Traversing Scales of Brain and Behavioral Organization I: Concepts and Experiments

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1 Introduction

In this paper, and the ones following, we will present an approach to understanding behavior, brain and the relation between them. The present contribution provides a sketch of the strategy we have adopted toward the brain-behavior relation, notes its main tenets and applies them to a new and very specific experiment that uses large scale SQuID arrays to determine how the human brain times individual actions to environmental events. A second paper (Fuchs, Jirsa and Kelso this volume) will describe in more detail the various methods we and others have used to analyze and visualize the spatiotemporal activity of the brain and to extract relevant features from experimental data. Finally, in a third paper (Jirsa, Kelso and Fuchs this volume) we will spell out a theory, grounded in the neuroanatomy and neurophysiology of the cerebral cortex, that serves to connect neural and behavioral levels of description for the paradigmatic case of bimanual coordination. Our collective goal in these three papers is to set the stage for a principled move from phenomenological laws at the behavioral level to the specific neural mechanisms that underlie them. With respect to the history of science our approach is entirely conventional. Fundamentally, it begins with the identification of the macroscopic behavior of a system and attempts to derive it from a level below. Even for physical systems, however, the derivation of the "macro" from the "micro" is nontrivial. Only in the 70's, for example, was it first possible to derive the behavior of ferromagnets (as described by Landau's mean field theory) from more fundamental grounds using the so-called renormalization group method that earned Kenneth Wilson the Nobel Prize in 1982. Likewise, it took the genius of Hermann Haken to derive the behavior of a far from equilibrium system like the laser from quantum mechanics (Haken 1970). Thus, some 70 years after atoms were discovered did it become possible to derive macroscopic properties of certain materials and optical devices from a more microscopic basis, and only then using rather sophisticated mathematical techniques.
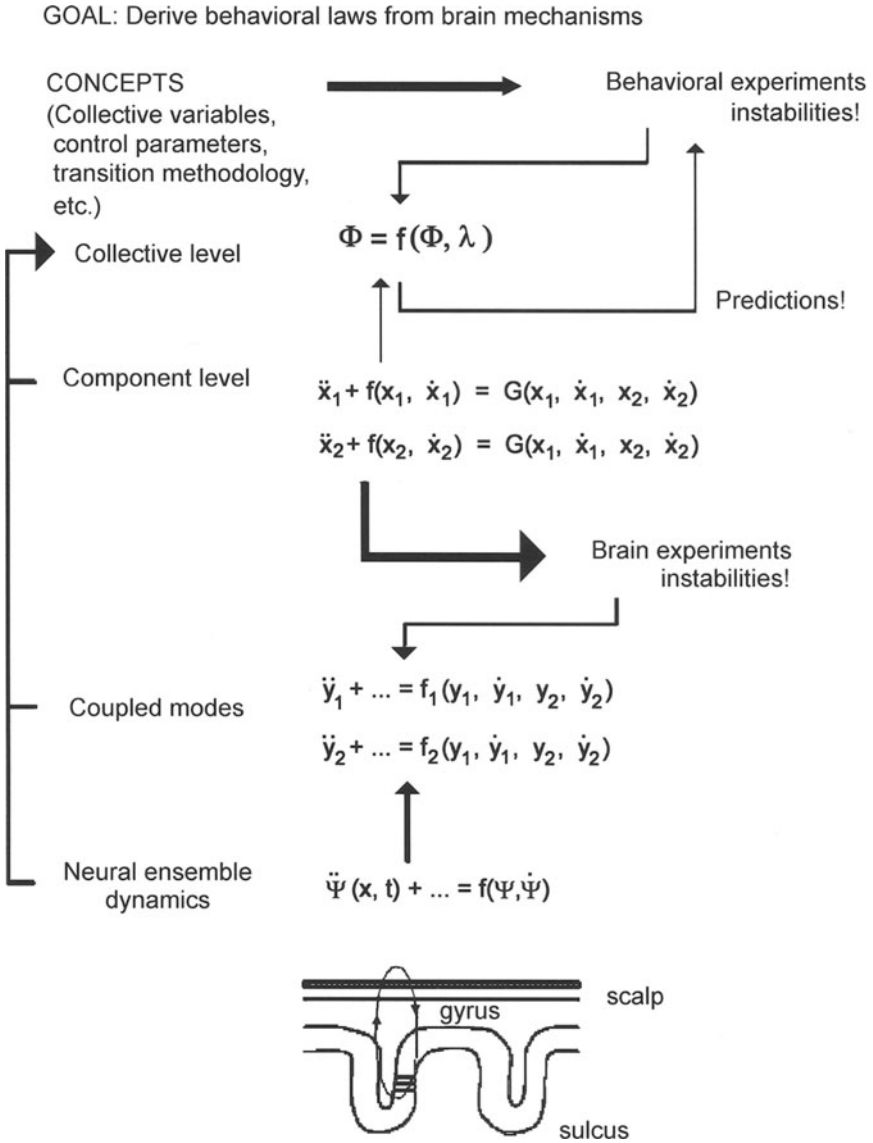
What lessons can be learned from such successes? One is that it is crucial to first have a precise description of the macroscopic behavior of a system in order to know what to derive. Another is that even in a system whose

microscopic constituents are homogeneous (unlike, say the neurons and neural transmitters of the brain) special methods are needed to handle events and interactions that are occurring simultaneously on many spatial and temporal scales. For example, even in a ferromagnet, it is not possible to derive the macro from the micro in a single step. Rather the so-called block spin technique proceeds in a series of steps each of which must be repeated many times in order to calculate the overall level of magnetization (Wilson 1979). Likewise, in a heterogeneous, hierarchically organized system like the nervous system, it is necessary to proceed in a level by level fashion with an intimate interplay between theory and experiment.

