Spontaneous recruitment and annihilation of degrees of freedom in biological coordination

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Whereas bifurcations within an already active set of components are well-known in biological coordination (e.g. gait transitions), less well understood is the process by which previously quiescent degrees of freedom are spontaneously activated. We introduce a simple paradigm to explore how complex, biological systems flexibly recruit and annihilate degrees of freedom according to parametric task requirements. A sequence of transitions within and across planes of motion is observed as a control parameter is varied. Such transitions are invariably preceded by enhancement of fluctuations in trajectory related variables. Our results suggest a theoretical model in which the main qualitative changes observed experimentally are a consequence of two consecutive Hopf bifurcations.

An essential, but poorly understood feature of complex biological systems is their ability to flexibly assemble and disassemble patterns of coordinated behavior according to functional demands. For example, to reach for a cup of coffee close by may require only the coordinated extension of the elbow and shoulder. A cup located further away, however, may require forward lean of the trunk or even, if one is seated, rising from the chair (a transition from a three- to two-point stance). Such flexible and spontaneous recruitment of previously quiescent biomechanical degrees of freedom (d.f.) and the simultaneous elimination of no longer relevant d.f. according to task or boundary conditions is accomplished effortlessly by human beings and animals, but not by robotic devices.

Here we introduce a simple experimental paradigm to explore the dynamical process of flexibly recruiting and annihilating biomechanical d.f. according to parametric task requirements. The present work follows along the footsteps of previous research (see e.g. refs. [1–3]) showing that coordination in complex biological systems may be understood using the theoretical concepts of self-organization and pattern formation in nonequilibrium systems and the language of nonlinear dynamics. Specifically, the formation of rhythmically coordinated movement patterns and switching among different coordinated states has been demonstrated to arise via an instability when a control parameter is systematically varied. Predicted features associated with instabilities, such as enhancement of fluctuations in an identified order parameter and slowing down near the transition region [2,3] have been verified in a number of different experimental systems (see e.g. refs. [4–7]). In the foregoing cases, transitions are always of the order → order type: the *same* biomechanical d.f. are spontaneously re-ordered at a critical value of the control parameter. Depending on the symmetry of the system, transitions may take the form of (subcritical) pitchfork (see e.g. ref. [1]) or saddle-node bifurcations (see e.g. ref. [8]). Much less studied (indeed, not studied at all) are situations in which *new* biomechanical d.f., e.g. muscles, neuronal groups, are recruited (and "old" ones annihilated) under parametric influences. Such a case is reminiscent of one of the most fundamental processes in dissipative dynamical systems, namely the creation and destruction of orbits as a parameter is increased (see e.g. ref. [9]).

Our main goal in this paper is to elucidate how available (in the sense of potential) d.f. are recruited and already active d.f. are annihilated when performing a rhythmic task. The underlying reason is that a system containing a set of active components that have been self-organized for a particular movement pattern is now no longer able to support that behavior in a stable fashion when a control parameter (here the frequency of motion) crosses a critical value. The new movement pattern may still be topologically equivalent to the previous one (e.g. both may be limit cycles) but additional d.f. are required to perform the task.

The present experiment builds upon a serendipitous finding briefly described some years ago by Kelso and Scholz [10] in their studies of human bimanual coordination. Earlier work in which motion was confined to horizontal planar movements involving flexion and extension of the index fingers had shown that transitions from anti-symmetrical patterns (homologous muscles contracting alternately) to symmetrical patterns (homologous muscles contracting together) occur as frequency of oscillation is increased. In order to obtain measures of underlying neuromuscular activity, Kelso and Scholz studied repetitive bimanual motion in the x-y plane. After the anti- to in-phase transition, now involving abduction and adduction movements in the horizontal (x) plane, they noted that further increases in cycling frequency produced yet another transition, this time from the horizontal to vertical (flexion-extension) plane of motion. Occasionally, the motion of the fingers became rotary in nature before the transition to the vertical plane. This phenomenon may be qualitatively understood as follows. Observed reproducible patterns correspond to stable attractive states of coordination (described in terms, e.g. of the relative phase between oscillatory components). When motion is restricted to the horizontal plane only the symmetric and antisymmetric modes of coordination are stably performed over a range of frequencies. For frequencies above this range, no comparably stable pattern is available on the horizontal plane of motion. In order to achieve stability, previously quiescent d.f., i.e. in the vertical dimension are spontaneously recruited. With the availability of this added d.f. the system becomes multistable and transitions among the various patterns have both a temporal and spatial character. We now identify experimentally what these patterns are, the pathways between these patterns and the nature of the transitions (abrupt or continuous) from one ordered pattern to another[#1]. We propose a preliminary theoretical model at the individual oscillator level of description, and suggest how the collective level may be handled.

