4. TRAJECTORY FORMATION IN TIMED REPETITIVE MOVEMENTS

Ramesh Balasubramaniam

Sensorimotor Neuroscience Laboratory, School of Human Kinetics, University of Ottawa, Canada

Abstract

In skills as diverse as piano playing or swinging a racquet in tennis, movements comprise a pattern that involves going to and away from the target, anecdotally referred to as attack and release. Although all such voluntary actions involve timing, timed repetitive movements involve bringing an end effector periodically to a certain location in the workspace in relation to a sensorimotor event. Research in this area has involved the characterization of synchronization errors, identification of sources of variability in synchronization, and determination of neural structures involved in organizing such behavior. While much is known about the timing errors made while synchronizing with respect to external beat, not much is understood about what kind of movement trajectories are needed for timing accuracy. In this chapter, I review some recent work that links the ideas from the trajectory formation literature to what we currently know about timing accuracy in repetitive movements. Additionally, I present a paradigm that offers to bring together the dynamical systems approach with the information processing accounts of movement timing.

Introduction

There are two well identified traditions in movement timing research: the information processing approach and the dynamical systems approach. In the former, time is considered to be mental abstraction that is represented independent of any particular effector system (Wing, 2002; Vorberg & Wing, 1996). In this view, our ability to carry out an action such a playing the piano or hitting a ball at various speeds, to speak or draw fast or slow, depends on central timing processes.

Time is represented independent of the motor apparatus, although it is generally understood that central timing processed might indeed make contact with the motor system. Said differently, according to this approach the central timing processes are functionally contained in that they do not need any particular effector system to be instantiated. While the timing processes may be set to initiate movements at certain times these movements' other parameters, such as force, amplitude or direction, can be specified independently (Semjen, Schulze & Vorberg, 2000).

In the dynamical systems approach, timing is considered to be an emergent property of the organizational principles (i.e., dynamical equations of motion) that govern coordinated action (Turvey, 1990; Kelso, 1995; Yu & Sternad, 2003). Thus the characteristic timing of an action is part and parcel of other movement dimensions of that action, such as frequency or its dynamical equivalents, stiffness and damping. A rhythmic activity such as piano playing may be carried out with regular timing but that is a consequence of a dynamical regime specifying a sequence of finger movement directions and amplitudes under particular stiffness constraints. In this approach, time as such is not an explicitly controlled variable, but follows from dynamical equations of motion and their parameter settings (for review see Schöner, 2002). The CNS does not deal with the abstract notion of time without reference to the moving parts of the body. So for example, the control of timing in the production of a musical pattern may thus be said to follow from the effector system used to implement movement and its interaction with the environment. The key concept in the dynamical systems approach is that like all physical systems, brains and indeed behavior are governed by

the laws of motion and change. The idea here is that *atomisms* or sub-symbolic units of behavior, emerge into organized, stable and meaningful structures on the basis of simple extremum principles or lawful constraints (Turvey, 1990). For example bringing an end effector to a specific point in the workspace in time, involves the collective action of several neuromuscular events whose macroscopic stability leads to the production of stable timed rhythmic behavior.

While the two approaches have divergent views on the nature of how temporal information is made available to and treated by the nervous system, they have also employed very different experimental paradigms (Wing & Beek, 2002; Balasubramaniam, Wing & Daffertshofer, 2004). The information processing approach has largely been concerned with the study the synchronization event itself (Vorberg & Wing, 1996). Of special interest has been the statistical relationship between adjacent timing intervals in a sequence. The variability in the timing element of these movements has provided clues into how the nervous system organizes movement onsets, arrivals or departures with respect to a specified meter (internal or external), with respect to successive arrivals, and in response to perturbations in phase and period (Repp, 2001).