2   The Strategy

Our strategy for traversing scales is shown in Fig. 1. Inspired by synergetics (Haken 1983) the basic idea is to identify relevant variables characterizing coordinated or collective states of the system and the collective variable's dynamics (i.e. equations of motion for collective variables). Note that in complex neurobehavioral systems, these are not known in advance, but have to be found. The experimental method uses transition points to clearly distinguish different coordinated behaviors. In complex systems in which many features can be measured but not all are relevant, we assume that the variable that changes qualitatively is the most important one for system function.

   It is these collective variables that are mapped on to a dynamical system (see Collective level, Fig. 1). We remark that the behavioral dynamics for a given system must be understood on its own terms. Relative phase, ϕ, for example, proves to be a crucial collective variable or order parameter in a number of situations, but in others (e.g. trajectory formation of a single multijoint limb (DeGuzman, Kelso and Buchanan 1997) recruitment of additional degrees of freedom in coupled bimanual movements (Kelso, Buchanan, DeGuzman and Ding 1993) etc.) amplitudes play an important role and must be included in the collective variable dynamics. Likewise, equations of motion at the behavioral level must be (and have been) elaborated to include the influence of intention, environmental demands, handedness, learning, memory and attention (see refs. in Kelso 1995, and Treffner and Turvey 1996 for a recent example). Also, further experiments are necessary to identify the component dynamics and further theory is needed to derive the collective variable dynamics from nonlinear couplings among the components (see Component level, Fig. 1). We note that this step has been accomplished in a large number of different experimental model systems such as bimanual coordination (e.g. Haken, Kelso and Bunz 1985), multifrequency coordination (e.g. DeGuzman and Kelso 1991, Haken et al. 1996) coupled pendulum movements (see Turvey 1994 for review), trajectory formation (DeGuzman et al. 1997) with relevant experiments from laboratories in North America, Europe, and Australasia. We note also that theoretical predictions of the collective

GOAL: Derive behavioral laws from brain mechanisms

CONCEPTS
(Collective variables,
control parameters,
transition methodology,
etc.)

Behavioral experiments
instabilities!

Collective level

$$\Phi = f(\Phi, \lambda)$$

Predictions!

Component level

$$\ddot{x}_1 + f(x_1, \dot{x}_1) = G(x_1, \dot{x}_1, x_2, \dot{x}_2)$$

$$\ddot{x}_2 + f(x_2, \dot{x}_2) = G(x_1, \dot{x}_1, x_2, \dot{x}_2)$$

Brain experiments
instabilities!

Coupled modes

$$\ddot{y}_1 + \dots = f_1(y_1, \dot{y}_1, y_2, \dot{y}_2)$$

$$\ddot{y}_2 + \dots = f_2(y_1, \dot{y}_1, y_2, \dot{y}_2)$$

Neural ensemble
dynamics

$$\ddot{\Psi}(x, t) + \dots = f(\Psi, \dot{\Psi})$$

scalp

gyrus

sulcus

Fig. 1. The proposed level-building strategy connecting behavioral and brain dynamics (see text for details)

and component dynamics have been verified over and over again. The key notion behind our strategy, however, is to use this precise behavioral description and the methodology that allowed it, in order to probe other levels of analysis, in particular the brain. Here again, studies using large scale SQuID or multi-electrode arrays (e.g., Kelso et al. 1991, 1992, Wallenstein et al. 1995) and sophisticated analysis methods (e.g., Fuchs et al. 1992, see also Fuchs, Jirsa and Kelso this volume) have enabled us to identify relevant collective variables (such as spatial patterns and their time-dependent amplitudes). Signature features of self-organizing instabilities such as critical fluctuations and critical slowing down near transition points (Haken 1983) have been a prominent feature of these experiments. Elsewhere (Jirsa, Friedrich, Haken and Kelso 1994) we have summarized these results and presented a theoretical model that accounted for them in terms of the nonlinear interaction among spatial modes. We also showed how it was possible to derive the behavioral dynamics from this phenomenological brain mode theory (see arrow in Fig. 1 from coupled (brain) mode level back to collective behavioral level) hence providing a first glimpse of a possible connection between brain and behavioral levels. The bottom part of Fig. 1 shows a caricature of the neocortex with its sulci and gyri. Apical dendrites of pyramidal cells in columns are densely packed together and tend to discharge synchronously. A volume of cortex about $0.1mm^3$ contains enough neurons to generate a magnetic field which can be measured outside the head as MEG. The term neural ensemble dynamics in Fig. 1 reflects our initial attempts to formulate a theory of the measured magnetic field generated by intracellular dendritic currents that is grounded in the neuroanatomy and neurophysiology of the cerebral cortex. Using various known facts about intra- and cortico-cortical connections, and a number of simplifying assumptions Jirsa and Haken (1996) already showed how it was possible to obtain the earlier brain mode and behavioral models, hence setting the stage for a principled move from phenomenology to brain mechanism (One man's phenomenology is another's mechanism!). In this paper, and the ones that follow, we will describe some new theoretical and empirical developments that have emerged from the strategy illustrated in Fig. 1.

