Two hands, one brain: cognitive neuroscience of bimanual skill

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Bimanual coordination, a prototype of a complex motor skill, has recently become the subject of intensive investigation. Whereas past research focused mainly on the identification of the elementary coordination constraints that limit performance, the focus is now shifting towards overcoming these coordination constraints by means of task symbolization or perceptual transformation rules that promote the integration of the task components into a meaningful 'gestalt'. The study of these cognitive penetrations into action will narrow the brain–mind gap and will facilitate the development of a cognitive neuroscience perspective on bimanual movement control.

The majority of everyday movements require some degree of collaboration between the hands. With the evolution towards upright standing in higher primates including humans, the hands have developed into a highly sophisticated system that is used for manipulative activities such as tool use, preparing and eating food, and making gestures. As a result of cultural pressure, the complexity of the human bimanual skills has increased tremendously. Bimanual movements are highly adaptive and context-dependent. Some tasks require bilaterally isomorphic actions such as pulling or pushing a large box, or alternating arm movements supporting locomotion. Other tasks require a more differentiated role for each hand, such as sewing, opening a bottle, driving a car, playing musical instruments, etc. These examples suggest that the control of bimanual movements has a high degree of modularity. Goal invariance is preserved by flexible covariation of the individual limb movements [1,2].

Even though bimanual movements are more abundant than unimanual skills, they have been studied less intensively. However, since the seminal work of Kelso and co-workers [3], bimanual movement control has gained increasing research attention for several reasons. First, complex bimanual skills are favorite examples for the study of higher cognitive functions. Second, they represent a special case of multitasking, informing us about how the central nervous system (CNS) orchestrates the organization of multiple command streams. Third, bimanual tasks are rewarding tools to reveal motor dysfunctions in general and processes of lateralization and asymmetry in particular, following neurodegenerative diseases and other brain pathologies [4].

The present review will explore this adaptive bimanual control system in which the movements of each limb can be combined in various ways to accomplish various goal-directed behaviours. We will first discuss two principal theoretical frameworks that have dominated thinking over the past years, followed by an attempt to categorize coordination constraints. Then, we will address the overruling of coordination constraints through cognitive intervention. Finally, recent progress in establishing the neural network underlying 'bimanual coordination effort' will be discussed.

Theoretical frameworks for the study of bimanual control

Two theoretical frameworks have dominated the scientific exploration of bimanual control: the information-processing and dynamic pattern perspective. Within the information-processing perspective, bimanual movement is considered a special case of dual-task performance that is faced with structural interference as a result of limitations in neural resources [5–9]. The concept of neural crosstalk (NC) assumes that neural leakage can occur during bimanual motor programming and execution as well as at different levels of the central nervous system, from cortical to spinal. Here, the focus has been on studying limitations in performance when the task assigned to each limb differs with respect to one or more parameters, such as timing, amplitude, force, direction etc [5–9]. Bimanual tasks can be performed successfully as long as the neural interference can be suppressed as a result of practice and/or by integration of both tasks into a meaningful global control structure. Motor learning requires overcoming neural interference as a prerequisite for differentiated patterns of action to emerge [10].

Within dynamic-pattern theory (DPT), biological systems are formally described in terms of their time-dependent changes. Such systems are composed of many subcomponents that organize themselves into coherent global patterns, such as the swirling behaviour of a school of fish. Order is not prescribed by a superior command structure but emerges in a self-organized fashion as a consequence of cooperation among the subcomponents [11–15]. Similarly, motor coordination emerges as orderly behaviour in a system with many degrees of freedom at multiple levels. This approach emphasizes a physical

