends.

Finally, the lag one serial correlation is defined as:

$$\rho_I(1) = \frac{\mathrm{cov}(I_{j-1}, I_j)}{\mathrm{var}(I_j)} \qquad (4)$$

which simplifies to

$$\rho_I(1) = \frac{-1}{2 + (\sigma^2_C / \sigma^2_D)} \qquad (5)$$

and it can be shown that the strength of the dependence between adjacent IRI's as measured by $\rho_I(1)$ falls in the range (-0.5,0).

From the preceding four equations, we see that any correlation between adjacent IRI's may simply be due to the shared motor delay of the first IRI, rather than to any feedback process that may be occurring. We can also see that it is possible to estimate timer and motor delay variability by measuring $\mathrm{var}(I_j)$ and $\mathrm{cov}(I_{j-1}, I_j)$, which is exactly what Wing and Kristofferson did in order to see how σ^2_C and σ^2_D vary with tapping rate. What they found was that the motor delay variance was independent of the ISI while the internal timer process accounted for a greater proportion of variance of the IRI as tapping rate slowed.

While this two process model has been validated for the self-paced continuation phase, it is reasonable to ask whether it also holds for the synchronization phase when there is feedback from the external timer. Semjen, Schulze, and Vorberg (2000) showed that the Wing-Kristofferson model can be extended to incorporate a second-order linear phase correction that depends on the last two synchronization errors:

$$I_j = (C_j - \alpha A_{j-1} - \beta A_{j-2}) - D_{j-1} + D_j \qquad (6)$$

so that a certain proportion of the last two synchronization errors are subtracted from the internal timer's trigger interval. They found that, just as in the continuation phase, internal timekeeper variance in the externally paced phase increased as tapping rate decreased. Not surprisingly, they also found that timekeeper variance is greater in the continuation phase than in the paced phase. They further found that first-order error correction increased (increasing α) as the target tapping rate slowed, while second-order error correction decreased (decreasing β). Semjen et al. speculate that the error correction process may be too slow to incorporate the information from the previous tapping cycle at fast tapping rates and therefore gives more weight to the next to last cycle.

So far we have seen that the simplest model of unpaced tapping requires no element of feedback while the extension of this model to paced tapping shows that information from previous tapping cycles is used in the current one. If we break the finger tap response into two parts – the arrival, or downward flexion, phase whose end point of motion is the point of synchronization, and the departure, or upward extension, phase when the finger returns to its start position – one may next ask whether there is a dependency between these different phases of the motor response. In other words, does the time of arrival for a tap influence the time of departure for the same tap or does the time of departure influence the time of arrival for the next tap? Wing (1980) concludes that, at least for the unpaced continuation phase, neither is the case but rather that a central timekeeper triggers all phases independently of the motor delay of adjacent phases.

While the motor response phases may be temporally independent, at least in the continuation phase, they may nevertheless be related kinematically. In other words, are there aspects of finger movement that are correlated between the extension and flexion phases? One may also ask if there are aspects of the movement comprising the motor response that are characteristic of the synchronization process. In light of the independence of the timer and motor delays assumed by the Wing-Kristofferson model, these may appear to be superfluous questions to ask. However, given that the extension of the model to the synchronization phase does incorporate a feedback mechanism, it is not unreasonable to hypothesize that movement is being adaptively planned in order to help maintain synchronization. Certainly for other kinds of tasks in which a synchronization constraint is not present, accurate, efficient movement has been found to be characterized by the optimization of certain kinematic parameters. For example, one aspect of motor control that is present in many kinds of tasks is the tendency to produce smooth movements after sufficient learning of the task, where smoothness is operationalized as jerk, the derivative of acceleration, so that the smaller the magnitude of jerk, the smaller the changes in acceleration and the smoother the movement (Shadmehr & Wise, 2005). Indeed, Flash and Hogan (1985) showed, in their minimum jerk model, that a trajectory in a two joint planar point-to-point movement minimizes a cost function related to the integral, over movement duration, of the square of jerk.

Translated into the domain of finger tapping, the minimum jerk model would lead one to predict that the optimally smooth trajectory for a repetitive movement such as finger tapping is a symmetric sinusoidal curve with equal time spent in flexion and extension (Balasubramaniam, Wing, & Daffertshofer, 2004). In a study that examined the kinematics of the motor response in sensorimotor synchronization, Balasubramaniam et al. found that finger tapping showed a departure not only from maximal smoothness but also from the symmetry of trajectory between flexion and extension phases that one might reasonably expect from the repetitive to and fro motion of the finger tap. They asked musicians to tap their right index finger in synchrony with a metronome beat at three different rates (every 1000ms, 750ms, or 500ms). In other conditions, the participants were asked to syncopate their tapping (that is, to tap off the beat) to the metronome at these same three rates and, finally, to extend the index finger upwards, rather than flex downwards, on the beat. When executing the synchronized response under all three styles of synchronization, whether by flexing with or against the beat or extending with the beat, subjects showed a significant asymmetry in their motor response in terms of trajectory and velocity. More precisely, when flexing on or off the beat, the time spent in the downward flexion phase of the finger tap was significantly less than the time spent in the upward extension phase, implying greater finger velocity in the flexion phase. Conversely, significantly less time was spent in the upward extension phase in conditions where subjects were asked to extend their fingers upward on the beat. For all three synchronization styles, this asymmetry decreased as the tapping rate increased and in an unpaced condition, in which participants simply move their right index fingers up and down in an oscillatory fashion in the absence of any auditory stimuli but at a regular rhythm, movement trajectories had no significant asymmetry.

The fact that the observed asymmetry was independent of synchronization style, and disappeared in the unpaced condition, implies that it was related somehow to the task of synchronization rather than to any physical constraints of the required motor response. This is further supported by an observed correlation between the degree of asymmetry and the degree of synchrony of the motor response such that the more asymmetric the movement, the greater the timing accuracy of the response.

Balasubramaniam et al. (2004) also showed that the durations of the slow and fast phases of movement were negatively correlated with each other and that this correlation was negatively correlated in turn with asynchrony. In other words, the stronger the dependence between the velocities of the two movement phases, the better the synchrony. Therefore, while motor delays may be independent of the central timer, as posited in the Wing-Kristofferson model, and while the two movement phases may be triggered independently of each other, at least in the continuation phase as reported by Wing (1980), there does appear to be a dependency between the velocities of the two phases that suggests the presence of an error correction process that uses feedback from the previous motor response phase.

For their study, Balasubramaniam et al. (2004) also measured the smoothness of movement by calculating the mean squared jerk for the entire duration of tapping for each condition. They found that mean squared jerk decreased as tapping rate increased and the unpaced condition yielded the smoothest movement of all. This makes intuitive sense if we think of synchronized tapping as converging to a constant oscillatory motion as tapping frequency increases to threshold. Given that smoothness and symmetry decrease while asynchrony increases as the tapping rate slows, one could say that as prediction gets more difficult with slowing tapping rate, jerkiness of movement increases and we may ask if it something about the predictive nature of sensorimotor synchronization that is making the movement jerky.

