



Drawing lines while imagining circles: Neural basis of the bimanual coupling effect during motor execution and motor imagery



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ARTICLE INFO

Article history:

Accepted 25 October 2013

Available online 2 November 2013

Keywords:

Bimanual coupling effect

Motor execution

Motor imagery

Circles–Lines paradigm

Intention–programming system

fMRI

ABSTRACT

When people simultaneously draw lines with one hand and circles with the other hand, both trajectories tend to assume an oval shape, showing that hand motor programs interact (the so-called “bimanual coupling effect”). The aim of the present study was to investigate how motor parameters (drawing trajectories) and the related brain activity vary during bimanual movements both in real execution and in motor imagery tasks. In the ‘Real’ modality, subjects performed right hand movements (lines) and, simultaneously, Congruent (lines) or Non-congruent (circles) left hand movements. In the ‘Imagery’ modality, subjects performed only right hand movements (lines) and, simultaneously, imagined Congruent (lines) or Non-congruent (circles) left hand movements. Behavioral results showed a similar interference of both the real and the imagined circles on the actually executed lines, suggesting that the coupling effect also pertains to motor imagery. Neuroimaging results showed that a prefrontal–parietal network, mostly involving the pre-Supplementary Motor Area (pre-SMA) and the posterior parietal cortex (PPC), was significantly more active in Non-congruent than in Congruent conditions, irrespective of task (Real or Imagery). The data also confirmed specific roles of the right superior parietal lobe (SPL) in mediating spatial interference, and of the left PPC in motor imagery. Collectively, these findings suggest that real and imagined Non-congruent movements activate common circuits related to the intentional and predictive operation generating bimanual coupling, in which the pre-SMA and the PPC play a crucial role.

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Introduction

If you perform simultaneous, Non-congruent movements with your hands, you will realize that each hand’s movement is affected by the movement of the other hand. Different kinds of modulation (both spatial and temporal) can be observed, depending on the action performed. These effects are collectively known as “bimanual coupling”. The present study focuses on the directional component of bimanual spatial coupling (Franz et al., 1991), involving functional magnetic resonance (fMRI) tasks in which Congruent (Lines–Lines) or Non-congruent (Circles–Lines) movements are executed by both hands (“Real” tasks), and tasks where the movements of one hand are performed while the movements (both Congruent and Non-congruent) of the other hand are only imagined (“Imagery” tasks). The study was designed to

investigate how motor parameters (drawing trajectories) and the related brain activity vary during bimanual Non-congruent movements, both in real execution and in motor imagery tasks.

In the classical Circles–Lines paradigm often used to reveal the reciprocal influence of hand actions in the spatial domain, subjects are asked to continuously draw straight lines with one hand and circles with the other. In this case, bimanual spatial coupling manifests as the tendency of both hand trajectories to assume an oval shape. In other words, lines tend toward circles and circles tend toward lines (Franz et al., 1991). The effect generalizes to bimanual tasks involving more discontinuous shapes, such as drawing squares combined with circles (Franz, 2003). It is important to note that, although the present study was only focused on directional features, spatial coupling effects may also pertain to amplitude parameters. In some previous studies, for example, amplitude parameters were manipulated by having subjects perform left and right limb movements with either the same or different amplitude specifications (for a review of spatial and other constraints, see Swinnen, 2002; Swinnen and Wenderoth, 2004; for experimental studies on

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spatial interference with a directional and/or amplitude component, see Swinnen et al., 2001, 2002; Wenderoth et al., 2005a).

Other bimanual coupling effects have taken temporal parameters into account. Although a reliable temporal relationship exists between distance and time for simple unimanual reaching movements (different reaching distances imply different reaching durations), movement initiation and termination occur in a more coupled fashion during bimanual tasks with different target distances (Kelso et al., 1979; Pia et al., 2013). Similarly, healthy subjects who are asked to tap rhythms bimanually using non-harmonic relations are unable to produce two clearly distinct timing patterns without interference (Klapp, 1979; Peters, 1977). It is also well known that bimanual coordination in the mirror-symmetrical (in-phase) mode, in which homologous muscles are active simultaneously, is more stable than in the anti-parallel (out-of-phase) mode, in which homologous muscles are engaged in an alternating fashion (Swinnen et al., 1997). When subjects bimanually rotate disks with their index fingers in the out-of-phase mode, for example, increasing the movement frequency ultimately results in transition toward the in-phase mode, but the opposite transition does not occur (Kelso, 1984).

Many fMRI studies have investigated bimanual coordination, focusing on comparisons between unimanual and bimanual movements, and between in-phase and out-of-phase bimanual movements. The first comparison, between unimanual and bimanual movements, has been discussed primarily under two alternative hypotheses. One view argues that bimanual coordination is achieved by recruiting networks additional to those involved in unimanual hand movements (Debaere et al., 2004; Koeneke et al., 2004; Nair et al., 2003; Toyokura et al., 2002; Wenderoth et al., 2005b). The other view argues that a different temporal modulation of the same unimanual network is sufficient to sustain bimanual movement, without recruiting additional brain regions (e.g. Grefkes et al., 2008; Macaluso et al., 2007; Walsh et al., 2008). Very recently, it has been proposed that neural dynamics are dominated by temporal modulation of unimanual networks during execution of stable bimanual coordination patterns, with recruitment of additional areas during periods of instability or transition (Banerjee et al., 2012).

