Perception–Action Coupling During Bimanual Coordination: The Role of Visual Perception in the Coalition of Constraints That Govern Bimanual Action

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ABSTRACT. Constraints pertaining to interlimb coordination have been studied extensively in the past decades. In this debate, F. Mechsner (2004) has taken a provocative position by putting primary emphasis on perceptual principles that mediate coordinative stability. Whereas the present authors agree that the role of perceptual principles is of critical importance during coordination, they take issue with Mechsner's extreme position and with the evidence forwarded to support a purely perceptual-cognitive approach to bimanual coordination. More specifically, the authors emphasize that current knowledge about brain function argues against a dualism between perception and action, criticize the presented evidence that posture manipulations during coordination provide decisive evidence against motoric and muscular constraints, and report on potential pitfalls associated with the use of visual transformation procedures to support complex coordination patterns.

Key words: bimanual coordination, directional constraints, symmetry principles

Mechsner's (2004) viewpoints have generated considerable debate within the field of interlimb coordination. Along the lines of his previous work, Mechsner provides provocative data on the role of perception during bimanual coordination in his review. Even though the notion of a "psychological approach to human voluntary movements" (p. 355) is ill defined, he should be credited for drawing our attention to the role of perceptual-cognitive principles in bimanual coordination and for encouraging us to think about exploiting such principles in the case of control of action in general. However, we would like to raise some concerns and comments with respect to his viewpoint for the following reasons: (a) Rather than further bridging the perception–action gap, his position appears to implicitly promote a dualism and dissociation between perception and action. (b) The experimental evidence provided in support of perceptual and against so-called motoric constraints is currently deficient. (c) A purely perceptual-cognitive approach without reference to constraints pertaining to the organization of movement is insufficient in view of the difficulties performers often encounter when recalibrating the mapping between perception and action during visual transformations (such as mirror drawing). Moreover, a unified framework of candidate perceptual principles that facilitate movement control is lacking, and more investigation is required so that researchers can assess the boundary conditions under which such principles can support action. That caveat also implies an assessment of the degree (or lack) of convergence between the principles of visual perception and proprioception. We discuss those issues in more detail next.

A Unifying Framework for Perception and Action: Neural Evidence

One of the important contributions of cognitive neuroscience is that this expanding field has provided convincing evidence for a strong link between perception, action, and imagery. Medical imaging studies have revealed that the cortical networks involved in performing a movement, perceiving somebody else's movement, and imagining a movement are partly overlapping (Kosslyn, Ganis, & Thompson, 2001). Apparently, when watching somebody else's movement, the observer maps his intentions onto those of the performer (Kosslyn et al.; Rizzolatti, Fogassi, & Gallese, 2001). The important conclusion to be drawn from that observation is that the neural substrates for perception and action are closely intertwined and refer to a continuum rather than a dualism. That conclusion implies that any attempt to strictly dissociate perception from action is meaningless from a neural and behavioral perspective, even though it may be desirable to experimentally manipulate one or the other so that their coupling may be better understood. The consequence of those overlapping brain networks is also that movement control should be understood against the context of a multitude of constraints referring to perception, action, and their integration. Every movement is associated with perceptual consequences, and perception guides our actions. Their underlying neural architecture constrains our behavior.

Digging Deeper Into the Biomechanical and Neuromuscular Consequences of Posture Manipulations

The experimental evidence Mechsner (2004) provided to discount what he considers motor constraints and to argue in favor of perceptual constraints is faced with weaknesses. At issue is the role of spatial (directional) constraints in bimanual coordination and whether those should be understood within an intrinsic or an extrinsic reference frame. Two coordination constraints are prominent in the current bimanual coordination literature (Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997; Swinnen, Jardin, et al., 1998), that is, *egocentric*, converging upon the intrinsic tendency to activate homologous muscle groups simultaneously but extending beyond strict homologous muscle coupling (Temprado, Swinnen, Carson, Tourment, & Laurent, 2003), and *allocentric*, referring to a general preference for moving the limbs in the same direction in extrinsic space. Abundant evidence has been generated for the role of constraints related to muscle homology (Byblow, Carson, & Goodman, 1994; Kelso, 1984; Lee, Almeida, & Chua, 2002; Park, Collins, & Turvey, 2001; Riek, Carson, & Byblow, 1992; Semjen, Summers, & Cattaert, 1995; Swinnen, 2002; Swinnen, Jardin, et al., 1997; Swinnen, Jardin, et al., 1998).