3   Knowing What to Derive: Dynamics of Behavioral Function

But let's start at the beginning. The goal of experiment is to invent or discover paradigms that allow us to understand essential aspects of biology and behavior (e.g. formation of synergies, multifunctionality, stability and flexibility of function, invariance under change, pattern selection etc.). Thus we study the simplest system that contains these interesting properties. Following this approach, (1) represents an elementary equation of motion for how just two biological components are coordinated:

$$\dot{\phi} = \delta\omega - \lambda_1 \sin\phi - \lambda_2 \sin 2\phi + \sqrt{Q}\xi_t \qquad (1)$$

This dynamical law was progressively established in a series of detailed experiments and theoretical steps (Kelso 1984, Haken, Kelso and Bunz 1985, Schöner, Haken and Kelso 1986, Kelso, DelColle and Schöner 1990, see also Fuchs and Kelso 1994). It constitutes a macroscopic description of the behavior of the system and contains three essential kinds of parameters:

- one that reflects whether the individual components are the same or different ($\delta\omega$). In general $\delta\omega$ may be viewed as an asymmetry parameter the sources of which are many (e.g. handedness, laterality, locus of attention, etc.);
- one that reflects external or internal factors (control parameters) that govern the strength of coupling between the components (λ_1, λ_2);
- and one that reflects the fact that all real systems contain noise or fluctuations (ξ_t) of a given strength Q.
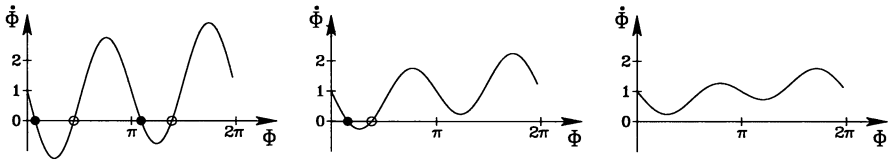
Fig. 2. An elementary law of behavioral coordination (see text for details)

Experiments showed that the relevant collective variable describing the functional synergy or spatiotemporal ordering between individual components is the relative phase, ϕ. For high values of the coupling ratio $\frac{\lambda_2}{\lambda_1}$, both modes of behavioral organization coexist, the essentially nonlinear property known as bistability (Fig. 2, left). Bistability (or, in general, multistability) confers multifunctionality on the system. That is, at least two forms of behavior are possible for exactly the same control parameter values. Notice that each is stable (negative slopes of the function cross the x-axis, denoted by solid circles, open circles mark unstable states) over a range of coupling, though the degree of stability may change. In this (bi)stable region (Fig. 2, left) the system's behavior will be restored despite any slight perturbation. As the coupling ratio is decreased, however, the system switches from one mode of behavior to another (Fig. 2, middle). Near the critical point, the slightest fluctuation will kick the system into a new form of stable organization. We may refer to this spontaneous transition or bifurcation as a form of pattern selection or decision-making which underlies the flexibility of the system's behavior. Switching is due to instability: under certain conditions, one mode of behavioral organization is less stable than another. On the right side of Fig. 2, there are no longer any stable states in the system. Due to

changes in control parameters or coupling ratio, the entire function has lifted off the x-axis. Note however that the function retains its curvature; there is still attraction to, or remnants of, previously stable states (so-called metastability). This effect is entirely due to broken symmetry in the dynamics, itself due to the fact that the individual parts of the system or their properties are not the same. As a consequence of such broken symmetry, the system produces a far more flexible form of behavioral organization in which the individual components are free to express themselves yet still work together in a looser kind of harmony. Metastable dynamics may help us understand a longstanding either-or conflict in brain theory, namely how "global" integration in which parts of the brain are locked together, may be reconciled with localized, independent activity in individual brain areas. Metastable dynamics says that the brain, like other complex living systems, uses a subtle blend of both. Finally, if the direction of the control parameter values changes after the transition shown in Fig. 2 (middle), the system stays in the stable state around $\phi = 0$, i.e., it exhibits hysteresis, a primitive form of memory. In Jirsa, Fuchs and Kelso (this volume) we will derive the coordination dynamics shown in Fig. 2 from neural ensemble properties for the paradigmatic case of bimanual coordination.

4   Brain-Behavior Experiments

It is well-known that animals and humans can accomplish the same goal using different body parts and end-effector trajectories, even when the path to the goal is disrupted or perturbed (Kelso, Bateson, Tuller and Fowler 1984). Likewise, people can accomplish the same temporal rhythm using different anatomical structures. Think of the pianist whose fingers, feet, torso and head all conform to the basic beat. Or of people dancing at a rock concert. What is going on in the brain when humans produce this kind of "motor" (more properly, functional) equivalence? How is the spatiotemporal activity of the brain related to the actual behavior produced? Recent studies of single cell activity in monkeys suggest that certain parameters of voluntary movement such as direction may be specified in the motor cortex independent of the particular muscles required to execute the act (Georgopoulos 1997 for review). Here, using a full-head SQuID array to record ongoing brain activity, we demonstrate 1) a robust relationship between time-dependent activity in sensorimotor cortex and movement velocity, independent of the direction of movement and the explicit timing requirements of the task and 2) dynamic patterns of brain activation that are specific to task demands alone. Taken together, we believe these new results provide evidence of "motor" or "function" equivalence in humans at the level of cortical function.

Recently we performed two experiments (Kelso, Fuchs, Lancaster, Holroyd, Cheyne and Weinberg 1998) The main one required human volunteers to perform four different coordination tasks: Simple flexion or extension move-

ments of the preferred index finger either on the beat of a metronome or in-between metronome beats, the frequency of which was fixed at 1Hz. One hundred cycles of continuous movement were recorded in each condition. Notice that these experimental conditions may be grouped with respect to the kinematics of motion (flexion versus extension movements), or with respect to the coordination task (synchronization or syncopation). Figure 3 shows plots of the relative phase between stimuli and movement peaks on a cycle-by-cycle basis for all four conditions. As requested, the peak of the movement is closely synchronized to the stimulus in the flexion-on-the-beat and extension-on-the-beat conditions. Likewise, subjects are able to place a movement in between stimuli in the flexion-off-the-beat and extension-off-the-beat syncopation conditions.

