Haptic information stabilizes and destabilizes coordination dynamics

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Goal-directed, coordinated movements in humans emerge from a variety of constraints that range from 'high-level' cognitive strategies based on perception of the task to 'low-level' neuromuscular–skeletal factors such as differential contributions to coordination from flexor and extensor muscles. There has been a tendency in the literature to dichotomize these sources of constraint, favouring one or the other rather than recognizing and understanding their mutual interplay. In this experiment, subjects were required to coordinate rhythmic flexion and extension movements with an auditory metronome, the rate of which was systematically increased. When subjects started in extension on the beat of the metronome, there was a small tendency to switch to flexion at higher rates, but not vice versa. When subjects were asked to contact a physical stop, the location of which was either coincident with or counterphase to the auditory stimulus, two effects occurred. When haptic contact was coincident with sound, coordination was stabilized for both flexion and extension. When haptic contact was counterphase to the metronome, coordination was actually destabilized, with transitions occurring from both extension to flexion on the beat and from flexion to extension on the beat. These results reveal the complementary nature of strategic and neuromuscular factors in sensorimotor coordination. They also suggest the presence of a multimodal neural integration process—which is parametrizable by rate and context—in which intentional movement, touch and sound are bound into a single, coherent unit.

Keywords: coordination dynamics; neuromuscular–skeletal constraints; haptic information; stability; transitions

1. INTRODUCTION

General laws and principles of biological coordination— to the extent that they exist—are by definition abstract and mathematical. Yet these laws are always conditioned and realized by specific mechanisms (Kelso 1994*a,b*, 1995). Using the field of coordinated movement as an entry point, it has been shown over the last two decades that the same coordination dynamics (equations of motion, the parameters of which alter the stability and change of coordination patterns over time along with the nonlinear coupling between the components that gives rise to them) apply to the functional coordination between anatomically different parts, including but not limited to the rhythmic motions of two or more fingers and limbs (Kelso 1981, 1984; Haken *et al.* 1985; Schöner *et al.* 1990; Kelso & Jeka 1992; Fuchs & Kelso 1994; Swinnen *et al.* 1994; Carson *et al.* 1995; Peper *et al.* 1995; Treffner & Turvey 1996), coupling between the joints of a single, multijointed limb (Kelso *et al.* 1991*b*; Buchanan & Kelso 1993; Carson *et al.* 1999*a*), perception–action coupling between visual and auditory stimuli and motor responses (Kelso *et al.* 1990, 1998; Wimmers *et al.* 1992; Stins & Michaels 1999) including postural sway (Dijkstra *et al.* 1994; Jeka *et al.* 1997; Bardy *et al.* 1999) and visually mediated coordination between two people (Schmidt *et al.* 1990; Amazeen *et al.* 1995). In numerous situations co-ordination dynamics—at both the coordinative level and at the level of the nonlinear interactions between the components—explicitly incorporate the role of specific neuromuscular–skeletal constraints. For instance,

eigenfrequency differences between coupled limb move-ments (Kelso & Jeka 1992; Fuchs & Kelso 1994; Sternad *et al.* 1995) as well as neurally based informational couplings between auditory or visual stimuli and move-ment are known to shape or sculpt the form of coordina-tion observed (Kelso *et al.* 1990). Influences of attention (Amazeen *et al.* 1997; Carson *et al.* 1999*b*; Temprado *et al.* 1999), intention (Kelso *et al.* 1988; Schöner & Kelso 1988*a*; Lee *et al.* 1996) and learning (Schöner *et al.* 1992; Zanone & Kelso 1992, 1997; Kelso & Zanone 2001) have also been demonstrated, both empirically and theoreti-cally. Neural correlates of the stability of and change in behavioural coordination have been revealed using high density Superconducting Quantum Interference Device (SQuID) and EEG arrays (Kelso *et al.* 1991*b*, 1992; Fuchs *et al.* 1992, 2000*a,b*; Wallenstein *et al.* 1995; Mayville *et al.* 1999, 2001; Daffertshofer *et al.* 2000; Frank *et al.* 2000), as well as functional magnetic resonance imaging and posi-tron emission tomography (Fuchs *et al.* 2000*c*; Ullen *et al.* 2000; Meyer-Lindenberg *et al.* 1999). Theoretical work at the neural level has progressed from phenomenological modelling at the behavioural (Haken *et al.* 1985; Schöner *et al.* 1986, 1990; Kelso *et al.* 1990, 1993; Treffner & Turvey 1996) and brain levels (Jirsa *et al.* 1994; Uhl *et al.* 1995) to neurobiologically grounded accounts of both uni-manual (Jirsa & Haken 1997; Frank *et al.* 2000; Fuchs *et al.* 2000*a*) and bimanual coordination (Jirsa *et al.* 1998) that are based on known cellular and neural ensemble properties of the cerebral cortex. Recent work (Jirsa & Kelso 2000) has extended this neural theory to include the heterogeneous connectivity between neural ensembles in the cortex. Once general laws at the behavioural and brain levels have been identified, it has proved possible to

derive them from a deeper theory founded on neuroanatomical and neurophysiological facts, thereby causally connecting different levels of description (see Kelso *et al*. 1999 for a review). The neural theory in turn poses a number of challenges to be tested, such as how synaptic and cellular properties are influenced by learning, arousal and attention (Kelso 2000).