On the contrary, the dynamical systems approach has looked at movement trajectories and their stability with respect to keeping with an external beat. Interesting experimental paradigms have looked at the stability of the phase of the movement of the end effector (1) with respect to an external event (Kelso, Delcolle & Schöner, 1990) or (2) with respect to another limb (Haken, Kelso & Bunz, 1985; Swinnen, 2002). Unearthing the nature of the "attractor" that keeps the movement of the effector in a phase relationship with the event in question has been a key question driving this approach. For example what kind of attractor mechanism governs the behavior when one flexes the index finger to synchronize with a beat or syncopate to a beat (flexes the finger midway between two beats)? In the theory of dynamical systems, two well known attractors have been commonly used to describe timed repetitive movements: (1) The point attractor or stable fixed point (nearby trajectories converge onto a point; e.g., the equilibrium point of a mass-spring system) and (2) the periodic attractor or a limit cycle (trajectories converge onto a closed orbit; e.g., the periodic oscillations of a pendulum with an escapement to sustain the oscillations). The stability and variability of these movement patterns (along with their proclivities towards stable states) have provided clues into the preferences shown by the nervous system in organizing rhythmic behavior. Such models

have shown considerable success in explaining the relative stability of one regime with respect to another (Riley & Turvey, 2002).

PACED RESPONDING AND INTERVAL PRODUCTION

Behavioral studies of motor timing commonly focus on relatively short intervals up to a few seconds to span the timescale of voluntary movements. As mentioned in the earlier section, a frequently used paradigm in the information processing approach involves repetitive responding to produce a series of inter-response intervals I_j. Experimental control over mean (I) is obtained by including a period at the beginning of a trial in which the subject synchronizes responses with an auditory pulse train with inter-pulse interval set to T. When the pulses stop the subject is instructed to continue at the same rate for a further 30 to 50 responses. During the unpaced phase it is found that subjects maintain mean (I) within a few milliseconds of T, but with variability that increases with mean (I), a phenomenon first reported by Stevens (1886). A key characteristic of unpaced responding (also called continuation) is that successive I_j, I_{j+1} are negatively correlated between zero and minus one half. A theoretical account for this phenomenon was proposed by Wing and Kristofferson (1973). They suggested a hierarchical two-level model in which intervals generated by a central timer C_j are subject to delays in motor implementation D_j before the occurrence of observable responses. This model is henceforth referred to as the Wing & Kristofferson (W-K) model. The details of the working of the W-K model are presented in Figure 1.

LIMIT CYCLE OSCILLATORS AND THE W-K MODEL

Following a suggestion by Schöner (1994), it has been assumed that the lag-one autocorrelation effect predicted by the W-K model can be accounted for by the modulation of stiffness and damping of an autonomous limit cycle oscillator. A formal attempt has been made to account for empirically observed patterns of temporal variability in the W-K model with autonomous limit cycle oscillators. Daffertshofer (1998)—following an earlier suggestion of Schöner (1994)—examined both analytically and numerically the minimal conditions under which limit cycle models with noise consistently produce a negative lag-1 serial correlation between consecutive periods of oscillation (with a value between 0 and −0.5). Contrary to earlier intuitions, he showed that a single (autonomous) limit cycle oscillator that is
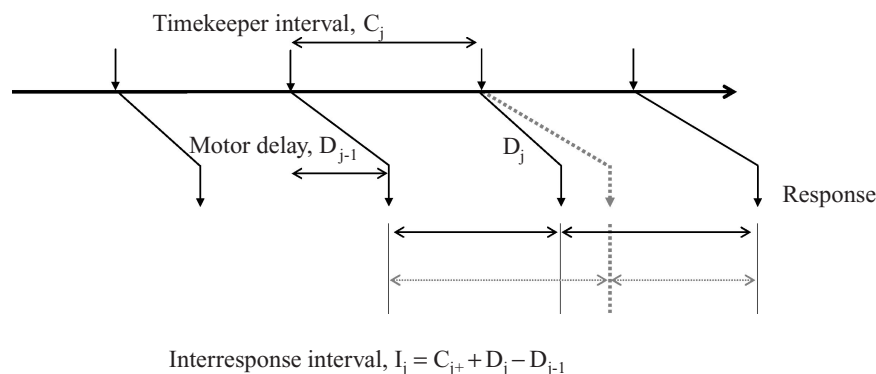
FIGURE 1. The operation of the Wing-Kristofferson (W-K) timing model. Variable timekeeper intervals subject to random motor implementation delays result in inter-response intervals that are negatively autocorrelated at lag 1 and bounded between zero and negative one half.