Six normal adults volunteered for participation in this study. The experimental task consisted of bimanual and unimanual rhythmical coordination of the index fingers about the metacarpophalangeal joint. The experimental task consisted of four bimanual initial conditions: horizontal in-phase (ten trials) and anti-phase (ten) (i.e., abduction-adduction) in the transverse plane and vertical in-phase (five) and anti-phase (five) in the sagittal plane (i.e., flexion-extension). In the unimanual conditions, the subjects performed abduction-adduction movements of the left and right fingers (five trials of each) starting in the transverse plane. All trials consisted of twelve frequency plateaus (twelve cycles per plateau) starting at 1.5 Hz and increasing to 4.25 Hz in 0.25 Hz steps. The subject's primary task was to produce one full cycle of movement with each finger, for each beat of a metronome. The subjects were instructed that should they feel the pattern begin to change, they should not intervene, but rather adopt the pattern that was most comfortable under the current conditions. Emphasis was placed on maintaining a 1:1 relation with the metronome. Before each condition, the required pattern was demonstrated for the subject, who was allowed to practice a few cycles of the pattern before the experiment proper began.

The Watsmart/Watscope image processing system (Northern Digital Inc., Waterloo, Canada) was used to record the x-y coordinates of light-weight infrared emitting diodes (IREDs) attached to the fingertips and knuckles of the subject's index fingers. A custom

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[#1] In doing so, we provide a response to a question raised by Professor H. Swinney concerning whether additional bifurcations are possible in the bimanual system (see ref. [11]). The answer turns out to be yes in at least two respects. One, which we do not explore here concerns transitions among frequency-lockings, e.g. 4:3 to 1:1, 5:2 to 2:1 etc. [12,13]. The other, presented here, concerns spatial transitions that occur when the experimental system affords motion in the x-y plane and initial conditions are appropriately established.

made apparatus consisting of two plastiform molds and a horizontal grip bar was used to support and restrict the movement of the subject's forearms, wrists, and digits III through V. Mounted on the wall directly behind the subject was an auditory metronome. The signal was simulated by a series of 50 ms square wave pulses output through a RS232 port on a MacIntosh personal computer. Metronome frequency was controlled by a computer program and a PC AT was used for data acquisition and on-line monitoring.

The data were sampled at 200 Hz and a detailed analysis of the movement trajectories was performed off line. The two-dimensional x–y coordinate values of the IREDs were recorded in the form of a time series of the trajectory images projected onto the camera plane. The two two-dimensional time series, one from each camera, for each IRED were converted into a three-dimensional time series using using a direct linear transformation. The data were smoothed and transformed into individual angle files which were then displayed as trajectories over time and used to compute point estimates of relative phase and frequency values.

The raw trajectories of the two fingers shown in fig. 1 illustrate the variety of transitions within and across planes of motion as the frequency of oscillation is increased. We refer to transitions between patterns within a single plane of motion as *interlimb transitions*, while transitions from one plane of motion to another are referred to as *spatial transitions*. Roughly speaking, when the initial conditions specify horizontal motion and the movement rate is relatively low, movement is largely confined to the x dimension on the x–y plane. As rate increases beyond a certain critical value, oscillations on the y dimension spontaneously emerge, the superposition of the x and y dynamics producing a rotary-like pattern in the x–y plane. As rate is increased further, passing another critical region, oscillations in the x dimension diminish and the observed pattern is largely confined to the y dimension. Distortions of this scenario are quite modest (see fig. 1), probably due to the recording arrangement and the constraints of finger joint geometry (e.g. the motions of the y dimension at high movement rates contain a modest horizontal component).

