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Synergies: Stabilities, instabilities, and modes

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Nashner & McCollum (N & M) have addressed the question of whether muscle synergies exist for complex skilled activity, and if so, how they are organized (see also Kelso & Tuller 1983/1984; Lee 1984). The authors argue that muscle synergies exist for postural stability tasks in the form of a small set of discretely represented control entities, and that postural corrective movements of the dynamically continuous musculoskeletal system are organized through the operation of these discrete synergy elements. In this commentary, we make two main points: first, that N & M's arguments are not supported sufficiently by their data (i.e., the data do not allow one to distinguish between their discrete synergy model and other model types); we will describe the sort of data that would be convincing. And second, because N & M stress the "universality and importance of global schemes" for sensorimotor coordination and "principles governing the interactions among elements" that lead to "testable hypotheses," we mention briefly a theoretical framework that is attractive to us (e.g., Kelso 1984; Kelso & Saltzman 1982; Kelso & Tuller 1983/1984; Kugler, Kelso & Turvey 1980; 1982) because it treats cooperative phenomena in multicomponent systems on the basis of first principles (e.g., Haken 1975). We feel that this framework can: (1) offer a firmer basis for some of N & M's existing experimental observations; and (2) promote an experimental strategy that would illuminate N & M's hypothesis of region-specific discrete synergies.

N & M describe distinct patterns of EMG (electromyogram) bursts in response to distinct patterns of postural perturbation (e.g., vertical or front–back platform translation) in the context of given support conditions (e.g., different platform sizes). Each EMG pattern is characterized by a temporally ordered sequence of bursts within a subset of three agonist–antagonist muscle pairs (ankle, thigh, and trunk muscles). N & M hypothesize that each such pattern or synergy operates with respect to a corresponding distinct control structure. Each structure controls corrective postural movements within a limited subregion of postural configuration space (e.g., ankle angle versus hip angle plane), such that when the body is perturbed the associated (fine-tuned) EMG burst pattern will return the body to a balanced posture. In principle, however, such synergistic EMG patterns could also be generated by alternative models (e.g., Litvintsev 1972; Saltzman & Kelso 1984) in which control laws dependent on task (i.e., maintain balance), support condition, and postural configuration serve continually to specify corrective joint torque vectors that return the body from an unbalanced to a balanced posture. If one defined a further mapping from torque vectors to "muscle element" vectors (e.g., Jerard & Jacobsen 1980; Saltzman 1979) for which muscle elements were activated only after inputs exceeded a given threshold, then ongoing corrective torques would be mapped into patterns of discrete EMG bursts in those muscles appropriate for producing the required torques. This sort of control-law model augmented by thresholds for muscle element recruitment should generate consistent "synergistic" patterns of postural EMG in response to given types of destabilizing inputs, without reference to discretely organized synergy control structures. For stabilizing movements initiated from most locations in the postural configuration space, therefore, the above discrete and control-law hypotheses predict qualitatively similar EMG activity patterns. However, the discrete synergy model predicts that there will be certain regions of the configuration space for which the EMG predictions will be different for discrete and control-law models.

For the discrete control hypothesis, partitioning the configuration space into distinct (possibly overlapping) synergy subregions implies that border-lines (or border regions) will be defined between the different control domains (see N & M's Figure 5). N & M's notion implies that the system will behave differently along (or within) these borders than when operating away from them. Furthermore, when the postural system adapts from one support condition to another (e.g., from long to short platform lengths) the implication is that the border layout itself shifts correspondingly. Let us focus on the "simpler" adapted case for which border structure is assumed to be relatively constant. In this instance, the control structures associated with adjacent configurational domains should com
pete equally at the borders for access to the final common path
of muscular output. There are at least four possible outcomes o
such competition: (a) opposing effects will cancel each other an
no muscle activity will occur; (b) competing synergies will b
observed simultaneously in a mixture of EMG patterns; (c) ther
will be a repetitive alternation or "jittering" between the EM
patterns of each competing synergy; or (d) a totally novel EM
pattern might be observed. Experimental demonstration of an
of these patterns near N & M's hypothesized synergy borders i
support-condition-adapted subjects would provide strong su
port for the discrete model, since the control-law model woul
not behave differently on, near, or away from those border
These data are lacking, however, or at least have not bee
presented in the target article. The strongest data offered by
& M in favor of their hypothesis is the sequential mixing of ank
and hip "synergies" during adaptation to suddenly chang
platform sizes (see N & M's Figure 7). However, these findin
seem equivocal at best, given the concomitant shifts in bord
structure that presumably accompany such adaptation. Ther
fore, perturbation studies that use adapted subjects and th
explore a sufficiently large sample of the postural space could:
help to identify synergy borders and (2) constitute a direct test
the discrete synergy model.