Current research and theory views coordination as arising from the mutual interplay of constraints on multiple levels of description—ranging from the intrinsic properties and modes of interaction between cellular ensembles in the brain circuitry to biomechanical influences at the behavioural level all the way to cognitive and task constraints (Bressler & Kelso 2001). Indeed, coordination dynamics is not only a theoretical framework, but also a research programme that explicitly attempts to incorporate and connect known constraints at multiple levels of description (Kelso 1994*b*, 1995; Friston 1995, 1997; Haken 1996; Strohman 1997). For instance, coordination dynamics has been successfully used in identifying (Haken *et al*. 1985) and later quantifying the form of the nonlinear coupling between the interacting components (see Schöner & Kelso 1988*b* for a review). In showing that the stability of and change in behavioural coordination is due to nonlinear interactions between individual components (see also Collins & Stewart 1993; Golubitsky *et al*. 1999) coordination dynamics has removed some of the mysticism behind the contemporary terms 'emergence' and 'self-organization'.

In motor control, the field to which coordination dynamics owes its origins (Kelso 1984; Haken *et al*. 1985; Kelso & Scholz 1985; Schöner *et al*. 1986; Beek 1989; Turvey 1990; Byblow *et al*. 1994; Swinnen *et al*. 1994; Carson *et al*. 1995; Peper *et al*. 1995; Sternad *et al*. 1995; Carson 1996; Treffner & Turvey 1996; Wallace *et al*. 2000), it has proven useful to try to isolate the role of various constraints on coordinated movement and how they are mediated by the central nervous system. On the one hand, this strategy has helped identify the different factors that serve to stabilize coordination under conditions in which it may otherwise become unstable and susceptible to change. Such factors include the selective recruitment (and disengagement) of biomechanical degrees of freedom in order to accomplish a task (Kelso *et al*. 1993; Buchanan & Kelso 1999; Fink *et al*. 2000*a*) and the well-known 'anchoring' effect (Byblow *et al*. 1994) that arises because specific aspects of the movement trajectory tend to become coupled to specific sensory stimuli (Fink *et al*. 2000*b*). Recruitment and anchoring have been modelled mathematically within the existing theoretical framework of coordination dynamics (Fink *et al*. 2000*a*; Jirsa *et al*. 2000).

On the other hand, focusing on isolating particular constraints can lead, albeit unwittingly, to dichotomies (e.g. coordination principles versus neuromuscular–skeletal implementation) that may not be so useful. For example, studies of humans synchronizing flexion and extension movements to a metronome have shown that transitions from extension-on-the-beat to flexion-on-the-beat patterns occur as movement frequency is increased (Byblow *et al*. 1995; Carson 1996). The influence of posture and the preference for flexors over extensors led Carson *et al*. (1999*b*) to conclude that neuromuscular–skeletal factors are a principal determinant of the stability

of coordination (Carson & Riek 1998). Of course, this should not negate the fact that the same coordination dynamics describe and predict the nature of coordination between different kinds of components. Thus, although the relative phase dynamics of bimanual (Kelso 1984; Haken *et al*. 1985), sensorimotor (Kelso *et al*. 1990; Wimmers *et al*. 1992) and social coordination (Schmidt *et al*. 1990; Amazeen *et al*. 1995; Turvey & Schmidt, 1994) are the same, the anatomical, mechanical and physiological mechanisms instantiating these dynamics are obviously not.

In reality it seems safe to conclude that a coalition of constraints acting on multiple levels impinges upon the stability of coordination depending on the task context. For example, the multilevel theory offered by Kelso (1995) connected task goals (level 1) to constraints on nonlinear oscillators (level 3), the interactions between which create the coordinated patterns observed (level 2). Thus, rather than pose 'abstract laws of coordination dynamics' against 'neuromuscular–skeletal determinants of coordination', it is more important to understand how the balance between the expression of various constraints is mediated by the central nervous system. Here we study a situation in which two possible constraints, one arising from neuromuscular–skeletal factors and the other arising from neural information processes (haptic sources), are placed in competition with each other. Specifically, following a paradigm introduced by Kelso *et al*. (1990), we asked subjects to coordinate finger flexion or extension with an auditory metronome, the frequency of which was systematically increased. On the basis of previous work (Byblow *et al*. 1995; Carson 1996) we expected and observed a slight preference for subjects to switch from extend to flex on the beat rather than vice versa. However, in other conditions we introduced an apparently innocuous requirement. Subjects were asked to touch a physical stop actively, the location of which was either coincident with or counterphase to the auditory metronome. We found that, when haptic contact was coincident with the auditory stimulus, coordination was stabilized (that is, no transitions were observed), regardless of whether finger flexion or extension was synchronized with the metronome. However, even more telling was the fact that, when subjects made haptic contact that was counterphase to the metronome, transitions occurred from both extend on the beat to flex on the beat and (equally likely) from flex on the beat to extend on the beat. Thus, any putative superiority of flexors over extensors was actually reversed in the present experiment, rather strongly suggesting, in the present context, that afferent input arising as a result of active touch can override the influence of flexor versus extensor muscles in determining the stability (and instability) of coordinated movement.