stochastically forced by (additive or multiplicative) white or by colored noise cannot produce the desired period correlation but results in phase diffusion, except under conditions of unrealistic stiffness values. In order to obtain reliable negative correlations, it is necessary either to introduce two conveniently placed interacting noise sources (regressing to the original WK model), or to add a second oscillator that is coupled to the limit cycle oscillator of interest (as a forcing function), thus stabilizing its phase. Thus if one were to take an oscillator based approach to account for the W-K results, a different strategy is needed. One obvious way to bring the two paradigms together is to look at movement trajectories of timed movement (Balasubramaniam et al, 2004; Delignieres et al, 2004).

Despite ideological differences between the two approaches, 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 (organization of movement parameters to meet interval requirements). What might be the constraints that would drive the requirements of a model that combines the two approaches? And more importantly, what kind of movement trajectories do we need to produce accurate movement timing?

Timing research has also historically paid little attention to the literature on trajectory formation. This is partly because models of trajectory formation and optimization have looked largely at discrete movements such as aiming and pointing. In discrete aiming movements, an important principle control principle

is that of smoothness, based on jerk or the third derivative of position (Flash & Hogan, 1985). A sinusoidal trajectory (symmetric in position and velocity in the out and back phases) is a maximally smooth movement in that it minimizes the mean squared value of jerk (Flash & Hogan, 1985; Wann et al, 1988). It has been shown that the movement trajectories that have different velocity profiles in the two phases of a movement (hence asymmetric) typically have higher values of mean squared jerk (Nagasaki, 1991).

CEREBELLUM AND TIMING

A recent finding about the cerebellum's role in event timing and repetitive response production (Spencer, Zelaznik, Diedrichsen & Ivry, 2003) offers an interesting perspective on the two approaches. Spencer and colleagues found that patients with cerebellar damage (uni- and bilateral) could perform implicit timing tasks such as air tapping or circle drawing with little difficulty. However their ability to perform tasks with clearly defined temporal landmarks such as tapping to a beat with surface contact was quite seriously compromised. They suggest that the cerebellum, which is considered essential in setting and representing explicit temporal goals, plays a less important role in continuous movements. 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 a trajectory optimality criterion such
minimization of jerk.

MODES OF COORDINATION

There are two basic modes of coordinating movement
with respect to an external metronomic event. They
are (1) *Synchronization*: e.g. flexing the finger to strike
on the beat and (2) *Syncopation*: e.g. flexing to strike
off the beat or midway between beats, commonly seen
in jazz. In musical contexts, syncopation is the more
difficult skill and at higher frequencies shows an invol-
untary switch to synchronization. The skill is some-
times trained by redefining the focus of the task as
extending the finger on the beat (Kelso et al, 1990).
Thus flexion off the beat is achieved as a secondary
consequence. In several laboratory studies it has been
shown that extending on the beat is more stable than
flexing off the beat, especially at higher frequencies,
though not as stable as flexing on the beat (Kelso et al,
1998; Carson & Riek, 1998). Hence the definition of
coordination with respect to an external metronome
(Aschersleben & Prinz, 1995; Vorberg & Wing, 1996)
should include not only task goals (synchronize vs.
syncopate) but also motor goals (flexion vs. extension
or pronation vs. supination).

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

EVIDENCE AGAINST
SYMMETRICAL TRAJECTORIES

In an experiment involving synchronization and
syncopation to an external auditory metronome,
Balasubramaniam et al (2004) have shown that the
nervous system produces movement trajectories that
are asymmetric with respect to time and velocity in the
out and return phases of the repeating movement cycle
(as shown in Figure 2). This asymmetry is task specific
and is independent of motor implementation details
(flexion vs. extension). Unpaced trajectories, however,
do not show this asymmetry in movement times or

velocity in either direction of motion. Additionally,
they found that timed trajectories are less smooth
(higher mean squared jerk) than unpaced ones.