The above suggestion exemplifies a general experimen
strategy for explicating the cooperative behavior of multicom
nent, open, nonlinear systems. A common feature of all su
systems is that when control parameters are changed beyo
certain critical values, new "modes" or spatiotemporal patte
may appear (for many examples in physics, chemistry,
biology see Haken 1977; 1983; Prigogine 1980; Yates 1982; Ya
& Iberall 1973; for examples in motor behavior, see Coh
Holmes, & Rand 1982; Kelso & Tuller 1983/1984; von H
1973). The beauty of this formulation is that the modes (e
synergistic patterns) may themselves be described by a se
dynamical equations derived via transformation proced
from the equations describing the behavior of the orig
subsystems (e.g., muscle elements). Under the influenc
continuous parameter scaling a given mode may suddenly
come dominant and "capture" the behavior of the subsyst
Such bifurcations result from the competition, as it w
between the "forces" or inputs that are parametrically sc
(corresponding, for example, to the translation of a platfo
and the "forces" holding the system together (i.e., the
ergistic constraints among muscles).

In Figure 1 we show an example from our own work on
behavior in a parametrically scaled, bimanual movement sy
exhibiting such a bifurcation. In the figure, the displacen
time profiles of left and right hands are plotted against
other on the Lissajous plane. Here the phase relation bet
the movements of the right and left hands describes the
tiotemporal ordering among corresponding flexor and ext
muscle activities. Starting in the antiphase modal pattern
right flexion [extension] is accompanied by left exte
[flexion]), the parameter of movement frequency is volun
increased in a continuous manner. As the frequency incr
the antiphase mode becomes less stable, as exemplified b
increase in phase variance. At a critical value (which turns
be a dimensionless function of each individual's preferr
cling rate), the system bifurcates and a different, in-
modal pattern appears (for a more complete analysis, see
1984). Extrapolating the above concepts to the postural d
of N & M, we envisage one "discrete strategy" as giving
another at critical borders in the postural parameter

Several points, therefore, are pertinent to N & M's an
First, transitions from one synergistic pattern of musc
ments to another may be discontinuous, even though the
controlling the process can change continuously. Secon
continuities of muscular pattern (giving rise to a descripti
apparently discrete properties) are observed not becaus