Converging neuroimaging data show that, in right-handed subjects, the (left) dominant hemisphere plays a principal role in performing bimanual symmetrical (in phase) movements, whereas the (right) non-dominant hemisphere has a key role during the execution of bimanual asymmetrical (out of phase) movements (Aramaki et al., 2006a; Maki et al., 2008; Meyer-Lindenberg et al., 2002; Sadato et al., 1997; Wenderoth et al., 2004). Within this right-brain network, the activity of certain brain areas has been described repeatedly. Increased activation during asymmetric movements has been observed in the dorsal premotor cortex (PMd) (Aramaki et al., 2006b; Sadato et al., 1997; Wenderoth et al., 2004); the cingulate motor area (CMA) (Ehrsson et al., 2002; Immisch et al., 2001); parietal areas (Diedrichsen et al., 2006; Ehrsson et al., 2002; Wenderoth et al., 2004, 2005a, 2005b); the cerebellum (Debaere et al., 2004; Nair et al., 2003); and in the Supplementary Motor Area (SMA) (Aramaki et al., 2006a; Debaere et al., 2004; Ehrsson et al., 2002; Immisch et al., 2001; Matsuda et al., 2009; Meyer-Lindenberg et al., 2002; Sadato et al., 1997).

The present study, incorporating both Real and Imagery tasks, was designed with two main goals: 1) to investigate the magnitude of spatial bimanual coupling during the Real and Imagery tasks; and 2) to evaluate and compare brain activity related to bimanual coupling for such task conditions. Previous studies have investigated the afferent versus efferent locus of bimanual coupling. These studies suggested that the interference effect cannot be modulated by manipulating afferent sources of information, and they concluded that spatial interference primarily emerges at the efferent level of movement planning and organization (Swinnen et al., 2003). Accordingly, in pathological conditions, spatial coupling effects should be observed even in the absence of actual movements of one hand. Garbarini et al. (2012) described bimanual coupling effects in left hemiplegic patients affected by anosognosia for

hemiplegia (denial of paralysis), who claimed to move their paralyzed hand when asked to draw lines with the right hand and circles with the left hand. Although no movement of the left hand occurred, lines drawn with the right hand showed clear “ovalization”. Using the same Circles–Lines paradigm, similar results were also found in amputees with illusory movements of the phantom limb (Franz and Ramchandran, 1998) and in brain-damaged patients affected by an atypical form of hemisomatoagnosia, who identified other people's limbs as belonging to themselves (Garbarini et al., 2013). In these lesional studies, the actual movement execution seemed unnecessary for bimanual coupling to occur: motor intention and programming was sufficient to trigger the interference effects.

This raises the question whether similar effects are present during a motor imagery task, in which normal subjects imagine that the left hand is drawing circles while the right hand is actually drawing lines. Many studies have shown that cerebral regions recruited during motor imagery and during motor execution overlap substantially (Ehrsson et al., 2003; Frak et al., 2001; Gerardin et al., 2000; Jeannerod and Frak, 1999; Parsons, 2001; Porro et al., 2000; Sacco et al., 2006), with brain activity during motor imagery associated more closely with that during the pre-executive (preparation) stage of real movement than that during the movement execution stage and analysis of sensory afferents (Hanakawa et al., 2008). Given the commonality of circuits between planned and imagined actions, it is reasonable to hypothesize that motor imagery triggers a similar motor intention-programming cascade of events as motor execution. If this is the case, then it is expected that, at the behavioral level, imagining drawing a circle with one hand will influence the trajectories of the other hand actively engaged in drawing lines. Importantly, although behavioral performance is difficult to assess in many imagery experiments, the tasks employed in the present study are designed to objectively and quantitatively reveal how imagery ability interacts with motor behavior, based on the amount of ovalization in line drawings.

Regarding the second goal of the present study, and based on the literature cited above, a similar brain activity is expected in both Real and Imagery tasks within the network related to the intention-programming system, mostly involving prefrontal–parietal circuits (e.g., Desmurget and Sirigu, 2009; Haggard, 2008). The use of both Real and Imagery tasks in the same study provides further information with respect to the existing pertinent functional neuroimaging literature involving actual movement execution. Specifically, the approach allows discrimination between two different components of bimanual coupling: one strictly related to actual execution of the Non-congruent movement, and the other related to selection and planning of the Non-congruent motor program. The first component is expected to be specific to the Real task; the second is expected to be common to both Real and Imagery tasks. Several lines of evidence suggest that two candidate brain regions will be crucially implicated in the latter prediction: medial wall motor areas, and parietal areas. For both areas, a role in bimanual movements has been previously described (e.g., Sadato et al., 1997; Wenderoth et al., 2004), as well as a functional distinction between regions subserving motor execution or motor intention and planning (e.g., Andersen and Buneo, 2002; Picard and Strick, 2001). In particular, based on the existing literature we predict that our experimental design will emphasize the functional role of the medial prefrontal and posterior parietal areas in the “abstract” selection of Non-congruent (CL) motor programs, irrespective of task (Real or Imagery).

Materials and methods

Subjects

Twelve healthy young subjects were recruited for the present study (mean age = 28.8, SD = 3.3). Two subjects were excluded from the analysis because of technical problems during data acquisition. All subjects had no history of psychiatric or neurological illness, and all were

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