

Ramesh Balasubramaniam · Alan M. Wing ·
Andreas Daffertshofer

Keeping with the beat: movement trajectories contribute to movement timing

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Abstract Previous studies of paced repetitive movements with respect to an external beat have either emphasised (a) the form of movement trajectories or (b) timing errors made with respect to the external beat. The question of what kinds of movement trajectories assist timing accuracy has not previously been addressed. In an experiment involving synchronisation or syncopation with an external auditory metronome we show that the nervous system produces trajectories that are asymmetric with respect to time and velocity in the out and return phases of the repeating movement cycle. This asymmetry is task specific and is independent of motor implementation details (finger flexion vs. extension). Additionally, we found that timed trajectories are less smooth (higher mean squared jerk) than unpaced ones. The degree of asymmetry in the flexion and extension movement times is positively correlated with timing accuracy. Negative correlations were observed between synchronisation timing error and the movement time of the ensuing return phase, suggesting that late arrival of the finger is compensated by a shorter return phase and conversely for early arrival. We suggest that movement asymmetry in repetitive timing tasks helps satisfy requirements of precision and accuracy relative to a target event.

Keywords Jerk minimisation · Movement synchronisation · Movement timing · Movement trajectories · Timed repetitive actions

Introduction

Studies of movement timing often employ repetitive movements of the finger, the wrist or the whole arm, performed in time to a metronome beat. The variability in the accuracy of these movements has provided clues into how the nervous system organises movement onsets, arrivals or departures with respect to a specified internal or external meter (Aschersleben and Prinz 1995; Swinnen 2002), with respect to successive arrivals (Vorberg and Wing 1996), and in response to perturbations in phase and period (Repp 2001). It is generally understood that control of timed repetitive actions should satisfy two goals: one directed at phase (precision and accuracy in timing) and the other at period (organisation of movement parameters to meet interval requirements). What are the control variables involved in organising movement parameters to meet these requirements of timing?

There are two basic modes of coordinating movement with respect to an external metronomic event. They are (a) *synchronisation*, for example, flexing the finger to strike on the beat, and (b) *syncopation*, for example, flexing to strike off the beat or midway between beats, commonly found in jazz. In musical contexts syncopation is harder to perform than synchronisation. The skill is sometimes trained by redefining the focus of the task as extending the finger on the beat. Thus flexion off the beat is achieved as a by-product. In laboratory studies it has been shown that extending on the beat is more stable than flexing off the beat, especially at higher frequencies, although it is not as stable as flexing on the beat (Carson and Riek 1998; Kelso et al. 1998). Hence the definition of coordination with respect to an external metronome (Aschersleben and Prinz 1995; Vorberg and Wing 1996) should include not only task goals (synchronise vs. syncopate) but also motor goals (flexion vs. extension or pronation vs. supination).

Repeated to-and-fro movement is often approximately sinusoidal in form and hence assumed to be symmetric in the sense that the form and velocity of movement is similar in the out and back phases. This suggests constancy or symmetry of movement kinematics in the

R. Balasubramaniam (✉) · A. M. Wing
Behavioural Brain Sciences Centre, School of Psychology,
University of Birmingham,
Edgbaston, B15 2TT, UK
e-mail: ramesh@uottawa.ca
Tel.: +44-121-4143683
Fax: +44-121-4144987