2. METHODS

Ten participants (six male and four female graduate student volunteers aged between 22 and 28 years) took part in this experiment. Each participant was seated with their right forearm supported and wrist held at *ca.* 10° of flexion, with their index finger placed in a sleeve that pivoted around an axis, thereby limiting motion to flexion and extension of the metacarpophalangeal joint. Haptic information was provided at

Table 1. *Summary of the percentage of trials (n = 30) demonstrating a transition and the means and standard deviations of the critical frequencies for each condition collapsed across all participants*

(Critical frequencies were calculated using only those trials in which a transition occurred. A dash indicates those conditions in which a mean or standard deviation could not be calculated.)

				critical frequency	
condition	contact	synchronization	trials showing transitions (%)	mean (Hz)	s.d. (Hz)
1	none	flexion	17	2.3	0.3
	none	extension	38	2.2	0.3
2	flexion	flexion	0	—	—
	extension	extension	0	—	—
3	flexion	extension	58	1.8	0.4
	extension	flexion	63	2.0	0.3
4	both	flexion	3	1.6	—
	both	extension	3	2.0	—

locations where the sleeve containing the finger contacted padded plastic stops. Motion of the index finger was sampled at 256 Hz using a potentiometer connected to an analogue–digital converter (Optotrack 2010 ODAU unit). Metronome signals (50 ms and 250 Hz) were generated by a PC and sent to the analogue–digital converter as well as to headphones worn by the participant.

The task was to synchronize either peak flexion (flex on the beat) or extension (extend on the beat) of the index finger with an auditory metronome, the frequency of which increased from 1.0 to 2.6 Hz in 0.2 Hz increments every ten cycles. Four contact conditions were tested for both flexion and extension: (i) no contact present (the condition studied by Carson *et al.* (1999*b*)), (ii) contact coincident with the synchronization point (e.g. contact at peak flexion when the task was to flex on the beat), (iii) contact counterphase to the synchronization point (i.e. contact at peak flexion when the task was to extend on the beat and vice versa), and (iv) contact at both peak flexion and extension. The conditions are summarized in table 1. The subjects were instructed to close their eyes in all conditions, make contact with the stops if present and not to intervene if they felt the primary task (flex on the beat or extend on the beat) begin to change, but instead continue synchronizing with the metronome in whichever pattern was most comfortable.

The order of the trials was randomized except that the first trial was always in a condition in which no contact was present. This was done in order to identify the normal range of movement for each subject so that in subsequent trials the stops could be placed in locations covering the natural range of motion. Three trials were performed for both flex and extend on the beat in each condition, with 30 s of rest provided between each trial.

Time-series of finger position and the metronome were analysed in order to calculate a point estimate of relative phase between finger motion and the onset of the metronome beat. Separate relative phases were calculated for both flexion and extension in each trial. Depending on the task condition, synchronization was defined by a relative phase of zero between the metronome beat and peak flexion or peak extension. Coordination was classified as flex on the beat, extend on the beat or wrapping based on the following criteria.

(i) If the relative phase of flexion was closer to zero (synchron-ization) than the relative phase of extension in three consecutive movement cycles the pattern was classified as flex on the beat.

(ii) If the relative phase of extension was closer to zero (synchronization) than the relative phase of flexion in three consecutive movement cycles the pattern was classi-fied as extend on the beat.

(iii) All other patterns were classified as phase wrapping.

For purposes of analysis, trials that displayed a pattern other than the original flex- or extend-on-the-beat pattern were considered to have undergone a transition and, thus, trials were divided into transition and no-transition categories for each frequency plateau.

3. RESULTS

A summary of the percentage of total trials (*n* = 30 for each cell) exhibiting transitions or the lack thereof is presented in table 1. First, notice that no (or virtually no) transitions were observed for either flex on the beat or extend on the beat when haptic contact was coincident with the synchronization point (contact conditions 2 and 4). Thus, locally available haptic contact information actually helped to stabilize coordination. Second, without such haptic contact at the synchronization point, coordi-nation is known to destabilize and switch (contact condi-tion 1). Some support for the greater stability of flexion on the beat over extension on the beat may be gleaned from the fact that there were more transitions in the latter (38%) than the former (17%) condition, although the mean critical frequency at which they switched was approximately the same. Third, with haptic contact at the peak of the flexion phase of the cycle, extend on the beat switched to flex on the beat in 58% the trials. This result might be expected on the basis of intrinsic preferences for flexion over extension (Carson 1996; Carson & Riek 1998; Carson *et al.* 1999*b*). Remarkably, however, this effect was reversed when there was haptic contact on extension: flex on the beat switched to extend on the beat in 63% of the trials. Differences in the percentage of trials showing transitions between contact conditions were confirmed with a χ^2-test ($\chi^2_3 = 79.04$ and $p < 0.0001$). No significant differences were found between flex and
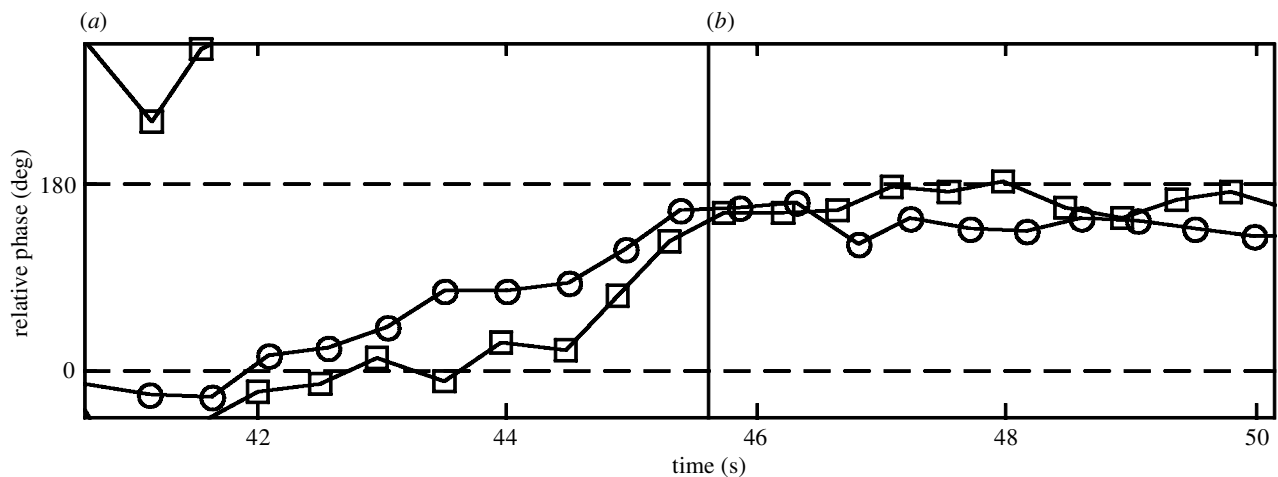
Figure 1. Time-series of the relative phase for representative trials of flex on the beat (circles) and extend on the beat (squares) for contact condition 3 (haptic contact at extension and flexion, respectively). Two frequencies, (*a*) 2.0 and (*b*) 2.2 Hz, are shown with a transition from in-phase (*ca.* 0°) to anti-phase (*ca.* 180°) occurring in both trials at 2.0 Hz.

