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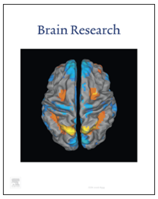

Research Report

Brain activation profiles during kinesthetic and visual imagery: An fMRI study

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ABSTRACT

The aim of this study was to identify brain regions involved in motor imagery and differentiate two alternative strategies in its implementation: imagining a motor act using kinesthetic or visual imagery. Fourteen adults were precisely instructed and trained on how to imagine themselves or others perform a movement sequence, with the aim of promoting kinesthetic and visual imagery, respectively, in the context of an fMRI experiment using block design. We found that neither modality of motor imagery elicits activation of the primary motor cortex and that each of the two modalities involves activation of the premotor area which is also activated during action execution and action observation conditions, as well as of the supplementary motor area. Interestingly, the visual and the posterior cingulate cortices show reduced BOLD signal during both imagery conditions. Our results indicate that the networks of regions activated in kinesthetic and visual imagery of motor sequences show a substantial, while not complete overlap, and that the two forms of motor imagery lead to a differential suppression of visual areas.

1. Introduction

In the context of theories of embodied cognition, motor imagery (MI) is said to involve fundamentally the same neuronal circuit as the execution of complex voluntary acts (e.g. Decety, 1996; Jeannerod, 1995; Jeannerod and Decety, 1995; Jeannerod and Frak, 1999). In the case of hand movements like finger tapping, this circuit involves, among other brain structures, the region corresponding to the arm and hand representation in the primary motor (M1) and somatosensory (S1) cortex of the contralateral hemisphere, the premotor cortex (Witt et al., 2008) and, in the case of self-initiated actions, the supplementary motor area (SMA) (Nachev et al., 2008). The suggestion that imagined actions are likely to involve the same circuit as actually executed (and observed) ones is based on the notion that a motor image is the conscious representation of a non-executed action (Jeannerod, 1994, 1995).

There is ample evidence that imagined actions bear the same temporal regularities and the same responsiveness to physical laws as their overt counterparts (Anquetil and Jeannerod, 2007; Decety et al., 1989; Sirigu et al., 1995a, 1995b) and that real and imagined hand movements share partially overlapping neuronal networks (Ehrsson et al., 2003; Gerardin et al., 2000; Lotze et al., 1999; Nair et al., 2003; Porro et al., 2000; Roth et al., 1996; Sharma et al., 2008). However, despite the general consensus regarding regional overlap between imagery and sensory processing, there is disagreement concerning the set of areas that support the generation of mental motor representations and, more so, when subjects have to form these representations adopting different perspectives (Hetu et al., 2013). An important area whose involvement in motor imagery has been repeatedly debated is the primary motor cortex (M1) (Dechent et al., 2004; Guillot et al., 2012; Hetu et al., 2013).

There are several factors that can account for the discrepancies concerning the set of areas activated during motor imagery and the activation of M1 in particular (Dechent et al., 2004; Hetu et al., 2013; Lotze and Halsband, 2006). It has been suggested that the lack of agreement among studies could be due to the inadequate sensitivity of the neuroimaging methods to capture small or transient activations (e.g. Dechent et al., 2004; Hetu et al., 2013).

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Specifically, that the whole brain analysis that is used in many studies, may be inadequate to capture such activations and a regions of interest (ROI) approach may be a more sensitive method (Hetu et al., 2013); or, as it has been suggested that the usually employed general linear model has limitations which may be surpassed using multivariate models (e.g. Norman et al., 2006; Peelen and Downing, 2007; Sauvage et al., 2011). A second reason for the diversity of the results could be the type of action that subjects are imagining. For example, imagery of simple movements may or may not recruit different neuronal populations than imagery of complex motor acts (e.g. Gerardin et al., 2000) as could imagining novel versus skilled, overlearned movements (e.g. Lacourse et al., 2005).

Another, quite plausible reason for the discrepancies in the literature, may be the strategy employed during performance of the task. Imagining an action can involve visual, kinesthetic or both imagery strategies (e.g. Guillot et al., 2009; Madan and Singhal, 2012). One may engage predominantly in “external visual imagery” meaning that one imagines someone else performing the imagined action (Callow and Hardy, 2004; Fourkas et al., 2006; Lorey et al., 2009; Moran, 2009; Ramsey et al., 2010) which coincides with what others call imagery from the third person perspective (e.g. Jackson et al., 2006; Holmes and Calmels, 2008; Guillot et al., 2009). Alternatively one may engage instead in “internal visual imagery” involving imagining oneself performing the action. However, as many investigators have commented (e.g. Ruby and Decety, 2001; Callow and Hardy, 2004; Lorey et al., 2009; Jiang et al., 2015), this form of strategy may confound visual and kinesthetic imagery. More explicitly, when people resort to such a strategy they may imagine the sensation one experiences during performance of an act (kinesthetic imagery) or visualize themselves performing this act as being the spectators of their own actions (visual imagery). Consequently, instructions to the subjects to either visualize themselves performing the act or to use kinesthetic imagery and imagine themselves moving in the appropriate way (e.g. Jiang et al., 2015) are essential to avoid complicating interpretation of the neuroimaging data.