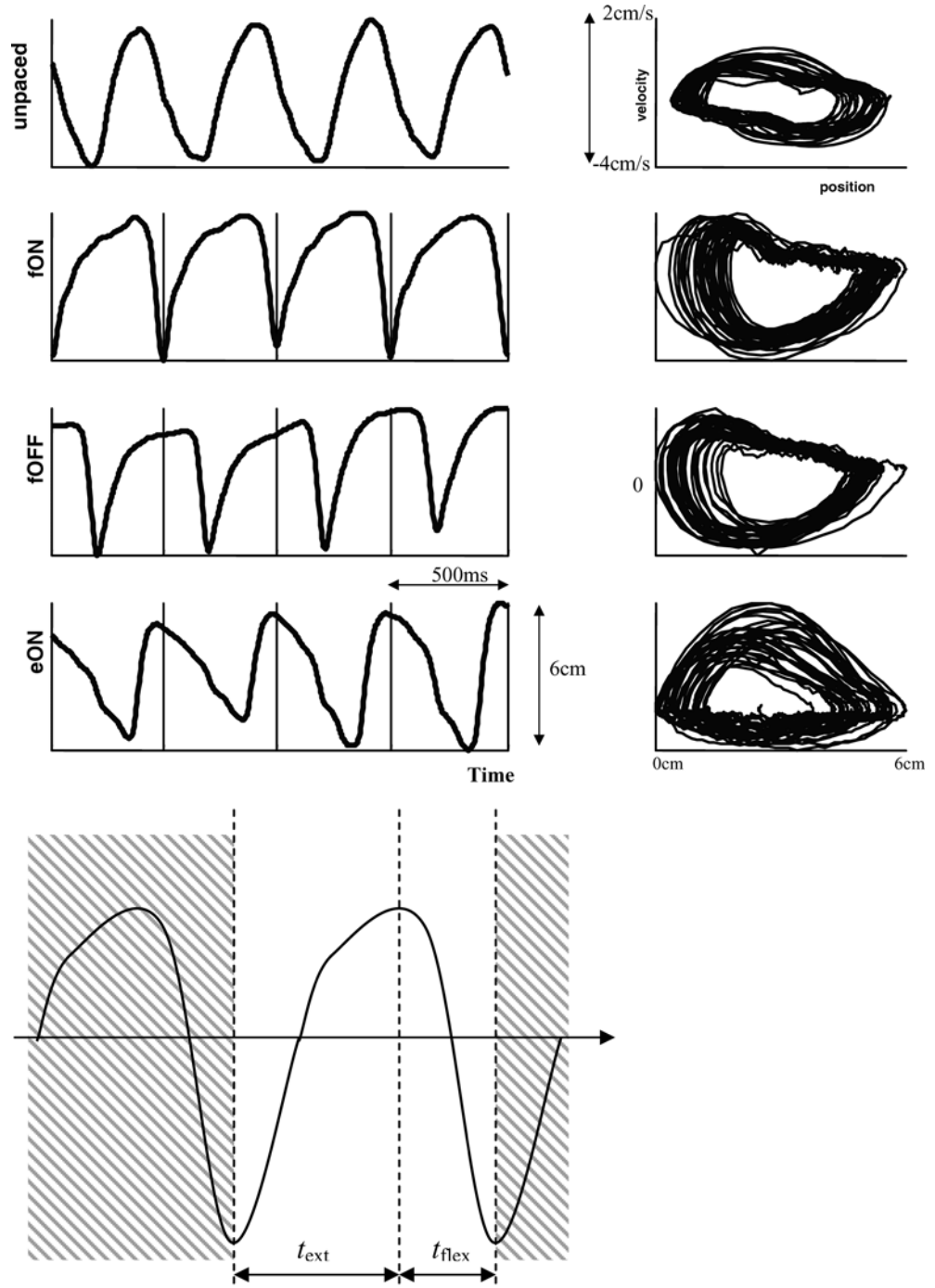
A. Daffertshofer
Faculty of Human Movement Sciences, Vrije Universiteit,
Amsterdam, The Netherlands

two phases. Symmetry in form is found even though the muscle activation required in each phase may be quite different due to dynamic factors such as the effects of gravity (Vallbo and Wessberg 1993), unequal muscle forces (Cheney et al. 1991) and different sensori-motor cortical activation patterns (Yue et al. 1998). This symmetrical movement form has been used in several modelling efforts that have attempted to capture an oscillator description of finger movements, often involving limit cycles (Kay et al. 1991).