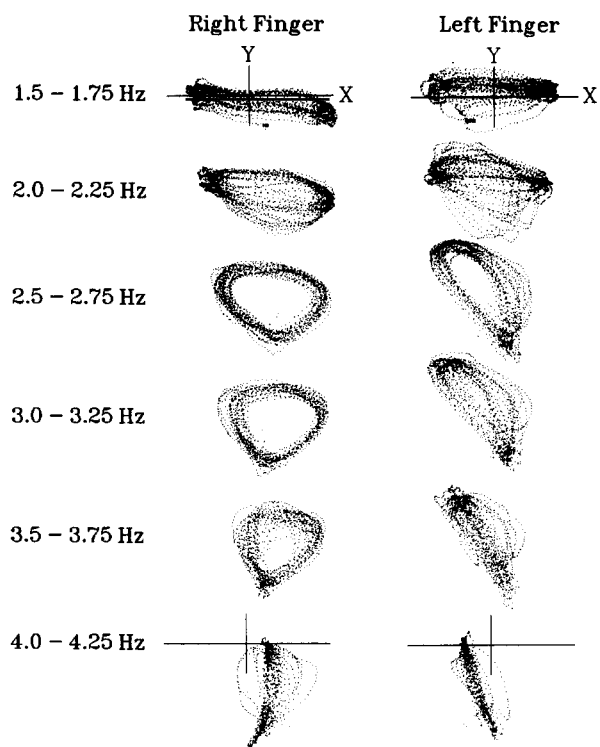A total of 80/90 (88%) abrupt *interlimb* transi-

Fig. 1. Raw trajectories of the finger movements in the x–y plane. In this example, the initial condition is horizontal in-phase coordination and the frequency of motion increases from top to bottom.

tions from bimanual anti-symmetrical to symmetrical patterns of coordination were observed (horizontal anti-phase to in-phase 50/60; vertical anti-phase to in-phase 30/30). By abrupt, we mean that spontaneous shifts in the phasing between components usually occurred within 2–3 cycles of motion. Thirty-seven (76%) of the horizontal anti-phase to in-phase transitions occurred between cycling frequencies of 1.75 and 2.25 Hz. The range of critical frequencies for vertical interlimb transitions was from 1.75 to 3.0 Hz. These results are consistent with many other findings in the bimanual paradigm (see e.g. refs. [1,11]).