To account for the deviation from maximal smoothness that they observed, Balasubramaniam et al. (2004) suggested that higher movement velocity in the flexion phase may provide additional feedback to an error correction process allowing for accurate movement timing. If this is true, then varying the sensory feedback during tapping should affect movement asymmetry such that greater tactile feedback should reduce the dependence of the synchronization process on feedback from a high velocity arrival phase and result in a reduction of the asymmetry of the finger tap trajectory. More specifically, we would expect movement asymmetry to decrease as tactile feedback from the tapping surface increases and we would expect this effect to be most pronounced at the slower tapping rate, when prediction is more difficult and reliance on the high velocity arrival, or flexion, phase is greatest. To test this hypothesis, we investigated synchronized finger tapping at two different rates and on three different tapping surfaces with varying degrees of tactile feedback.

Methods

Participants

Nine right-handed subjects (4 males), ranging in age from 20 to 29 years (M = 23.2 years) were recruited, primarily from the undergraduate and graduate student population of Concordia University in Montréal, Québec. Handedness was determined by administering a widely used handedness questionnaire adapted from Crovitz and Zener (1962) and reproduced in Appendix A. The subjects had a mean score of 24.8 (SD=2.6), indicating that the sample was strongly right-handed. Additionally, prospective subjects were first given questionnaires to screen out those with health problems that could affect fine motor movements (see Appendix B) and to screen out participants with greater than three years of musical training or who were currently engaged in musical instruction or regular practice, including voice and dance (Appendix C). The study was approved by the Concordia University Human Research Ethics Committee and informed consent was given by all participants (Appendix D), who were debriefed about the goals of the experiment following their testing.

Apparatus, Task, and Stimuli

The finger motion of study participants was recorded using the Visualeyez VZ3000 3D motion tracking system, manufactured by Phoenix Technologies. For each participant, small light-emitting diodes (LED's), attached by thin copper wire to a central controller, were affixed with Velcro tape to the tip of the fingernail, the distal interphalangeal joint, the proximal interphalangeal joint, and the metacarpophalangeal joint, all of the right index finger. An additional marker was placed at approximately the centre of the top of the right hand. Nine infrared-sensitive cameras tracked the position of each marker in three dimensional space at a sampling rate of 200Hz and to a spatial resolution of 0.015mm.

Each participant was seated on a desk chair whose seat and armrest heights were independently adjustable. The right armrest was reinforced and extended with wood covered in soft cloth so that participants could comfortably keep their entire forearm, wrist, and most of their right hand supported and immobile during the experiment. The LED marker wires had sufficient slack to allow for complete freedom of movement of the right index finger.

Participants were asked to tap their right index finger in synchrony with 60 cycles of an auditory pacing stimulus (a 1kHz pulse of 20ms duration heard through a pair of Sony Professional stereo headphones). There were two tapping rates, 1 Hz and 2 Hz, in each of three conditions, tapping in the air, on the key of a Yamaha PSR-90 MIDI keyboard, or on a key of the same keyboard but that was blocked from descending so that it acted as a hard surface with no give. This resulted in six different tapping conditions in all.

Custom software, written in the C# programming language and run on the Windows XP operating system, controlled delivery of the auditory stimulus and synchronized the recording of the motion capture data. Motion capture data was then exported to the Matlab programming environment for analysis.

Procedures

Once participants were seated in the modified desk chair, the seat and armrest heights were adjusted so that they would be able to tap under all three tapping surface conditions without altering their body position. They were instructed to support their entire right forearm and as much of their hand as possible on the extended armrest and told not to move any part of their body, other than their right index finger, to help them keep time with the beat. Participants were instructed to tap their right index finger "on the beat"; that is, in synchrony with the onset of the auditory stimulus. Additionally, the desired tapping motion of flexion using only the metacarpophalangeal joint of the right index finger was demonstrated by the experimenter for each participant.

Every participant was tested under each of the six tapping conditions described above after an initial practice block of 60 trials at a tapping rate of 1.33Hz. The ordering of the six paced conditions was determined by using a Latin square for counterbalancing of the different levels of independent variables. Each condition consisted of a block of 60 presentations of the auditory stimulus at the given rate.

Data Analysis

In order to test our hypothesis that the degree of symmetry of finger motion would vary with the degree of feedback from the tapping surface, various dependent measures related to movement symmetry were extracted from the data. Following Balasubramaniam et al. (2004), we calculated trajectory asymmetry by dividing each tapping cycle into flexion and extension phases and using the average time spent in flexion versus extension as a measure of trajectory asymmetry with respect to time. We then took a finer grain approach by conceptualizing the tapping cycle as consisting of three phases instead of two by introducing an intermediate phase between flexion and extension, in which the finger is more or less stationary. This intermediate phase was then factored out of the calculation to arrive at a more conservative measure of trajectory asymmetry, especially at slower tapping rates when this idle phase can account for a sizeable proportion of the total tapping time. Additionally, we focused on the velocity curve of the flexion phase by extracting a volume asymmetry index and by calculating the maximum velocity reached in this phase of tapping, reasoning that lower maximum velocities on surfaces that provide greater tactile feedback to the finger would be consistent with our hypothesis.

The motion capture data were analyzed with custom software written in Matlab, version 7.5.0.342 (R2007b). All analyses were carried out solely on the z-coordinate of the marker placed on the fingertip, roughly corresponding to the vertical motion of the finger.

As a first step common to all of the analyses carried out, the raw motion capture data was first smoothed with a fifth order Savitsky-Golay filter of window size 79 and then detrended to remove any linear drift that might have occurred over time. While linear drift would not necessarily affect the search for movement landmarks that is described next, it could affect the calculation of some of the dependent measures described later.

In the second step of the analysis, landmarks in the finger trajectory data corresponding to movement initiation and termination in each tapping cycle were identified (Figure 1). Consistent with Balasubramaniam et al. (2004), we calculated the time spent in flexion versus extension by using the maximum and minimum points of each tapping cycle as the points of initiation and termination respectively and then simply calculated the time it took to go from a maximum to the subsequent minimum as the time spent in downward flexion for a given tapping cycle. Extension time was similarly defined as the time from a minimum to the next maximum and the ratio of flexion to extension time was calculated such that values less than 1.0 indicate that more time was spent in extension than in flexion.

A limitation of this measure, especially at slower tapping rates, is that it includes a certain amount of time when the finger is more or less stationary (ignoring normal physiological tremor) and will apportion this time partly to the extension phase and partly to the flexion phase, depending on where the local maximum occurs. In order to treat this time interval in a systematic way, we reanalyzed the motion capture data by defining the point of movement initiation as the point in the downward, or flexion, phase of a tapping cycle where 5% of the maximum velocity of that phase was first reached. The points of movement termination in the upward, or extension, phase of each tapping cycle were similarly defined. The tap itself was defined to be the minimum point of the trajectory in a given cycle. Using these three points in the trajectory of each cycle, motion was deconstructed into three stages: (1) the Waiting phase, or the period between movement termination of the previous tapping cycle and the onset of movement of the current tapping cycle, (2) Response, defined as that part of the trajectory running from the point of movement onset to the point of the tap, and (3) Recovery, comprised of that part of the trajectory from the tapping point until the point of movement termination (Figure 1).

To find the points of delineation of these three stages of the tapping cycle, we first found the tapping point of each cycle by searching for the local minimum on the trajectory curve in a neighbourhood centred on the point of stimulus presentation and with a width defined by the sampling and tapping rates. Next, the local maximum between adjacent tapping points was found, the velocity curve was computed, and the point between a local maximum and the subsequent local minimum of the trajectory at which five per cent of maximum velocity was first attained was defined as the point of movement onset. Similarly, the last point between the minimum and the next local maximum at which five per cent of maximum velocity was attained was taken as the point of movement termination for that tapping cycle.

