



## Neuroimaging Coordination Dynamics in the Sport Sciences

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### ABSTRACT

Key methodological issues for designing, analyzing, and interpreting neuroimaging experiments are presented from the perspective of the framework of Coordination Dynamics. To this end, a brief overview of Coordination Dynamics is introduced, including the main concepts of control parameters and collective variables, theoretical modeling, novel experimental paradigms, and cardinal empirical findings. Basic conceptual and methodological issues for the design and implementation of coordination experiments in the context of neuroimaging are discussed. The paper concludes with a presentation of neuroimaging findings central to understanding the neural basis of coordination and addresses their relevance for the sport sciences. The latter include but are not restricted to learning and practice-related issues, the role of mental imagery, and the recovery of function following brain injury.

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### 1. Introduction

Common to all forms of sport and exercise is the need to coordinate movements in a constantly changing environment. Despite the apparent computational problems inherent in such complex coordination [1], the human brain easily integrates information across multiple sensory modalities and multiple muscles and joints in order to generate a broad repertoire of adaptive behavior. Of particular relevance to sports is the need to understand the behavioral and neural mechanisms underlying performance and its improvement, including the processes underlying recovery of function from sports injury and surgery. At the neural level, this entails uncovering the cortical and subcortical circuitry responsible for the formation and change of patterns of coordination. *Coordination Dynamics* is a theoretical and empirical approach based on the concepts, methods, and tools of informationally coupled self-organizing dynamical systems [2]. In the context of physical activities and sport sciences, Coordination Dynamics offers a window into uncovering neural processes of complex behavioral patterning and performance as well as understanding how patterns can change spontaneously in response to various forms of learning and practice. Meaningful influences on the behavioral dynamics include such factors as intention, attention, and imagination [2]. Moreover, together with brain imaging techniques, Coordination Dynamics provides a framework for uncovering how coordination

may be altered as a result of mild and severe brain injury and for establishing effective routes to retraining and recovery.

The goal of the present paper is to outline key methodological issues for designing, analyzing, and interpreting neuroimaging experiments undertaken within the Coordination Dynamics framework. In Section 2, we present a brief overview of the Coordination Dynamics approach, introducing key concepts and tools, the basic experimental setting, and cardinal empirical findings. In Section 3, we provide greater experimental detail, outlining basic methodological issues for designing and implementing coordination experiments with specific focus on neuroimaging. Section 4 will provide an overview and discussion of pivotal neuroimaging findings for understanding the neural basis of coordination and its application to the sport sciences. We will conclude in Section 5 with a brief summary and some forward-looking remarks.

### 2. Coordination Dynamics—approach and theory

Coordination Dynamics, defined broadly as the science of coordination [see 2–5] describes, explains, and predicts how patterns of coordination form, adapt, persist, and change in natural systems. It uses the language, methods, and tools of self-organizing dynamical systems [e.g. 6,7] to provide a conceptual and theoretical framework for understanding coordination at multiple levels, from behavior to brain [2,8,9]. A primary goal of Coordination Dynamics is to understand the laws, principles, and mechanisms governing how patterns of behavior form in space and time at multiple levels of description (molecules, cells, circuits, brain, behavior, etc.); how

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these patterns are maintained; how they change in response to environmental or physiological demands; and how they are (re)organized in an adaptive way, often allowing for the adoption of new patterns.

Coordination Dynamics treats the problem of coordination between multiple effectors [10–13], between oneself and the environment [14,15] and even between different people performing movements while watching each other (e.g. [16–18], see [19] for a review) as a dynamic, pattern forming process [2]. Coordination is operationally defined by the spatiotemporal relationship between two or more coupled agents or components. Although in the paradigmatic bimanual case the components are the fingers or wrists of the two hands [2,10], components may be defined quite broadly to include a range of environment stimuli—from simple computerized displays or sounds [14,20] to the actions (and intentions) of another individual [16–18,21]. Such inherent flexibility represents a major advantage of the Coordination Dynamics approach, underscoring the applicability, and translation of simple experimental paradigms to the study of complex human actions across a broad range of contexts including athletics. Hence Coordination Dynamics has been employed to investigate and shed new light in many physical activities or sports such as the relation between respiration and locomotion [22], juggling [23,24], gymnastics [25], running [26], tennis [27], swimming [28], boxing [29] skiing [30], golf [31], and even riding horses [32] to name only a few.

Within the framework of Coordination Dynamics, coordination is defined in terms of collective or coordination variables that specify the spatiotemporal ordering between component parts. In principle, biological movement systems are high-dimensional, involving a large number of elements that can be measured and quantified in many different ways. Inspired by theories of self-organization in physics and chemistry [6,7], a key result in Coordination Dynamics is that in the vicinity of critical points, emergent behavior is governed by the low-dimensional dynamics of collective variables (e.g. [10,33]). This low-dimensional dynamics is revealed by manipulating one or more non-specific *control parameters* whose role is simply to move the system through a series of state changes. Adopting this strategy in the case of human behavioral coordination has identified relative phase between component subsystems as a crucial *collective or coordination variable* (or order parameter) and rate of coordination as a key control parameter [10,33]. In short, the quantitative change of the control parameter leads to qualitative changes of the order parameter. Thus, when rate is systematically increased, instabilities in coordination develop, and spontaneous switches between patterns of coordination ensue. It is these transitions and the features that surround them that have established the self-organizing nature of human brain and behavior [34,35].

For the present discussion, the key aspect of the essentially ‘non-linear paradigm’ of Coordination Dynamics is that it provides a convenient entry point for investigating the dynamics of pattern formation and change at both behavioral and brain levels. Systematic manipulation of the relevant control parameter, in this case movement rate, provides experimental control over key features of behavioral coordination and allows for direct investigation of the neural mechanisms underlying pattern formation, change, and improvement with learning and experience. Importantly, actions and the underlying brain dynamics can be quantified in terms of coordination and stability of coordination in contrast (or as a complement) to other commonly used performance measures such as reaction time and response accuracy. Moreover, the relative simplicity of the behavioral paradigm is easily implemented in imaging environments without the need for expensive or complicated recording devices and using only small flexion/extension movements that minimize motion related artifacts. Under the pro-

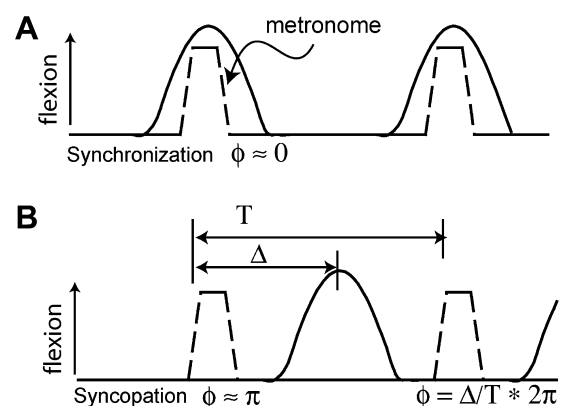
posal that coordination patterns are generated and maintained functionally independent of (or at least complementary to) the component parts recruited during movement (e.g. motor equivalence), the results from fMRI studies using simple finger coordination experiments may provide powerful insight into the neural mechanisms of the sport related selection, development, and maintenance of complex patterns of action.