Availability of additional d.f. resulted in two distinct spatial bifurcation routes from horizontal to vertical motion. Histograms in figs. 2A and 2B represent the evolution of horizontal to vertical motion as a function of cycling frequency and initial coordinative pattern. Within the two bimanual horizon-
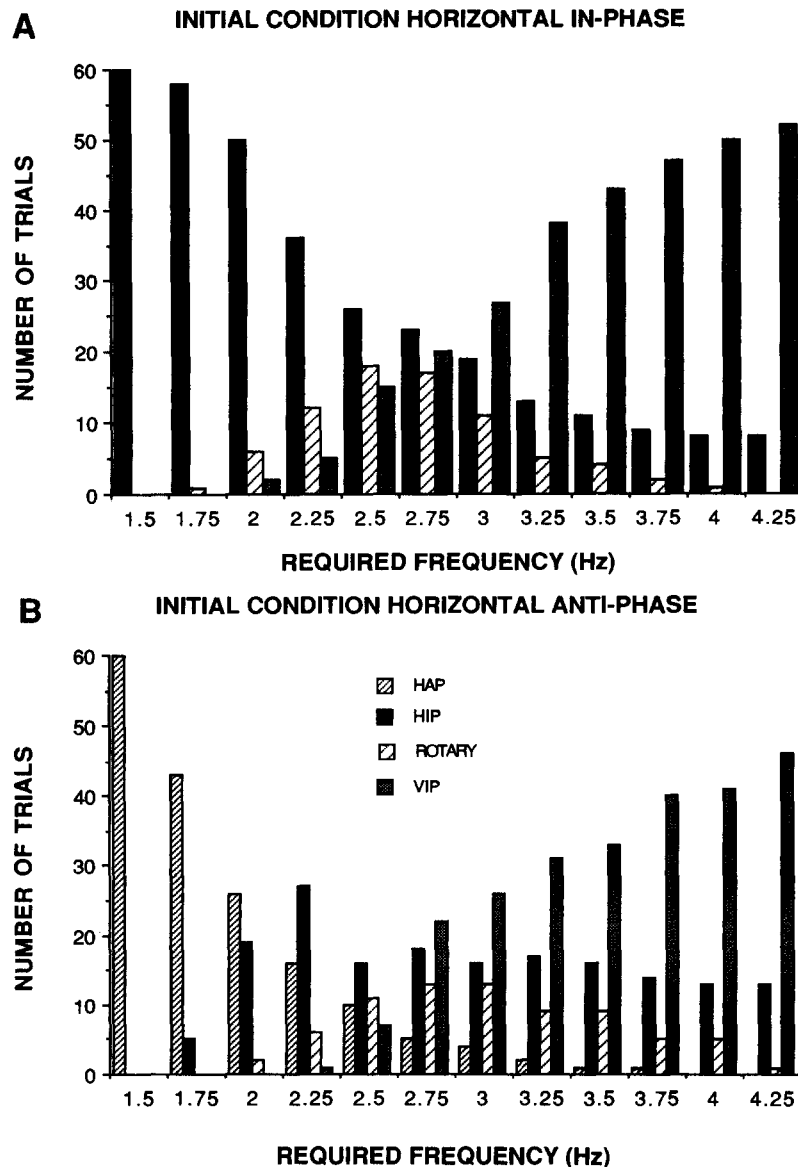
Fig. 2. Histograms showing the number of trials displaying a particular coordination pattern as the frequency increases. HAP=horizontal anti-phase pattern; HIP=horizontal in-phase pattern; ROTARY=rotary pattern; VIP=vertical in-phase pattern.

tal conditions, 98/120 (82%) transitions to the vertical plane of motion were observed. Of these, 53 were abrupt, occurring (like interlimb transitions) within 2–3 cycles of motion. Rotary motion was identified in 46/120 (38%) trials across both horizontal conditions. Rotary transitions were characterized by a more gradual increase in the amplitude of vertical

oscillation. Such changes are evident in the representative trajectories shown in fig. 1. Quantitative analysis showed that the relative phase between components hovered around $\phi \approx 0$, i.e. the limbs remained phase-locked throughout. In the rotary pattern, within-component phasing was bounded between 45° and 135°. Across both individual finger

conditions, spatial transitions to either rotary or vertical motion were observed on a total of 50/60 (83%) trials. Of these transitions, 30 were abrupt (HRF, 12; HLF, 18) and 20 were rotary (HRF, 12; HLF, 8).

A stability analysis of all the patterns was performed by calculating the standard deviation of the appropriate relative phasing measures on a given frequency plateau before and after transitions. Due to the range of critical frequencies, pre-transition analysis consisted of lining up plateaus from the transition point and working backwards. For horizontal interlimb transitions, the anti-phase pattern was consistently less stable than the in-phase pattern ($p < 0.01$). Vertical interlimb transitions followed suit ($p < 0.01$). In the latter, but not the former (perhaps because of a higher starting frequency than earlier experiments and because transitions occurred quite quickly starting in the horizontal plane) variability was significantly enhanced in the anti-phase pattern as rate increased ($p < 0.01$). This fluctuation enhancement in the hypothesized order parameter, relative phase, is fully consistent with the instability mechanism proposed for such transitions [1–3].

For spatial transitions, analysis revealed that the horizontal in-phase pattern was less stable than the vertical in-phase pattern ($p < 0.05$). Moreover, a pattern by frequency plateau interaction was also significant ($p < 0.01$). This was the result of an increase in variability for the horizontal in-phase pattern before the transition. Such a result suggests the possibility that the nature of the spatial bifurcation may be dependent upon the stability of the system before the transition. Analysis of rotary motion supports this idea: variability of rotary motion increased with frequency ($p < 0.05$) and was always less stable (more variable about the mean relative phase) than the vertical in-phase pattern. Likewise, for the individual fingers there was a significant increase in variability as frequency increased that dropped after the spatial transition to vertical (flexion–extension) motion.