Stimulus-Response Relations for all Task Conditions
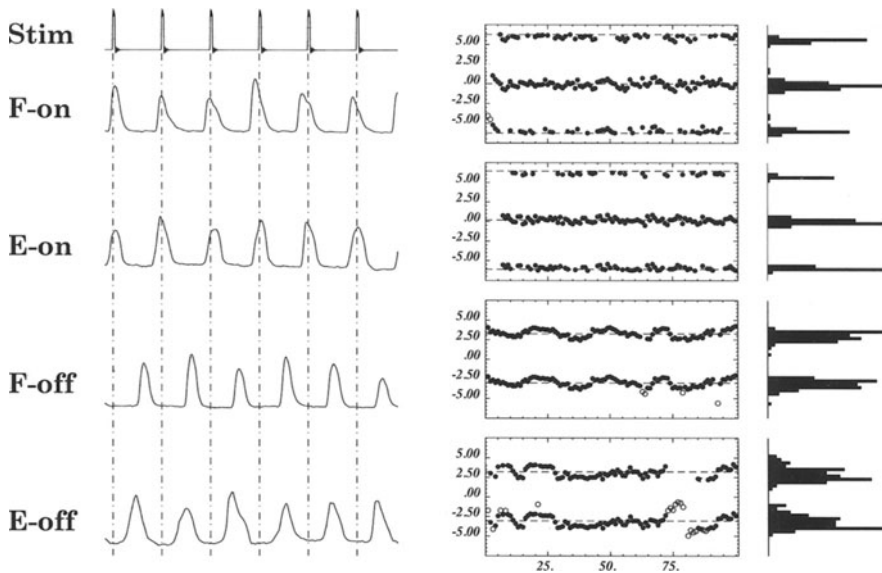
Fig. 3. Relative phase (in radians) on a cycle by cycle basis for all conditions (top rows: synchronization; bottom rows: syncopation) for a representative subject. Solid circles indicate cycles within a ±60° range of the average phase. Open circles are outside this range and were rejected from further analysis

Also shown are histograms, the width of which is a measure of the quality of performance. In general, the distributions for the syncopate conditions are broader, hence more variable than those of synchronization. Subjects tended to have more difficulty syncopating than synchronizing, which conforms to everyday experience and detailed behavioral experiments (Kelso et al. 1990).

Brain activity was recorded continuously as subjects performed these tasks using a 64 channel magnetometer (CTF Systems Inc., Vancouver) sampled at 250 Hz. This device consists of gradiometers arranged radially around the subject's head, each gradiometer consisting of a pair of parallel, axially centered, oppositely wound detection coils coupled to a SQuID. All the magnetic fields generated by the brain are due to the flow of electrical current, which is mainly ionic and is generated in the dendrites and somas of cortical neurons. About 10 000 neurons must be synchronously active to produce fields in the order of 200 fT (femtoTesla). Thus, any spatial patterning of activity within the brain is at the level of neuronal ensembles (see next section).

What is the relation between this evolving brain activity and the actual behavior produced? Figure 4 shows cortical activity patterns displayed in polar coordinates on the plane (see Fuchs, Jirsa and Kelso this volume for details) for each task averaged across subjects sampled at various points (shown by the red line) throughout the movement. Also shown (in green, inside the boxes) is the average amplitude profile of the movement. To ease visualization across conditions the movement profiles are all plotted in the same positive going fashion. Notice the presence of a strong dipolar field in the sensorimotor area of the left hemisphere during the first part of the movement, regardless of whether it involves flexion or extension. Notice also that the field reverses just after the peak movement (column 5) and then becomes much weaker and more distributed.

