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Shared neural resources between left and right interlimb coordination skills: The neural substrate of abstract motor representations

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ABSTRACT

Functional magnetic resonance imaging was used to reveal the shared neural resources between movements performed with effectors of the left versus right body side. Prior to scanning, subjects extensively practiced a complex coordination pattern involving cyclical motions of the ipsilateral hand and foot according to a 90° out-of-phase coordination mode. Brain activity associated with this (nonpreferred) coordination pattern was contrasted with pre-existing isodirectional (preferred) coordination to extract the learning-related brain networks. To identify the principal candidates for effector-independent movement encoding, the conjunction of training-related activity for left and right limb coordination was determined. A dominantly left-lateralized parietal-to-(pre)motor activation network was identified, with activation in inferior and superior parietal cortex extending into intraparietal sulcus and activation in the premotor areas, including inferior frontal gyrus (pars opercularis). Similar areas were previously identified during observation of complex coordination skills by expert performers. These parietal-premotor areas are principal candidates for abstract (effector-independent) movement encoding, promoting motor equivalence, and they form the highest level in the action representation hierarchy.

Introduction

Once a motor skill is acquired, it can often be performed with effectors not previously involved in practice. A typical example of this is handwriting, where the necessary strokes that were initially acquired by the dominant hand, can also be produced with the non-dominant hand, foot, or other segments (Wright, 1990). This ability to accomplish the same goal by variable means is referred to as motor equivalence (Lashley, 1930) and suggests that an abstract movement representation is engraved during practice, independent of the specific muscle activations. This observation has inspired considerable research efforts into identification of the motor program's content, defined as an abstract code of motor information in memory, without specific reference to the effectors recruited for skilled performance (Schmidt, 1975).

Considerable behavioral support for limb-independent movement representations has been obtained from transfer studies evaluating the influence of learning a task with one effector on performance with another (Imamizu and Shimojo, 1995; Grafton et al., 1998; Criscimagna-Hemminger et al., 2003; Vangheluwe et al., 2004, 2005). However, much less is known about their neural implementation within the central nervous system. More than hundred years ago, Liepmann elaborated upon the limb-independent neural foundation for motor skills and proposed that movement representations (i.e. "movement formula") are stored in the left parietal cortex and forwarded to bilateral frontal areas, controlling movements at either body side (Liepmann, 1905).

Examining commonly activated areas across motor skills performed with the right versus left limbs, imaging work has supported the important role of the left hemisphere in controlling movements bilaterally, generally supporting Liepmann's viewpoint (Kuhtz-Buschbeck et al., 2003; Haaland et al., 2004). Furthermore, studies have also explored neural representations of abstract codes for movements performed with effectors on the same body side. However, none of the aforementioned studies addressed this question in the context of acquisition of new complex coordination skills with both sides of the body. This is not a trivial matter because the search for shared neural resources and the associated lateralization of brain activity depends on many factors, such as the type of effector, task complexity, skill level, and the amount of task experience.

Here, we used fMRI to trace the neural basis of motor equivalence, inferring shared (effector-independent) neural activations across newly acquired left and right limb coordination tasks. A novel approach was used, consisting of three stages. First, to guarantee

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the formation of a new motor representation, subjects were involved in substantial practice of an unfamiliar ipsilateral coordination task, requiring cyclical flexion-extension movements of the right (or left) hand and foot, such that one segment lagged with respect to the other by a quarter of a cycle (also known as 90° out-of-phase, $\Phi = 90°$). This new pattern differs from the preferred ipsilateral coordination mode in which both limb segments are moved in the same direction in extrinsic space (i.e., isodirectional, $\Phi = 0°$). Whereas the latter pattern can be produced spontaneously and with minimal effort, the acquisition of nonpreferred phase relations requires substantial practice (for bimanual coordination examples, see Lee et al., 1995; Swinnen et al., 1997a,b; Debaere et al., 2004b; Zanone and Kelso, 1992). Second, to focus on the formation of new motor representations, the activations obtained during the learned (nonpreferred) coordination mode were contrasted against those of the isodirectional (preferred) mode. Third, the regions that were commonly active across the learned left and right limb coordination modes were identified by means of a conjunction analysis.

This procedure allowed us to identify critical candidate areas supporting the abstract (effector-independent) features of the central representation, developed during skill acquisition. Although previous studies have compared brain activations associated with left and right limb movements, use of a learned complex coordination pattern involving upper and lower limb segments has not been made, nor has the aforementioned three-stage analysis approach been implemented. Using this new approach, brain areas within the parieto-frontal network were targeted, as identified by Liepmann's seminal work and subsequent ideomotor apraxia studies (Haaland et al., 2000). Furthermore, based on recent action observation studies of complex gross motor skills (Calvo-Merino et al., 2005; Cross et al., 2006), we anticipated that the superior and inferior parietal lobe and the inferior frontal gyrus, would play a prominent role in the abstract spatiotemporal codes for complex coordination skills.