These spatial transitions, first the recruitment of previously quiescent d.f. in the vertical dimension and then the annihilation of horizontal oscillation, can be regarded as the result of two consecutive Hopf bifurcations. Similar mechanisms have been proposed to model the transition, e.g. from standing to

walking in gait dynamics [14]. The essential difference here lies in the fact that, in our situation, such a bifurcation is utilized as a vehicle to maximize the stability (i.e. reduce fluctuations) of the performed pattern while fulfilling the task requirement stipulated by the environment, whereas in the case of gait changes, bifurcations simply provide a mechanism that converts one functional state to another. Our experimental system is rather more analogous to the spontaneous recruitment of "back bending" in quadrupedal gaits such as the gallop, and goes beyond gait changes per se. Bifurcations in coupled oscillator models of gaits pertain to an already active set of dynamical variables, but do not presently accommodate the self-organization of previously quiescent d.f.

In what follows we illustrate the foregoing notions with a simple oscillator model and compare the result with experimental observations. Theoretically, the phase space for describing the kinematics of a single end-effector, in the present case the finger tip, is $(x, \dot{x}, y, \dot{y})$. Previous work has shown that the dynamics of one dimensional, planar movements can be modelled by a nonlinear oscillator controlled by parameters such as the movement rate [2,15]. thus the trajectories seen in fig. 1 can be considered as the Lissajous figures produced by the two oscillators. The simplest system that captures the main observed characteristics is the following pair of nonlinear oscillators,

$$\dot{r}_i = r_i[a_i(f) - r_i^2] , \tag{1a}$$

$$\dot{\theta}_i = 2\pi f , \tag{1b}$$

where r_i and θ_i are the polar coordinates of oscillator i ($i = x, y$ denotes the x and y directions respectively) and $a_i(f)$ are parameters of the oscillators which are functions of the cycling frequency f. The solutions for eq. (1b) can be written as

$$\theta_i(t) = \theta_i(0) + 2\pi f t ,$$

where $\theta_i(0)$ are the initial phases at $t = 0$. The relative phase between the y and x oscillators is then defined as

$$\phi = \theta_y(t) - \theta_x(t) = \theta_y(0) - \theta_x(0) .$$

For $a_i(f) \leq 0$, the origin $r_i = 0$ is a stable fixed point attracting all initial conditions in the r_i–θ_i plane. If $a_i(f)$ is increased above 0, the origin becomes an un-

stable fixed point and a limit cycle attractor appears at $r_i = \sqrt{a_i(f)}$ giving rise to the oscillations in the i direction, i.e. a Hopf bifurcation. If $a_i(f)$ is decreased from above 0, then an inverted Hopf bifurcation takes place eliminating the existing oscillations in the i direction.

For concreteness, we assume that the parameters $a_i(f)$ depend on the movement rate f in the following manner,

$$a_x(f) = k_x(f_2 - f) , \qquad (2a)$$

$$a_y(f) = k_y(f - f_1) , \qquad (2b)$$

where k_x and k_y are constants of dimension [length^2 time] with numerical values of unity. The simple expressions used in eqs. (2) may be regarded as approximations of more realistic forms of a_i near the bifurcation points f_1 (the onset of rotary motion) and f_2 (the onset of purely vertical motion). For numerical computations, we choose $f_1 = 2$ Hz and $f_2 = 4$ Hz for eqs. (2), and consider f being increased from 1.5 to 4.5 Hz.

Figure 3A shows the trajectory for a single end-effector confined to the x direction in the x–y plane for $f = 1.50$ Hz $< f_1$. For $f = 2.75$ Hz $< f_1$, the trajectory forms an ellipse whose orientation in the x–y plane is determined by the relative phase ϕ. Figure 3B shows the case where $\phi = 90°$. For $f = 4.5$ Hz $> f_2$, the oscillation in the x direction disappears due to an inverted Hopf bifurcation at $f = f_2$ and the motion is confined to the y direction (fig. 3C). Trajectories

with noise added to the dynamical equations are shown in fig. 4 for the same set of parameters as in fig. 3. The addition of random noise produces effects more like the rhythmical motions actually observed.