Several measures related to the asymmetry of motion were calculated based on these movement landmarks. First we recalculated trajectory asymmetry as the average ratio of the time spent in the Response phase to the time spent in the Recovery phase. A value of 1.0 implies equal amounts of time spent in each phase while values less than one indicate that the subject spent less time in the Response phase compared to the Recovery phase, which implies, in turn, relatively high velocity motion in the Response phase.

Next, focusing on the velocity of the Response phase, the velocity asymmetry index (Nagasaki, 1989), defined as the ratio of the time it takes to reach maximum velocity over total movement time, was calculated for this specific portion of motion in each tapping cycle and then averaged over all trials of a condition for each subject. (Strictly speaking, we are, in fact, looking for minimum velocity as the finger moves in the negative z direction in the downward flexion of the Response phase.) A value of 0.5 for this index indicates that maximum velocity occurs in the middle of the segment, while values greater than 0.5 signify that maximum velocity is reached somewhere past the midway mark of the trajectory.

An additional measure related to the velocity of the Response phase is the maximum velocity reached in the Response phase, averaged over all trials of a condition for a given subject. Combined with the time-based measure of trajectory asymmetry and the velocity asymmetry index of the Response phase, this measure helps to characterize variations in the motion of the Response phase across different tapping surfaces and at different rates, allowing us to validate our hypothesis of the effects of greater tactile feedback on the velocity profile of synchronized finger tapping.

Finally, the degree of asynchrony between the onset of the auditory stimulus and the associated motor response was defined as the difference in time between the onset of the playing of the metronome tone and the point at which the tap occurs, defined above. Per cent asynchrony was then calculated by dividing this difference by the duration of the ISI. Thus per cent mean asynchrony was calculated as the average of these across all trials of a block of finger tapping.

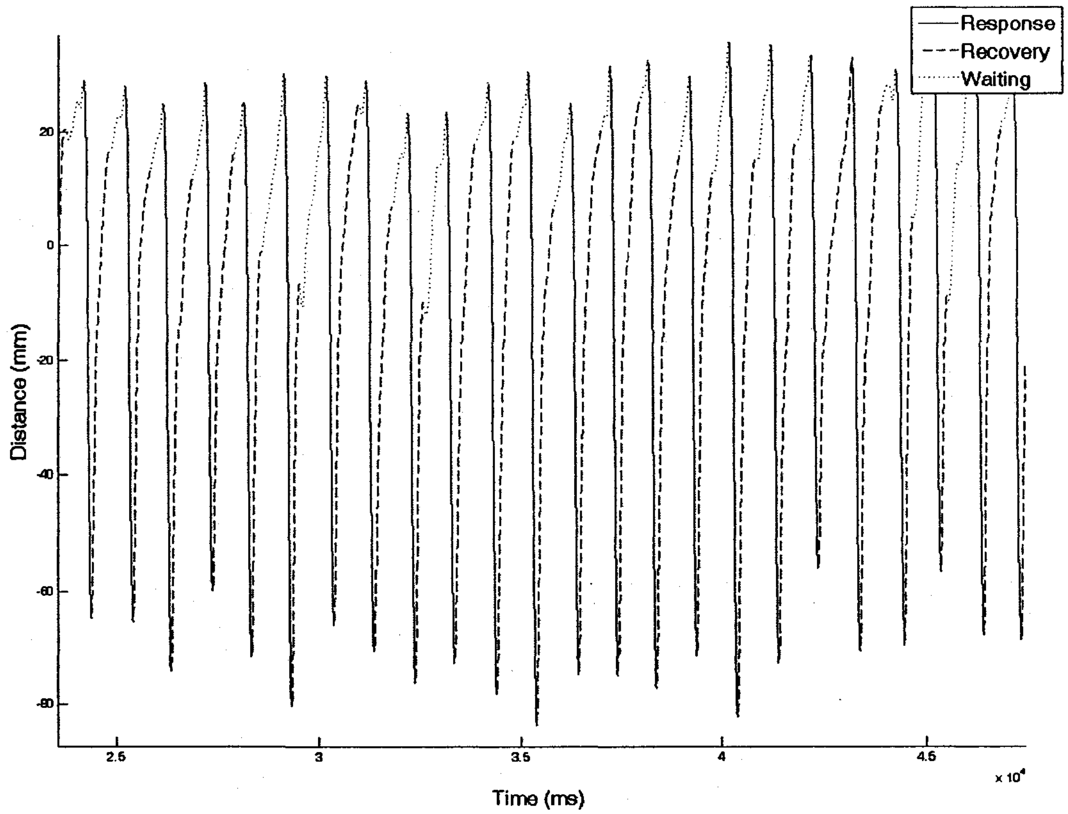

Figure 1. The z-coordinate of motion of a subject's tapping in the air at 1Hz. The movement of each tapping cycle is divided into three phases.

Results

We initially looked at the ratio of flexion to extension time as a measure of trajectory asymmetry, using the local minima and maxima of the trajectory curve as delineation points for the different phases of movement (Figure 2). A 2 x 3 (frequency x surface) repeated measures ANOVA did not reveal any significant main or interaction effects. Nevertheless, a comparison employing a Bonferroni correction showed that tapping in the air was more symmetric at 2Hz than at 1Hz ($p = 0.001$), consistent with the findings of Balasubramaniam et al. (2004).

When we divided each tapping cycle into three phases using five per cent of minimum and maximum velocity as the points of movement initiation and termination respectively and then computed the ratio of Response to Recovery time, we found a main effect of frequency ($F(1,8) = 5.682$, $p < 0.05$, partial $\eta^2 = 0.415$) such that tapping became significantly more symmetric with increasing tapping frequency (Figure 3). Additionally, pairwise comparisons using a Bonferroni correction revealed that this frequency-dependent pattern of trajectory asymmetry was found in the air and blocked key conditions ($p < 0.05$) but not in the piano key condition. Therefore, while we did not find the expected main effect of surface on trajectory asymmetry, we did find that it does have some influence on this dependent measure.

Under all conditions, the velocity asymmetry index of the Response phase was greater than 0.5, indicating that the maximum velocity always occurred somewhere past the midpoint of the Response (Figure 4). A significant main effect of surface ($F(2,16) = 17.086$, $p < 0.001$) was found and post-hoc comparisons with a Bonferroni correction showed that when tapping on the blocked key, the velocity curve was significantly more asymmetric (maximum velocity was achieved significantly later) compared to the other two tapping surfaces ($p = 0.01$). Meanwhile, the effect of frequency trended to significance ($p = 0.076$) with the 1 Hz condition always slightly more symmetric. While there was no interaction found, pairwise comparisons revealed a significant difference of velocity asymmetry between the two tapping rates when tapping in the air such that the velocity profile is more symmetric at the slower 1 Hz tapping rate ($p=0.026$).

Figure 5 shows the velocity profile of one of the subjects tapping in the air at 1 Hz. The maximum velocity achieved by the right index finger during the Response phase (Figure 6) differed significantly across surfaces ($F(2,16) = 9.809$, $p = 0.002$) such that it was greatest when tapping in the air compared to tapping on the piano key or blocked key ($p < 0.02$). No significant differences were found between the piano key and blocked key conditions.