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account of coordination whereby two paradigms have been explored extensively: bimanual finger coordination [12,13] and pendulum swinging by the hands [15]. The system's macroscopic state or emerging coordination pattern is described by an order parameter, for example, relative phase (ϕ) or the difference in phase angle between effectors. Two patterns have been studied extensively: the in-phase mode ($\phi = 0^\circ$), requiring the synchronized activation of homologous muscle groups, and the anti-phase pattern ($\phi = 180^\circ$), resulting from the simultaneous activation of non-homologous muscle groups. At low cycling frequencies, both patterns can be produced with high stability and constitute attractive states. However, the anti-phase pattern becomes increasingly destabilized at higher frequencies, resulting in a transition to the more stable in-phase mode (a phase transition). A mathematical description of this attractor landscape, or so-called coordination dynamics as a function of cycling frequency as critical control parameter, has been provided by the Haken, Kelso, Bunz (HKB) model [16]. This model is a landmark in the study of coordination dynamics (for an overview, see [12,14]). In addition, behavioural and cortical dynamics have recently been linked with each other [17]. Within DPT, learning is regarded as a dynamic process whereby new patterns emerge through behavioural information. This corresponds to the stabilization of a novel attractive state (e.g. $\phi = 90^\circ$) by deformation of the initial potential landscape ($\phi = 0^\circ$ and 180°) through practice [18]. Even though the NC and DPT frameworks differ substantially, they share the search for the principal constraints that affect motor coordination.

Limitations in bimanual coordination: a coalition of constraints

The search for coordination constraints vs preferred patterns of coordination represents two sides of the same coin. This is an important endeavour because it is highly informative about CNS limitations in dealing with multitask organization of a multiple degrees-of-freedom system. However, whereas some bimanual constraints are uniquely associated with coordination, others are merely an expression of those observed during movement of a single limb.

Various coordination constraints have been identified but a coherent framework is lacking. Constraints related to sensory input versus motor output are described in Box 1. This is an arbitrary division within the perception–action cycle because performing a movement, perceiving somebody else performing a movement, or imagining a movement, involve the recruitment of partially overlapping brain networks [19]. A useful working hypothesis is that coordination emerges at multiple levels, from 'high-level' cognitive perceptual to low-level neuromuscular [20]. The basic rule of thumb is that the more the constraints act in coalition, the more stable and accurate the coordination pattern will be. Conversely, when constraints are in conflict with each other, performance will deteriorate.

Box 1. Bimanual coordination constraints

Constraints associated with sensory input

Perceptual input constrains bimanual coordination. Similar to in-phase/anti-phase bimanual coordination, stability differences are also observed when moving a single effector in-phase (same direction) or in opposite phase (different directions) with a moving visual stimulus [71,72], when moving an effector in synchrony with an auditory beat (synchronization) versus in alternation (syncopation) [73,74], or when strictly perceiving two visual stimuli with different relative phasings [75]. Therefore, some have proposed that the difference in quality between in-phase and anti-phase motor coordination is mediated by (visual) perception. Exploring links between static and dynamic principles of visual symmetry perception [76] and coordination represents an interesting direction for future research.

Constraints associated with motor output

On the processing-output side, constraints are closely associated with the effectors and muscles used for controlling movement (musculoskeletal constraints).

(1) Patterns of in-phase and anti-phase coordination are abundant in invertebrate and vertebrate species. With respect to human bimanual coordination, the relative timing of homologous muscle activation has been studied most intensively. When moving the fingers, wrists or forearms towards and away from the body midline, requiring simultaneous homologous muscle activation (in-phase), a more stable pattern of coordination emerges than when non-homologous muscle groups are activated together (anti-phase).

(2) When moving at the pace of an auditory metronome, a preference emerges to flex rather than extend the finger or wrist on the beat, and to pronate rather than supinate the forearm. This is evident when moving either one limb or both [44,77].

(3) When changing the posture of the forearm or the axis of rotation during wrist movements, activation patterns shift as a result of muscle length and orientation changes and these intrinsic properties of the neuromuscular-skeletal system have an impact upon the stability of bimanual coordination [78].

