PATTERN SWITCHING IN HUMAN MULTILIMB COORDINATION DYNAMICS

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A relative phase model of four coupled oscillators is used to interpret experiments on the coordination between rhythmically moving human limbs. The pairwise coupling functions in the model are motivated by experiments on two-limb coordination. Stable patterns of coordination between the limbs are represented by fixed points in relative phase coordinates. Four invariant circles exist in the model, each containing two patterns of coordination seen experimentally. The direction of switches between two four-limb patterns on the same circle can be understood in terms of two-limb coordination. Transitions between patterns in the human four-limb system are theoretically interpreted as bifurcations in a nonlinear dynamical system.

1. Introduction. In the study of biological motor control a primary question is how spatiotemporal patterns (e.g. locomotory patterns) form in systems composed of a large number of components. Theoretically the question is whether their behavior can be described by a few well-chosen state variables, no matter the number of components involved. For example, the behavioral patterns found between two rhythmically moving fingers have been characterized by a single state variable, the relative phase between the fingers (Kelso, 1984). This low-dimensional description was motivated by the assumption that the movement of each finger reflects the output of a distinct oscillator (Haken et al., 1985). From this viewpoint, the coordination between fingers arises from the interactions between two coupled oscillators. Under general assumptions, when oscillators are weakly coupled,

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their dynamics are well approximated by a function of their relative phases (Cohen et al., 1982; Ermentrout and Kopell, 1984). Such a relative phase description is also valid in certain cases of strongly coupled oscillators (Ermentrout and Kopell, 1991).

Applying the same approach as above, Schöner et al. (1990) proposed a model of quadruped locomotion, using three relative phases as state variables. Assuming left-right and front-hind symmetry they analysed the stability of common coordination patterns, i.e. equilibrium points of the dynamics. In this paper we modify the model of Schöner et al. and use it to interpret experiments on the coordination between human limbs. We consider changes in the system as a parameter is varied and focus on pattern switching: bifurcations in which an equilibrium disappears or becomes unstable and the system moves to another equilibrium point.

2. Summary of Experimental Results.

2.1. General design of experiments. In the human multilimb experiments we summarize here (see Kelso and Jeka, 1992, for additional information) a person is seated in a specially designed chair which allows her to rhythmically move her forearms, bending at the elbows, and her lower legs, bending at the knees. All movements are made in planes parallel to the median plane of the body. The position of each limb is characterized by its absolute phase modulo $2\pi$. The absolute phase $0 = 2\pi$ is assigned to the upward peak of a limb's movement and is defined to increase at a constant rate in between upward peaks. The downward peak of a limb's movement occurs at an absolute phase of approximately $\pi$. The relative phase $\phi$ between two limbs is defined as the difference in their absolute phases. If two limbs are in-phase ($\phi \approx 0$), both are moving up and down together, while if two limbs are antiphase ($\phi \approx \pi$), one limb is moving down while the other is moving up. Relative phases between limbs are calculated every time a certain target limb passes through the absolute phase $0$.

An experiment consists of a series of trials starting in various initial relative phase patterns. The subject is instructed to maintain the prescribed initial pattern and to cycle her limbs smoothly and continuously at a frequency set by an auditory metronome. Although instructions emphasize maintaining a one-to-one relation between the limbs and the metronome, no particular phase relationship between the metronome and the limbs is specified. The metronome frequency is systematically increased during each trial. The subject is instructed that should she feel the pattern begin to change, she should not try to resist the change, but instead perform whatever pattern seems most comfortable. (Although not done so here, subjects are capable of switching to a previously specified pattern, if so instructed; Jeka and Kelso, 1989.) All subjects were able to perform the