Relative timing in brain and behavior: Some observations about the generalized motor program and self-organized coordination dynamics

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Abstract

Recent functional brain imaging studies show that relative timing is a key variable capturing the coordination activity of both brain and behavior. Switching among relative timing patterns takes the form of a critical instability indicating that the underlying neural representation is dynamical and self-organized.

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An oft-cited goal of human movement science is to analyze motor control and learning not only in terms of externally observed variables, but also in terms of hypothetical internal variables used by the central nervous system to control movement. Although such an approach may allow us to correlate the former with the latter, correlations, as we all know, often fall far short of explanation. Presumably, not any empirically adequate language suffices to describe the ‘internal’ behavior of the brain, and the ‘external’ world of overt behavior. One

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might ask, without commensurability of description how is it possible to see the connection between the two? Just as space and time were unified in the theory of relativity, might a common conceptual language be found to reconcile the apparently very different domains of neural and behavioral events? Presumably, some variables — whether 'external' or their hypothetical 'internal' counterparts — are likely to be far more important than others. It may even be that when we find the essential quantities that capture the coordinative relations or coupling between brain and behavioral events, the need to infer one from the other might disappear (Kelso, 1992, 1995). Thus, instead of correlation or inference between 'internal' and 'external' variables, the task becomes one of finding relevant quantities and their dynamics that serve to bridge the two domains. Some recent evidence, reviewed briefly here, suggests that in certain specific cases this may, in fact, be possible.

Within the context of finding relevant variables for brain and behavior and a common conceptual language for each, the present paper addresses the two main theories of how the brain controls movement: the notion of motor programming and the set of theoretical concepts and methods that has come to be called coordination dynamics. There are many differences, both conceptual and empirical between the two approaches, but here attention is drawn to what I conceive to be a deep similarity between them. The original motor program idea (e.g. Keele, 1968) has evolved over time into the concept of generalized motor program (GMP), hypothesized to be an abstract representation stored in the central nervous system that controls 'most importantly' the temporal structure of an upcoming action (Heuer et al., 1995). More specifically, relative timing has been suggested as an invariant property common to a set of actions governed by the generalized motor program (Schmidt, 1982). Heuer et al. (1995) have noted that although ... "relative timing may not be perfectly invariant, it shows a conspicuous tendency toward invariance" (p. 344) in actions performed in so-called closed, stable environments. Although relative timing is the key hypothesized parameter controlled by the motor program in human motor skills, no one to my knowledge who subscribes to the program view has actually measured relative timing in the human brain, a fact that I shall return to shortly. Studies conducted so far infer relative timing as the main program parameter from behavioral observations, that is, as an invariant feature that is preserved across changes in force, amplitude, velocity, and so forth.

There is, of course, a vast body of literature showing that relative timing is a prominent property of the patterns produced by neural circuits in invertebrate and lower vertebrates (Grillner, 1996). It is not clear, however, how this work relates to the notion of generalized motor programs in the brains of people.
Also, because of the extreme multifunctionality and flexibility of these circuits, a number of prominent neurobiologists have dropped the term 'central pattern generator' altogether (for review, see Kelso, 1995, Ch. 8). Regardless of terminology, it is assumed here that both the proponents of the GMP and coordination dynamics would embrace the facts of dynamic pattern generation in neural circuits (e.g. Schmidt, 1988; Schöner and Kelso, 1988).

Coordination dynamics has its ancestry in the notion of coordinative structure or functional synergy, task-specific ensembles of neuromuscular and skeletal components constrained to act as a single unit (e.g. Boylls, 1975; Turvey et al., 1978; see also Edelman, 1987). Like the GMP, a conspicuous signature of a coordinative structure is relative timing, seen not only in actions such as locomotion, but also in voluntary discrete movements of the upper limbs (Kelso et al., 1979). Whereas invariant (or almost so, Heuer et al., 1995) relative timing has been used to bolster the GMP hypothesis, in coordination dynamics relative timing has come to reflect the central theoretical concept of temporal stability. The reason is, of course, that there are now many experiments showing: (1) that coordination patterns are differentially stable; (2) that systematic shifts in relative timing occur depending on the components being coordinated and their biomechanical properties; (3) that temporal stability may be lost when parameters (independent variables in the language of experimental design) are continuously varied over a sufficiently wide range; and (4) that additional biomechanical degrees of freedom may even be recruited and others suppressed while preserving temporal stability among the interacting components. Fluctuations in relative timing measures are known to precede the switching from one coordinative state to another. Fluctuation enhancement, transitions and other experimentally verified features such as multistability, hysteresis, phase trapping and slippage, recruitment, and so forth are predicted features of self-organized coordination dynamics, not a GMP (Kelso, 1994; Kelso and Haken, 1995; Turvey, 1994). At best, only the output of the motor program, not the program itself is subject to 'noise' (Schmidt et al., 1979), which, unlike in coordination dynamics, plays no constructive role. The role of fluctuations in coordination dynamics is both practical and conceptual: fluctuations probe the stability of coordinative states and allow the system to discover new coordinative states according to current environmental and task demands.