A significant interaction between surface and frequency was also found for the maximum velocity measure ($F(2,16) = 3.683$, $p < 0.05$). The maximum velocity attained when tapping in the air was greater compared to tapping on the piano at 1 Hz but there was no significant difference between tapping in the air and on a blocked key at this tapping rate. At 2 Hz, the maximum velocity for tapping in the air exceeded that of both the piano key and blocked key conditions ($p <= 0.02$ with a Bonferroni adjustment for multiple comparisons).

No significant differences were found for per cent mean asynchrony amongst the various conditions (Figure 7) and the correlation between asynchrony and the ratio of time spent in Response versus Recovery was examined but no significant correlation was found for either the pooled data or for any specific condition.

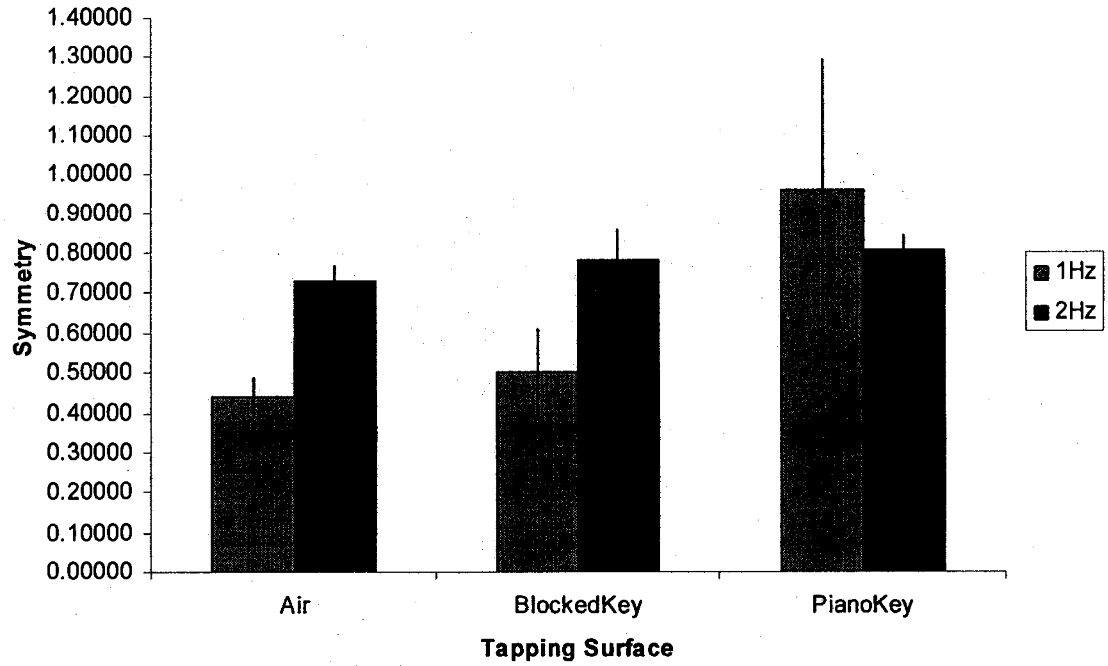

Figure 2. Trajectory asymmetry defined as the average ratio of time spent in Flexion versus Extension, using the maximum and minimum points of each tapping cycle to define movement initiation and termination respectively. A significant difference between the 1 Hz and 2 Hz conditions was found for tapping in the air.

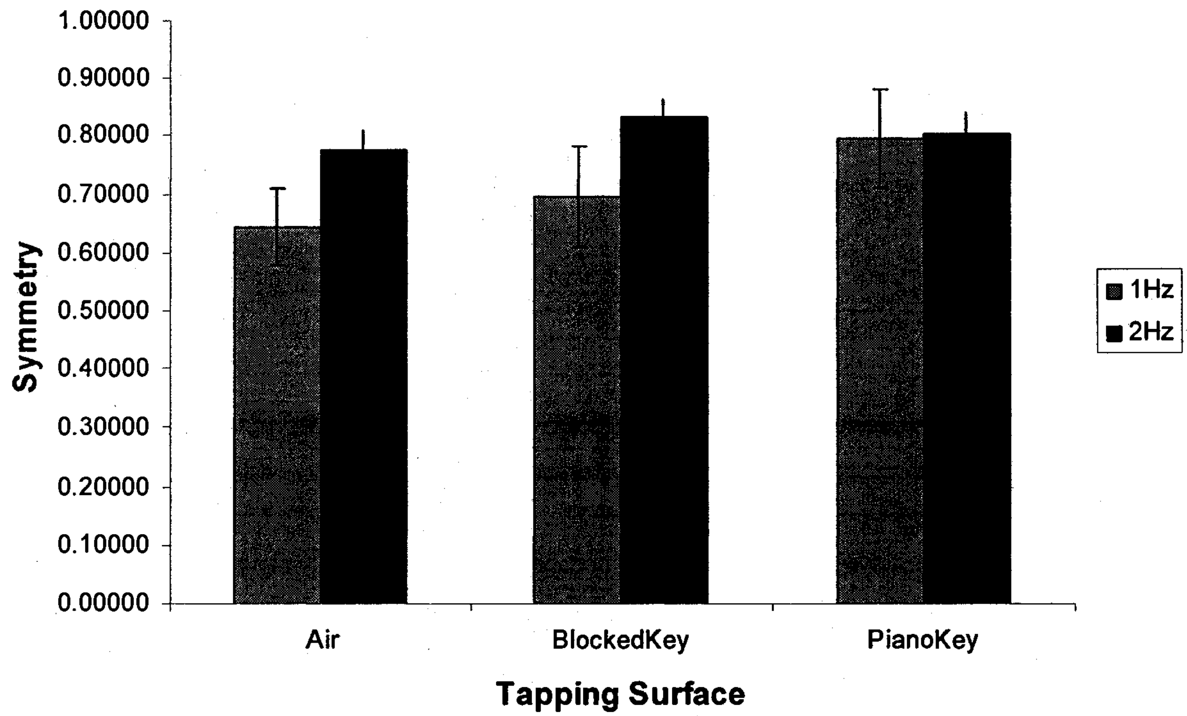

Figure 3. Average ratio of time spent in Response versus Recovery using percentage of maximum velocity to define movement initiation and termination and factoring out Waiting time. Symmetry of trajectory increases significantly with tapping rate for the air and blocked key conditions but not the piano key condition.