Recently it has been proposed (Spencer et al. 2003; Zelaznik et al. 2000) that timing behaviour in continuous

movement tasks such as circle drawing or to-and-fro movements without surface contact does not require explicit temporal representations. In contrast, periodic surface contact in tapping defines an event whose timing is subject to explicit control. In aiming movements an important principle control principle is that of smoothness, based on jerk or the third derivative of position (Flash and Hogan 1985). In cyclic movements a sinusoidal trajectory (symmetric in position and velocity in the out and back phases) is a maximally smooth movement in that it minimises the mean squared value of jerk (Flash and Hogan 1985; Wann et al. 1988). Spencer and colleagues

Fig. 1 Visualising the asymmetry. *Upper left panel* Four cycles of displacement from a sample trial of a subject in the unpaced condition followed by fON, fOFF and eON; *dotted lines* The metronome event. *Right panel* Corresponding phase plots (position×velocity). Notice that the kinematic traces are symmetrical about flexion and extension in the unpaced condition and not so in the others. We also draw attention to the fact that while fON and fOFF have similar extension/flexion profiles, eON is different. *Lower panel* Illustration of extraction of parameters from the asymmetric movement trajectories (t_{ext} , t_{flex}) in the fON condition. Peak velocities, v_{ext} and v_{flex} were also computed for each cycle



(2003) suggested from work on patients with cerebellar lesions that the control of continuous movements is based on an optimality principle such as minimisation of jerk, and that apparent temporal control is an emergent property.

We report a task-modulated departure from the movement symmetry implicit in limit cycle models and sinusoidal trajectory assumptions when the movements are paced by an external metronome, a phenomenon which is less evident in unpaced repetitive movements. We ask: How is the asymmetry in the movement trajectory related to task and motor goals? What are its implications for timing? We also tested the possibility that although synchronisation by extending on the beat may be functionally equivalent to syncopation by flexing off the beat (in terms of meeting the task goal), movement trajectories in these two cases which have been assumed to be kinematically similar are not, in fact, equivalent.

Materials and methods

Subjects

Eight healthy right-handed adult volunteers at the University of Birmingham (six men, two women; aged 25–37 years) took part in this study. All subjects had some musical training that provided them with the ability to syncopate at higher frequencies. None of the subjects reported any neurological or skeleto-muscular disorder or injury at the time of the experiment. The protocol was approved by the human subjects ethics committee of the University of Birmingham, and all subjects gave informed consent prior to the experiment.

Procedure

Seated subjects performed repetitive right index finger movements in the absence and presence of an auditory metronome that produced a 1 kHz tone for 20 ms every 1000 ms (1 Hz), 750 ms (1.33 Hz) or 500 ms (2 Hz). The kinematics of the movement trajectories were recorded at 200 Hz by a three-camera motion capture system (Qualisys ProReflex). A marker was placed on the tip of the index finger for the kinematic recordings. Reference markers were placed at the metacarpophalangeal joint and at a calibrated reference point of origin on the workspace. Subjects rested their right arm on an elevated surface on a desk from which they could make right index finger movements without any mechanical contact with objects or surfaces. Subjects were instructed to synchronise their index finger movement to the metronome (peak flexion on the beat: fON or peak extension on the beat: eON) or syncopate (peak flexion off the beat: fOFF). There were ten trials in each condition, with each trial involving 60 cycles of responses. In a further unpaced condition subjects were instructed to oscillate their index fingers at a comfortable frequency and amplitude in the absence of a metronome (ten trials with 60 cycles in each trial). In all of

these conditions the right index finger made no contact with any surface during the movement trials. The kinematic data from the sagittal plane (in the vertical direction) and corresponding analogue metronome data were stored onto a conventional PC for reduction and analysis in MATLAB (Mathworks, Natick, Mass., USA). Prior to each differentiation (for velocity, acceleration and jerk), signals were smoothed using a 5th order Savitzky-Golay polynomial filter (frame size 79 samples). Time of response to the metronome was taken as the peak flexion position in the fON and fOFF conditions and peak extension position for the eON condition.