Decomposition of the brain's magnetic field into components corresponding to localized current sources is an ill-posed problem. Nevertheless, the spatial patterns of cortical activity shown in Fig. 4 suggest that the underlying neural ensemble is quite localized and fairly stationary during particular phases of the task. We decomposed the brain signals into spatial patterns and time-varying amplitudes using so-called Karhunen–Loève (K-L) decomposition or Principal Components Analysis (e.g. Fuchs, Jirsa and Kelso this volume). Tangential currents naturally produce spatial correlations (the field entering the scalp at one location and leaving at another), and the resulting principal components may capture this dipolar structure. Figure 5 shows that the first two spatial modes (1st and 2nd columns) capture about 80% of the variance in the brain signals. Because the top spatial mode, like the underlying neural ensembles, is under no orthogonality constraint, it is identical to the dominating spatial pattern of brain activity observed experimentally. The remarkable result shown in Fig. 5 is that its time-dependent amplitude tracks the velocity profile extremely well, especially for the initial velocity peak associated with the active phase of the coordination task. The second velocity peak constitutes the less active phase of the task and the match to the brain signal is weaker. It seems likely that the corresponding minimum in the brain signal occurs after movement onset and reflects reafferent activity from the periphery to somatosensory cortex (Cheyne and Weinberg 1989) although precentral sources may remain active throughout the movement.
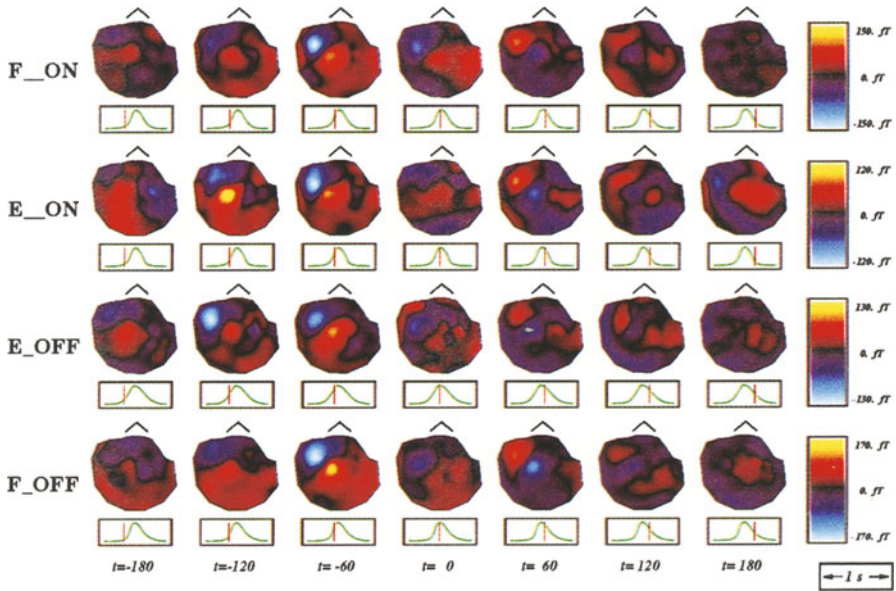
Fig. 4. Brain activity patterns averaged across cycles and subjects (N = 5) at time points t (in ms) for all conditions. The time point $t = 0$ is the peak movement amplitude. The green curve in the box shown below each pattern is the average amplitude profile for each condition. The red line indicates the time ($t = \pm180$ms) at which brain activity is sampled during the movement cycle. Each condition has been scaled separately to highlight the peak fields. In general, the activity for flexion conditions has a slightly higher amplitude range than the extension conditions (adapted from Kelso et al. 1998)

These results are even more striking because the K-L mode decomposition simply minimizes the mean square error without regard to the movement at all. A second method calculates the spatial patterns that best fit the movement and its derivatives (Uhl, Friedrich and Haken 1995). The results of that procedure (see Fuchs, Jirsa and Kelso this volume) once again show that the largest mode corresponds to movement-related brain activity, specifically the velocity of finger flexion or extension.

Two questions arise from these results. First, is the strong relationship between average movement velocity and the time course of cortical activity a mere coincidence or is it consistent across different manipulations of the velocity profile? In particular, does this relationship hold across a number of peak velocities (with the same length timecourse) and does it hold across a number of movement rates (similar peak velocity, but shorter timecourse)? Second, what, if any, influence does the task alone contribute to patterns of brain activation? The issue of motor equivalence is double-sided, requiring an identification of both invariant and task-specific aspects of brain activity. To answer the first question we performed two different manipulations. First,

KL–expansion

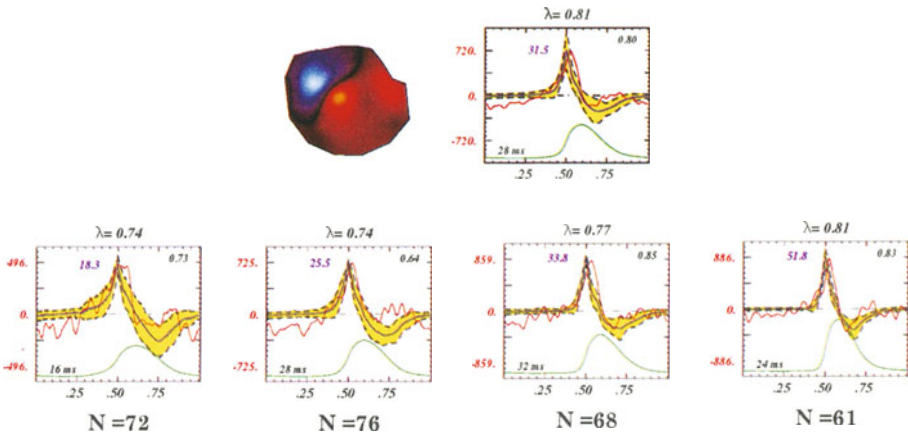— Brain signal   — Movement velocity
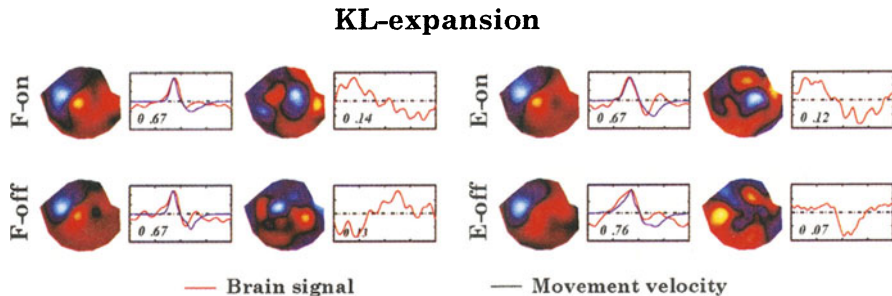
Fig. 5. Decomposition of the spatiotemporal signal into spatial patterns and corresponding time-dependent amplitudes for all conditions. The first two modes of a Karhunen-Loeve decomposition and their time-dependent amplitudes (in red). The numbers in the lower left corner of each box indicate how much of the variance of the entire signal is contained in a given mode. Notice the first two modes cover about 80% in all conditions. Overlaid in the first column is the movement velocity (in blue). The tight relationship between time-dependent neural activity and movement velocity is apparent especially for the first peak for all task conditions (F_ON and E_ON refer to flexion and extension movements on-the-beat. F_OFF and E_OFF refer to flexion and extension movements off-the-beat)

we sorted the existing data from all four original task conditions into sets representing different peak velocity ranges, from slowest to fastest. The data from four different peak velocity ranges for a representative subject are shown in Fig. 6. The brain signal (again the time-dependent amplitude of the top spatial mode) is plotted (in red) along with the velocity profiles (in blue) for the overall data (left box) and four non-overlapping bins in which velocity increases from left to right. The steepness of the displacement profile (in green) reflects the derivative, actual values of which are shown in blue. Notice that each graph in Fig. 6 is scaled individually, highlighting the correspondence between the brain signal and the velocity profile. The degree of covariance, given by the correlation value on the top right of each box, is high.