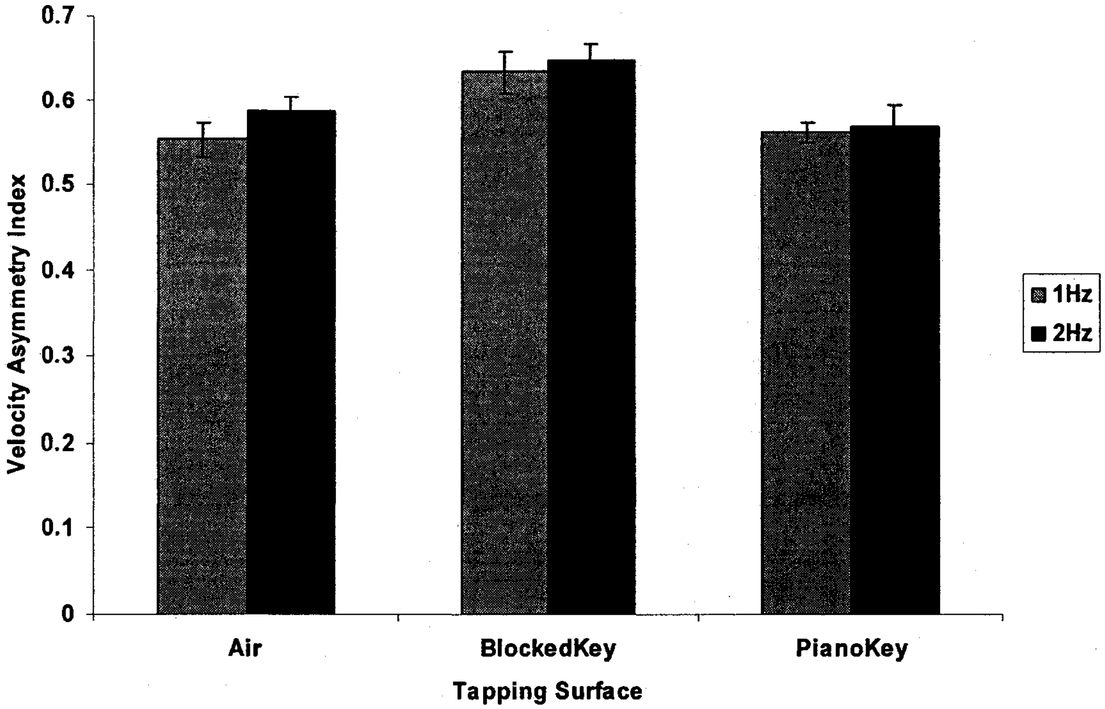

Figure 4. Velocity asymmetry index of the Response phase. A value of 0.5 indicates perfect symmetry such that maximum velocity is obtained at the midpoint of the Response phase.

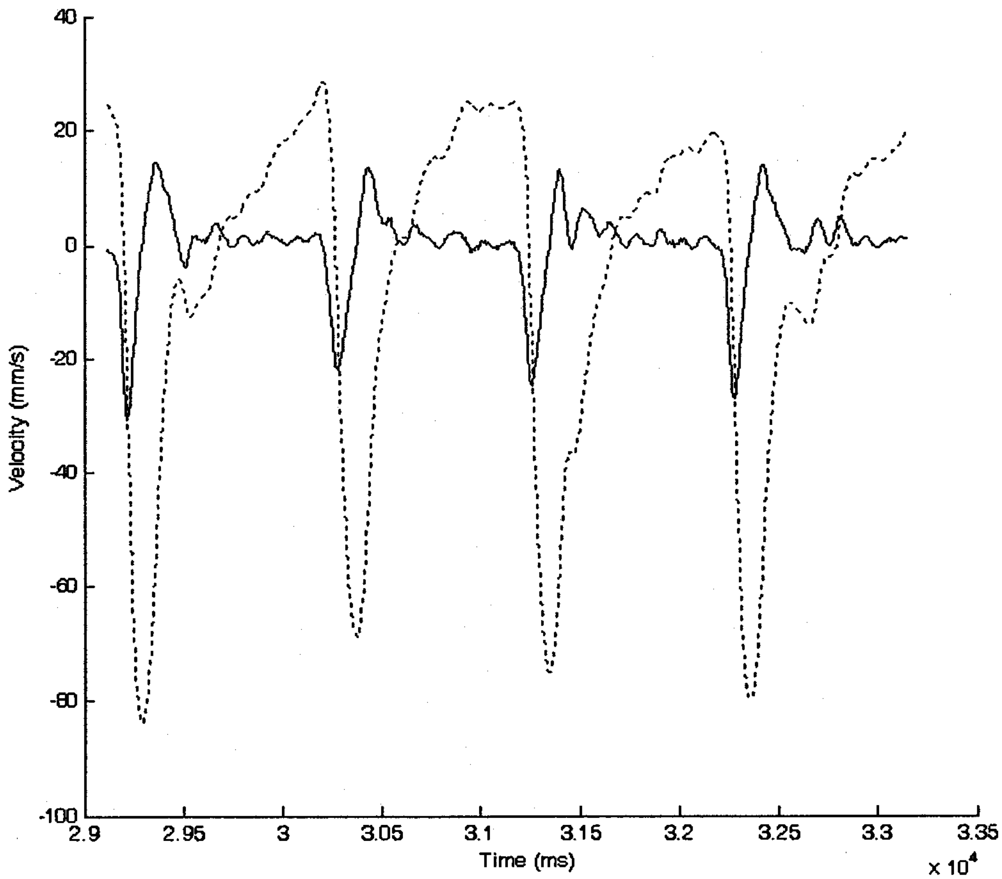

Figure 5. Velocity (solid line, scaled up by a factor of 20) overlaid on trajectory (dashed line). Four tapping cycles from a single subject tapping in the air at 1 Hz.

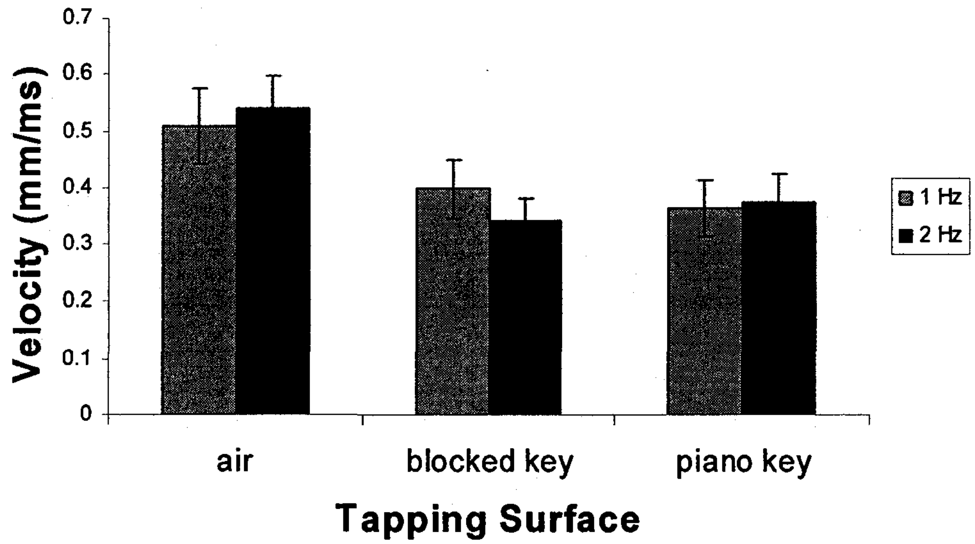

Figure 6. Average maximum velocity (in absolute value) of the Response phase. The air condition has greater maximum velocity than the piano key condition at both tapping rates. The air condition is statistically the same as the blocked key condition at 1 Hz but significantly greater at 2 Hz.