The mean squared jerk for the movements with a
metronome present was much higher than the un-
paced ones (as shown in Figure 3). Thus the timed
movements showed a shorter, faster movement to-
wards the target followed by a slower and longer move-
ment away from the target. For example, in the con-
dition flexing on the beat (fON), the flexion phase
was shorter and faster than the extension phase, but
the converse was true in the extend on the beat con-
dition (eON). The trajectory in the Flexing off the
beat (fOFF) condition resembled fON and not eON
(which it is believed to be functionally equivalent
to).

Additionally, negative correlations that were greater
than −0.5 were observed between synchronization
timing error and the movement time of the ensu-
ing return phase suggesting that late arrival of the
finger is compensated by a shorter return phase and
conversely for early arrival. Balasubramaniam and
colleagues suggest that movement asymmetry in repet-
itive timing tasks helps satisfy requirements of preci-
sion and accuracy relative to a target event. Trajectory
asymmetry was present in all conditions where sub-
jects had to synchronize to an auditory metronome.
In all the metronome paced conditions, subjects made
more rapid movements of shorter duration towards
the target and slow movements in the return phase.
The degree of this asymmetry and consequently mean
squared jerk decreased at higher metronome frequen-
cies. In general, greater trajectory asymmetry was as-
sociated with better timing accuracy. Additionally,
relative asynchrony (early or late arrival) was nega-
tively correlated with the following slow phase.

It is interesting to note that duration of the "to"
phase (such as flexion in fON), varies much less than
the duration of the "away" phase across frequency
conditions. One might suppose that the relative in-
variance of the "to" phase duration might underlie
the changes in durational asymmetry of the move-
ment trajectories. But a careful look at the correla-
tions implicates the existence of a closed-loop control
mechanism. Open-loop models of timing such as the
Wing-Kristofferson (W-K) model (Wing & Kristof-
ferson, 1973) predict that, in the absence of an exter-
nal 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. The existence of a cor-
relation between cycles greater than −0.5, as reported
by Balasubramaniam and colleagues, suggests the
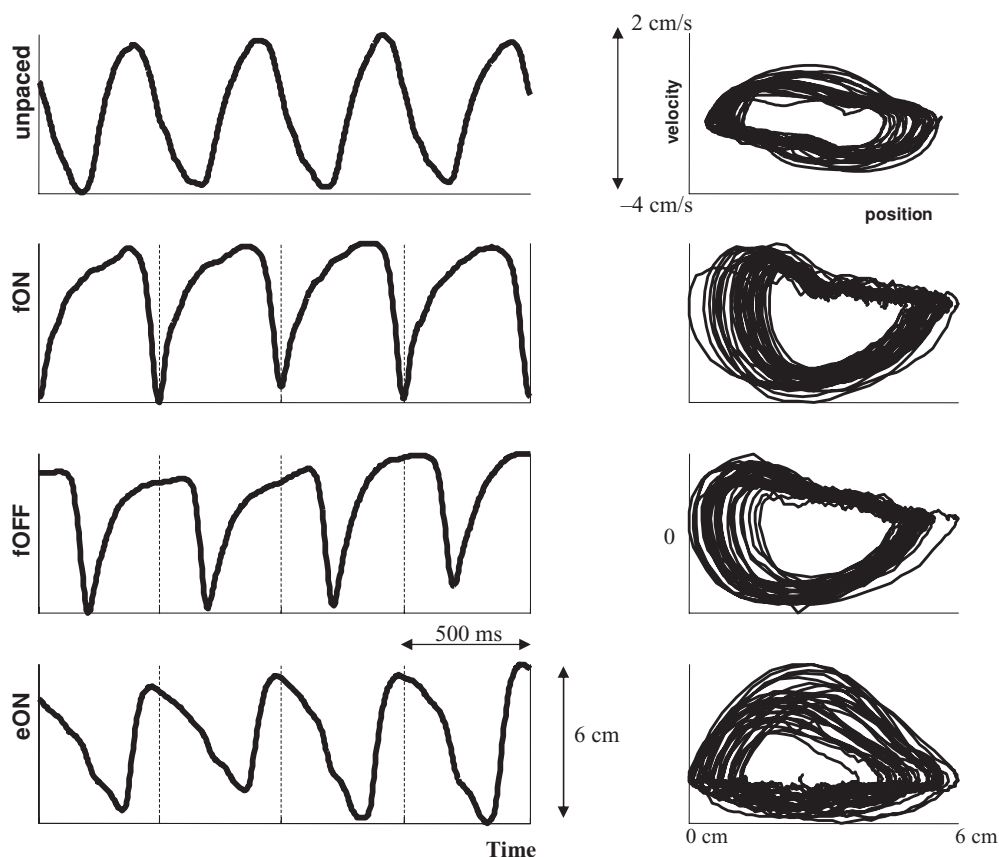presence of error correction or closed-loop control