Materials and methods

Subjects

Fourteen subjects (eight males and six females, age 19–28 years) participated in the experiment. They were all right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and naive with respect to the task. Prior to participation, subjects were informed about the experimental procedure and provided written informed consent. The study design was approved by the local Ethics Committee of Biomedical Research at K.U. Leuven and was in accordance with the guidelines of the Declaration of Helsinki (1964).

Experimental design

Task

Subjects acquired a left/right cyclical ipsilateral hand-foot coordination task, requiring rhythmical flexion and extension movements, with one limb required to lead the other by a quarter cycle, resulting in a phase offset of 90° (90° TASK). This task can only be performed after substantial practice, implying that a novel representation of the task has to be acquired (for bimanual examples, see Lee et al., 1995; Zanone and Kelso, 1992). By contrast, isodirectional coordination, in which both limb segments are moved upwards and downwards simultaneously (ISO task), is inherent to our motor system and does not require practice for successful performance (Baldissera et al., 1982; Carson et al., 1995; Swinnen et al., 1995). Preferred coordination modes do not exhibit substantial changes in brain activation when practiced extensively (for a preferred bimanual pattern, see Debaere et al., 2004a). Moreover, preferred (isodirectional) movements produce the same net motor output (i.e., flexion-extension of the same effectors), but with a different spatio-temporal pattern. Accordingly, it is an optimal control condition to ensure equality of kinematics. All movements were metronome paced (KORG DTM-12, Tokyo, Japan) at a movement frequency of 1.1 Hz (66 beats per minute), whereby an entire movement cycle had to be completed on every beat. The coordination tasks were performed at the right (r) and left (l) body side. Compared with the sequencing and adaptation tasks predominantly used in medical imaging studies on learning, the present coordination task combines successive as well as simultaneous motor elements into an integrated complex spatiotemporal organizational structure, i.e., directional relations between the limb segments change at each quarter cycle. Moreover, the principles governing interlimb coordination are not a mere extrapolation of those involved in unimanual tasks (Swinnen, 2002).

Kinematic registration

Laying supine inside the actual or "dummy" scanner, subjects' forearms and lower legs were supported by a cushion to facilitate free wrist and ankle rotation. The limb segments were positioned in non-ferromagnetic wrist–hand and ankle–foot orthoses, restricting the movements to flexion-extension in the sagittal plane. The anatomical joint axis was aligned with the axis of rotation of the orthosis. High precision shaft encoders (4096 pulses per revolution, sampling frequency 100 Hz) were fixed to the frictionless movement axis of each orthosis to register angular displacements of the joints on-line during both training and scanning.

Training

Before scanning, the 90° out-of-phase pattern was intensively practiced during five successive days. At the start of each daily learning session, subjects performed five trials (30 s per trial) of the isodirectional coordination task ($\Phi = 0°$) with their right and left body side. Then, they practiced the 90° out-of-phase coordination task for 60 trials per day, subdivided into twelve blocks of five trials (30 s per trial), amounting to >8000 individual movement cycles across the 5 days of practice. Organization of training, using the left or right body side, was randomized across subjects. Participants switched to a different body side following every three practice blocks. During learning, augmented visual feedback was provided by means of a Lissajous figure, which represented the wrist movement on the X-axis and the ankle movement on the Y-axis. A circle appeared on the screen when participants correctly performed the 90° out-of-phase coordination task, providing them with on-line feedback in real time to support performance. To learn to generate the task internally (i.e., without any visual feedback), the number of visually guided trials was gradually decreased across the 5 learning days, i.e. from five to two feedback trials per block across days 2 to 5 (fading feedback schedule).

Scanning

The general experimental setup was the same as in the dummy scanner. Participants performed the following conditions in the scanner: (1) the learned 90° out-of-phase task with their left (90° l) and (2) right (90° r) body side, (3) the isodirectional task with their left (ISO l) and (4) right (ISO r) body side, and (5) a rest condition in which no movements were performed (rest). Movement imagery conditions were also included but these are not reported here. The condition order was randomized across subjects. All conditions were performed without visual feedback and were metronome paced. To avoid confounding eye movements, participants were trained to fixate a cross, displayed in front of them. Head movements were restricted by a bite-bar. The mean translation and rotation parameters for the whole group of subjects were 0.36, 0.54, 0.80 and 0.47, 0.40. and 0.34, respectively.

Following training, task related changes in neural activity were determined by measuring the blood oxygen level-dependent (BOLD) signal using echoplanar imaging on a 3 T Intera MR scanner (Philips, Best, The Netherlands), with a 6-element SENSE head coil (MRI