Putting aside semantic hang-ups, I propose that the regularities (such as 'invariant' relative timing) that motivated the GMP and related 'schema' notions may, at least in a number of key situations, already be subsumed within the formal, mathematical structure of coordination dynamics. After all, coordination dynamics is a law-based mathematical structure describing the coordination
activity of a system, whether it be the central nervous system, an organism interacting with its environment or even organisms interacting with themselves (Kelso, 1994). Like the GMP, in coordination dynamics relevant variables such as relative timing are abstract and task-related, even though the dynamics are always measurable. In coordination dynamics, the same equations of motion (e.g., Haken et al., 1985; Schöner et al., 1986; Kelso et al., 1990) have been shown to govern the behavior of different structures in similar tasks and across different coupling media. Moreover, several different coordinative patterns and pattern switching have been shown to be governed by the same abstract dynamics (see also Beek et al., 1995; Schöner, 1994; Turvey, 1994). In contrast, in its present formulation the GMP concept postulates different invariant motor programs for different tasks. So far, the GMP is a static theory motivated by human-made artifacts (the computer). Coordination dynamics is a dynamic theory motivated by, and grounded in, the behavior of natural, evolving, self-organizing systems (Haken, 1977). In this respect, it should be kept in mind (pardon the pun) that although all computers are dynamical systems, not all dynamical systems are computers.

Coordination dynamics, like the GMP, has shown that relative timing is a key (order) parameter, but goes on to predict a good deal more about the dynamics of relative timing variables (and how to derive them from lower levels) that the GMP does not. Given the numerous extensions of coordination dynamics to embrace intentional change, learning, perception–action coupling, speech production, discrete movements and even, in recent years corresponding brain activities (see following), a denouement with GMP theory seems possible, even imminent. Just as thirty-odd years ago the motor program theory required familiarity with the operations of a computer and computational concepts, so coordination dynamics requires some familiarity with the concepts, tools, and methods of complex, pattern forming dynamical systems and related informational aspects. This takes time and effort on the part of those who find the approach useful or appealing. Computers will play an evermore crucial role, of course, but as a window and an aid into understanding brain and behavior, not (at least as we presently know them) as the basis for a theory of mind.

One of the main purposes of this paper is to draw attention to several experimental facts that may be of great relevance to both theories of GMP and coordination dynamics, and any possible reconciliation between them. I refer to recent work in which functional brain imaging has been used in conjunction with the bimanual and sensorimotor coordination paradigms employed by my colleagues and I (e.g. Kelso, 1981, 1984; Kelso et al., 1990). In each case, subjects produce either in phase or antiphase behavior in response to a stimulus
whose frequency is systematically increased. The following behaviors are typically observed: (1) strong tendencies for phase- and frequency synchronization in both inphase and antiphase conditions for low movement rates (bistability). This is tantamount to saying that relative timing is 'almost invariant' across a range of frequencies. Measurements of the mean and variance of the relative timing among components and perturbation studies indicate, as noted earlier, that the key concept is temporal stability not invariance (see also Tuller and Kelso, 1990); (2) spontaneous transitions from antiphase to inphase coordination at a critical movement rate. No such transitions are observed when subjects begin in the inphase mode; and (3) hysteresis, when the direction of parameter change is reversed, subjects stay in the inphase mode. Although different brain areas are selectively activated in time to accomplish these tasks, the result of chief interest here is that relative timing measures capture both the brain behavior (internal?) and the overt behavior (external?), whether it be the timing relation between movement and a sound (Kelso et al., 1991, 1992; Fuchs et al., 1992), movement and a light (Wallenstein et al., 1995) or between the finger movements themselves (Kelso et al., 1994). In each case, the relative timing of the underlying brain activity maps onto the relative timing of the overt behavior in a one to one fashion.