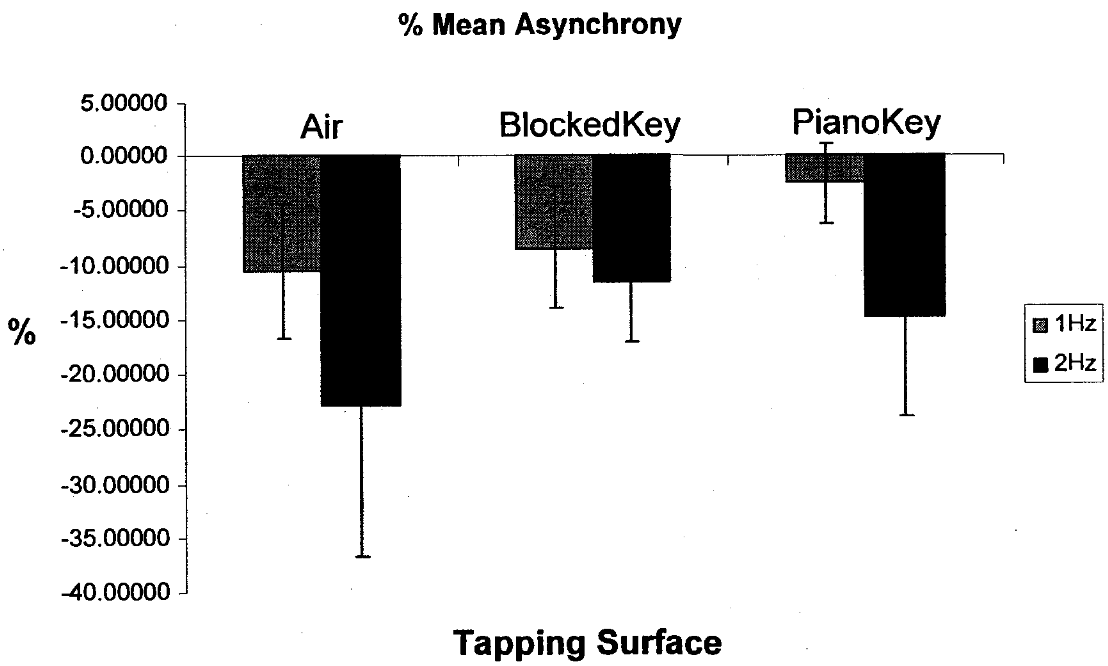

Figure 7. Per cent mean asynchrony. No significant differences were found.

Discussion

This study was designed to test the hypothesis that the degree of asymmetry of finger trajectory and velocity in a sensorimotor synchronization paradigm could be manipulated by controlling the amount of sensory feedback the finger receives from the tapping surface. In particular, it was expected that tapping in the air would produce the most asymmetric trajectories, followed by tapping on a piano key and finally tapping on a blocked key. As tactile feedback increased across tapping surfaces, it was expected that the asymmetry of finger trajectory and velocity would progressively decrease. It was further expected that this decrease would be most pronounced at the slower tapping rate, when synchronization is more difficult and the additional tactile feedback would presumably have a greater impact in decreasing the reliance on additional proprioceptive information from the high velocity flexion phase. If this turned out to be the case, it would support the theory that the observed deviation from symmetry of finger trajectory and velocity serves a functional purpose as part of a feedback process meant to improve timing accuracy.

Using the methodology of Balasubramaniam et al. (2004) to define the flexion and extension movement phases in each tapping cycle, we were able to reproduce their result, showing that trajectory asymmetry decreases as tapping rate increases for the air condition. When we used our own more conservative measure that removes the effect of a Waiting phase in between the current flexion and previous extension phases, we found an effect of frequency in the air and blocked key conditions, with the expected pattern of decreasing asymmetry with increasing tapping frequency.

The one surface condition for which both trajectory asymmetry measures showed significant differences between the two tapping frequencies was tapping in the air. If we compare these two measures of trajectory asymmetry in the air condition alone, then using the local extrema to define the flexion and extension phases, we get a partial η^2 of 0.785 for the measure of Balasubramaniam et al. (2004), or what we shall call measure A. If we use five per cent of minimum and maximum velocity and remove the Waiting phase (our measure, B), then we arrive at a partial η^2 of 0.471, which can certainly be considered a large effect of frequency on asymmetry but which is 40% smaller than the effect size arrived at when the Waiting phase is not factored out. Figures 8 and 9 compare the two methods of dividing up the trajectory.

In other words, our measure B accounted for 40% less of the variance in asymmetry compared to measure A. Removing the Waiting phase from each tapping cycle decreases the variance between frequency group means and referring to Figures 8 and 9, it appears that at the slower tapping rate, when the Waiting phase is of more substantial duration, most of this phase is being accounted for as part of the Extension phase in measure A, leading to a greater value for asymmetry than that calculated by measure B. It could thus be argued that measure A gives a more biased estimate of trajectory asymmetry compared to measure B and that this bias increases in inverse proportion to tapping rate.

We did not find a main effect of surface on trajectory asymmetry but it should be noted that the observed power of 0.386 is low. This could be due to the small number of subjects tested and a possibly small effect size of the surface tactile feedback. While we did not find a main effect or a significant interaction between frequency and surface, pairwise comparisons did show that the effect of tapping frequency did behave differently in the air and blocked key conditions compared to the piano key condition. One interpretation of the fact that frequency of tapping had no effect when tapping on the piano key surface is that, contrary to our assumptions, this surface is supplying the largest amount of tactile feedback compared to the air and the blocked key. In retrospect this makes sense since the finger has two contact points with the piano key, one at surface contact and the other at key bottom. Thus the initial point of contact serves as a cue that the finger is close to the point of synchronization and can slow down. If this is indeed the case, that the ascending ordering of surfaces for degree of tactile feedback should be "air, blocked key, and piano key", not "air, piano key, and blocked key", then one could argue that in the piano key condition, tapping at 1 Hz becomes no more difficult than tapping at 2 Hz because of the additional feedback from the surface. An additional experiment with this specific hypothesis in mind would have to be carried out to confirm this. Furthermore, we would need to show that there is a negative correlation between asymmetry and asynchrony, indicating that the asymmetry is related to timing accuracy.

Turning next to the velocity measures of the Response phase, we see that the velocity asymmetry index indicates that the time to maximum velocity occurs later for the blocked key condition compared to air or piano key and that the average maximum velocity is greatest for tapping in the air. This provides partial support for the hypothesis that greater tactile feedback from the tapping surface results in decreased velocity of the Response phase (and therefore decreased trajectory asymmetry) because subjects are using information from the tapping surface, rather than proprioception, to adjust their movements. On the other hand, if the piano key is supplying the greatest feedback, we would have expected to see that maximum velocity was lowest in the piano key condition, but we found no significant difference between the piano key and the blocked key on the maximum velocity measure. It could simply be that when tapping on the blocked key, the finger travels a shorter distance and essentially crashes into the surface, resulting in a smaller (compared to the air condition) and later (compared to the air and piano key conditions) maximum velocity for this condition. Thus the finger does not have a chance to achieve as high a velocity as it does in the other surface conditions.

No differences in asynchrony were observed across conditions, suggesting that subjects were able to modify their tapping strategies to achieve accurate performance in all conditions. However, it should be noted that standard errors were large for this dependent measure, possibly due to a relatively small number of responses per condition and small sample size.

In summary, we were able to show that trajectory asymmetry decreases as tapping rate increases, as predicted. We were unable to demonstrate that asymmetry also decreases as tactile feedback increases, possibly due to low statistical power. However we did observe that tapping on a piano key is no less asymmetric at 1 Hz than at 2 Hz, lending some support to our hypothesis that tactile feedback from the surface is aiding the synchronization process so that it becomes less dependent on proprioceptive feedback from a high velocity Response phase. Consistent with this finding, we also observed that the maximum velocity of the Response phase is smaller when tapping on the piano compared to tapping in the air. Therefore, the results of our study lend partial support to the hypothesis of Balasubramaniam et al. (2004) that the high velocity descent of the finger provides proprioceptive feedback that aids in synchronization.