extend on the beat ($\chi_1^2 = 0.54$ and $p > 0.05$). Thus, whereas in one context haptic contact stabilized coordination, in another context (contact counterphase to the synchronization task) it destabilized coordination. These stabilization and destabilization effects held true regardless of any intrinsic anatomical and physiological asymmetries between flexion and extension.

Figure 1 shows a typical, relative-phase time-series for the extend-on-the-beat (squares) and flex-on-the-beat conditions (circles) with haptic contact on flexion and extension, respectively (contact condition 3). In line with the percentages shown in table 1, in which transitions occurred in approximately equal numbers for both directions, switching in figure 1 is seen in both flex and extend on the beat at similar frequencies. Note in particular that a transition from flex on the beat to extend on the beat (shown in circles) would never be expected if neuromuscular–skeletal constraints (e.g. stronger flexors than extensors) were the dominant factor determining the stability of movement coordination.

Quantitative analysis bore this picture out. A $4 \times 2 \times 9$ (contact condition × synchronization point × frequency) analysis of the mean relative phase for each frequency plateau revealed a significant condition × frequency interaction ($F_{24,216} = 3.74$ and $p < 0.0001$) and a significant three-way interaction ($F_{24,216} = 1.67$ and $p < 0.05$). The mean relative phase for all four contact conditions is shown in figure 2. The source of the two-way interaction is obvious; transitions occurred in contact conditions 1 and 3, but not in conditions 2 and 4, regardless of whether the subjects were synchronizing flexion or extension. There was a significant difference between flex and extend on the beat (e.g. between 1.8 and 2.2 Hz in contact condition 1 and at 2.2 Hz in contact condition 3) at a few frequency plateaus, giving rise to the three-way interaction, but these differences were minor compared to the differences between contact conditions.

4. DISCUSSION

Much research on human motor control has established the essentially nonlinear nature of coordinated movement.

Two complementary aspects of coordinated behaviour have been a major focus of study. On the one hand, phase transitions have been observed in a number of different experimental model systems, ranging broadly from bimanual and interlimb coordination, to coordination within a single, multijointed limb, to coordination between a single limb and auditory or visual stimuli, to social coordination between two people (see Kelso 1995; Haken 1996 for reviews). Phase transitions play a dual role. First, they provide a special entry point for experimentally identifying the collective variables characterizing states of coordination and the (control) parameters that influence the coordination dynamics. Second, phase transitions provide biological systems with an important mechanism for stability and flexibility: as internal or external parameters are varied, coordination patterns may remain stable over a range of parameter values. However, at critical parameter values, coordination may suddenly switch from one mode of coordination to another. This ability to switch between well-defined coordination states provides the motor system and living things in general with an important source of flexibility.

On the other hand, an equally important issue for understanding biological coordination concerns how coordination states are stabilized under conditions in which they might otherwise become unstable and switch. Recent work, which is confirmed by the present results, has shown that coupling specific aspects of an individual movement to specific sensory information from the environment serves to stabilize coordination globally (Fink *et al.* 2000*b*; Jirsa *et al.* 2000).