### 3. Concepts and issues in experimental design and analysis

The key to the Coordination Dynamics approach is in mapping relevant coordination variables and control parameters onto brain function to uncover neural circuits of pattern formation and change. As such it is critical in designing experiments within this framework to understand experimental factors that can alter the behavioral pattern dynamics and associated neural dynamics. In what follows we provide a general overview of the key experimental paradigm and factors to consider when investigating the neural processes of coordination.

#### 3.1. The sensorimotor coordination paradigm

Coordination entails coupling between two or more individual components or agents that may themselves be of a variable nature. For illustration, however, we will consider a well-studied case of sensorimotor coordination [14], where temporal coupling is between a finger flexion/extension movement and a periodic stimulus. In the majority of cases discussed in the following sections the stimulus is an auditory signal, usually in the form of a short beep, however, visual presentations have also been employed [36]. The task requires participants to coordinate in one of two or more possible patterns. Although a repertoire of patterns are possible, particularly with learning and practice [37–42] two patterns tend to dominate (Fig. 1). *Synchronization* is defined by the temporal coincidence between peak finger flexion/extension and the environmental stimulus, whereas *syncopation* requires each action to be performed directly between consecutive beats. Very many skills are of this type: from skipping where one must synchronize one’s action with the periodicity of the rope, to dribbling a basketball, to dancing, to stepping onto an escalator, and so forth. In biology, numerous examples exist of external periodic stimuli entraining biological “pacemakers”—cells possessing a spontane-



**Fig. 1.** (A) Stylized depiction of a synchronized coordination pattern requiring temporal coincidence between peak finger flexion (solid line) and the auditory metronome (dotted line). (B) Syncopation requires the temporal placement of peak flexion directly between consecutive metronome pulses. The relative phase ( $\phi$ ) between metronome and movement is the temporal difference ( $\Delta$ ) between the signals divided by the inter-beep interval ( $T$ ). When expressed in degrees, ideal synchronization and syncopation have a relative phase of  $0^\circ$  and  $180^\circ$ , respectively.

ous rhythmic ability [14]. The Coordination Dynamics of these simple patterns has been revealed through systematic increases in metronome frequency (our control parameter) typically starting at 1 Hz and increasing to 3.5 Hz in steps of 0.25 Hz [14]. Instructions emphasize the importance of maintaining a 1:1 relationship between finger movement and metronome at all times, and if the pattern changes “not to intervene” or to intentionally restore the pattern (see also [43,44]).

A rich and reproducible set of behaviors flows from this paradigm as depicted in Fig. 2. At low metronome rates a strong tendency exists toward frequency- and phase-locking in both conditions. That is, both patterns are performed in a stable manner with relative phase between finger and metronome close to 0 (synchronization) or 180 (syncopation) degrees (see Section 3.2.2 for a description of relative phase). As the rate of the movement is parametrically increased, a spontaneous transition from syncopation to synchronization is observed at a *critical frequency* [14,45–47] marking the change from a bistable regime (where both patterns are possible and may be said to coexist) to a monostable one where synchronization predominates. In some cases further increases in rate induce a loss of entrainment between the finger and metronome resulting in phase wandering and various patterns of phase drift. Transitions between coordination patterns are typically preceded by an increase in the variability of the relative phase between sensory and motor events (Fig. 2B and C). Such fluctuation enhancement in the vicinity of transition points, referred to as *critical fluctuations*, indicates a characteristic loss of stability typical of non-equilibrium pattern forming systems in nature [6,48].

### 3.1.1. Translating paradigms to fMRI experiments

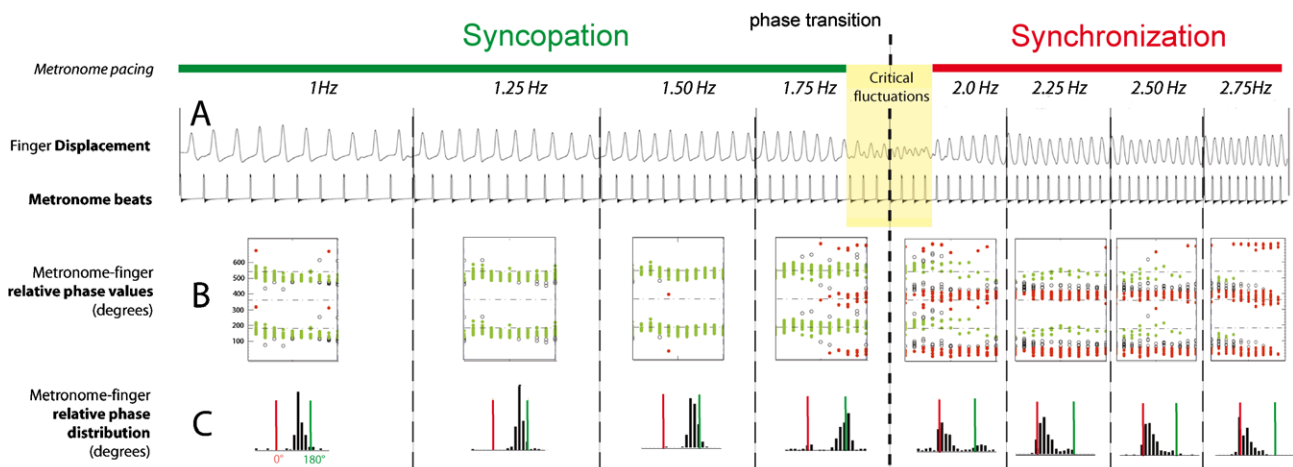
The advantage of Coordination Dynamics is that it allows for examination of the neural mechanisms of single coordination patterns or a set of patterns under controlled manipulation of stability. In turn the paradigm affords a portal into how stability changes with learning, experience, damage, and so on. The continuous movement or ramping paradigm has been successfully employed in both EEG and MEG studies to investigate the neurophysiological correlates of behavioral dynamics revealing shared behavioral and brain dynamics [49–54]. However, the tight temporal coupling between experimental conditions (rates) inher-

ent in ramping designs are problematic in fMRI experiments due to the poor temporal resolution of the instrument and the inherent low pass filter properties of the hemodynamic response [55]. Coordination and stability change too quickly under such conditions to accurately map these behavioral measures on the BOLD response. Hence, in order to investigate neural processes underlying coordinated behaviors using fMRI, movements may be performed in discrete blocks defined by a single coordination pattern and rate. A canonical block design is then fashioned by simply alternating coordination blocks with rest conditions. The foregoing approach has the advantage of allowing for a direct comparison between key coordination parameters such as rate, pattern type and stability with BOLD amplitude (e.g. [56–58]; see also [59,60] for reviews).

In contrast to conventional block paradigms, event-related designs are required for the investigation of the neural mechanisms of spontaneous and intentional pattern switching (see Section 4.3). Event-related designs allow for the post experiment definition of key moments of interest such as the appearance of critical fluctuations, loss of pattern stability, and the occurrence of switching between patterns [61]. The ability to classify events based on quantitative evaluation is critical given the subject and experiment dependent changes in coordination variables. Once identified, BOLD signal changes in response to, or prediction of such coordination events can then be evaluated using standard analyses [62]. Moreover, the long temporal interval between trials precludes efficiency issues related to the temporal proximity between events [63].