(4) The combination of effectors used, determines the quality of coordination patterns. Isofrequency (1:1) coordination of homologous effectors (both forearms) is associated with higher accuracy and stability than when non-homologous effectors (a forearm and leg segment) are involved [29–31]. Conversely, multifrequency patterns (e.g. a 2:1 frequency ratio) are produced more successfully with non-homologous than homologous limbs [31]. This suggests that lower stability during preferred coordination is associated with higher flexibility to adopt less familiar coordination modes. In other words, it appears more difficult to produce different rhythms with both hands than with hand and foot.

Space and time represent pervasive constraints on interlimb coordination that result from the architecture of the central nervous system. The general preference to move all effectors within a common time frame, such as moving the whole body to a familiar beat, reflects a basic tendency for neural synchronization. Simple rhythms (1:1, 2:1) in which the frequency of one limb motion is an integer multiple of the other, are produced more successfully than polyrhythms (3:2, 5:3) in which non-integer combinations are realized [21]. When stressing performance by increasing cycling frequency during polyrhythm production, loss of the pattern and a regress to simple ratios can be observed [22]. In addition to temporal ratios, the relative phasing between limbs also impacts upon coordinative difficulty: Patterns that deviate from the in-phase ($\phi = 0^\circ$) and anti-phase modes ($\phi = 180^\circ$) are associated with lower degrees of stability (such as $\phi = 90^\circ$, when one limb lags a quarter of a cycle with respect to the other) [18,23]. This is not unique to bimanual performance *per se* but can also be a consequence of the performers' natural preference to perceive and produce simple time intervals, indicative of limitations in representing complex temporal relationships [24].

Spatial constraints become apparent when movements with different amplitudes [6–8] and/or directions [25–28] have to be performed simultaneously. When performing a short- and long-amplitude movement with both arms simultaneously, assimilation effects occur whereby the amplitudes become more similar to each other [6–8]. Similar evidence has been generated during the simultaneous production of movements in different directions or with different orientations, such as stretching out one arm in front of you and the other sideways [25–27]. In addition to the preference to move both limbs together towards and away from the body midline in the mediolateral plane (same muscle groups, different directions), bimanual movements performed along the sagittal plane (same muscle groups, same directions) are produced with even higher stability. This suggests that two constraints reinforce each other to enhance coordinative performance, namely the principle of homologous muscle grouping and of direction in extrinsic space (isodirectionality) [26,28,29]. Directional constraints are also apparent when arm and leg movements are performed together: Segments moved in the same direction (isodirectional, wrist and foot up or down) are performed more easily and with higher accuracy than movements in different directions (non-isodirectional, wrist up and foot down, or vice versa) [30,31,32]. Thus, directional coding is more abstract than strictly referring to muscle homology principles. Moreover, this prompts questions about the reference frames in which movements are encoded: relative to the midline of the body (an intrinsic or radial egocentric reference) or by reference to the external world (an extrinsic or allocentric reference) [29]. Such reference frames can co-exist and task context determines the relative prevalence of one versus the other [33,34].

In summary, it appears that the default state of neural control refers to the specification of the same movement parameters to limbs that are moved simultaneously. Coordination arises from the mutual interplay of constraints from multiple sources and at different loci of the CNS, from high level perceptual and abstract processing codes to low-level neuromuscular. Constraints can be more or less compelling, depending on task context and individual characteristics (such as age, pathology, medication, etc.) [4].

Cognitive–perceptual penetrations into coordinated action

Even though coordination constraints confront the performer with limitations, they can be overcome as many everyday tasks involving differentiated limb patterns attest. Driving cars, tying shoelaces, or opening a drawer while grasping a pen are well-known examples. Sometimes, the overruling of constraints is easily accomplished. At other times, it requires considerable practice, as expert athletes, dancers or musicians can testify. A primary goal of motor learning is to overcome basic coordination constraints that often give rise to persistent errors in performance. There are various ways to accomplish successful coordination. For example, intention [35] and the deployment of attentional strategies [2,36] are helpful to stabilize otherwise unstable patterns of coordination. The use of conceptualization strategies – instructional means to promote task integration, and/or visual transformation procedures – has recently become the focus of increasing attention, and is discussed next.