The present study brings both themes together in a single experiment and places them squarely within a unified conceptual framework. First, active touch coincident with auditory input stabilized coordination throughout a broad range of movement rates. Second, haptic information served to destabilize coordination causing transitions when it was not coincident with the auditory metronome. Without any haptic contact, there was a small tendency to see more and earlier transitions from extend on the beat to flex on the beat, presumably because of the greater efficacy with which flexion is
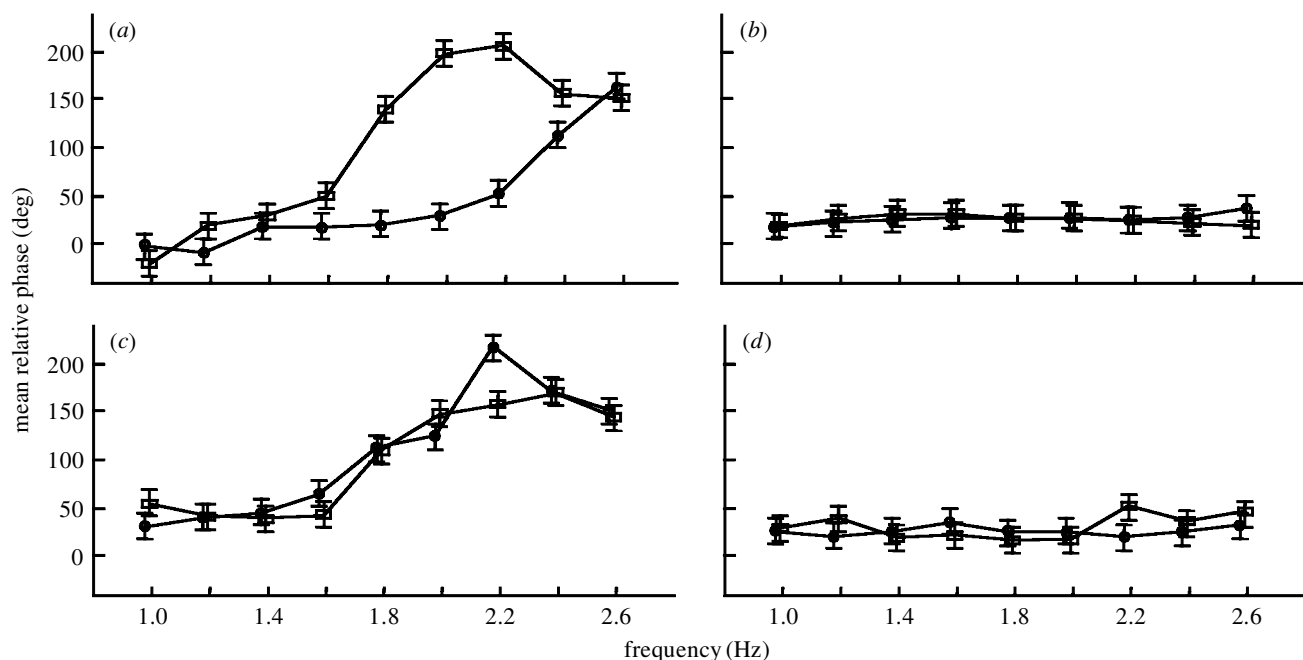
Figure 2. Haptic stabilization and destabilization of coordination. Mean relative phase as a function of movement frequency for the four contact conditions: (*a*) condition 1, (*b*) condition 2, (*c*) condition 3 and (*d*) condition 4. Circles denote flex on the beat and squares denote extend on the beat. Shifts away from a zero relative phase, which are indicative of transitions, are found in contact conditions 1 (no contact) and 3 (contact off the-beat), whereas no shifts are found in the other two contact conditions.

generated by the neuromuscular–skeletal system (Carson 1996; Carson & Riek 1998). However, such an account by itself does not accommodate transitions from flexion to extension as was observed here, nor the stabilization effects that are present for both effectors.

Although a number of possible hypotheses might help explain the observed pattern of results, an appealing possibility concerns multimodal integration. The basic idea is that subjects, regardless of whether they use flexion or extension for synchronizing with a metronome, are drawn to synchronize movement when both sound and active touch coincide in time. At low frequencies the two modalities can be kept separate. However, as frequency increases a conflict arises between coordinating one phase of movement with sound and the other with touch. At higher frequencies these conflicting demands are resolved: it is easier to coordinate movement when both sound and active touch go together in time. The two modalities are thus 'bound' or neurally integrated into one coherent action–perception unit. A novel aspect of this hypothesized neural integration process, which was demonstrated here, is that it is parametrizable by rate and task context. The observed stability of coordination across all frequencies when active haptic contact and sound were coincident also suggests less demand on attentional resources, a result that is consistent with recent evidence on bimanual coordination (Temprado *et al.* 1999) as well as neurophysiological findings (Mayville *et al.* 2001).

Regardless of how tests of this hypothesis of integrative neural processing turn out, the present results suggest that the central nervous system stabilizes and destabilizes coordinated behaviour in a task-specific, informationally meaningful fashion (Kelso 1995). This is not to say that neuromuscular–skeletal constraints do not contribute

importantly to coordination dynamics, only that they are not the sole or necessarily overriding determinant. For example, in a number of cases, biophysical factors such as eigenfrequency differences between interacting components (e.g. Kelso & Jeka 1992; Sternad *et al.* 1995) must be (and have been) explicitly incorporated into theoretical models (Kelso *et al.* 1990; Schöner *et al.* 1990). However, it should be emphasized that such factors shape or sculpt the coordination dynamics only to the extent that their influence is mediated by the central nervous system (Kelso 1994*b*). After all, an individual can write their name with a pen attached to their big toe, but the efficacy of the anatomical, mechanical and physiological mechanisms involved in moving the big toe surely affect the quality of their signature.