### 3.1.2. Critical frequency and stability

The critical frequency (coordination rate at which one observes spontaneous pattern switching) can be a useful dependent measure in studies of coordination and learning because it provides a probe of the underlying dynamics of the system and offers a means of quantifying experimental changes in those dynamics e.g. [64]. Due to its reliance on the underlying Coordination Dynamics, the critical frequency will vary as a function of parameters that influence the dynamics and therefore must be determined individually across participants and experimental contexts. For example, the critical frequency is sensitive to musculoskeletal factors and may vary substantially across participant and experimental setting



**Fig. 2.** Behavioral dynamics of non-linear phase transitions. In the paradigmatic sensorimotor coordination experiment participants start out performing the syncopated pattern (top green bar) by timing finger flexion/extension movements (A, top trace) with an auditory metronome (A, bottom trace). Metronome frequency is increased from 1 to 2.75 Hz with a 0.25 Hz increment every ten cycles. (B) Relative phase between the peak finger flexion and metronome onset computed on each movement cycle provides a measure of the coordination pattern which tends towards 180° (syncopation, green circles) and 0° (synchronization, red circles). (C) The distribution of relative phase across a plateau. The red vertical line indicates perfect synchronization and the green line indicates perfect syncopation. Panels (A–C) demonstrate a clear phase transition from syncopation to synchronization as the rate is increased from 1.75 to 2.0 Hz. The yellow area preceding the phase transitions highlights the presence of critical fluctuations characterized as an increase in phase variability. Adapted from [60].

depending on the limbs being coordinated [65–67], whether coordination involves flexion or extension [53,68], the relative position or spatial configuration of limbs being coordinated [69,70], different planes of motion [71], and the specific muscles being used [72]. Moreover, coordination stability and the critical frequency can be modified by the modality over which information is presented, the perceptual mapping of the responses [73] or the intention of the participant to either maintaining the pattern [74,75] or switching to a different pattern [43,44,76]. Pattern stability and the critical frequency can also be more permanently altered through experience and learning [38–40,42,69,77–79]. All these facts, taken together, underscore the potential importance of determining individual critical frequencies for specific paradigms and individual participants [38,44].

### 3.1.3. Appropriate frequency ranges

Selection of an appropriate experimental frequency range may be particularly important in cases where one is interested in the neural mechanisms of stability in relation to patterns of coordination, learning, practice and disease. In particular, the slowest rates should not slip below the range typically considered rhythmic [47] and at which prediction of upcoming stimuli is possible [45]. Rates of coordination below approximately 0.75–1.0 Hz are more likely to tap into neural mechanisms related to response selection and reaction rather than coordination and stability [45]. At high frequencies coordination may enter an unstable regime characterized by a range of possible behavioral outcomes including pattern switching, phase wrapping or phase wandering and the adoption of uninstructed temporal relationships such as 2:1 patterns [80]. Such unpredictability may confound the mapping between neural activity and performance features and thus, unless one is specifically interested in the neural correlates of this regime it is advantageous to maintain coordination at rates below approximately 4 Hz. Since the tasks are intended to probe stability and information processing demands, fatigue should also be minimized.

Behavioral studies have focused on the transition between bi- and monostable regimes as indicated by switches from syncopation to synchronization at a critical frequency. However, because the occurrence of spontaneous pattern switching introduces a potential confound in fMRI studies, coordination has often been maintained below the critical frequency. General guidelines suggest that syncopation becomes unstable at approximately 2 Hz in auditory motor coordination and a number of studies have respected this threshold [58,59]. But, in keeping with the overall message of this section, it is critical to be mindful of the fact that there are a large number of experimental factors that can alter the stability of coordination. Growing evidence supports the role for a coalition of constraints in guiding coordination and modulating pattern stability across a range of experimental contexts [21,67,71,73,81,82]. Such constraints may work both at the level of perceptual or environmental input [83], and at the level of the movement, for instance in the form of haptic feedback [68,81].

## 3.2. Analysis of coordination data

### 3.2.1. Collecting kinematic data

Special consideration must be given to devices for recording kinematics during coordination tasks in magnetically sensitive environments (e.g. fMRI, MEG). Several options are available each with unique advantages and disadvantages. The number of commercial and custom devices available for use in fMRI and MEG are too numerous to fully consider here. Instead we will describe commonly used options with focus on devices with which we have some experience.

It is likely that the most easily accessible device for recording the result of simple finger flexions is a button box that provides

a single digital pulse each time a key or button on a non-magnetic response pad is depressed. The button press may be taken as a measure of peak flexion and therefore be used to compute a point estimate of relative phase (see Section 3.2.2). Under such assumptions, computation of relative coordination requires information concerning the timing of the key press and the time of the corresponding external stimulus (or additional component being coordinated). Button boxes have the disadvantage that they do not provide a measure of the kinematics, only a measure of the point of contact with an external surface. Lack of full kinematics precludes inquiry based on position and velocity which both theory [84] and data [53] suggest is highly relevant. Moreover, haptic feedback provided by tapping the response pad can alter the dynamics of coordination, affecting stability, and switching time as well as the relative stability between patterns [68,81].

Examples of elaborate alternative devices designed by individual labs measure angular displacement by means of shaft encoders [85] or measure finger position by means of fiber optics [86]. In principle, such devices are perfectly acceptable and have the advantage of providing a continuous, time dependent signal of the entire movement cycle (i.e. kinematics). One caveat is that such devices are often relatively large and are either fixed in position or worn by the participant in some way thereby limiting their application to a relatively small range and orientation of motion. Care must also be taken to ensure that such devices do not interfere with the movement they are meant to measure by providing additional sources of information through haptic or other feedback or by restricting the degree of movement (e.g. unintentionally restricting degrees of freedom). Moreover, the cost of developing, building (or purchasing) and maintaining elaborate non-magnetic devices may be prohibitive for some labs.

A simple and low cost alternative that we have adopted is to quantify finger position as pressure changes in a small, non-magnetic air pillow (e.g. [53,56,87]). Air filled blood pressure bladders are connected to a transducer via several meters of plastic tubing. Movement induced changes in pressure in the bladder are converted to an analogue signal by a pressure transducer located outside of the MRI or MEG suite. The resulting signal, depicted in Fig. 3, is then digitized (together with the relevant stimulus and time locking signals from the magnet) and stored on disk. The device has no moving parts and, because the cuffs are plastic, it is completely non-magnetic. Moreover, the pillows are light, small, and flexible and therefore do not interfere with the movement while allowing for a range of postures and applications.