FIGURE 2. Asymmetry in movement trajectories. The left hand panel shows four cycles of displacement from a sample trial of a subject in the unpaced condition followed by fON, fOFF and eON. The dotted lines indicate the metronome event. The right hand panel shows the 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. Also note that while fON and fOFF have similar extension/flexion profiles, eON is different.

(Vorberg & Wing, 1996; Pressing, 1999), which is characteristic of phase locking. It is important to mention here that the correlation that I have described is different from that used in the W-K model. While Balasubramaniam et al (2004) showed possible correctional mechanisms between relative asynchronies and the following movement phase, the W-K model refers to correlations between successive intervals. I am suggesting here that the trajectory asymmetry described here might provide a basis for and facilitate error correction.

It has been demonstrated that neural activity in proprioceptive pathways is scaled with the velocity of the movement (Delong et al, 1985; Gandevia & Burke, 1992; Grill & Hallett, 1995 & Matthews, 1991).

Thus the modulation of velocity in timed movements (Turner et al, 1998) might be an active strategy employed by the CNS to detect proprioceptive sensory information. I would like to argue that high velocity movements towards the target may provide perceptual information relevant to phasing (accuracy in synchronization) and the slower return phase accommodates error correction and period adjustment. The general reduction of timing errors for higher movement frequencies or shorter time intervals (Aschersleben & Prinz, 1995), might also be related to movement velocity. Further experimentation in this area is required to clarify the role of movement velocity in the proprioceptive regulation of timing (Drewing et al, 2004).
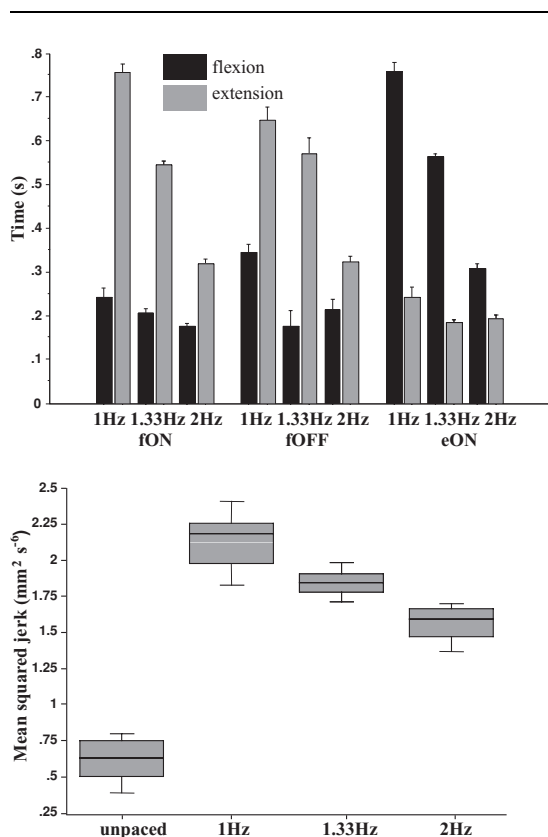
FIGURE 3. Statistical tests of asymmetry. The upper panel shows mean flexion and extension times for the fON, fOFF and eON conditions are plotted for each frequency. The lower panel shows that the mean squared jerk was significantly higher for the timed repetitive movement trajectories than the unpaced ones, with the slowest of the timed movements (most asymmetric) exhibiting the highest jerk.