Results

All subjects completed the tasks successfully without any abrupt or unforced transitions from the required phasing of the movements in each condition. The mean timing asynchrony in the synchronisation conditions (fON and eON) was -29.4 ± 16.2 ms, suggesting that the finger arrived slightly earlier than the metronome signal, which is consistent with previous reports (Aschersleben and Prinz 1995). Syncopation in the fOFF condition showed similar performance in the mean (relative to the midpoint between pacing tones) but with greater variability -31.3 ± 28.1 ms. Sample trajectories from each condition are shown in Fig. 1.

Trajectory asymmetry

Visual inspection of Fig. 1 (upper) reveals that, compared to the unpaced condition, all of the kinematic profiles in the paced conditions show a marked asymmetry. Note that in the paced conditions (fON, fOFF) the flexion or downward phase of the movement has a much steeper slope than the extension or upward phase. Conversely, the eON condition appears reversed in form compared to fON and fOFF, in that the extension phase shows a steeper slope. We tested this difference statistically by calculating the time spent in extension or flexion (t_{ext} , t_{flex}) and the peak velocity achieved in flexion or extension (v_{ext} , v_{flex}) as a function of task and frequency.

The results (Fig. 2) clearly demonstrate that in the fON and fOFF conditions, the flexion phase of the movement is of shorter duration, and the converse is true in the eON condition. Analysis of variance revealed a significant interaction effect, between the factors of task (fON, fOFF and eON), frequency (1, 1.33 and 2 Hz) and phase (flexion and extension): $F_{(4,28)}=110.21$, $P<0.0001$. Post-hoc means comparisons revealed that in general $t_{ext} > t_{flex}$ in the fON and fOFF conditions and $t_{flex} > t_{ext}$ in the eON condition. All movement trajectories were more symmetrical with increasing frequency. The peak velocities in both phases yielded the complementary result ($v_{flex} > v_{ext}$ for fON and fOFF; $v_{ext} > v_{flex}$ for eON) confirmed by a significant interaction between task, frequency and phase: $F_{(4,28)}=35.153$, $P<0.001$. In the unpaced conditions, no

significant differences in movement time or velocity ($F < 1$) were observed between flexion (mean $t_{flex} = 0.236$ s and mean $v_{flex} = 0.306$ ms⁻¹) and extension (mean $t_{ext} = 0.254$ s or mean $v_{ext} = 0.287$ ms⁻¹).

It is important to underscore that the two phases in a given cycle (slow and fast) are functional (related to task) and not attributable to or independent of motor factors (such as biomechanical differences between flexion and extension). This is indicated by the reversal of time and velocity properties between the flexion and extension phases in the eON condition. Interestingly, no movement amplitude changes were found either in the overall movement form or during each phase between the synchronisation and syncopation conditions. It also seems reasonable to conclude that syncopation in fOFF is equivalent to synchronisation with a virtual metronome (providing targets between beats), given that the trajectory properties resemble fON more than eON.