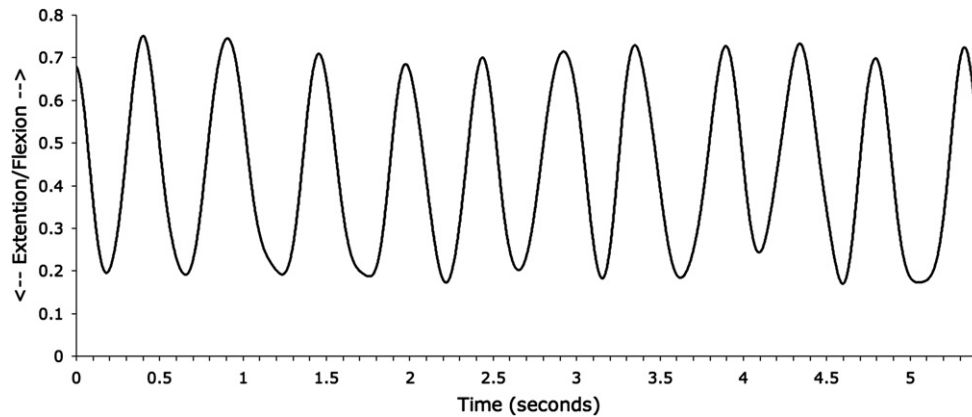
### 3.2.2. Computing coordination variables

Earlier we introduced the relative phase between interacting components as a key order parameter [10,33] or coordination variable [2] that characterizes the system's collective behavior. Relative phase qualifies because under parametric manipulation of a non-specific control parameter such as rate, measures of relative phase stability (variability, relaxation times following small perturbations, switching times, etc.) index behavioral pattern formation and anticipate spontaneous switching between patterns [2,8,34,35,88]. For example, in the bimanual case, the relative phase represents both the position and velocity of the end effector thereby capturing four degrees of freedom in a single quantity. A point estimate of the relative phase ( $\Phi$ ) is calculated according to the following:

$$\Phi = \Delta / T 2\pi \quad (1)$$

where  $\Delta$  is the time difference between maximum flexion of the moving finger (limb) and the preceding stimulus (see Fig. 1B) and  $T$  is the time distance between the onset of successive stimuli. As discussed previously and illustrated in Fig. 1, perfect coordination results in  $\Phi = 0^\circ$  for synchronization and  $\Phi = 180^\circ$  for syncopation.





**Fig. 3.** Illustration of a finger flexion/extension movement recorded as pressure changes in a small air filled bladder. The trace shows several seconds of a movement performed at approximately 2 Hz. An upward deflection in the trace indicates index finger flexion. The movement signal was recorded at 500 Hz and low passed filtered below 5 Hz. The non-magnetic bladder offers a convenient and cost effective means of recording movement kinematics from inside the MR scanner.

A similar calculation has been used to compute the relative phase between components across a number of contexts including bimanual skill learning [38], coordination between wrist displacement and grip aperture [89], coordination to an external event [14,20,68], inter- and intra-limb coordination [10,12,26,40,71,90] as well as interpersonal coordination e.g. [16,17,21,91–95]. This simple formula thus provides a useful metric for investigating the spatiotemporal relationship between coordinated structures across a range of contexts and tasks.

The average coordination performance is represented simply as the circular mean relative phase for a given pattern across a block of trials at constant frequency. Stability of the coordination pattern is represented by the variability in performance over the block as given by the circular deviation of the relative phase. Because of the circular nature of the phase measure  $\Phi$ , mean ( $M\Phi$ ), and standard deviation ( $SD\Phi$ ) must be computed using circular statistics [96–98] as follows:

$$M\phi = a \tan(X, Y) \quad (2)$$

$$SD\phi = \sqrt{2(1 - \sqrt{X^2 + Y^2})} \quad (3)$$

where

$$X = \left( \frac{1}{n} \sum_{j=1}^n \sin \phi_j \right) \text{ and } Y = \left( \frac{1}{n} \sum_{j=1}^n \cos \phi_j \right)$$

It is worth noting that relative phase can also be computed in a continuous fashion ([48]; see also [39] for a comparison of continuous and point estimate methods on the same dataset). For example, quantitative evaluation of relative coordination can also be investigated in the frequency domain, provided by the FFT Power Spectrum Overlap (PSO) between the movements of limbs [99]. PSO measures the percentage of movement frequencies common to both partners in a pair. Defined as the area of intersection between each participant's normalized spectral plots, the PSO is an indicator of the strength of the frequency entrainment between elements to be coordinated including between two individuals [17,99].

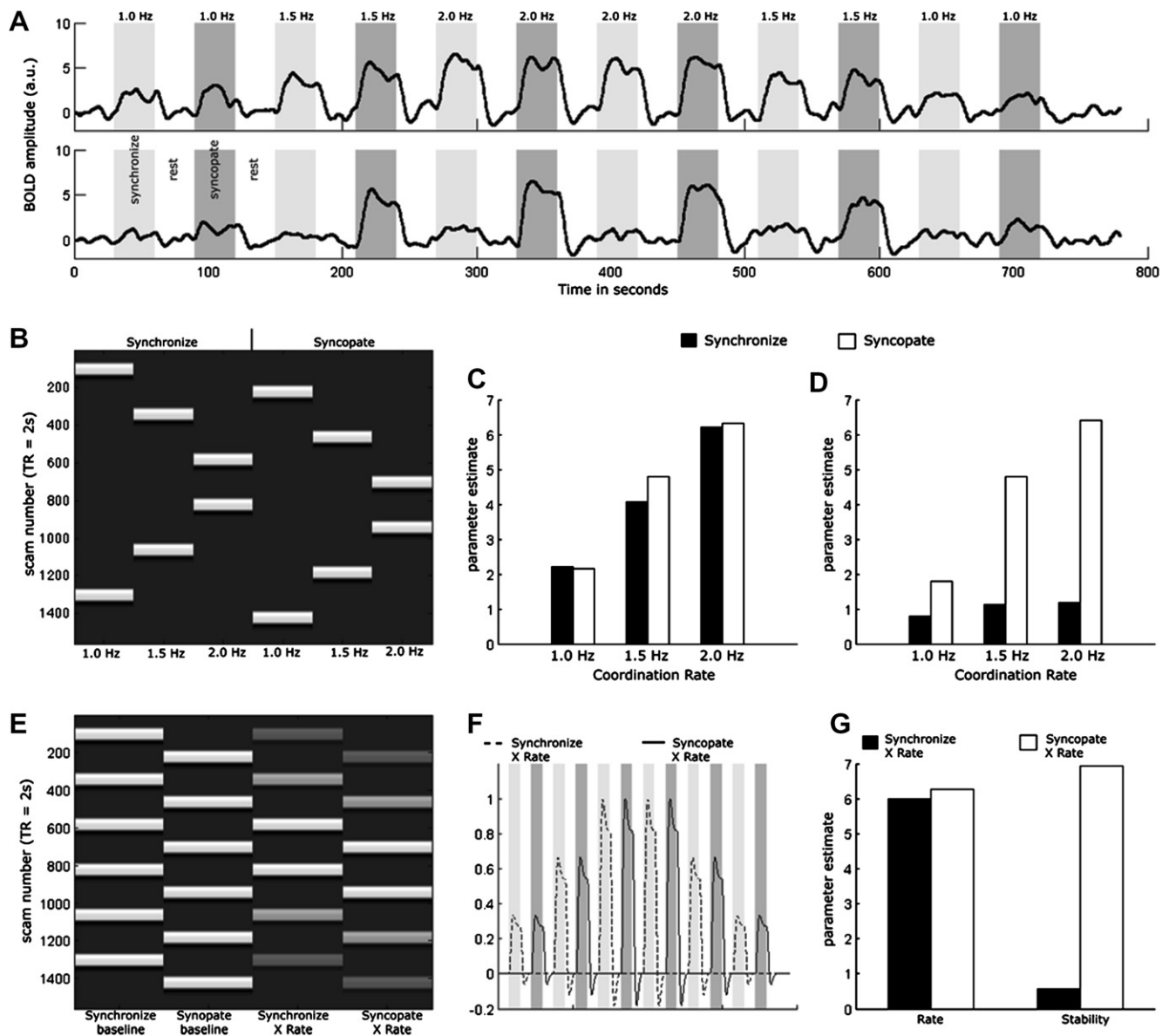
### 3.3. Analysis of neuroimaging data

In most cases, analysis of fMRI data can be performed using accepted linear models [100] and standard software packages. Introduction to fMRI analysis is also available in a number of recent texts which are highly accessible [55,101,102]. Hence the topic will not be considered further here. Instead, attention will be given to a specific parametric mapping approach adopted for detection of