Obviously, if f_1 is close to f_2 one may see an *abrupt* transition from horizontal to vertical motion which, as we have observed experimentally, occurs on approximately half of the trials. Figure 5 shows the experimental time series of the x (fig. 5A) and y (fig 5B) components of both index fingers. It is quite clear that damping of horizontal motion and growth of vertical motion occur simultaneously, exactly as the Hopf model would predict.

Despite the good qualitative agreement between two consecutive Hopf bifurcations and the present observations, questions remain. For example, we have assumed in eqs. (1) and (2) that oscillations are generated or annihilated through *supercritical* Hopf bifurcations. That is, the oscillation amplitude increases gradually from zero or decreases gradually toward zero. But, as we have seen experimentally (see fig. 5), the onset of y oscillations may also be sudden with a large amplitude, resembling that of a subcritical Hopf bifurcation. A further study using small increments of movement rate as a control parameter may elucidate this issue. A further feature that we have not explicitly tested here concerns hysteresis. With some certainty, however, we can assert that the present experimental system is strongly hysteretic. That is, once the system has switched to the most stable vertical in-phase motion it does not switch back
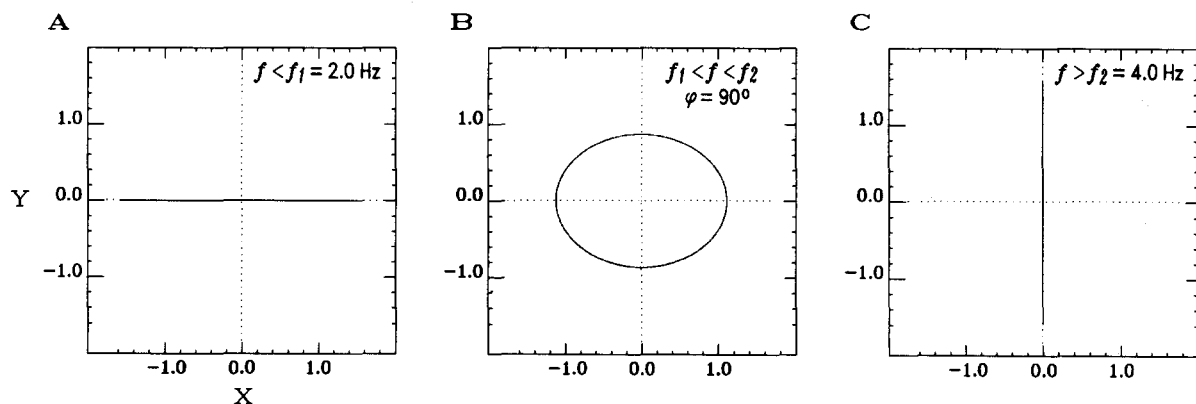