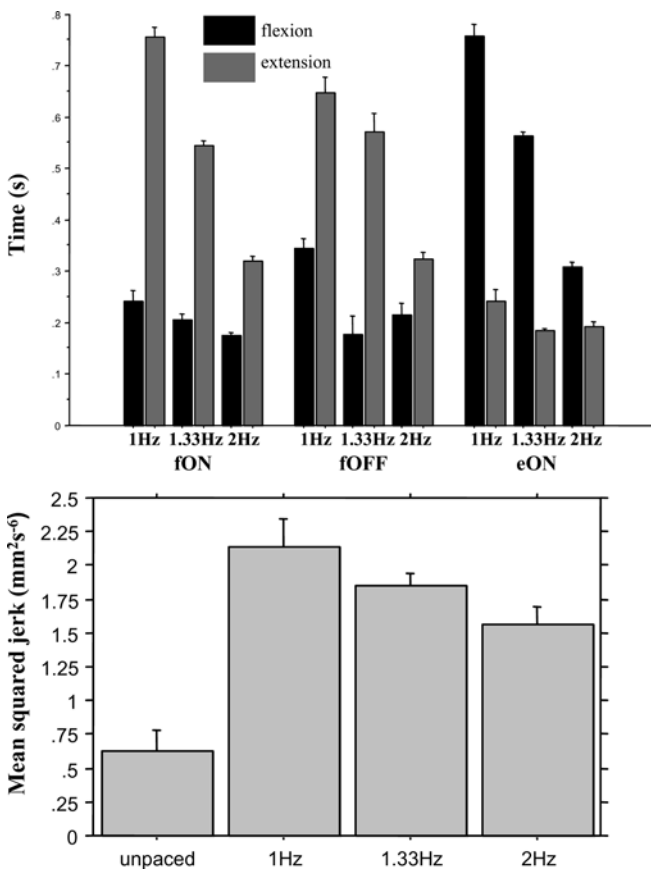


Fig. 2 Statistical tests of asymmetry. *Upper panel* Mean flexion and extension times for the fON, fOFF and eON conditions are plotted for each frequency. *Lower panel* The mean squared jerk was significantly higher for the timed repetitive movement trajectories than the unpaced ones, with the slowest of the timed movements (most asymmetric) exhibiting the highest jerk. In both plots the error bars stand for 1 SD

Movement smoothness

As noted above, sinusoidal symmetric cyclic movements minimise mean squared jerk. Our results show that timed repetitive movements made with the metronome are less sinusoidal and exhibit greater mean squared jerk than movements that are unpaced (shown in the lower panel of Fig. 2). Analysis of variance revealed a main effect of movement frequency on mean squared jerk: $F_{(2,8)} = 127.22$, $P < 0.001$. No significant effects of task factors (fON, fOFF and eON) or interactions between task and frequency on the values of mean squared jerk were found. In general, the mean squared jerk in the paced conditions was two standard deviations or greater than for the unpaced movements. This raises the question of what movement principle (Harris and Wolpert 1998) the nervous system follows in producing such markedly asymmetric movements, with a fast and slow phase, in the paced conditions.

Relationship between movement trajectories and timing errors

We posited that the systematic departure from symmetry (and smoothness) is related to the reduction in timing errors. This was confirmed by the fact that the more asymmetric the trajectory (for each cycle), the closer to zero was the asynchrony; $r = -0.69$; $P < 0.0001$, for the pooled data from all subjects in all the paced movement trials. We also found that relative asynchrony was strongly negatively correlated with the slow movement phase of the following cycle ($r = -0.63$, $P < 0.001$). This was true in the fON, fOFF and eON conditions ($r = -0.61$, -0.67 , -0.62 respectively, all $P < 0.001$) across all movement frequencies. This suggests that early arrival of the finger, producing a larger asynchrony, is compensated by a longer return phase that tends to correct the asynchrony. Correspondingly, a late arrival is compensated by a shorter return phase.

Additionally, we observed that the durations of low and high velocity phases were strongly negatively correlated ($r = -0.61$, $P < 0.0001$). Moreover, this correlation was itself negatively correlated with the asynchrony error ($r = -0.58$, $P < 0.0001$) such that the stronger the dependence between the two movement phases, the closer to zero is the asynchrony.

Discussion

In this study we sought to determine the relationship between trajectory form and accuracy of timing in movements paced by an external metronome beat. Trajectory asymmetry was present in all conditions in which subjects had to coordinate their movements with the metronome. In these conditions subjects made more rapid movements of shorter duration towards the temporal target and slower movements in the return phase. Although such unequal velocities in out and back phases of repetitive

movements have been reported previously (Wacholder and Altenburger 1926 cited in Sternad 2001; Nagasaki 1991), no links were made to timing goals. Here we have shown that asymmetry is closely linked to timing. In general, greater trajectory asymmetry was associated with better timing accuracy. Additionally, relative asynchrony (early or late arrival) was negatively correlated with the ensuing slow phase.