Task interference and context specificity

Contextual means to alleviate task interference refer to how task goals or movement targets are represented. Amplitude interference between limbs during bimanual pointing can be reduced or even eliminated when direct visual cues (target light illuminates) instead of symbolic cues (e.g. a verbal representation of the required movement amplitudes) are used to trigger movement [37,38]. It appears that the direct visual representation of targets drives each limb to the correct location in space with reduced or without (mutual) interference. Thus, the manner in which actions are conceptualized and represented, affects the amount of interference observed. Even though alternative interpretations exist [38], it is noteworthy to emphasize that different networks are recruited when movement is externally (visually) driven or internally generated. Whereas the parietal–premotor pathway dominates in the former case, the basal ganglia–supplementary motor area circuit prevails during the latter case and this may have differential implications for neural crosstalk [37,39,40] (see Figure 1). Further work is necessary to verify this hypothesis.

Motor binding by means of task conceptualization

Complex tasks that are seemingly difficult to perform can become easy when familiar events, acts or symbols are

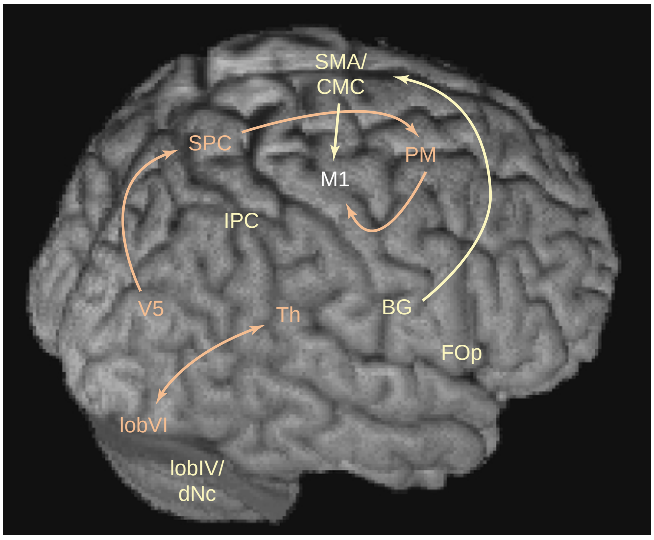

Figure 1. Differential brain networks during visually-guided (external) and non-visually-guided (internal) bimanual movement generation. During visually-guided movement generation (orange arrows), hMT/V5, superior parietal cortex (SPC), premotor cortex (PM), thalamus (Th), and cerebellar lobe VI (lobVI) show higher activation. During internal generation (yellow arrows), the basal ganglia (BG), supplementary motor area (SMA), cingulate motor cortex (CMC), cerebellar lobule IV-V/dentate nucleus (lobIV/dNc), the inferior parietal cortex (IPC), and the frontal operculum (FOp) are more active. These differences are relative rather than absolute. M1 is primary motor cortex. The arrows indicate the potential connections and tentative flow of information among brain areas. Adapted from [40].

called upon. For example, it is generally difficult to produce a 90° out-of-phase finger-tapping pattern but learners can catch the trick by referring to the sound made by a galloping horse. Cognitive strategies serve as binding rules to integrate the individual task components into a meaningful gestalt. Originally proposed in relation to resolving ambiguities in the visual scene, binding is also a meaningful concept in motor control [41,42]. In the present context, binding refers to how movement parts become spatiotemporally united to give rise to the unified experience of ‘coordination’.

Experimental evidence supporting the role of conceptualization processes has been obtained during the simultaneous production of semicircles with both hands [43]. When these geometrical forms are drawn in the air such that the overall pattern results in a full circle, performance is easy (Figure 2a, left). When the semicircles start and end far apart but approach each other in the middle (making an ‘X’ symbol), performance is much more difficult (Figure 2a, right) [43]. Both tasks are similar in their relative phasing but differ in familiarity of the symbols that are brought to mind to unify it into a meaningful ‘gestalt’. Whereas this example refers to spontaneous behaviour, conceptualization strategies can also be imposed by means of augmented feedback to promote progress in skill (see later).