Fig. 3. Plots of an end-effector trajectory computed from a simple model of the recruitment process (see text for details) using non-linear oscillators.
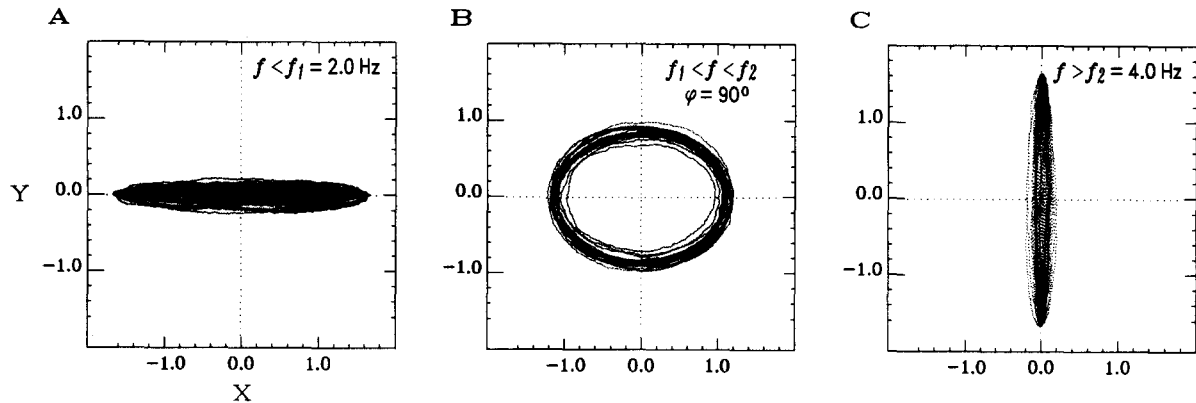
Fig. 4. Trajectories for an end-effector for the same set of parameters as in fig. 3 with added noise in the dynamical equations.
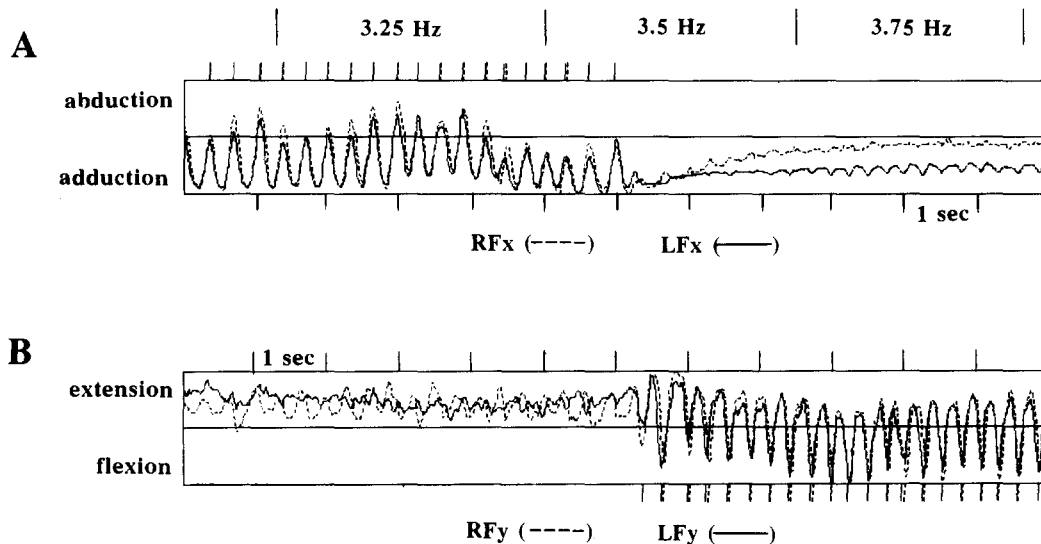

Fig. 5. Experimental time series of the x (A) and y (B) components of the left and right index fingers showing the damping of the horizontal motions and subsequent recruitment of the vertical d.f. as the cycling frequency is increased. In this case, the transition is from horizontal in-phase to vertical in-phase, bypassing rotary motion.

to a rotary or horizontal in-phase motion when the frequency is reduced. Elsewhere we have established and modelled this feature in planar motions along a single dimension [2]. When we consider simultaneous movements of two effectors in the x–y plane more complex dynamics arise. Again, previous work [16,17] shows that the dynamics in this case can be understood in terms of the relative phases between four oscillators.

Our main point here, however, was to show that

it is possible to observe a clear sequence of temporal (anti-phase to in-phase) and spatial (one plane to another) bifurcations in the present experiment. The spatial bifurcation route seems especially interesting because it characterizes the spontaneous creation and annihilation of movement-relevant degrees of freedom. We offer the Hopf scenario as a potentially model-independent mechanism for this essential aspect of flexibility in biological coordination. Elsewhere [18], we have considered other dynamical

mechanisms such as *antimonotonicity* [9], the simultaneous creation and destruction of periodic orbits near homoclinic tangency. Our results suggest that such a recruitment-annihilation process is one way biological systems achieve stability while fulfilling the task demand imposed by the environment.

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