It is interesting to note that the mean duration of the “to” phase (such as flexion in fON), stays relatively constant compared to the duration of the “away” phase across frequency conditions. One might suppose that this relative invariance of the “to” phase duration might underlie the changes in durational asymmetry of the movement trajectories. The strong negative correlations (more negative than -0.5) between the durations of the flexion and extension phases of the movement (across conditions) implicate the existence of closed loop control.

The Wing-Kristofferson (1973; W-K) model predicts that in the absence of an external metronome successive intervals between responses tend to exhibit a long and short alternation, resulting in a negative correlation that is theoretically bounded by zero and negative one-half. This is the case even though the model assumes open loop control of timing. An extension of the original W-K model proposed by Wing (1979) looked at the relationship between two movement phases (arrival and departure) of a cycle in continuation tapping. Negative correlations bounded by zero and negative one-half were found between the phases, which promoted the conclusion that initiation of each phase was centrally determined without reference to the time of occurrence of each preceding phase.

The existence of a correlation between cycles greater than -0.5 , as we have reported, indicates the existence of error correction or closed-loop control (Pressing 1999; Vorberg and Wing 1996). We suggest that the trajectory asymmetry (with negatively correlated flexion and extension phases) that we have described here might provide a basis for and facilitate error correction.

We posit that high velocity movements towards the target may provide perceptual information relevant to phasing (accuracy in synchronisation) and the slower return phase accommodates error correction and period adjustment. Further experimentation in this area is required to clarify the role of movement velocity in the proprioceptive regulation of timing, for example, in patients with sensory impairments (Drewing et al. 2004).

It is also worth noting that the degree of velocity asymmetry (and consequently mean squared jerk) decreased at higher metronome frequencies. Normally there is more variability in timing at lower frequencies (Wing 2002). We speculate that the introduction of asymmetry at lower frequencies helps to limit this increase in variability.

Our results suggest limitations on autonomous limit cycle oscillators as models of timed repetitive movements because they are inherently symmetric. Interestingly, such limit cycle models have not been able to account for a fundamental aspect of timed movements that is the

correlational structure between cycles as predicted by the W-K model (Daffertshofer 1998). An oscillator model of timed repetitive movements (e.g. Beek et al. 2002) must take into account both the movement asymmetry and the correlational structure. It would be interesting to see the development of models sensitive to the differing properties of each phase of the movement that also consider the optimisation criteria for flexion and extension separately. A starting point for such work might be to look at parameters such as jerk, in addition to stiffness and damping separately for flexion and extension.

As noted earlier, the trajectory in the fOFF condition was more similar in form to fON than to the eON condition. It has been assumed following the experiments of Kelso et al. (1998) that eON could actually be an alternative strategy for syncopation by fOFF. Our results suggest that the functional similarities and differences between eON and fOFF at both the behavioural (Carson et al. 1998) and cortical levels (Kelso et al. 1998) require a closer look.

Functional and neural implications

It has been suggested by Spencer et al. (2003) that the cerebellum, which is considered essential in setting and representing explicit timing goals, plays a less important role in continuous movements such as those presented here. They argue that timing in continuous tasks is an emergent property that arises from the interactions of the neuromuscular system with the environment, without explicit temporal representations that involve the cerebellum. Spencer et al. (2003) also suggested that “timing” in continuous movements (in the absence of cerebellar involvement) is likely to originate from an optimality criterion such as minimisation of jerk. Here we have shown that jerk minimisation which works well in the case of discrete movements such as spatial aiming might not be important in the control of timing in rhythmically paced movements. We postulate that the alternating directions of movement with high and low velocity phases provide contrast in acceleration patterns that may be useful landmarks for sensory (proprioceptive) regulation of timing.

Our results show the benefits of combining two contrasting approaches (Wing and Beek 2002) to timing: discrete *event-based* approaches that have looked at errors and their correction in synchronisation and *continuous* approaches that have almost exclusively dealt with the stability of movement trajectories. The question of what kind of optimality principles are used by the CNS during trajectory formation in timed repetitive movements that satisfy constraints of accuracy and period stability is likely to be an important avenue for future research.

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