predicted relationships between BOLD intensity and behavioral stability. The approach, introduced by Büchel and colleagues [103], uses a general linear model to reveal the (non)-linear relationship between stimulus or behavioral parameters and BOLD activity. In coordination experiments such an approach allows for the detection of brain areas that: (1) show a linear relationship between stimulus rate and BOLD intensity; and (2) show an interaction indicating brain areas where BOLD intensity increases with decreasing stability. The latter is critical for identifying brain circuits underlying pattern formation, persistence, and change.

Key elements of the analysis are illustrated in Fig. 4 showing data from a simulated block design coordination experiment requiring synchronization and syncopation at one of three demonstration rates (1.0, 1.5, and 2.0 Hz). The presentation of the experimental conditions together with two resultant time series is shown in Fig. 4A. The upper trace is from a voxel in which BOLD amplitude increases with increasing rate for both coordination patterns; that is, this voxel is rate dependent. The voxel depicted in the lower trace is sensitive to pattern stability because BOLD amplitude increases during syncopation, as stability decreases, but not during the synchronization pattern when stability is unaffected by rate. The relationship of the two time series to the experimental and theoretical parameters is shown in Fig. 4B and D. Parameter estimates are derived by a linear fitting of the covariates, shown in the design matrix at left (B), to each time series. Fitting the model to the rate dependent time series gives the parameter estimates plotted in Fig. 4C. The relationship between BOLD and rate is revealed by the systematic increase in the parameter estimate as rate increases for both synchronization (black bars) and syncopation (white bars). Fitting the same model to the stability-dependent time series yields parameter estimates (Fig. 4D) that mirror observed patterns of behavioral stability [14,59,60]. The patterns of BOLD activity depicted in Fig. 4C and D have been observed recently in the literature and taken as evidence that primary sensory and motor areas are sensitive to rate changes, whereas BOLD amplitude in premotor areas and cerebellum are sensitive to pattern stability [58,59].

Identifying specific brain areas that demonstrate the theoretically predicted relationship between rate and stability can be achieved by modeling BOLD activity directly as a function of rate (Fig. 4E–G). To create the covariates of interest one multiplies a time series modeling the presence or absence of movements on each block by the corresponding rate of coordination for that block. Applying this approach separately to synchronization (dotted line) and syncopation (solid line) conditions yields the two covariates plotted in Fig. 4F. Each covariate models a rate by movement



**Fig. 4.** A sample linear analysis illustrating approaches for determining the relationship between coordination parameters and BOLD amplitude is shown. The two virtual time series in (A) exemplify that BOLD amplitude in different brain regions may vary as a function of movement rate ((A) upper trace) or as a function of pattern stability ((A) lower trace). Each task block (gray region) is defined by a coordination pattern (synchronize or syncopate) performed at a specific rate (1.0, 1.5 or 2.0 Hz). Fitting the data with a design matrix in which each experimental condition is modeled as a single covariate (B) yields a set of parameter estimates that qualitatively identify both rate (C) and stability (D) dependent activity. In (C), BOLD amplitude increases with increasing rate for both coordination patterns. In (D), BOLD activity follows pattern stability, which decreases during syncopation and not synchronization. Quantitative assessment of the predicted relationships can be assessed by modeling the BOLD response as a function of rate for each coordination pattern (E and F). The design matrix in (E) includes baseline covariates (left two columns) to account for main effects of movement for each pattern and covariates to model the movement by rate interaction (right two columns). A movement by rate interaction was modeled separately for each coordination pattern by multiplying the modeled hemodynamic response on each block by the corresponding coordination rate (F). Shown in (G) are parameter estimates that indicate both rate dependence (G, left) and stability dependence (G, right). See text for more detail.

interaction, the presence of which is indicated in our example by the amplitude of the associated parameter estimate. The resulting design matrix, including requisite baseline models to account for the main effect of movement [103], is shown in Fig. 4E and the parameter estimates obtained from fitting this model to the simulated data are given in Fig. 4G. The parameter estimates for the fit to the first voxel reveal the expected rate  $\times$  movement interaction for both synchronization and syncopation (left two bars in Fig. 4G). The parameter estimates for the fit to the second, stability-dependent voxel accurately reveal that BOLD increases with rate occur only during syncopation and not synchronization indicating a specific rate  $\times$  movement  $\times$  pattern interaction (*cf.* Fig. 4D). When applied to Coordination Dynamics paradigms, the approach outlined

here and provided in detail elsewhere [103] provides a means to describe theoretically predicted patterns of BOLD activity across a large number of conditions using only one or two parameter estimates and the contrast between them.

#### 4. Key neuroimaging findings with relevance to sports

##### 4.1. Stability-dependent cortical circuitry

Recent studies investigating the relationship between large-scale measures of brain function and coordination using PET, TMS [58], and fMRI [59,85] have uncovered the neural circuitry associated with the stability of temporally evolving patterns of

coordination. Meyer-Lindenberg and colleagues [58] measured cerebral blood flow from participants performing in-phase and anti-phase bimanual movements at four movement rates (1.0, 1.5, 1.7, and 2.0 Hz) below the critical frequency. In a similar and complementary investigation, Jantzen and Kelso [59] investigated the mapping between BOLD amplitude, movement frequency and stability of unimanual sensorimotor coordination patterns. In this latter example, participants coordinated right hand finger flexion with an auditory metronome in either a synchronized or syncopated pattern at five different movement rates (0.75, 1.0, 1.25, 1.50, and 1.75 Hz), all below the critical frequency at which spontaneous transitions from syncopation to synchronization are known to occur.

Taken together, results of these two studies provide neurophysiological evidence for the existence of two separate but interacting brain networks underlying basic patterns of coordination. In both experiments moving at increasingly higher rates resulted in a significant reduction in stability only for anti-phase (syncopated) movements, a finding compatible with well-known studies of coordination and theoretical predictions thereof. Measures of neural function revealed greater activity concomitant with increasing instability in bilateral dorsal premotor cortex, SMA, and cingulate as well as the left frontal operculum (insula), and ipsilateral cerebellum (see example in Fig. 4A). In contrast, activity in contralateral sensorimotor cortex and primary auditory cortex demonstrated a linear increase in activity for both patterns, a finding consistent with a modality dependent processing role associated primarily with the elementary sensory and motor demands of the task [59].