Reviewing the relevant literature one can find many examples that demonstrate how different strategies applied by subjects may introduce ambiguity in the interpretation of the results. For example, Leonardo et al. (1995) used a simple finger-to-thumb opposition movement and asked their participants to imagine themselves performing this action. This study does not clarify the strategy the participants used and the general statement (i.e. “… imagine themselves performing…”) does not allow us to appraise their finding of activation of the contralateral sensorimotor cortex. Similarly, Lotze et al. (1999) found M1 activation when they asked their participants to imagine forming a fist without explicitly reporting the imagery strategy that was used. Later studies too, in which the motor imagery modality was not specified, also replicated the finding of M1 activation (e.g. Diers et al., 2010). On the other hand, other studies where it was also not specified whether the participants adopted the kinesthetic or visual strategy during the internal imagery, did not report activation of M1 in the imagery condition. In one such study, the researchers used simple and complex flexion/extension finger movements and asked the participants to imagine performing these movements (Gerardin et al., 2000).

Equally puzzling results are also observed in studies where the modality of imagery is specified. For example, Porro et al. (1996) reported increased activation in M1 during mental representation of sequential finger movements, when the instructions for motor imagery were “to imagine using the right hand to perform movements and feeling the sensations associated with finger-tapping”, therefore urging the participants to employ both visual and kinesthetic imagery. Furthermore, studies in which participants used only kinesthetic imagery (e.g. Guillot et al., 2008; Zhang et al., 2011) do find activation of M1, perhaps pointing to the direction that kinesthetic rather than visual imagery is essential for recruiting M1. However, the same data indicate that M1 recruitment may depend on the different imagery capabilities of the participants and not on the specific type of imagery (Guillot et al., 2008). On the other hand, there is accumulated evidence that M1 is not recruited either in the visual or in the kinesthetic imagery (e.g. Stephan et al., 1995; Hanakawa et al., 2008; Guillot et al., 2009; Fleming et al., 2010; Chang et al., 2011; Szameitat et al., 2012). Moreover, whether kinesthetic or visual imagery is adopted may depend on how well subjects may have already developed their internal motor representations (e.g. Olsson et al., 2008).

Therefore, a major challenge in imaging the circuits that mediate imagining motor acts is the choice of the appropriate experimental design as well as the specification of the kind of mental imagery subjects are to engage in during scanning, given the many and varied imagination strategies people are able to adopt.

The aforementioned studies are few examples in the vast literature on motor imagery which indicate that we have yet to reach a solid conclusion regarding the network that is consistently activated during motor imagery and whether this network involves M1, in particular. In fact, a recent meta-analysis of 122 motor imagery experiments (from 75 papers) reports that only 22 of them mention activation of M1 and 100 do not (Hetu et al., 2013).

To minimize such confounds and maximize the use of either kinesthetic imagery while subjects imagined themselves performing an act or visual imagery when asked to imagine someone else performing the act, we trained our subjects in these two strategies using concrete examples of an act they had first to actually perform and actually observe during an execution and observation condition. Specifically, to reduce the uncertainty associated with the strategy used during motor imagery tasks, it was necessary to provide individuals with concrete examples of precisely what was to be imagined. Accordingly, we trained a group of participants to perform finger tapping movements and then to imagine performing the same movements (kinesthetic imagery). Moreover, we instructed them to observe the same videotaped action performed by someone else and immediately afterwards to imagine what they had just observed (visual imagery). This way, by specifying the strategies that individuals adopt in performing tasks, one could probably identify the cortical regions that are differentially activated in the two modalities, and the possible contribution of the primary motor cortex in each case (Fig. 1).

2. Results

As detailed in Table 1 and in Fig. 2(a), for the condition of action execution, the entire sensory-motor circuit, including the contralateral premotor, motor, somatosensory and parietal cortices, was significantly activated as expected (Witt et al., 2008). In particular, activations were observed in the primary motor and somatosensory cortices (BA 4 and BA 2/3) at the level of representation of the upper limb, the dorsal and ventral parts of the premotor cortex (BA 6), the inferior parietal area BA 39, the prefrontal areas BA 8 and BA 9, as well as in frontal areas BA 46 and BA 47. Visual areas BA 17 and BA 18 were significantly activated bilaterally, since the execution task was carried out with the eyes open whereas the control condition with the eyes closed. Finally, action execution induced activations in the cerebellum ipsilateral to the moving hand as well as in the contralateral putamen of the basal ganglia.

For the condition of action observation (Table 2 and Fig. 2(b)), significant activations were found in the primary visual cortex (BA 17) as well as in the middle and inferior occipital gyri (BA 18 and