Mechsner (2004) suggested that the results of his and his colleagues' finger abduction–adduction study with posture manipulations indicate a weakening of the so-called motoric coordination constraint. However, in the absence of detailed kinematic measures, electromyography results, or both, it is unjustified and misleading to make bold claims about underlying coordination constraints. A more rigorous experimental approach is warranted here. The implicit assumption in Mechsner's work is that turning the hand from pronation to supination will not alter the muscle activation patterns required for finger or wrist abduction–adduction movements. As a consequence, Mechsner argues, homologous muscle groups are activated simultaneously during symmetrical movements with the same limb postures and during asymmetrical movements with different limb postures. Such assumptions greatly undermine the contribution of neuromuscular constraints on coordination. For example, Carson, Riek, Smethurst, Lison, and Byblow (2000) showed that unimanual pronation–supination movements made about the neutral (or semiprone) posture differed in stability on the basis of the axis of rotation (aligned with the ulna versus aligned with the radius). In a bimanual context, when aligning the axes of rotation on the bottom or top, mirror-symmetric patterns (in-phase) were found to be more stable than isodirectional patterns (antiphase), as one would expect. However, with the axes mixed, one on top in alignment with the radius, and the other aligned with the ulna, antiphase patterns were more stable than were in-phase patterns. In that configuration, and under frequency-scaling conditions, participants switched spontaneously from in-phase to antiphase patterns. Therefore, the stability of bimanual patterns were composites of the most stable unimanual patterns, and those were, in turn, determined by the mechanical efficiency of the muscles that gave rise to the movement (Carson et al., 2000).

In contrast to Mechsner (2004), we argue more strictly that one can assume with confidence muscle homology between the upper limbs only when both hands adopt the same posture. Under different posture conditions, there is no guarantee that movement kinematics and the simultaneous timing of homologous muscle activation are preserved. Consequently, in the absence of strict coactivation of homologous muscles, other principles come into play with respect to directional constraints. Directional or spatial coding of movement is not, however, the exclusive territory of brain areas that are typically associated with perceptual processing (such as the parietal cortex) but has also been observed in various motor-related areas (e.g., premotor and motor cortex; for a review, see Georgopoulos, 1995). A recent imaging study on the simultaneous production of two tasks with different directional requirements identified the locus of spatial interference within a parietal as well as a premotor subnetwork (Wenderoth, Debaere, Sunaert, Van Hecke, & Swinnen, in press). Interference and pattern stability are therefore considered interdependent phenomena. That interdependence demonstrates again that it is more fruitful to consider the convergence of constraints across perception and action networks rather than assigning priority to one over the other.

On the basis of the aforementioned evidence, we conclude that a paradigm making use of hand posture manipulations is highly problematic for the following reason: The torque-generating capacity of the muscles and the manner in which muscle torque is translated into joint motion are modified as a function of the mechanical context (hand posture), because muscle lengths and muscle moment arms involved in the muscle–joint complex change considerably (Li, Levin, Carson, & Swinnen, 2004).

In a recent study, Li et al. (2004) replicated Mechsner, Kerzel, Knoblich, and Prinz's (2001) hand posture experiment. They studied the effect of forearm posture (prone or supine) on bimanual abduction–adduction movements of the wrist in isodirectional and nonisodirectional modes of coordination, performed in the horizontal plane (Li et al.). Irrespective of forearm posture, nonisodirectional (mirror-symmetric) coordination was observed to be more stable than parallel (isodirectional) coordination, supporting Mechsner's observations. However, those observations do not invalidate at all the dominant role of muscle homology. Indeed, a more detailed assessment of the kinematics revealed that with elevations in cycling frequency, the performers recruited extra mechanical degrees of freedom in the vertical plane, principally via flexion–extension of the wrist. The increases in movement amplitude in the vertical plane were accompanied by decreasing amplitudes in the horizontal plane. Thus, in spite of the fact that participants were instructed to move strictly in the horizontal plane, they progressively recruited motions in the vertical plane that reflected the simultaneous activation of homologous muscle groups (Li et al.). Fink, Kelso, Jirsa, and De Guzman (2000) also demonstrated such recruitment of degrees of freedom across different planes under demanding conditions. That finding is not surprising, because flexion–extension is a much more natural and preferred joint motion for the wrist or fingers than is the more awkward and difficult abduction–adduction motion. Mechsner et al. limited motions to the horizontal plane, which increases the likelihood that performers recruited homologous muscle activation patterns that supported flexion–extension motion. Moreover, Li et al. observed that the condition in which the muscles were activated simultaneously with both wrists in the same posture (mirror-symmetrical movements) resulted in the most stable coordination pattern. Thus, whereas at first sight, perceptual symmetry principles appeared to dominate bimanual coordination, independent of underlying muscle activation patterns, a more profound analysis of movement kinematics suggested that the relative timing of homologous muscle activation acted as a principal constraint upon the stability of interlimb coordination. This is not to deny the role of perceptual organization principles in the organization of bimanual action (Bogaerts, Buekers, Zaal, & Swinnen, 2003). Rather, the lesson to be learned from that work is that the use of manipulations of limb posture in investigating the role of perceptual versus motor classes of constraints should be approached with great caution and does not justify unqualified statements.