The parametric approach of the Coordination Dynamics paradigm thus allows for the differentiation between brain networks related to (a) dynamic features of coordination that represent the global organization of the behavioral pattern, in particular its stability properties and (b) those related to more elementary modality dependent sensory and motor features. Overall the foregoing results demonstrate how activity across a network that minimally includes SMA, lateral premotor cortex, and cerebellum is linked to the degree of behavioral stability. Moreover, TMS studies have demonstrated that depending on how close the brain is to an instability, disruption of this network may result in the destabilization, and eventual dismantling of a less stable pattern in favor of a more stable one [58,104,105].

#### 4.2. Switching and selection between patterns of coordination

Behavioral coordination requires complementary neural mechanisms to both maintain complex behavioral patterns as they become unstable and to intentionally switch between patterns in order to meet changing demands. Efficient selection and switching between behavioral patterns are of critical importance in athletics where performance depends on rapid transitions in response to the demands of play such as the actions of an opponent and so forth. Switching between patterns of coordination may occur spontaneously as stability of one pattern gives way to another as experimental or task related demands vary [2]. The spontaneous transition from running to walking is one such example [26]. Much less investigated, however, are interactions between the purposeful intention to adopt a specific coordination pattern or switch between patterns and the underlying intrinsic dynamics. The term “intrinsic dynamics” expresses the fact that the system (which may include the brain)—prior to any specific input—already possesses a repertoire of behavioral patterns that are unique to each individual [2,10].

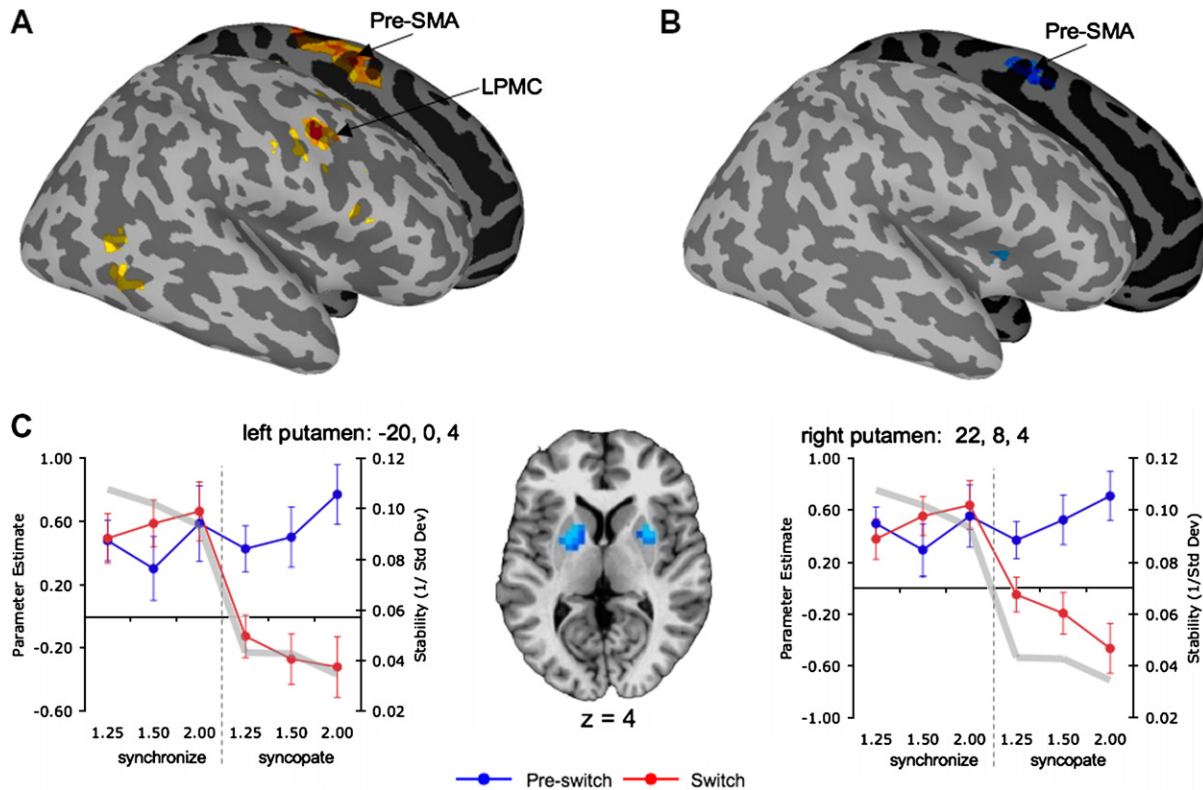
Behaviorally, intention acts to parameterize the intrinsic dynamics by destabilizing an ongoing pattern and stabilizing a target pattern [43,44,74,75]. In addition, intention may act as a ‘forc-

ing’ on the dynamics that stabilizes an intrinsically unstable pattern that under the current circumstances, e.g. high movement rate, is prone to switch ([2], Chapter 5). Measurement of switching time reveals that intention both acts upon and is constrained by the intrinsic dynamics of coordination [43,44]. Initial work investigating neural changes associated with spontaneous transitions between bimanual coordination patterns adopted an event-related approach in which events in the fMRI signal are defined by the occurrence of transitions in the behavioral response [61]. This approach revealed that switching between patterns was associated with activity in prefrontal, premotor, and parietal regions [61]. The general network reported by Aramaki and colleagues is compatible with the stability-dependent circuits described here and elsewhere [59]. The increased activity reported in specific brain regions may reflect the loss of pattern stability that precedes spontaneous pattern switching.

Preliminary event-related fMRI work is underway using a bimanual coordination paradigm to explore the neural basis of the interaction between pattern stability and intentional switching (Fig. 5). BOLD activity was recorded while participants coordinated flexion/extension movements between left and right index fingers in either an in-phase or anti-phase pattern at three different pacing frequencies (1.52, 2.0, and 2.5 Hz). In keeping with our general experimental approach, increasing coordination rate destabilized the anti-phase but not the in-phase pattern, thereby providing experimental control of the relative stability of the pre and post switch patterns. On each trial participants received an auditory signal to switch between patterns. Switches were either from anti-phase (less stable) to in-phase (more stable) or vice versa. In agreement with existing behavioral findings and dynamical theory [43,44], switching time was shorter when moving from the less (anti-phase) to the more stable (in-phase) pattern and decreased in duration with rate dependent decreases in pattern stability [88]. During switching, BOLD activity in Basal Ganglia (BG), pre-SMA, precentral gyrus and prefrontal cortex, was inversely related to the stability of the initial pattern (Fig. 5B and C). That is, BOLD activity was greater when switching from a more stable to a less stable pattern. Stability-dependent activity in BG was present only during the switch, implicating this region in the intentional process of switching among patterns. Support for this hypothesis comes from previous findings that BG plays a role in the selection of desired actions and in the inhibition of competing ones [106]. Importantly, the pattern of BG activity suggests that the selection/inhibition process is modulated by the relative stability of the behavioral patterns such that BG may act to parameterize the intrinsic Coordination Dynamics.