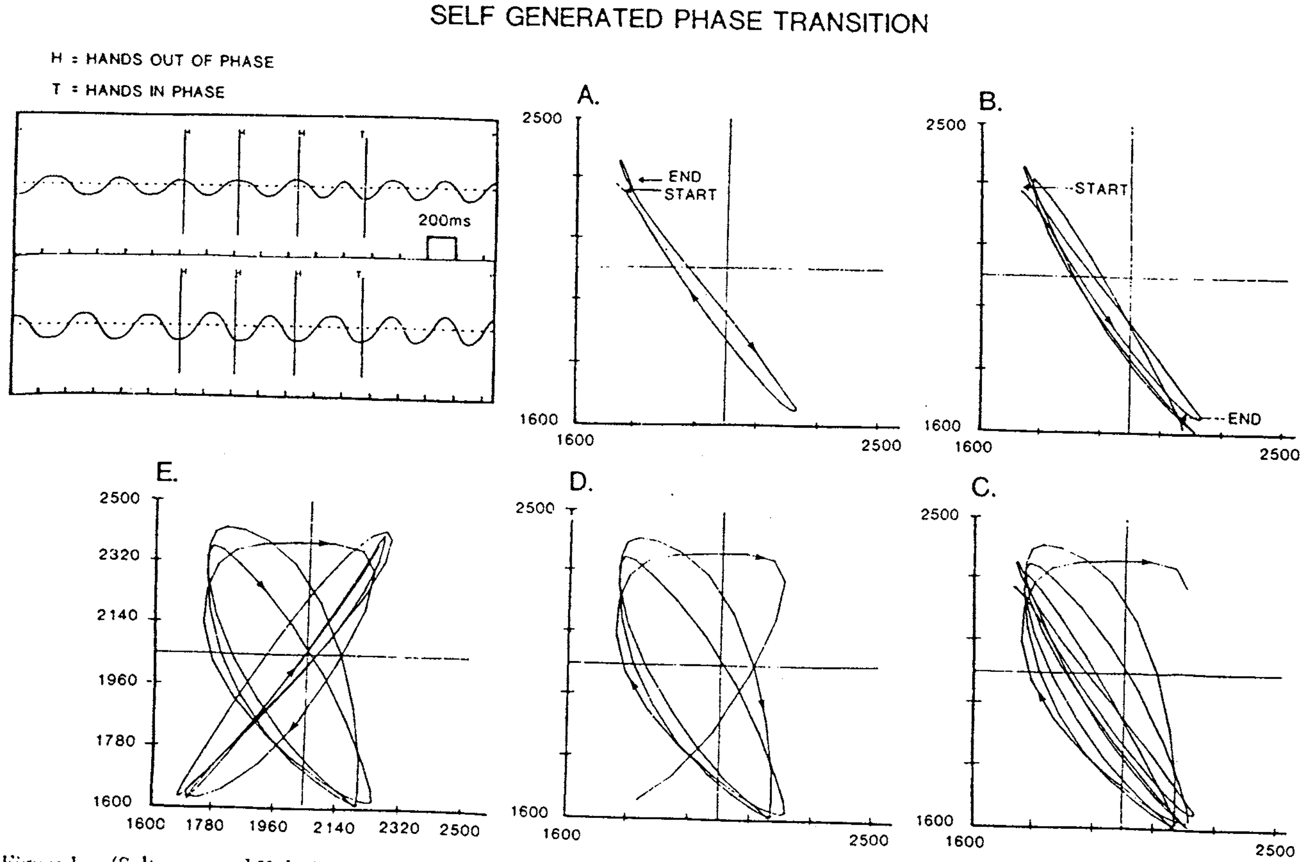

Figure 1. (Saltzman and Kelso) Angular position–time profiles of left and right hands (upper left) and position of each plotted against the other on the Lissajous plane (A–E). Left and right hand positions are plotted on the X and y axes respectively. "Hands out of phase" means that flexion of one hand is accompanied by extension of the other and vice versa. "Hands in phase" means that both hands flex and extend at about the same time. Phase becomes less stable (1C) as evident in the widening of the Lissajous trajectory, until an abrupt transition occurs (1D) (from Kelso & Tuller 1983/1984).

are no intervening behavioral states, but because none of them is stable (see possible experimental outcomes above). Thus, there may be a large number of ways for a system to exhibit continuous change but only a small number of ways for it to change discontinuously. To conclude, therefore, that discrete logical control is *imposed* upon a continuous mechanical system may not be warranted. Rather, synergistic muscular activities may *emerge* as modal patterns from appropriately scaled neuromuscular dynamical systems. Finally, although discrete logical states could be used to represent distinct modal patterns, it should be recognized that much of this apparent discreteness reflects the larger time constants of the dominant modes relative to the time constants of the subsystems. With reference to postural control, synergistic patterning among muscles appropriate to a given region of the associated parameter space is defined over longer time spans than, say, those involved in motor unit recruitment. Thus, the discrete–logical versus continuous–dynamical distinction drawn by Nashner & McCollum may be more apparent than real.

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