Next, we performed another experiment in which we asked the same subjects to perform the two basic syncopation tasks at six different movement rates. Beginning either in the flexion- or extension-off-the-beat conditions, subjects were instructed to syncopate with the metronome, the rate of which was increased every 10 cycles from 1.25 Hz to 2.5 Hz in 5 steps of 0.25 Hz. It is known that transitions from syncopation to synchronization occur spontaneously in both brain activity and behavior as movement rate is increased beyond a critical value (Kelso et al. 1990, Kelso et al. 1992) but the relationship of interest here has not, to our knowledge, been examined before. The results were unequivocal across subjects, initial conditions and movement rates. A representative example is shown in Fig. 7 for the flexion-off condition. Once again, the same basic dipolar-like spatial pattern was observed at all movement rates. For ease of visualization, the velocity profile (in blue)

Peak Velocity Binned Data

Fig. 6. The relationship between brain activity and movement velocity. The top box indicates the average data for all conditions for a representative subject. In the four boxes below these data are sorted according to different peak velocities which increase from left to right. Displacement profiles shown in green are represented on a common scale and increase in magnitude and steepness across the four bins. The time-dependent amplitude of the top spatial mode is plotted in red (eigenvalues are indicated above each box); the velocity profile and its standard deviation in blue and yellow, respectively. Labels on the y-axis (in red) indicate the range and magnitude of the brain signal, which increase from left to right. Blue numbers indicate the mean peak velocity for a given bin. From left to right, the ranges of peak velocity (in arbitrary units) in each bin are: 11.5 to 73.4 (average), 11.5 to 22.9, 23.0 to 28.5, 28.6 to 39.9, and 40.0 to 73.4. Black numbers indicate the correlation value between brain and velocity profile (top right of each box) and corresponding lag in ms (bottom left) (Adapted from Kelso et al. 1998)

is superimposed on the brain signal (here the best fit spatial pattern). The corresponding value of the correlation function at the time lag between the first velocity peak and the brain signal is also reported in the top right of the boxes. Given the predictive, rhythmical nature of the task it is not unexpected to find that the peak movement velocity leads the cortical activity by a small amount (shown in the lower left corner of Figs. 6 and 7). Yet the similarity in the neural and velocity profiles is once again striking, especially in the initial active phase of voluntary movement.

To answer the second question about task-specific brain activity, we removed the dominant velocity-related spatial pattern from the recorded brain signals (see accompanying paper by Fuchs, Jirsa and Kelso for details and results). These residual brain patterns turn out to be similar for the syncopation tasks, which in turn are very different from the corresponding brain activity patterns for synchronization. Thus, any differences attributable to
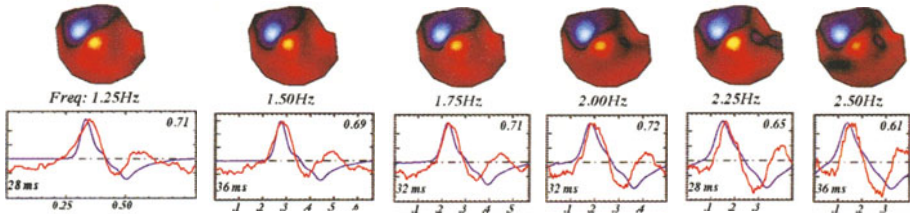
Fig. 7. The relationship between brain activity and movement rate (1.25 Hz to 2.5 Hz) for the Flexion-on-the beat condition (the other conditions are very similar). The number in the lower left corner of the boxes represents the shift between the brain signal (red) and the movement velocity (blue). In the upper right corner the correlation value for the two curves is shown. The smaller boxes as one moves from left to right reflect the number of points sampled in a given cycle which decreases with movement rate (adapted from Kelso et al. 1998)

movement direction (e.g., flexion-on and extension-off are kinematically similar) are far outweighed by differences due to the task, i.e., the goal of the subject's action.

In summary, the demonstration of a robust relation between movement velocity and the time course of cortical activity across a broad range of initial conditions, peak velocities and movement rates complements single-cell studies in monkeys which show that one of the most clearly represented parameters associated with motor cortical activity is movement direction (Georgopoulos 1997 for review). Although obtained in a rhythmic, not discrete movement context, our results are congruent with very recent findings which show that speed is directly represented in the discharge rate of cells in primary motor cortex when the directional component of the discharge pattern is removed (Moran and Schwartz in press). During the task of synchronization, the cortex appears to control the speed of movement so as to arrive or "collide" at the target (the metronome beat) at the right time. For syncopation the cortex must even plan for a virtual target in-between metronome beats. Of course, our results do not deny and even suggest that somatosensory information is used both in the planning and execution phases of the tasks. Nor do they exclude a role for other brain areas (e.g. cerebellum, putamen and thalamus) that appear to be involved in the internal generation of precisely timed movements (Rao et al. 1997). Nevertheless, our findings help resolve a longstanding question in studies of human synchronization, namely, how the brain coordinates actions in time with external events. Cortical correlates of the velocity profile hold across different movement directions, rates and task demands. At the same time, patterns of brain activation appear to be task-specific, conforming to particular modes of coordination. Taken together, these results reveal signatures of motor equivalence in dynamic patterns of cortical activity.