#### 4.3. Learning and practice-related changes in coordination and brain activity

A key issue for the application of neuroimaging in sports and exercise is to understand how different forms of practice and training can improve performance and how such enhancement is manifested at the neural level. The dynamic systems approach to skill learning aims at identifying key principles of adaptive change that apply to an entire coordination landscape, not just a single behavior [38]. A major tenant of the Coordination Dynamics approach to learning is that the to-be-learned pattern emerges as a modification of existing intrinsic dynamics. That is, the route to learning will depend on the degree of competition or compatibility between the new pattern and preexisting coordination preferences and tendencies [40]. Thus, two key features of learning demonstrated experimentally using simple coordination paradigms are that (1) learning progress and strategy depend on the relationship between to-be-learned patterns and existing coordination tendencies and (2) learning a new pattern can alter the entire coordination



**Fig. 5.** A bimanual coordination paradigm was used to explore the neural basis of the interaction between pattern stability and intentional switching. BOLD activity was recorded while participants coordinated movements between left and right index fingers in either an in-phase or anti-phase pattern at three different pacing frequencies (1.52, 2.0, and 2.5 Hz). On each trial, participants were signaled to intentionally switch between patterns. Switches were either from anti-phase (less stable) to in-phase (more stable) or vice versa. Areas demonstrating a pre-switch relationship between BOLD activity and pattern stability are colored in (A). In both the rostral supplementary motor area (pre-SMA) and lateral premotor cortex (IPMC) BOLD amplitude increased linearly with decreasing pattern stability. The relationship between BOLD amplitude and stability during intentional switching is shown in (B and C). During intentional switching, BOLD amplitude in both the pre-SMA (B) and bilateral putamen (C) (shown in blue) was greater when switching from a stable compared to unstable pattern. This relationship is observed in the line graphs (C) plotting the BOLD amplitude in Basal ganglia for each condition (plots in C). Pre-switch BOLD activity is shown in blue and switching activity in red. The stability of the preceding pattern (indexed as the inverse of the circular deviation of the relative phase) is shown in gray. Results provide a clear demonstration of how the role of the basal ganglia in pattern selection and switching (red) is parameterized by the stability of the preceding pattern.

repertoire by reshaping the landscape of the dynamics [38,39,42]. Therefore, when considering learning within the Coordination Dynamics framework, it is critical to account for individual differences in initial ability and to consider how the learning of a new pattern may interact with other existing coordination patterns.

The basic paradigm uses a scanning technique to establish the intrinsic dynamics of each participant (e.g. [38–40,64,79]) prior to learning of a new behavioral pattern. During and following learning the full repertoire of coordinative patterns can be probed to quantify both progress in learning and how practice modifies the entire dynamical landscape [40,79]. Using approaches outlined by the present framework, researchers have investigated behavioral and neural mechanisms of learning [38,39], transfer [40], and the interplay between learning and attention [79]. The latter may be of particular importance in sports because it provides a means to quantify the process of automatization of well-learned behaviors that is an oft-stated goal in athletics.

A growing number of studies have begun to investigate the neural consequences of coordination practice and performance improvement. One MEG investigation reported neural changes associated with training the intrinsically unstable syncopation pattern by having participants practice at their individual critical frequency [64]. Practice with feedback resulted in improved performance as indicated by a shift to a higher critical frequency in all subjects. Pre-training differences in neural oscillatory activity between synchronization and syncopation were reduced following

learning such that similar neural dynamics was associated with both patterns. Moreover, although training was restricted to the critical frequency, learning related changes in neural activity were observed at all movement rates below the critical frequency attesting to the generalizability of learning. Complementary behavioral findings suggest a similar outcome for transfer across effectors [40], but appropriate imaging experiments have not yet appeared.

Learning to perform a novel coordination pattern such as a 90° relation between wrist flexion movements results in performance related activity decreases across several premotor cortex regions [41]. Similar decreases in secondary motor areas have been reported in piano players relative to controls during a motor sequence learning task [107]. Areas demonstrating learning dependent activity decreases included lateral premotor cortex and the SMA, both of which are sensitive to coordination stability [59]. By extension, such findings suggest that coordination learning acts across stability-dependent cortical circuits to stabilize patterns of behavior. The complex interplay between context, practice and coordination is further demonstrated in an fMRI study of syncopation practice [57]. Participants who simply practiced a syncopated pattern in the absence of explicit error feedback showed a decrease in the syncopation related BOLD response in superior temporal gyrus and cerebellum. A paradoxical increase in BOLD activity was found during post practice synchronization in SMA, inferior frontal gyrus and superior temporal gyrus. Despite lack of changes in behavioral performance, such results hint at how learning can alter the neural



activity related to a larger repertoire of coordinated behaviors than the one explicitly practiced or learned.

Potential follow up questions in the area of learning are (1) how large-scale cortical function reflects increased stability achieved through practice and (2) how changes in neural activity reflect the cooperative and competitive mechanisms that underlie the relationship between the patterns being learned and preexisting intrinsic dynamics. Learning studies within the Coordination Dynamics framework could ultimately aid in establishing individualized training approaches that maximize performance increases by selecting optimal routes to learning that may include action observation and imagination. For instance, Calvo-Merino and colleagues analyzed brain activity of experts in classical ballet, experts in capoeira, and non-dancers who viewed videos of ballet or capoeira actions [108]. A strong influence of motor expertise on action observation was found when comparing the brain activity of dancers watching their own dance style compared to another style. Such results underscore the sometimes underappreciated intimacy between perception and performance, particularly as it relates to athletics.

#### 4.4. Imagery and coordination

Motor imagery, or the mental practicing of motor actions in the absence of overt performance [109,110] is another strategy for learning new patterns of coordination. The neural processes underlying imagination of a given motor task are generally similar to the ones required to physically execute it [111–113]. For instance, during motor imagery the processing of relevant stimulus parameters and the constraints that they impose, including timing, are similar to that observed during execution [110,113–118]. By decoupling the sensory aspects of the coordination task from motoric constraints the processing demands at two levels (sensory input and sensory motor integration) can be investigated while a third (motor execution) is removed. Thus the relative contribution of certain brain areas to some of these levels can be identified. In a motor imagery version of the classic sensorimotor coordination paradigm Oullier and colleagues [87] compared brain activity of two coordination patterns (synchronization and syncopation) to their covert equivalent. It was also possible for the first time to compare the neural underpinnings of the two imagined tasks. Results revealed that the typical differences found when comparing brain activity underlying executed synchronization and syncopation [56,57,119] persisted for the imagined coordination patterns [87]. Such results suggest that the neural indices (demands on timing and motor preparation) of tasks of inherently different stability persist in the absence of movement [87]. The foregoing findings also extend recent ones that have revealed context-independent neural signatures of behavioral instability after contrasting brain activity when performing various unstable compared to stable rhythmic coordination patterns (uni-, bimanual, and interlimb coordination; [59,60]). All the foregoing findings support the notion of stability-dependent neural circuitry, i.e. brain regions that are specifically sensitive to pattern stability independent of the components being coordinated and the physical execution of movement.