The results of our study are consistent with the work of Goebl and Palmer (2008) which also examines the role of tactile feedback from a surface. In their study of pianists playing various melodies on a piano, they found that larger acceleration changes at initial piano key contact were associated with greater temporal accuracy. They associate these large acceleration changes with greater tactile feedback from the piano key surface and interpret their findings as suggesting that this tactile information is being used to better plan subsequent motor responses. Their analysis also suggests that it would be fruitful to examine acceleration profiles in addition to trajectory and velocity. Additionally, it would be useful to extend our analysis by subdividing the Response phase for the piano condition into pre- and post-key-contact sub-phases to better understand the role of the piano key surface.

The synchronization of a motor response with a regularly occurring external event is an important aspect of behaviour, the understanding of which will lead to a greater knowledge of how the brain perceives time, how it predicts events, and how it integrates information from multiple sources to adaptively modify responses. In this study we sought to shed light on how the motor response is modified under varying conditions of sensory feedback. We provided evidence showing that the degree of tactile feedback from the tapping surface does influence trajectory and velocity. If the degree of sensory feedback from the tapping surface could be somehow quantified, then it might be possible to mathematically define the relationship between the amount of information received from the tapping surface and the asymmetry of the response. Additionally, further study is needed to verify that the influence of tapping surface increases as synchronization gets harder at slower frequencies.

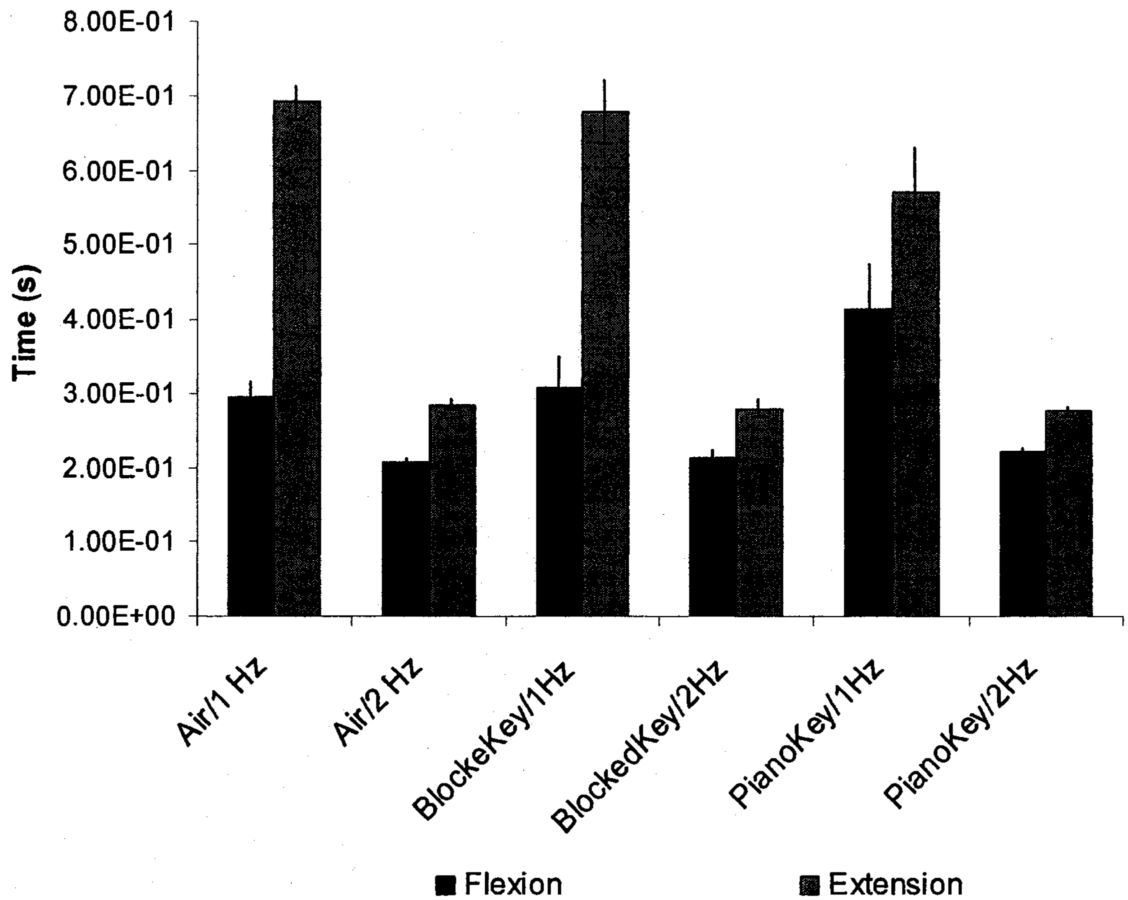

Figure 8. Flexion and extension times using the maximum and minimum points of each tapping cycle to define movement initiation and termination respectively.