Binding rules are also crucial when performing complex polyrhythms (e.g. a 3:2 or 5:3 frequency ratio). Polyrhythms can be performed successfully when the subtasks become integrated into a common temporal structure in which the taps of each limb are interleaved [2,21]. Perhaps the advantage of such binding rules is that attention is no longer divided across the subtasks but is united towards the gestalt. Such rules can also be combined with a form of intermittent control in which cyclical task monitoring is simplified by focusing on kinematic anchor points (such as reversals in direction) rather than continuously monitoring both limbs’ trajectories. Anchor points serve as key landmarks of attention to monitor movement progress and to detect upcoming errors [44,45]. Anchoring can also be imposed or amplified by providing haptic contacts and auditory beats [20]. For example, finger tapping movements become more stable when haptic contacts (touch the desk surface) coincide with the metronome beat. Conversely, when haptic contact is counterphase to the metronome beat, coordination suffers. This points to a neural integration process whereby polysensory elements are bound together into a coherent unit [20]. Dedicated brain areas serve these integration processes (see section below).

Instructional aids can also be used to reduce coordinative complexity by provision of a simplified visual representation of the task. Bimanual turning movements with different frequency ratios become less difficult when using a simplified visual representation of a 1:1 frequency ratio (Figure 2b) [46]. Bimanual line drawing movements with orthogonal orientations benefit from their visual representation as parallel motions of two dots on a screen (instead of orthogonal dot motions) [47]. The advantage of such transformations is that basic principles of dynamic perception can be exploited to improve action (see Box 1). However, visual transformations do not always abolish execution-related interlimb interactions [34,48] and might require a recalibration of visuo-kinesthetic maps before performance benefits become apparent. The question also remains to what extent visual transformation procedures not only aid task performance but also learning and memory consolidation. It is well known that such sources of powerful augmented feedback can induce a temporary boost in performance which can disappear as soon as this information is withheld [49].