Motor imagery (or mental practice) is widely used in the context of rehabilitation and sports training. Future research may focus on how imagery of coordination patterns can stabilize previously unstable patterns and whether similar generalization and broad modulation of cerebral patterns is capable of inducing significant changes in overt performance. As mentioned earlier, the fact that similar constraints, especially movement sequence and timing, persist at a neural level in the absence of movement, makes motor imagery an interesting training tool that may enhance motor preparation and planning. In a study of golf imagery, Ross and colleagues [120] found that brain activation decreased

with increased golf skill level, particularly in supplementary motor area (SMA), and cerebellum. A recent study suggests that, in addition to its major role in motor preparation the SMA also plays a part in suppressing movements that are possible but not performed [121]. Such is often the case in motor imagery. More and more evidence points to a minimal activation of M1 in imagined compared to executed coordination [87]. However, in the context of imagined locomotion, recent findings suggest that training is associated with an expansion of active bilateral motor areas [122]. This finding, together with a reduction of visuospatial activation in right occipital regions, suggests a decreased role for visual imagery in the post-training period in favor of a motor-kinesthetic one [122]. Such evidence is complemented by the research of Fourkas and colleagues [123] who used TMS to show that muscles of expert tennis players exhibit enhanced corticospinal excitability during motor imagery of tennis but not golf or table tennis. Interestingly, no such modulation was found across sports for a group of non-expert tennis players who nevertheless practiced sports on a regular basis. Expertise appears to play an important role in modulating sensorimotor representations during mental practice of a given sport [123]: The higher the level of expertise, the more efficient the mental practice.

#### 4.5. Sport related brain injury, rehabilitation, and retraining

According to Coordination Dynamics, maladaptive patterns of behavior can interfere with the learning of new, more adaptive behaviors. Such maladaptive patterns may emerge from the formation of bad habits or develop in conjunction with compensatory or adaptive strategies for overcoming injuries. Embodied therapeutic approaches such as the Feldenkrais method [124] believe that directed attention to existing behavioral patterns can improve the ability to adopt new and more adaptive behaviors. That is, emphasis is placed on sensitivity to the coordination structure as opposed to the behavioral goals [124]. This approach has been used to achieve improved behavioral function in a patient 9 months after suffering a left middle cerebral artery stroke; a time after which traditional approaches provided no further improvement [112]. Simple unimanual and bimanual coordination paradigms—both actual and imagined—were used to reveal concomitant large-scale reorganization of cortical activity. Three scanning sessions performed over a 3-month period revealed an increase in activity of affected M1 and a simultaneous decrease in activation of premotor (SMA and PMC) and parietal regions. Such reorganization is indicative of the formation of flexible, stable coordination patterns [57,59] and demonstrates how Coordination Dynamics compatible learning and retraining paradigms may induce neural plasticity in support of behavioral rehabilitation. The occurrence of cortical plasticity is emphasized by the observation that similar adaptive changes in neural activity are observed even when the patient only imagines coordinating [112].

Sport related mild brain injury, or concussion, is of serious concern in athletics, and has attracted recent interest across a range of sports including football, soccer, baseball, hockey, and others. A critical goal in concussion research is the development of approaches to adequately quantify and assess the neural consequences of concussion and the progress of recovery. Neural indices of cognitive and motor dysfunction associated with concussion may eventually provide empirical data on which to base return to play decisions. Because functional magnetic resonance imaging (fMRI) provides task specific information about neural function, it is well suited to detect functional abnormalities associated with concussion and can be tailored to address the specific and most prevalent complaints of patients. In addition, BOLD measures are sensitive to deficits that may be related to dynamic aspects of neural function that are evident only under conditions of

cognitive load or information processing [125,126]. Functional MRI has an added advantage over other brain imaging techniques such as PET and SPECT since multiple sessions can be performed on a single subject within very short periods of time. This promotes the implementation of *prospective* neurophysiological investigations in which pre-injury baseline measures of neural function are obtained for each participant in anticipation of future deleterious events such as brain injury. Prospective approaches to the study of concussion have proven to be an essential approach in recent neuropsychological investigations [127–129] but have yet to be applied in neurophysiological settings. On the other hand, a prospective approach to brain injury receives great impetus from research on the Coordination Dynamics of learning ([2], Chapter 6, Section 4.4). That work demonstrated that each individual enters a new learning situation with his or her own predispositions and preferences (“intrinsic dynamics”) and that the relationship between new information (e.g. a task to be learned) and intrinsic factors determines the nature and rate of learning. Every brain shares similarities, but each brain is different. Grouping individuals together without attention to such ‘baseline differences’ hides the basic dynamics of the learning process, and by extension, how an individual brain recovers following injury.

The detection of between-session differences within a single subject is novel in functional neuroimaging and may prove a powerful advance in the assessment and monitoring of concussion for four primary reasons. First, a within subject approach allows each player to act as their own control thereby removing (or at least complementing) the need for large normative databases. Second, it may prove more sensitive to pathological changes within an individual that may be small relative to the typically large between subject variability observed when combining physiological data from larger subpopulations [130–132]. Such concussion related changes in neural activity, while apparent within an individual, would therefore go undetected when compared to so-called normal subjects. Third, in agreement with our overall individualized approach, no assumption is made about what constitutes a normal pattern of neural activity and whether a single subject’s individual brain responses deviate from normal. The pattern of neural activity for each individual is likely to reflect personal history and intrinsic capacity. Neural consequences of concussion will interact with this baseline state and thereby should be assessed within an individual. Finally, the pattern of recovery of function is likely to be highly individualized and as such is only adequately quantified with respect to each individual and their own preexisting pattern of neural activity.

Initial research adopting a within participant approach has been successful in identifying specific, within subject, neural signatures of mild head injury in athletes within one week following impact [133]. Both concussed athletes and control players performed a sensorimotor coordination paradigm similar to that employed for the investigation of stroke recovery [112]. Compared to their own baseline control data, concussed players showed significant alterations in functional activity across specific cortical regions including premotor and parietal cortices. Sensitivity of a within participant approach may be enhanced by adopting parametric coordination paradigms as discussed here and parametric cognitive paradigms to assess dysfunction in memory. Recent unpublished work from our lab demonstrates that such paradigms provide a dramatic decrease in variability across session, thereby increasing sensitivity to neural changes associated with brain injury and recovery of function.

## 5. Conclusions and future directions

Throughout this review we have tried to pinpoint exciting research possibilities for elaborating the role of neuroimaging in

sports, ranging from understanding the neural mechanisms of skill learning to recovery of function following brain injury. From the perspective of brain Coordination Dynamics, it is now recognized that complex cognition and action arise from cortical interaction between discrete and specialized neural regions. The dual tendency between long-range integration across multiple cortical sites and the neural segregation implied by local specialization of basic cognitive functions provides new challenges to understanding the brain. The theory of Coordination Dynamics has proposed metastability as a new principle of behavioral and brain function [2,134–136]. Metastable coordination, which expresses the joint tendency for the diverse regions of the brain to function autonomously at the same time as to coordinate together, allows for flexible switching in the brain on a time scale compatible with action and cognition. Although the neural pattern generating circuits associated with patterns of coordination and their involvement in attention, intention, learning, and recovery from brain damage are the subject of much investigation, the rich dynamics of the neural architecture is just beginning to be explored. Uncovering the Coordination Dynamics of brain and behavior on the same time scale requires true multidisciplinary approaches and the integration of multiple imaging modalities—in addition to theoretical modeling studies at both brain and behavioral levels.

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