5   A Little Theory

Our experimental findings can be interpreted from the viewpoint of a field
theoretical description that has been developed based on properties of exci-
tatory and inhibitory neural ensembles and their corticocortical (long range)
and intracortical (short range) interactions. The resulting spatiotemporal dy-
namics is represented by a set of retarded coupled nonlinear integro-differen-
tial equations for the excitatory and inhibitory neural activity (see Jirsa,
Kelso and Fuchs of this volume for details). Due to differences in spatial and
temporal scales this system can be reduced and transformed into one single
nonlinear partial differential equation:

$$\ddot{\psi}(x,t) + 2\,\omega_0\,\dot{\psi}(x,t) + \{\omega_0^2 - v^2\Delta\}\psi(x,t) = \left\{\omega_0^2 + \omega_0\frac{\partial}{\partial t}\right\}\rho(x,t) \qquad (2)$$

with

$$\rho(x,t) = S[\psi(x,t) + \sum_i p_i(x,t)] \ . \qquad (3)$$

Here $\psi(x,t)$ represents the spatiotemporal neural activity, $\omega_0 = v/\sigma$ a fre-
quency defined by the axonal propagation velocity v and the mean axon
length σ, S a sigmoid function, and $p_i(x,t)$ functional input and output
units. In the framework of this theory the experimental findings described
above can be represented as depicted in Fig. 8. There the behavioral level
may be represented by an equation of motion for the relative phase ϕ which
serves as a collective variable coupling the visual stimulus to movement (see
Fig. 2). At the brain level, a functional input unit $\alpha(x)$ embedded into the
cortical sheet receives input signals from the visual metronome. An output
unit in the motor cortex sends signals to the finger muscles which provide
sensory feedback from muscle spindles and joint receptors to a second input
unit located in sensormotor cortex. We seek an explicit account for the rela-
tion between finger displacement $r(t)$ and neural activity $\psi(x,t)$, represented
by:

$$r(t) = \int \mathrm{d}x\,\beta(x) \int \mathrm{d}\tau\,e^{-\gamma(t-\tau)}\,\psi(x,\tau) \qquad (4)$$

where $\beta(x)$ describes the localization of the output unit in the cortical sheet
and is to be identified with the dipolar mode observed experimentally (see
Figs. 5 and 6). Notice the finger motion $r(t)$ arises out of an integration in
space as well as time. Such a mechanism of spatial and temporal integration
is well-known neurophysiologically and serves to smoothen intrinsically noisy
brain signals. It is well known that $r(t)$ is the particular solution of

$$\dot{r}(t) + \gamma\,r(t) = \int \mathrm{d}x\,\beta(x)\,\psi(x,t) \qquad (5)$$

where the lhs represents a linear damped system driven by the neural sig-
nal (rhs). Figure 9 shows the reconstruction of the movement profile from

neural activity according to (4) for all task conditions. Note the reconstructed movement profile fits the experimentally observed movement particularly well in the active phase represented by its positive flank. The discrepancies mainly occur after peak displacement and are probably due to the influences of sensory feedback which are not accounted for by (4).
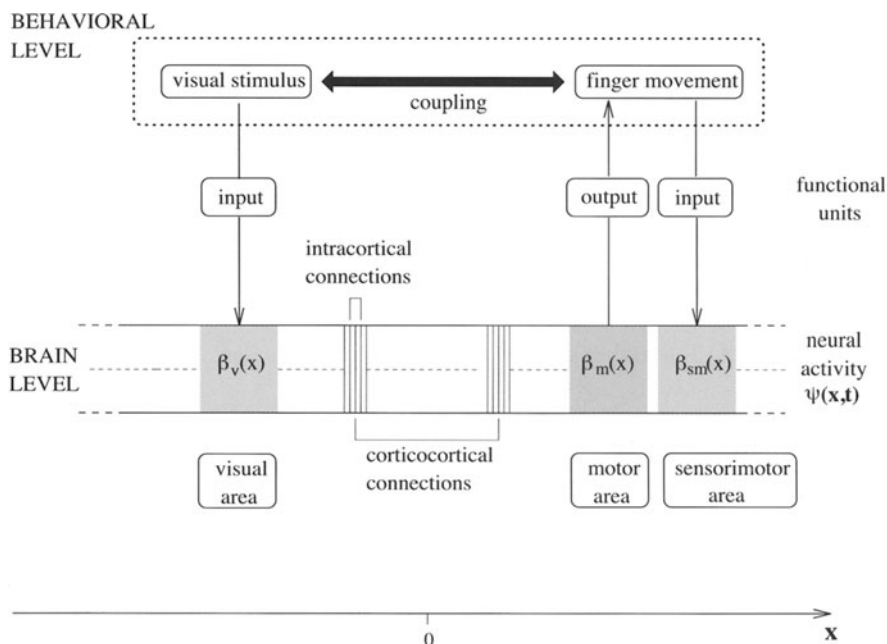

Fig. 8. Functional units embedded in a cortical sheet with long range and short range interactions (see text for details)