REFERENCES

Amazeen, P. G., Schmidt, R. C. & Turvey, M. T. 1995 Frequency detuning of the phase entrainment dynamics of visually coupled rhythmic movements. *Biol. Cybernet.* **72**, 511–518.

Amazeen, E. L., Amazeen, P. G., Treffner, P. J. & Turvey, M. T. 1997 Attention and handedness in bimanual coordination dynamics. *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 1552–1560.

Bardy, B. G., Marin, L., Stoffregen, T. A. & Boutsma, R. J. 1999 Postural coordination modes considered as emergent phenomena. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 1284–1296.

Beek, P. J. 1989 Timing and phase locking in cascade juggling. *Ecol. Psychol.* **1**, 55–96.

Bressler, S. L. & Kelso, J. A. S. 2001 Cortical coordination dynamics and cognition. *Trends Cogn. Sci.* **5**, 26–36.

Buchanan, J. J. & Kelso, J. A. S. 1993 Posturally induced transitions in rhythmic multijoint limb movements. *Exp. Brain Res.* **94**, 131–142.

Buchanan, J. J. & Kelso, J. A. S. 1999 To switch or not to switch: recruitment of degrees of freedom stabilizes biological coordination. *J. Motor Behav.* **31**, 126–144.

Byblow, W. D., Carson, R. G. & Goodman, D. 1994 Expressions of asymmetries and anchoring in bimanual coordination. *Hum. Move. Sci.* **13**, 3–28.

Byblow, W. D., Chua, R. & Goodman, D. 1995 Asymmetries in coupling dynamics of perception and action. *J. Motor Behav.* **27**, 123–137.

Carson, R. G. 1996 Neuromuscular–skeletal constraints upon the dynamics of perception–action coupling. *Exp. Brain Res.* **110**, 99–110.

Carson, R. G. & Riek, S. 1998 The influence of joint position on the dynamics of perception–action coupling. *Exp. Brain Res.* **121**, 103–114.

Carson, R. G., Goodman, D., Kelso, J. A. S. & Elliott, D. 1995 Phase transitions and critical fluctuations in rhythmic co-ordination of ipsilateral hand and foot. *J. Motor Behav.* **27**, 211–224.

Carson, R. G., Riek, S., Byblow, W. D., Abernethy, B. & Summers, J. J. 1999a The timing of intralimb coordination. *J. Motor Behav.* **31**, 113–118.

Carson, R. G., Chua, R., Byblow, W. D., Poon, P. & Smethurst, C. S. 1999b Changes in posture alter the attentional demands of voluntary movement. *Proc. R. Soc. Lond.* B **266**, 853–857.

Collins, J. J. & Stewart, I. 1993 Coupled nonlinear oscillators and the symmetries of animal gaits. *J. Nonlin. Sci.* **3**, 349–362.

Daffertshofer, A., Peper, C. E. & Beek, P. J. 2000 Spectral analysis of event-related electroencephalographic signals. *Phys. Lett.* A **266**, 290–302.

Dijkstra, T. M. H., Schöner, G., Giese, M. A. & Gielen, C. C. A. M. 1994 Frequency dependence of the action–perception cycle for postural control in a moving visual environment: relative phase dynamics. *Biol. Cybernet.* **71**, 489–501.

Fink, P. W., Kelso, J. A. S., Jirsa, V. K. & DeGuzman, G. C. 2000a Recruitment of degrees of freedom stabilizes coordination. *J. Exp. Psychol. Hum. Percept. Perform.* **26**, 671–692.

Fink, P. W., Kelso, J. A. S., Foo, P. & Jirsa, V. K. 2000b Local and global stabilization of coordination by sensory information. *Exp. Brain Res.* **134**, 9–20.

Frank, T. D., Daffertshofer, A., Peper, C. E., Beek, P. J. & Haken, H. 2000 Towards a comprehensive theory of brain activity: coupled oscillator systems under external forces. *Physica* D **144**, 62–86.

Friston, K. J. 1995 States of mind. *Nature* **375**, 643–644.

Friston, K. J. 1997 Transients, metastability and neuronal dynamics. *NeuroImage* **5**, 164–171.

Fuchs, A. & Kelso, J. A. S. 1994 A theoretical note on models of interlimb coordination. *J. Exp. Psychol. Hum. Percept. Perform.* **20**, 1088–1097.

Fuchs, A., Kelso, J. A. S. & Haken, H. 1992 Phase transitions in the human brain: spatial mode dynamics. *Int. J. Bifurcat. Chaos* **2**, 917–939.

Fuchs, A., Jirsa, V. K. & Kelso, J. A. S. 2000a Theory of the relation between human brain activity (MEG) and hand movements. *NeuroImage* **11**, 359–369.

Fuchs, A., Deecke, L. & Kelso, J. A. S. 2000b Phase transitions in the human brain revealed by large SQuID arrays. *Phys. Lett.* A **266**, 303–308.

Fuchs, A., Mayville, J. M., Purcott, K. L., Steinberg, F. & Kelso, J. A. S. 2000c Cerebellar activity distinguishes sensori-motor task difficulty in fMRI. *Soc. Neurosci. Abstr.* **26**, 1499.