In addition to those observations, we point out that motoric coupling (a) remains evident in the absence of afferent information sources at the level of movement planning (Swinnen, Young, Walter, & Serrien, 1991); (b) is so prominent that it hinders the generation of different movements in both limbs, as abundantly demonstrated; and (c) is supported by neural pathways and by the existence of mirror movements in exaggerated form as a result of central nervous system pathology. Mechsner (2004) appears to be more receptive to the idea of efference-related constraints in the present target article than in his previous work. He states: "The material and the perceptual-cognitive levels are certainly dependent on each other, but those levels are of a different kind" (p. 362). Our response is that if they are dependent on each other, then that implies that researchers should consider emerging constraints at both levels together rather than argue in favor of a "strictly" perceptual-cognitive approach. An efference-related or biomechanical account has also proven to be very insightful for a better understanding of constraints related to intralimb (intersegmental) coordination (Dounskaia, Swinnen, Walter, Spaepen, & Verschueren, 1998). We argue that knowledge about neuromuscular, mechanical, and effector-related constraints is a major step forward toward envisaging how perceptual-cognitive principles can support action.

Exploiting Perceptual Principles for the Control of Action: Problems and Pitfalls

A perhaps more convincing example of the role of perceptual principles was provided by Mechsner, et al.'s (2001) bimanual circle-drawing (cranking) task. Basically, a difficult temporal noninteger ratio (4:3) becomes easier when it is visually displayed as mirror-symmetric isofrequency (1:1) movements. We believe that line of research should be explored further because it may reveal profound insights into the role of visualization or task conceptualization strategies in the performance of difficult actions (Swinnen & Wenderoth, 2004). However, we are currently doubtful that that observation extends beyond the circle-drawing case, for example, cyclical motions involving more abrupt reversals in direction. The following remarks may provide some boundary conditions for the further elaboration of those phenomena.

1. Evidence that augmented visual feedback helps performers to overcome motoric constraints does not invalidate the latter's existence. On the contrary, exploring those constraints may point to those conditions in which visual or conceptualization principles can be of great assistance in overcoming muscle- or motor-related coordination constraints. It is important to add that motor-related constraints are associated with proprioceptive information by default and that the term *motor* is misleading as such.

2. To arrive at a coherent framework in future research, those principles of static and dynamic visual (symmetry) perception that support action may merit investigators' further exploration (Wagemans, 1997). They can use as a guideline the extensive research program that has already been deployed in the study of visual perception to investigate the role of perceptual principles in movement control. Mechsner (2004) does not explicitly state the principles that apply; neither does he provide a coherent framework for the presumed perceptual basis of interlimb coordination, although he admits that there may be a variety of such principles. He implicitly refers to principles of mirror symmetry, on the one hand, and to isodirectionality, on the other hand. Those principles need to be formalized more rigorously and their interactions assessed. That converges upon the previously discussed egocentric and allocentric spatial constraints that apply across different planes of motion (Swinnen, Jardin, et al., 1997). We agree with Mechsner, however, that there may be additional candidate principles. In addition, it currently remains obscure how the principles of visual perception relate to other sources of sensory information, such as proprioception.

3. Whereas we believe in the benefit of using principles of visual perception to support (bimanual) action, it is also important to be aware of potential drawbacks. In view of the normal coalescence of visual and proprioceptive maps, one should realize that the use of visual transformations to aid performance of difficult tasks is often associated with a disturbance of sensory convergence; that disturbance requires a subsequent recalibration between visual and proprioceptive maps (see prism-goggles and mirror-drawing experiments; Lajoie et al., 1992). As such, there may be a tradeoff between the benefits accrued from visual transformations to exploit perceptual constraints and the disadvantages of breaking down the normal calibration between both sensory maps. In an experiment in which the limbs were to move in different directions simultaneously, Swinnen et al. (2003) used visual directional transformations, displayed on a screen, to dissociate perception from action. They observed that mutual interference between both limbs was largely accounted for by the performers' actually produced rather than perceived movement. If perceptual-cognitive principles would flexibly enslave the sensorimotor networks, as suggested by Mechsner (2004), then the aforementioned difficulties should be overcome much more easily.