To return the argument made earlier, these results also 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) will have to take into account both the movement asymmetry and the correlational structure. It would be interesting and useful to see the development of models sensitive to the differing properties of each phase of the movement that also consider the optimization criteria for flexion and extension separately.

A starting point for such work might be to look at parameters like jerk, in addition to stiffness and damping separately for flexion and extension. Another avenue for further research might be to look at the optimization with respect to signal dependent noise present when issuing motor commands to move the finger (or an end effector) back and forth.

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 (1995) that eON could actually be an alternative strategy for syncopation by fOFF. These results suggest that the functional similarities and differences between eON and fOFF at both the behavioral (Carson et al 1998) and cortical levels (Kelso et al, 1995) 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. Hence, it has been argued 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. Systemic modulations of parameters such as stiffness and damping that are not mapped directly onto specific neural or anatomical structures are implicated in the production of regular timed sequences of action (for review see Beek et al, 2002). 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 minimization of jerk. Here it is shown that jerk minimization 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. It is postulated that the alternating directions of movement with high and low velocity phases provide contrast in acceleration patterns that are useful landmarks for sensory (proprioceptive) regulation of timing. Thus the informational basis for timed action arises from the action itself. Further studies of cerebellar patients should address the issue of perceptual regulation of timing more carefully (Bracewell, Balasubramaniam & Wing, 2005).

Conclusions

The body of work that has been reviewed and presented here shows the benefits of combining two contrasting approaches (Wing & Beek, 2002) to timing:

discrete *event based* approaches that have looked at errors and their correction in synchronization and *continuous* approaches that have almost exclusively dealt with the stability of movement trajectories. The question of what kind of optimality principles (Harris & Wolpert, 1998) 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. Interesting future experimental methods would include studying trajectory formation in timed repetitive movements in the context of perturbations involving elastic and viscous force fields. This would reveal the relative importance of position and velocity based information in the regulation of timing. The question of what kind of oscillator (forced or unforced) model would account for W-K results still remains.

Acknowledgements

References

Aschersleben G & Prinz W (1995). Synchronising actions with events: the role of sensory information. *Percept Psychophys* 57: 305–317.

Balasubramaniam R, Wing AM & Daffertshofer A (2004) Keeping with the beat: Movement trajectories contribute to movement timing. *Exp Brain Res* 159: 129–134.

Beek, PJ, Peper CE & Daffertshofer A. (2002) Modeling rhythmic interlimb coordination: beyond the Haken-Kelso-Bunz model. *Brain Cog* 48: 149–165.

Bracewell RM, Balasubramaniam R & Wing AM (2005) Interlimb coordination deficits in a case of cerebellar hemiataxia. *Neurology* (in press).

Carson RG & Riek S (1998). The influence of joint position on the dynamics of perception-action coupling. *Exp Brain Res* 121: 103–114.

Cheney PD, Fetz CE & Mewes K (1993) Neural mechanisms underlying corticospinal and rubrospinal control of limb movements. *Prog Brain Res* 87: 213–252.

Daffertshofer A (1998) Effects of noise on the phase dynamics of nonlinear oscillators. *Phys Rev E* 58: 327–338.

Delignieres D, Lemoine L & Torre K (2004) Time interval production in tapping and oscillatory motion. *Hum Mov Sci* 23: 87–103.

DeLong MR Crutcher MD & Georgopoulos AP (1985) Primate globus pallidus and subthalamic nucleus: functional organization. *J Neurophysiol* 53: 530–543.

Drewing K, Stenneken P, Cole J, Prinz W & Aschersleben G (2004). Timing of bimanual movements and deafferentation: implications for the role of sensory movement effects. *Exp Brain Res* 158: 50–57.

Flash T & Hogan N (1985) The coordination of arm movements: an experimentally confirmed mathematical model. *J Neurosci* 5: 1688–1703.