The first point one might make is that although brain correlates of other movement parameters such as direction have been found (e.g., Georgopoulos, 1991, for review), the present results provide direct evidence of stable relative timing in ensembles of cortical neurons in the human brain during movement coordination tasks. This is surely a positive result for the relative timing hypothesis, regardless of theoretical orientation. The second point is that relative timing in the brain, like behavior itself, is (bi)stable for low values of the manipulated parameter, but undergoes a transition from one timing relation to another at a critical movement or stimulus rate. At first blush, this might suggest a switch from one motor program to another. But then one might ask, what mechanisms cause the switch to occur? The answer is that switching is due to loss of stability, a predicted feature of self-organized coordination dynamics not the GMP. Note that stability and instability are dynamical concepts and play no role whatsoever in motor programming theory.

Evidence obtained from both large scale EEG (Wallenstein et al., 1995) and SQuID arrays (Fuchs et al., 1992; Kelso et al., 1991, 1992, 1994) indicates that relative timing measures of brain electrical and magnetic signals exhibit both critical fluctuations and critical slowing down prior to switching. The former is indicated by systematic growth in the variance of relative timing in the antiphase pattern prior to switching. The latter by the fact that after a perturbation it takes
longer and longer to return to the pre-perturbation relative timing value as the transition draws near. Thus, the human brain (as well as many studies of overt behavior) may be said to exhibit nonequilibrium phase transitions. By showing that switching among relative timing patterns is due to instability, these results confirm the thesis, proposed several years ago by Haken (1983), that the human brain is fundamentally a self-organizing, pattern forming dynamical system. By operating close to instability points, both brain and behavior are able to switch flexibly from one coherent (relative timing) state to another. Moreover, phase transitions in global patterns of brain activity offer a novel mechanism for the collective action of cortical neurons (Kelso et al., 1991, 1992).

In the past fifteen years, much evidence has accrued that certain integrative processes previously unexplained in psychology and neuroscience lie within the laws of pattern formation and change in nonequilibrium systems, suitably extended, of course, to incorporate the informational aspects of living things (e.g. see recent contributions in Beek and Van Wieringen, 1994). A major outcome of this research is that the same collective variable has been demonstrated to capture coherent states and state transitions in both brain and behavior. The observed temporal relations are direct not merely correlative, and have been modelled phenomenologically (Jirsa et al., 1994) very much in the style of the Hodgkin–Huxley equations for single neurons, but here at the level of neuronal ensembles. Current work is underway to derive these phenomenological equations (and the observed experimental effects) from basic cortical neurophysiology and anatomical considerations (see, e.g. Jirsa and Haken, 1996). Ironically, perhaps, the key relative timing quantities are precisely those hypothesized by proponents of the generalized motor program (GMP), until now only inferred, but never measured directly in the human brain. Unlike the GMP, however, the evidence shows that these relevant quantities and the way they form and change (their dynamics) display predicted signatures of self-organization. The ‘neural representation’ may therefore be said to be self-organized and is precisely described in dynamical terms, i.e., as equations of motion of relevant variables (coordination dynamics). Said coordination dynamics provides a formal mathematical structure that incorporates the hypothesized GMP feature of relative timing and, it seems, much more.

Significantly, the discovery of physiologically realized coordination variables and their dynamics that serve to bridge organism–environment, perception–action and brain–behavior relations may render the strict distinction between relevant ‘internal’ and ‘external’ variables dubious. Rather, such results suggest that movement science (and the contemporary brain and cognitive sciences?) consider a shift in theoretical strategy away from inferring or correlating the
outside and the inside, to a focus on the between. Moreover, to the extent that new technologies and experimental paradigms allow us to make appropriate measurements of the spatiotemporal dynamics of the human brain during motor control and learning tasks, and to draw logical conclusions from them, we may hope to replace the ‘hypothetical’ with the actual.

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References