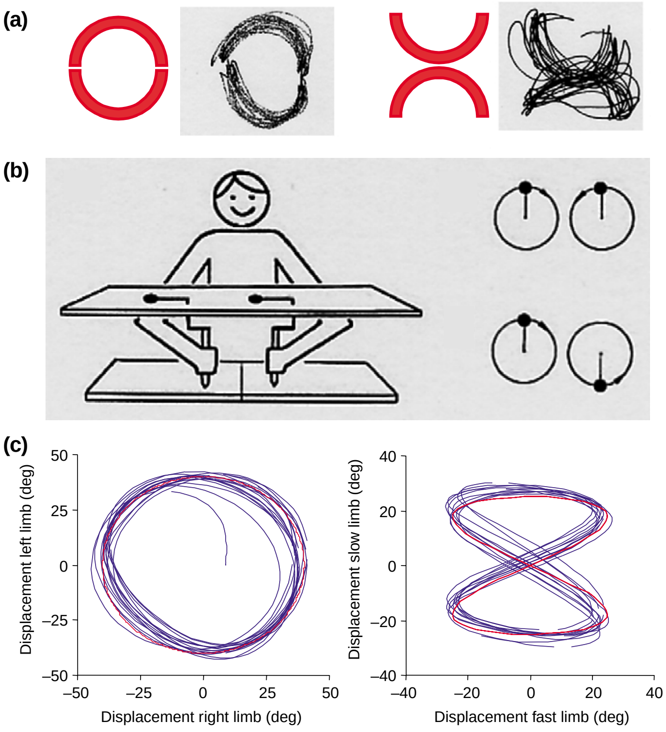

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Figure 2. Examples of conceptualization processes or visual transformations that promote task integration. **(a)** Participants are required to draw semicircles in front of them with both arms. They move in the air from left to right or vice versa. One task (left) requires starting and ending both fingers together in space whereas there is maximal separation in the middle of the trajectory. The other task (right) starts and ends with both fingers separated but the trajectories meet in the middle. When the resulting global pattern is represented by a circle (left), performance is more successful than when a less familiar pattern is generated (right), in spite of the similar relative phasing patterns in two-dimensional space for both tasks. The template is shown in red and actual performance in black. Adapted from [43]. **(b)** Participants circle two visible flags by way of two hand-held cranks that are hidden under the table (left). The flag controlled by the left hand circles directly above the left crank (hand) whereas the right flag circles in a 4:3 frequency ratio to the right crank (hand) as a result of a gear system. Thus, isofrequency in the visible flags is associated with a 4:3 frequency ratio in the non-visible hands. Participants circle the flags either in mirror symmetry or in anti-phase (see right picture). Performance of these hidden bimanual movements of unequal frequency becomes easier when they are visually represented as isofrequency movements Adapted from [46]. **(c)** Difficult relative-phasing patterns can be produced and acquired more easily when performers receive real-time augmented feedback displaying their displacements in an integrated fashion. Participants perform cyclical forearm movements in the horizontal plane while the Lissajous figures are represented on a screen in front of them. The left arm motion is presented in the ordinate and the right motion in the abscissa. Examples of patterns with a 1:1 (left) and 2:1 (right) frequency ratio in which one limb lags 90° with respect to the other. Mathematically generated ideal templates are shown in red, actual performance across a 15-s trial is indicated in blue. Adapted from [45,50].

Perceptual integration promotes bimanual coordination learning

One can take the aforementioned visual transformation examples one step further by representing the coordination between limbs more directly by an integrated signal instead of two separate signals representing each limb. When orthogonally plotting the displacement signals of each limb on-line during performance (i.e. generating a Lissajous figure), difficult coordination patterns become 'graspable' (Figure 2c) [23,45,50]. This low-dimensional type of augmented feedback provides direct information about the nature and quality of coordination and has been used successfully in the context of learning bimanual coordination patterns with a 1:1 and 2:1 frequency ratio involving a 90° phase offset. Depending on task complexity and organization of practice, performance can transfer more or less successfully to non-augmented feedback conditions. This is not surprising in view of the guiding role of feedback [49] but also because the neural networks, involved in movement production in the presence or absence of augmented Lissajous feedback, are vastly different. This converges upon the differential neural pathways for external versus internal movement generation (see Figure 1) [40].

In summary, the human motor system is sufficiently plastic and adaptive to overrule basic coordination constraints. Abstract binding or visual transformation rules can help to overcome these constraints by enslaving the sensorimotor networks. This is consistent with the notion of a hierarchy in movement control with higher-level abstract and lower-level muscle- or effector-specific codes.

Box 2. Principal brain areas involved in bimanual coordination

Cerebellum

When comparing activation during tasks requiring a high coordination effort to simple in-phase and unilateral tasks, cerebellar activation maxima are observed in clusters that mainly differ with respect to their anterior-posterior location in the hemispheres and superior-inferior location in the vermis (see Figure I). Areas within lobule VI of the cerebellar vermis and hemisphere become activated when movements are performed in synchrony to a predictable rhythm, as observed in the majority of metronome-paced interlimb coordination tasks. In addition, more posterior regions (hemisphere lobuleVI/Crus I, vermis lobule VII/VIII) appear to come into play when limbs are not moved in synchrony, but when an exact temporal delay between the limb movements has to be maintained. This might also involve processes of error monitoring and on-line correction of the spatial-temporal relationship between the limbs.

Supplementary motor area (SMA) and Cingulate motor cortex (CMC)

Activation of the medial wall areas is either more pronounced during coordination of the limbs as compared with single-limb conditions [51,53,54,58,60], or during less compatible as compared with more compatible coordination tasks [51,52,55–57,59,60]. SMA activation predominantly occurs within its dorsal part (SMA-proper) behind the VCA line, and often extends into the dorsal CMC [52,56,57] (Figure I). SMA is tentatively proposed to be important for simultaneously coding different actions of two or more effectors in addition to their temporal sequencing.