Golubitsky, M., Stewart, I., Buono, P.-L. & Collins, J. J. 1999 Symmetry in locomotor central pattern generators and animal gaits. *Nature* **401**, 693–695.

Haken, H. 1996 *Principles of brain functioning.* Berlin: Springer.

Haken, H., Kelso, J. A. S. & Bunz, H. 1985 A theoretical model of phase transitions in human hand movements. *Biol. Cybernet.* **51**, 347–356.

Jeka, J. J., Schöner, G., Dijkstra, T. M. H., Ribeiro, P. & Lackner, J. R 1997 Coupling of fingertip somatosensory information to head and body sway. *Exp. Brain Res.* **113**, 475–483.

Jirsa, V. K. & Haken, H. 1997 A derivation of a macroscopic field theory of the brain from the quasi-microscopic neural dynamics. *Physica* D **99**, 503–526.

Jirsa, V. K. & Kelso, J. A. S. 2000 Spatiotemporal pattern formation in neural systems with heterogeneous connection topologies. *Phys. Rev.* E **62**, 8462–8465.

Jirsa, V. K., Friedrich, R., Haken, H. & Kelso, J. A. S. 1994 A theoretical model of phase transitions in the human brain. *Biol. Cybernet.* **71**, 27–35.

Jirsa, V. K., Fuchs, A. & Kelso, J. A. S. 1998 Connecting cortical and behavioral dynamics: bimanual coordination. *Neural Comp.* **10**, 2019–2045.

Jirsa, V. K., Fink, P. W., Foo, P. & Kelso, J. A. S. 2000 Parametric stabilization of biological coordination: a theoretical model. *J. Biol. Phys.* **26**, 85–112.

Kelso, J. A. S. 1981 On the oscillatory nature of movement. *Bull. Psychonomic Soc.* **18**, 63.

Kelso, J. A. S. 1984 Phase transitions and critical behavior in human bimanual coordination. *Am. J. Physiol.* **15**, R1000–R1004.

Kelso, J. A. S. 1994a Elementary coordination dynamics. In *Interlimb coordination: neural, dynamical and cognitive constraints* (ed. S. Swinnen, H. Heuer, J. Massion & P. Casaer), pp. 301–318. San Diego: Academic Press.

Kelso, J. A. S. 1994b The informational character of self-organized coordination dynamics. *Hum. Move. Sci.* **13**, 393–413.

Kelso, J. A. S. 1995 *Dynamic patterns. The self-organization of brain and behavior.* Cambridge, MA: MIT Press.

Kelso, J. A. S. 2000 *The self-organized dynamics of human skill learning. Dynamical neuroscience VIII.* Bethesda, MD: NIMH Publications.

Kelso, J. A. S. & Jeka, J. J. 1992 Symmetry breaking dynamics of human multilimb coordination. *J. Exp. Psychol. Hum. Percept. Perform.* **18**, 645–668.

Kelso, J. A. S. & Scholz, J. P. 1985 Cooperative phenomena in biological motion. In *Complex Systems: Operational approaches in neurobiology, physics and computers* (ed. H. Haken), pp. 124–149. Berlin: Springer.

Kelso, J. A. S. & Zanone, P. G. 2001 Coordination dynamics of learning and transfer across different effector systems. *J. Exp. Psychol. Hum. Percept. Perform.* (In the press.)

Kelso, J. A. S., Tuller, B., Bateson, E.-V. & Fowler, C. A. 1984 Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *J. Exp. Psychol. Hum. Percept. Perform.* **10**, 812–832.

Kelso, J. A. S., Schöner, G., Scholz, J. P. & Haken, H. 1987 Phase-locked modes, phase transitions and component oscillators in biological motion. *Phys. Scripta* **35**, 79–87.

Kelso, J. A. S., DelColle, J. D. & Schöner, G. 1990 Action–perception as a pattern formation process. In *Attention and performance*, vol. 13 (ed. M. Jeannerod), pp. 139–169. Hillsdale, NJ: Erlbaum.

Kelso, J. A. S., Bressler, S. L., Buchanan, S., DeGuzman, G. C., Ding, M., Fuchs, A. & Holroyd, T. 1991a Cooperative and critical phenomena in the human brain revealed by multiple SQUIDS. In *Measuring chaos in the human brain* (ed. D. Duke & W. Pritchard), pp. 97–112. Singapore: World Scientific.

Kelso, J. A. S., Buchanan, J. J. & Wallace, S. A. 1991*b* Order parameters for the neural organization of single, multijoint limb movement patterns. *Exp. Brain Res.* **85**, 432–444.

Kelso, J. A. S., Bressler, S. L., Buchanan, S., DeGuzman, G. C., Ding, M., Fuchs, A. & Holroyd, T. 1992 A phase transition in human brain and behavior. *Phys. Lett.* A **169**, 134–144.

Kelso, J. A. S., Buchanan, J. J., DeGuzman, G. C. & Ding, M. 1993 Spontaneous recruitment and annihilation of degrees of freedom in biological coordination. *Phys. Lett.* A **179**, 364–368.

Kelso, J. A. S., 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, J. A. S., Fuchs, A. & Jirsa, V. K. 1999 Traversing scales of brain and behavioral organization. I–III. In *Analysis of neurophysiological brain functioning* (ed. C. Uhl), pp. 73–125. Berlin: Springer.