However, we would like to add that some of us have also generated evidence demonstrating the benefits of visual transformations in performing directionally less compatible bimanual movements, such as movements in orthogonal directions that were visually displayed as parallel movements on a computer screen (Bogaerts et al., 2003). Another example is using a visual stimulus to pace a bimanual pronation–supination task (both axes on the bottom): Participants produced antiphase patterns with greater stability, and spontaneous transitions to in-phase occurred at higher movement frequencies when the visual pacing stimulus and the hand movements started in the same direction than when they started in opposite directions (Byblow, Chua, & Goodman, 1995). In a bimanual circle-tracing task (Byblow, Chua, Bysouth-Young, & Summers, 1999), a directional visual stimulus was displayed between the two hands as participants performed mirror-symmetric or -asymmetric patterns. When the pacing was isodirectional with respect to the hands in symmetric patterns, pattern stability improved. In asymmetric patterns, when the stimulus direction was compatible with the nondominant hand (which reversed direction spontaneously when the hands moved asymmetrically at fast rates), patterns were more stable than they were when the visual stimulus was compatible with the dominant hand (which seldom reversed direction). Those are but two examples of the convergence of visual information onto the coordination dynamics, and in both cases, patterns in which homologous muscles were activated in synchrony emerged as the most stable.

4. Whereas some perceptual transformations may support performance (such as in Mechsner et al.'s [2001] arm-cranking study with different frequency ratios), the more important question is whether they also support learning. In Mechsner's as well as in the aforementioned cases, the perceptual transformations served only as performance boosters. Learning such patterns, however, will be more difficult and will involve overcoming constraints at multiple levels of the system's functioning. In that respect, it is noteworthy to bear in mind the guidance hypothesis of knowledge of results and augmented feedback, in general, in which it is proposed that such feedback may provide a temporary boost in performance but does not necessarily aid learning and retention (Salmoni, Schmidt, & Walter, 1984; Schmidt & Lee, 1999). Schmidt and coworkers have provided many occasions in which augmented feedback aided performance but hampered learning and retention. To complement that work further, Debaere, Wenderoth, Sunaert, Van Hecke, and Swinnen (2003) have recently shown that the brain networks involved during bimanual performance are considerably different in the presence of augmented feedback (external generation) than they are in the absence of augmented feedback (internal generation).

However, there are conditions in which visual transformations can aid bimanual skill learning. During the past decade, Swinnen and colleagues have made extensive use of relative motion plots (Lissajous figures) to support the acquisition of bimanual skills, such as 1:1 and 2:1 movements with a 90° phase offset between the limbs (Lee, Swinnen, & Verschueren, 1995; Swinnen, Dounskaia, Walter, & Serrien, 1997; Swinnen, Jardin, et al., 1998; Swinnen, Lee, Verschueren, Serrien, & Bogaerts, 1997; Verschueren, Swinnen, Dom, & De Weerdt, 1997). Those plots provide an orthogonal display of left and right limb motions in real time on a computer screen. In adolescents, transfer performance from augmented to nonaugmented visual feedback conditions is quite successful (but not perfect), whereas more difficulties are experienced in the elderly and in groups with pathologies (Swinnen, Verschueren, et al., 1998; Verschueren et al., 1997). The message emerging from those observations is that some visual transformation strategies can indeed support performance and learning and are apparently not hampered by intersensory (re)calibration problems. So far, the use of Lissajous figures has received little attention in the coordination literature, even though that may prove to be a fruitful avenue for exploring the acquisition of complex patterns of interlimb coordination in which perceptual strategies may play a prominent role.

In summary, the strong claims of Mechsner (2004) regarding a purely perceptual-cognitive approach currently lack firm experimental support. However, exploring the role of perceptual and conceptualization principles in enhancing action remains an interesting avenue for future research. In that endeavor, the development of a unifying framework of perceptual symmetry principles (visual and proprioceptive) may prove to be very useful. Rather than pursuing whether coordination constraints are strictly perceptual in nature, the available experimental evidence suggests that an integrated research program, in which musculoskeletal, neural, perceptual, and cognitive constraints are studied together, is bound to be a more promising road for studying the mysteries underlying movement coordination.

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