Premotor cortex (PM)

This area is subdivided into a dorsal part (PMd) and a ventral part (PMv). Activation spots evoked by bimanual coordination are predominantly identified within the caudal part of PMd (PMd-proper). The PMs in both hemispheres are highly interconnected via the SMA [79], which emphasizes their role in bimanual coordination. Activations during coordination usually occur in the vicinity of the precentral sulcus, either bilaterally or within the right hemisphere. PMd-proper might be involved in integrating both limbs into one sequence of appropriate muscle contractions and in the suppression of automated (mirror) movements. In more demanding coordination tasks, activations are also seen in the caudal part of PMv [40,59] (Figure I).

Corpus callosum (CC)

Whereas neural crosstalk between different-direction bimanual movements is often observed in normals [26,27,33], callosotomy patients do not exhibit this interference, suggesting that information between the spatial codes of both movements is normally exchanged between the hemispheres [25,66]. Timing is not affected in these patients when movements have discrete landmarks or reversals [25] but it is for continuous movements, such as cyclical circle drawing [67].

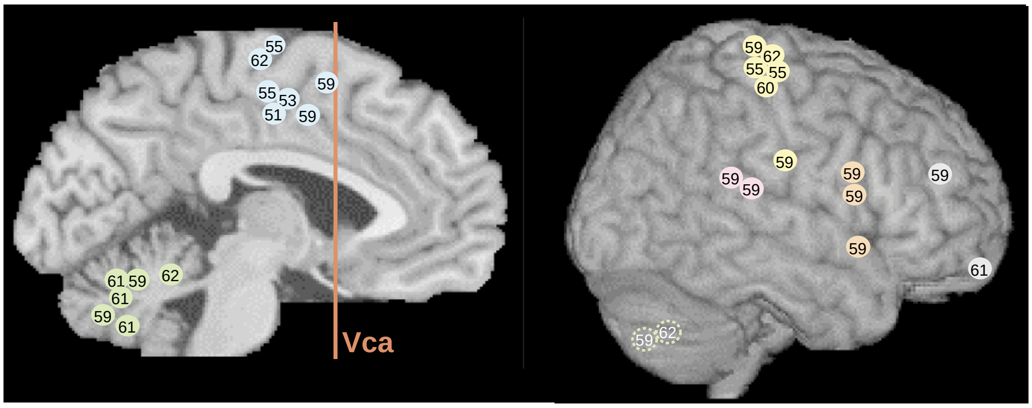

Figure I. Overview of areas that show higher activation levels during more difficult (1:1 anti-phase, 3:2) than during simple (1:1 in-phase) bimanual tasks. Principal foci of activation have been identified in the following areas: blue: sma; green: cerebellum; yellow: premotor cortex; orange: Broca's area, Insula; pink: secondary auditory cortex; gray: frontal cortex. The numbers refer to references (see list). Left, medial view; Vca-line refers to the anterior commissural landmark. Right, lateral view; the activation in the cerebellum is not on the surface but within the cerebellar hemispheres (dotted symbols).

The dynamic neural network involved in cyclical bimanual coordination

Even though the supplementary motor area (SMA) has traditionally been associated with the control of bimanual coordination patterns, there is mounting evidence to assign this complex function to a network rather than a single locus [1,4]. Medical imaging studies have recently investigated rhythmical tasks, requiring either bilateral finger [51–59] or forearm and wrist movements [60,61]. These tasks have consistently resulted in the activation of a general sensorimotor network that is similar to the one observed during unilateral task performance [4]. As such, a specialized structure acting as 'coordination controller' does not appear to exist (Box 2).