Lee, T. D., Blandin, Y. & Proteau, L. 1996 Effects of task instruction and oscillation frequency on bimanual coordination. *Psychol. Res.* **59**, 100–106.

Mayville, J. M., Bressler, S. L., Fuchs, A. & Kelso, J. A. S. 1999 Spatiotemporal reorganization of electrical activity in the human brain associated with a phase transition in rhythmic auditory–motor coordination. *Exp. Brain Res.* **127**, 371–381.

Mayville, J. M., Fuchs, A., Ding, M., Cheyne, D., Deecke, L. & Kelso, J. A. S. 2001 Event-related changes in neuromagnetic activity associated with syncopation and synchronization timing tasks. *Human Brain Mapping.* (In the press.)

Meyer-Lindenberg, A., Ziemann, U., Hajak, G., Cohen, L. & Berman, K. F. 1999 Cortical instability: Direct demonstration of nonlinear dynamics in the human brain using transcranial magnetic stimulation and positron emission tomography. *NeuroImage*, **9**, S287.

Peper, L., Beek, P. J. & Van Wieringen, P. C. W. 1995 Frequency induced transitions in bimanual tapping. *Biol. Cybernet.* **73**, 310–309.

Schmidt, R. C., Carello, C. & Turvey, M. T. 1990 Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *J. Exp. Psychol. Hum. Percept. Perform.* **16**, 227–247.

Schöner, G. & Kelso, J. A. S. 1988*a* A dynamic pattern theory of behavioral change. *J. Theor. Biol.* **135**, 501–524.

Schöner, G. & Kelso, J. A. S. 1988*b* Dynamic pattern generation in behavioral and neural systems. *Science* **239**, 1513–1520. (Reprinted in Kelner, K. L. & Koshland Jr, D. E. (ed.) 1989 *Molecules to models: advances in neuroscience*, pp. 311–325. Washington DC: AAAS Publications.)

Schöner, G., Haken, H. & Kelso, J. A. S. 1986 A stochastic theory of phase transitions in human hand movement. *Biol. Cybernet.* **53**, 247–257.

Schöner, G., Jiang, W.-Y. & Kelso, J. A. S. 1990 A synergetic theory of quadrupedal gaits and gait transitions. *J. Theor. Biol.* **142**, 359–391.

Schöner, G., Zanone, P. G. & Kelso, J. A. S. 1992 Learning as change of coordination dynamics: theory and experiment. *J. Motor Behav.* **24**, 29–48.

Sternad, D., Collins, D. & Turvey, M. T. 1995 The detuning factor in the dynamics of interlimb rhythmic coordination. *Biol. Cybernet.* **73**, 27–35.

Stins, J. F. & Michaels, C. F. 1999 Strategy differences in oscillatory tracking: stimulus–hand versus stimulus–manipulandum coupling. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 1793–1812.

Strohman, R. C. 1997 The coming Kuhnian revolution in biology. *Nature Biotechnol.* **15**, 194–200.

Swinnen, S., Heuer, H., Massion, J. & Casaer, P. (ed.) 1994 *Interlimb coordination: neural, dynamical and cognitive constraints.* San Diego: Academic Press.

Temprado, J. J., Zanone, P. G., Monno, A. & Laurent, M. 1999 Attentional load associated with performing and stabilizing preferred bimanual patterns. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 1595–1608.

Treffner, P. J. & Turvey, M. T. 1996 Symmetry, broken symmetry and handedness in bimanual coordination dynamics. *Exp. Brain Res.* **107**, 463–478

Turvey, M. T. 1990 Coordination. *Am. Psychol.* **45**, 938–953.

Turvey, M. T. & Schmidt, R. C. 1994 A low dimensional nonlinear dynamic governing interlimb coordination. In *Interlimb coordination: neural, dynamical and cognitive constraints* (ed. S. Swinnen, H. Heuer, J. Massion & P. Casaer), pp. 277–300. San Diego: Academic Press.

Uhl, C., Friedrich, R. & Haken, H. 1995 Analysis of spatiotemporal signals of complex systems. *Phys. Rev.* E **51**, 3890–3900.

Ullen, F., Ehrsson, H. H. & Forssberg, H. 2000 Brain areas activated during bimanual tapping of different rhythmical patterns in humans. *Soc. Neurosci. Abstr.* **26**, 458.

Wallace, S. A., Weeks, D. L. & Foo, P. 2000 A dynamical systems approach to understanding reaching movements with a prosthetic arm. *Nonlin. Dynam. Psychol. Life Sci.* **4**, 311–338.

Wallenstein, G. V., Kelso, J. A. S. & Bressler, S. L. 1995 Phase transitions in spatiotemporal patterns of brain activity and behavior. *Physica* D **84**, 626–634.

Wimmers, R. H., Beek, P. J. & Van Wieringen, P. C. W. 1992 Phase transitions in rhythmic tracking movements: a case of unilateral coupling. *Hum. Move. Sci.* **11**, 217–226.

Zanone, P.-G. & Kelso, J. A. S. 1992 The evolution of behavioral attractors with learning: Non-equilibrium phase transitions. *J. Exp. Psychol. Hum. Percept. Perf.* **18**, 403–421.

Zanone, P.-G. & Kelso, J. A. S. 1997 The coordination dynamics of learning and transfer: collective and component levels. *J. Exp. Psychol. Hum. Percept. Perf.* **23**, 1454–1480.