Harris, CM & Wolpert DM (1998) Signal-dependent noise determines motor planning. *Nature* 394: 780–784.

Gandevia SC & Burke D (1992) Does the nervous system depend on kinesthetic information to control natural limb movements? *Behav. Brain Sci.* 15: 614–632.

Grill S & Hallett M (1995) Velocity sensitivity of human muscle spindle afferents and slowly adapting type II cutaneous mechanoreceptors. *J Physiol* 489: 593–602.

Kay BA, Saltzman EL, Kelso JAS (1991). Steady-state and perturbed rhythmical movements: A dynamical analysis. *J Exp Psychol : Hum Percept Perform.* 17: 183–197.

Kelso JAS, Fuchs A, Holroyd T, Lancaster R, Cheyne D & Weinberg H (1998). Dynamic cortical activity in the human brain reveals motor equivalence. *Nature.* 392: 814–818.

Kelso, JAS., DelColle J & Schöner, G. (1990). Action-Perception as a pattern formation process. In M. Jeanerod (Ed.), Attention and Performance XIII, Hillsdale, NJ: Erlbaum, 139–169.

Kelso JAS (1995) Dynamic Patterns. Cambridge: MIT press.

Matthews PBC (1981) Muscle spindles: their messages and their fusimotor supply. In: *Handbook of Physiology. The Nervous System. Motor Control.* Bethesda, MD.

Nagasaki H (1991) Asymmetric velocity and acceleration profiles of human arm movements. *Exp Brain Res* 87: 653–661.

Pressing J (1999) The referential dynamics of cognition and action. *Psych Rev* 106: 714–747.

Repp BH (2001) Processes underlying adaptations to tempo changes in sensorimotor synchronization. *Hum Mov Sci* 20: 277–312

Riley MA & Turvey MT (2002) Variability and determinism in motor behavior. J Mot Behav 34: 99–125.

Schöner G (2002) Timing, clocks and dynamical systems. *Brain Cog* 46: 31–51.

Stevens LT (1886) On the time sense. *Mind* 11: 393–404.

Spencer RM, Zelaznik HN, Diedrichsen J & Ivry RB (2003). Disrupted timing of discontinuous but not continuous movements by cerebellar lesions. *Science* 300: 1437–1439.

Swinnen SP (2002) Intermanual coordination: from behavioral principles to neural-network interactions. *Nat Rev Neurosci*. 3: 350–361.

Turner RS, Grafton ST, Votaw JR, Delong MR & Hoffman JM (1998) Motor subcircuits mediating the control of movement velocity: a PET study. *J Neurophysiol* 80: 2162–2176.

Turvey MT (1990) Coordination. *Am Psychol* 48: 938–153.

Valbo AB & Wessberg J (1993) Organization of motor output in slow finger movements in man. *J Physiol (Lond)* 469: 673–691.

Vorberg D & Wing AM (1996) Modeling variability and dependence in timing. In Heuer H & Keele SW (eds). *Handbook of Perception & Action*. 181–262. Academic Press, San Diego.

Wann JP, Nimmo-Smith I & Wing AM (1988) Relation between velocity and curvature in movement: equivalence and divergence between a power law and a minimum-jerk model. *J Exp Psychol : Hum Percept Perform* 14: 622–637.

Wing AM (2002). Voluntary timing and brain function. *Brain Cog* 48: 7–30.

Wing AM & Kristofferson AB (1973) Response delays and the timing of discrete motor responses. *Percept Psychophys* 14: 5–12.

Wing AM & Beek PJ (2002) Movement timing—a tutorial. In Prinz, W and Hommel, B (Eds) *Attention and Performance XIX*. Oxford University Press. pp. 202–226.

Yue GH, Liu JZ, Siemionow V (2000) Brain activation during finger flexion and extension movements. *Brain Res* 856: 291–300.

Zelaznik HN, Spencer RM & Ivry RB (2002). Dissociation of explicit and implicit timing in repetitive drawing and tapping movements. *J Exp Psychol : Hum Percept Perform* 28: 575–588.