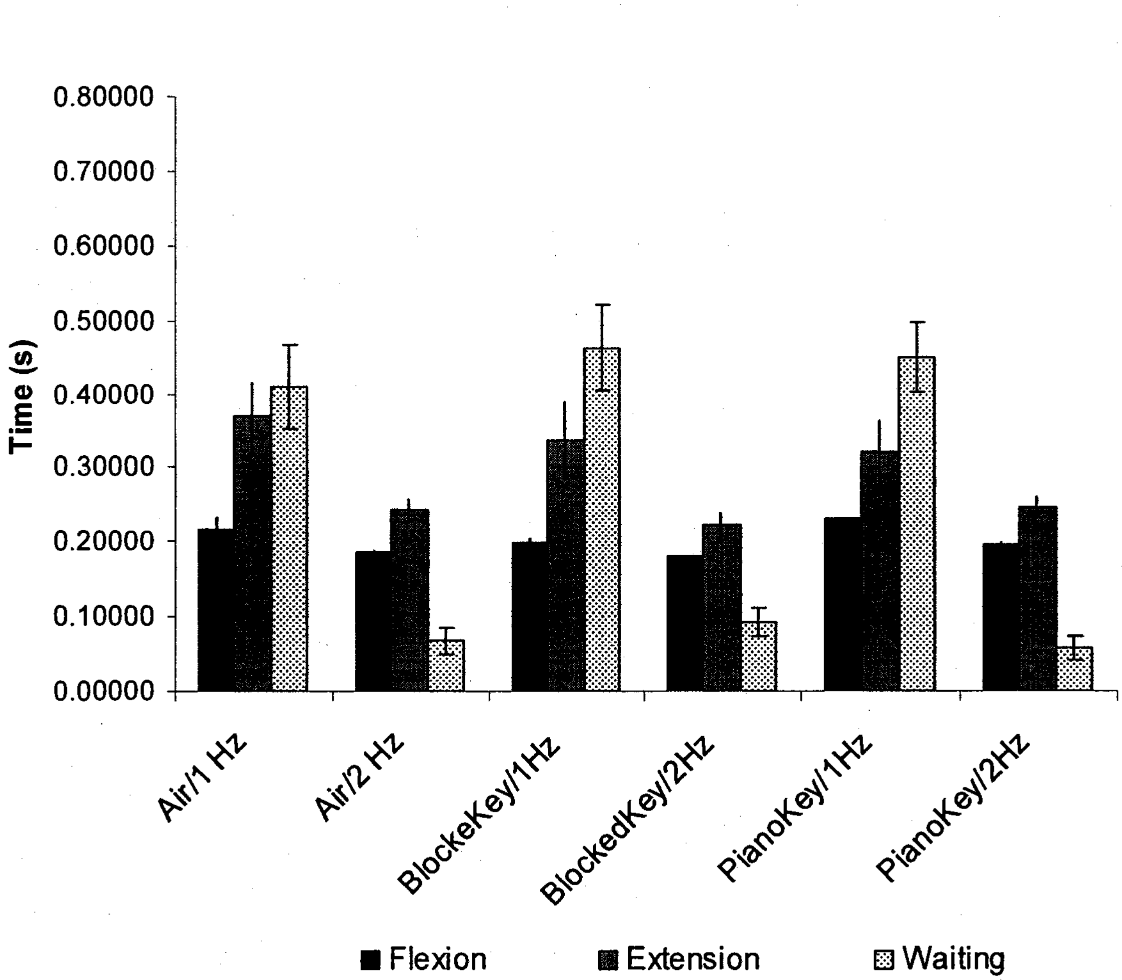

Figure 9. Flexion (Response), extension (Recovery), and waiting times using percentage of maximum/minimum velocity to define movement initiation and termination.

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Appendix A

Handedness Questionnaire

Handedness Questionnaire

ID: ____________ Date ____________

Ra	- right hand always (1/5)
Rm	- right hand most of the time (2/5)
E	- both hands equally often (3)
Lm	- left hand most of the time (5/2)
La	- left hand always (5/1)
X	- do not know which hand (0)

Which hand do you normally use to:	**R (1/5)**	**L (5/1)**
1. hold scissors when cutting	_____	_____
2. throw a ball	_____	_____
3. hold a slice of bread when buttering	_____	_____
4. hold a watch when winding it	_____	_____
5. hold a drinking glass when drinking	_____	_____
6. hold a needle when threading	_____	_____
7. hold a dish when wiping	_____	_____
8. insert a key into a lock	_____	_____
9. hold a pencil when writing	_____	_____
10. hold a comb when combing hair	_____	_____
11. hold a bottle when removing cap	_____	_____
12. hold a potato when peeling	_____	_____
13. hold a tooth brush when brushing teeth	_____	_____
14. dial a telephone number	_____	_____
15. hold a pitcher when pouring out of it	_____	_____
16. turn on a water faucet	_____	_____
17. hold a loaf of bread when cutting with a knife	_____	_____
18. hold nail when hammering	_____	_____
Total :	_____	_____
Score:	__________	

Appendix B

Health Questionnaire

LABORATORY FOR MOTOR LEARNING AND NEURAL PLASTICITY

GENERAL INFORMATION

Given name: ____________________ Family name: ________________________

Participant's ID: ____

Male _____ Female _____ Telephone number(s): (   )________________________

Email address: ____

Date of birth: ____________________________ Age: _____________________

Medical Condition

Head injuries: ____

Exclude if the person had a significant head injury and were actually hospitalized or were unconscious for more than 24 hrs.

Medication: ____

Exclude if taking medication for any neurological disease (i.e. Multiple Sclerosis etc.)

Hand injuries: ____

Exclude if any hand injury that could interfere with finger tapping.

Remarks: ____

I should tell you that there are other interesting studies being conducted in our department. Would I be able to pass on your name and number to a colleague? The info you have just given me will remain confidential.

☐ YES ☐ NO

Can we leave a message on answering machine?

____

Appendix C

Music Questionnaire

Musical Training/Experience Questionnaire

ID ____________________ Date ____________________

* Have you ever played a musical instrument (including voice/dance)? **YES** ☐ **NO** ☐

(The following questions are letter coded with respect to the first question, e.g. years of playing for instrument "a", instrument "b", etc.)

If yes, which instrument(s) (including voice/dance) in order of concentration:
a) __________________________,
b) __________________________,
c) __________________________

* How old were you when you first started playing/singing/dancing? a) ____________, b) ____________, c) ______

* How did you learn to play/sing/dance? a) __________________, b) ____________________, c) ______________

* For how many years did you play/sing/dance?

0-3 yrs:	a) ☐	b) ☐	c) ☐
4-8 yrs:	a) ☐	b) ☐	c) ☐
9-13 yrs:	a) ☐	b) ☐	c) ☐
14 + yrs:	a) ☐	b) ☐	c) ☐

ADD YRS: _________

If stopped playing, at what age did you stop playing/singing/dancing?
a) _________, b) _______, c) _______

<u>Musical Scale</u>

1 – No musical training or experience
2 – < 3 yrs musical training or experience/no current practice (i.e. stopped practicing > 1 yr ago)
3 – < 3 yrs musical training or experience/current practice (i.e. been practicing > 2-3 times/wk in past yr)
4 – > 4 yrs musical training or experience/no current practice (i.e. stopped practicing > 1 yr ago)
5 – > 4 yrs musical training or experience/current practice (i.e. been practicing > 2-3 times/wk in past yr)

Appendix D

Informed Consent Form

LABORATORY FOR MOTOR LEARNING AND NEURAL PLASTICITY

CONSENT FORM TO PARTICIPATE IN RESEARCH

Title of project: Performance changes in human motor skill learning I

Researchers: Dr. Virginia Penhune; Dr. Karen Li; Larry Baer (Graduate Student); Alejandro Endo (RA); Anthony Hopley (Research Assistant); Joannie Huberdeau (undergraduate volunteer)

This is to state that I agree to participate in a program of research being conducted in the Laboratory for Motor Skill Learning and Neural Plasticity in the Department of Psychology at Concordia University.

A. PURPOSE

The purpose of this study is to advance our knowledge of how we learn precise motor skills, similar to playing the piano. In the future, this knowledge may also increase our understanding of brain disorders resulting from disease or injury.

B. PROCEDURES

This experiment consists of a single testing session lasting approximately 45 minutes. At the beginning of the session, small infrared- emitting markers will be placed on the fingernail and knuckles of your right index finger. These markers allow us to measure the movement of your finger using a specialized camera system. You will also wear a set of headphones through which you will hear a regular metronome-like tone. You will be asked to tap your finger in synchrony with the tone, either in the air, on a tabletop, or on a piano keyboard. As you perform this task over a twenty to thirty minute period, the movement of your finger will be recorded. This is a noninvasive procedure and at no time will you be videotaped.

Advantages and disadvantages: Participation in this study has no personal benefits. On a long term basis, the study may help us gain knowledge about motor skill learning. There are no significant risks associated with participation in this experiment. The only possible risk is that of minor skin irritation related to placement of the markers. The only disadvantage of participation is the time spent doing the test and traveling to and from the laboratory. The investigator may end the study at any time for purely scientific reasons.

C. CONDITIONS OF PARTICIPATION

I understand that my participation is entirely voluntary and that I am free to withdraw my consent and discontinue my participation at anytime without negative consequences. I further understand that all records and test results of this study will be kept strictly confidential. No one but the experimenters will have access to any information about me or my performance. In addition, my name will not be used in any report or publication.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

Name

Signature Date

Witness signature Date

For further information about this study either before or after it is completed, please feel free to contact:
Dr. Virginia Penhune at 848-2424 x7535 (vpenhune@vax2.concordia.ca). If you have questions about your rights as a research participant, please contact Adela Reid, Research Ethics and Compliance Officer, Concordia University, at 514-848-2424 x7481 or by email at Adela.Reid@concordia.ca.