6   Concluding Remarks

Modern neuroscience at the end of the 20th Century is successfully reducing the brain to its physical elements, but it is becoming increasingly unclear how to put Humpty Dumpty together again, i.e., to understand how orchestrated biological functions arise from such structural complexity. New concepts and strategies are needed to handle such complex systems, and a vocabulary must be devised that is rich enough to characterize both behavioral and neural levels of analysis. A main idea behind our approach is that it is difficult, if not impossible, to integrate levels except in the context of well-defined behavioral functions. Thus, much work has gone into identifying the quite abstract, but

Reconstruction of Movement Profile from Brain Activity
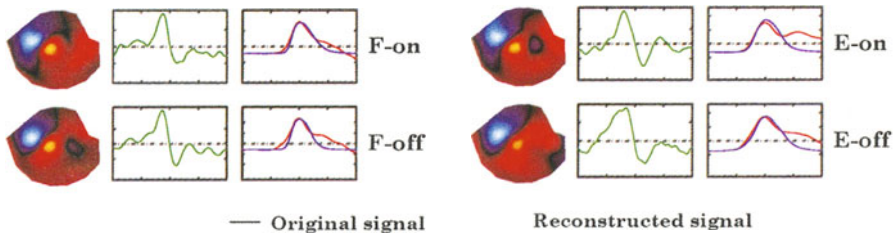
Fig. 9. Reconstruction of the movement profile using brain activity (the dipolar mode's amplitude over time, shown in green) as a driving signal for the finger oscillator

empirically-grounded phenomenological laws at behavioral and brain levels. These are then used as a necessary guide into the materially based mechanisms and principles that underlie them. Obviously the neurophysiology, neuroanatomy and neurochemistry of the central nervous system constitute a deeper basis upon which to derive phenomenological laws of behavioral function. But to start with the former without knowing the latter may be a grave mistake. Casting back to the conceptual scheme shown in Fig. 2, notice that the order parameters or collective variables are function, task or context dependent. Nothing subjective is implied by this statement. As a considerable amount of experimental research now shows, the same order parameters have been identified in a variety of contexts. Notice also in Fig. 2 that the order parameters are different at each level and that there may be mutability between order parameters and control parameters across levels. What is a collective variable at one level may be a control parameter at another, and vice-versa. The connection across levels – the traversing of scales in the title of this trilogy of papers – is by virtue of coupled spatiotemporal dynamics on all scales.

Acknowledgements

References

DeGuzman, G., Kelso, J.A.S. (1991): Multifrequency behavioral patterns and the phase attractive circle map, Biol. Cybern. 64, 485–495

DeGuzman, G., Kelso, J.A.S., Buchanan, J.J. (1997): Self-organization of trajectory formation. Biol. Cybern. 76, 275–284

Fuchs, A., Kelso, J.A.S., Haken, H. (1992): Phase Transitions in the Human Brain: Spatial Mode Dynamics, Inter. J. Bifurc. Chaos 2, 917–939

Fuchs, A., Kelso, J.A.S. (1994): A theoretical note on models of interlimb coordination, Journ. Exp. Psych.: Human Perception and Performance, 20, No. 5, 1088–1097

Georgopoulos, A.P. (1997): Neural networks and motor control, Neuroscientist 3, 52–60

Haken, H. (1970): *Laser theory.* Encyclopedia of Physics Vol. XXXV/2C, Springer, Berlin

Haken, H. (1983): *Synergetics. An Introduction*, 3rd ed., Springer, Berlin

Haken, H., Kelso, J.A.S., Bunz, H. (1985): A Theoretical Model of Phase Transitions in Human Hand Movements, Biol. Cybern. 51, 347–356

Haken, H., Peper, C.E., Beek, P.J., Daffertshofer, A. (1996): A model for phase transitions in human hand movements during multifrequency tapping, Physica D 90, 179–196

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

Jirsa, V.K., Haken H. (1996): Field theory of electromagnetic brain activity, Phys. Rev. Let. 77, 960–963

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

Kelso, J.A.S. (1995): *Dynamic Patterns. The Self-Organization of Brain and Behavior*, MIT Press, Cambridge, MA

Kelso, J.A.S., DelColle, J.D., Schöner, G. (1990): Action-perception as a pattern formation process, in: *Attention & Performance XIII*, Jeannerod, M., ed., 139–169, Erlbaum, Hillsdale, NJ

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. Let. A 179, 364–371

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. Let. A 169, 134–144

Kelso, J.A.S., Bressler, S.L., Buchanan, S., DeGuzman, G.C., Ding, M., Fuchs, A., Holroyd, T. (1991): Cooperative and critical phenomena in the human brain revealed by multiple SQUIDS. In: *Measuring chaos in the human brain*, Duke D., Pritcard W., eds., World Scientific, NJ

Kelso, J.A.S., Fuchs, A., Lancaster, R., Holroyd, T., Cheyne, D., Weinberg, H. (1998): Dynamic Cortical Activity in the Human Brain Reveals Motor Equivalence, NATURE 392, 814-818

Moran, D.W., Schwartz, A.B. (in press): Motor cortical representation of speed and direction during reaching, J. Neurophysiol.

Rao, S.M., Harrington, D.L., Haaland, K.Y., Bobholz, J.A., Cox, R.W., Binder, J.R. (1997): Distributed neural systems underlying the timing of movements, J. Neurosci. 17, 5528–5535

Schöner, G., Haken, H., Kelso, J.A.S. (1986): A Stochastic Theory of Phase Transitions in Human Hand Movement, Biol. Cybern. 53, 247–257

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. (1994): From Borelli (1680) and Bell (1826) to the dynamics of action and perception. J. of Sport and Exercise Psychology 16, 2, S128–S157

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

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

Wilson, K.G. (1979): Problems in Physics with many scales of length. Sci. Am. 241, 158