Two experimental strategies have been explored to identify coordination-related areas. First, brain activation levels during bimanual coordination have been compared with activation during single-limb task levels. This has revealed evidence in favor of an additional coordination effort from the nervous system that exceeds the sum of the single-effector demands [58,60,61]. In this respect, an increased involvement of the primary motor cortex (M1), premotor cortex (PM), and SMA [58,60] as well as the cerebellum, has been identified [61]. However, a stricter comparison between regions responding more strongly to the coordination task and the sum of the responses evoked by the single-limb subtasks, is mandatory in the future.

Second, brain activation patterns across different levels of coordination complexity have been compared whereby cycling frequency manipulations serve to amplify the differences [70]. Comparisons of in- and anti-phase bimanual patterns have revealed partially inconsistent results [52,56,57,59,60,62]. Whereas studies comparing both patterns at low frequencies (less than 1 Hz) have predominantly obtained an increased activity of the SMA, sometimes extending into the cingulate motor cortex (CMC), higher frequency studies (1 Hz or more) have also shown increased activations in PM and cerebellum, sometimes including activations in Broca's area as well as the secondary auditory and somatosensory cortex. Similar observations have been made during comparisons between 3:2 and in-phase 1:1 coordination patterns [59]. The role of the latter regions should be verified in future work. The caudal part of Broca's area (BA 44,46) and the insula of the left hemisphere also become activated during rhythm perception [63]. The secondary auditory cortex appears involved in integrating sensory information from multiple modalities, including auditory stimuli [64]. As such, these areas might not only be involved in producing rhythmic behaviour *per se* but also in monitoring whether the motor output of the different limbs matches the temporal requirements.

Following early work [65], recent studies with split-brain patients and those with agenesis of the corpus callosum (CC), have provided crucial support for the role of this neural pathway in bimanual coordination [25,66,67]. Whereas overtrained tasks (such as tying shoelaces) remain successful in these patients, learning new tasks is more difficult [68]. This suggests that the CC plays a crucial role in exchanging sensory information about both limb motions to accomplish goal-directed task integration. Whereas patients appear to have a particular advantage relative to normals in simultaneously producing unrelated movements, they incur difficulties when both limbs need to interact to accomplish new goal-directed actions.

The emerging picture is that the bimanual coordination network is not rigid and static but rather a dynamic entity that changes as a function of task complexity (spatiotemporal interlimb relationships), difficulty level (e.g. performance speed), and experience. With increasing task complexity, the basic coordination network is extended into parietal, temporal and prefrontal areas (depending on skill level) that serve many other functions. Moreover, practice and experience give rise to plastic changes in within- as well as between-hemisphere interactions, resulting in complex dynamic network changes [69,70]. In view of the wide distribution of this network, test batteries of bimanual function would be helpful in clinical contexts to assess the integrity of movement control in disordered groups.

Box 3. Questions for future research

- Where does cortical neural crosstalk primarily occur: between two interconnected control centres (inter-hemispheric) or between neuronal populations within a single lateralized control centre (intra-hemispheric)?
- How do integrative symbolization or conceptualization rules enslave the sensori-motor networks, thereby overruling basic coordination constraints?
- How does the neural architecture differ between subjects that can easily overcome coordination constraints to produce differentiated action patterns and those that are harnessed by basic neural synchronization?
- How do inter- and intra-hemispheric interactions among neuronal populations change as a result of bimanual motor learning and what role is being played by inhibitory and excitatory networks?
- What are the similarities and differences between the networks underlying interlimb coordination and those associated with other motor tasks?

Summary

Following two decades of behavioural research on the principles governing bimanual coordination, a neuroscientific approach has emerged recently that focuses on the brain networks involved in coordination and that addresses where and when neural activations occur. This is complemented by an increasing interest in mental processes associated with conceptualization and binding rules that serve to manage control over the sensorimotor networks that are faced with orchestrating a multiple degrees-of-freedom system. Understanding how cognition penetrates into action will also narrow the gap between behaviour and the neurosciences. In addition, the study of the dynamic changes in the bimanual networks as a function of task, environmental context and practice, will become primary foci of attention in the near future (see also Box 3).

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