

Mental imaging of motor activity in humans

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Motor imagery corresponds to a subliminal activation of the motor system, a system that appears to be involved not only in producing movements, but also in imagining actions, recognising tools and learning by observation, as well as in understanding the behaviour of other people. Recent advances in the field include the use of techniques for mapping brain activity and probing cortical excitability, as well as observation of brain lesioned patients during imaging tasks; these advances provide new insights into the covert aspects of motor activity.

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Abbreviations

fMRI	functional magnetic resonance imaging
MEP	motor-evoked potential
PET	positron emission tomography
SMA	supplementary motor area
TMS	transcranial magnetic stimulation

Introduction

Motor imagery is now becoming a hot topic in the field of cognitive neuroscience. A major conceptual advance in the past three or four years, which we will discuss in this review, has been to decouple the mental phenomenon of simulating an action from the conscious representation of that action. New methodologies are now being developed where subjects have to go through the process of mental simulation before they can give a response on the feasibility of a movement. Objective cues, such as pattern of responses or response time, can then be correlated with neural events observed during this mental activity.

The two sides of motor imagery: explicit and implicit motor images

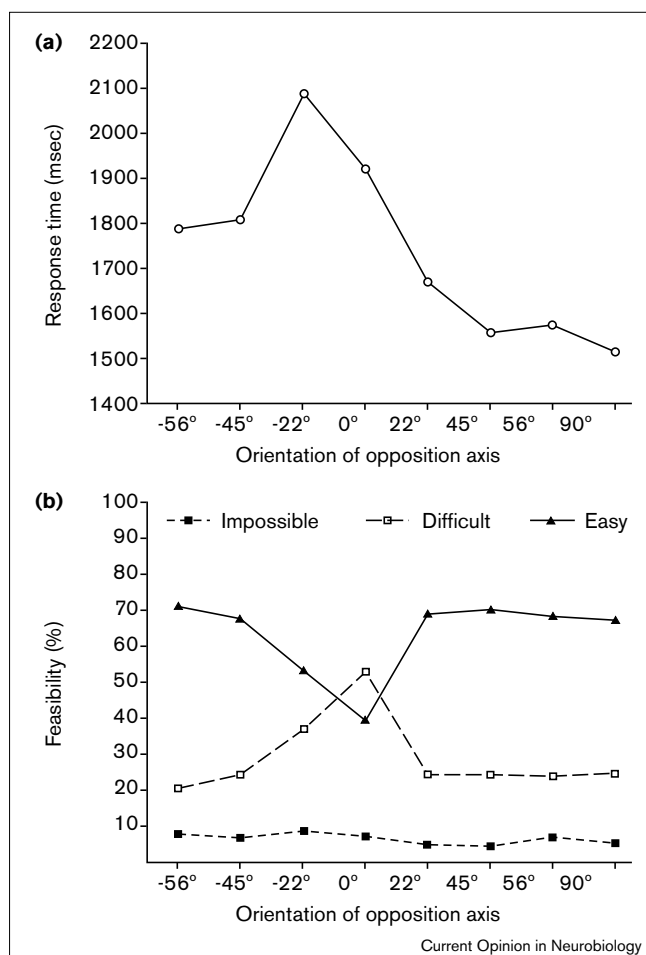
Whereas the term ‘motor image’ classically refers to explicit or conscious representation of an action (imagine yourself running or raising your hand), the same concept also includes other, implicit or unconscious, aspects of the same phenomenon. One example of implicit motor imagery is provided by Frak *et al.* (V Frak, Y Paulignan, M Jeannerod, unpublished data): subjects were shown a glass of water from above with an indication of where the thumb and the index finger should contact it. Subjects, without performing the action, had to judge (by pressing on different keys) whether the action of raising the glass and pouring the water in another container would be easy, difficult or impossible for each set of finger positions. Their pattern of responses followed the limitations that

the geometry of the upper limb would have imposed on real motor performance. This implies that although they received no instruction to do so, they unconsciously simulated the movement before giving the response. Their response times (within 1500–2000 ms) increased with the estimated difficulty of the task (Figure 1). This result is in line with other observations showing that recognition of the handedness of a visually presented hand depends on covert sensorimotor processes [1,2^{**},3–5].

As a rule, these experiments tend to converge on a common finding, namely that the time to give the response reflects the degree of mental rotation needed to bring one’s hand in a position adequate for achieving the task. This implicit process is the motor counterpart of the classical mental rotations or displacements used for giving responses about visual objects. Unlike three-dimensional shapes, however, which can be rotated at the same rate in any direction, rotation of one’s hand is limited by biomechanics of the arm joints [6]. According to Parsons and Fox [7], response times thus reflect biomechanically compatible trajectories, at the same rate seen for executed movements. Parsons *et al.* [2^{**}] further showed that in handedness recognition, these sensorimotor processes are also constrained by the neural structures controlling the side of the hand to be recognized. In two split-brain subjects, they found that handedness recognition was almost impossible when an image of a right hand was visually presented to the right hemisphere, whereas recognition was normal when it was presented to the left hemisphere (which controls the movements of the right hand). Interestingly, in normal subjects, response times also reflect a better recognition of handedness by the hemisphere contralateral to the presented hand [3].

Similar effects on response times have been observed when making judgements on how to use hand-held objects or tools. According to Tucker and Ellis [8], such objects automatically potentiate the actions they afford. Our implicit knowledge about actions influences the way we cognitively process the visual world [9]. Another form of implicit mental operation has been recently added to the realm of motor imagery — this is the cognitive process related to recognising and understanding actions observed from other individuals. It has often been suggested that an action can only be understood to the extent that it can be performed by the observer [10,11] — the general idea of ‘knowing by simulated doing’ [12]. Thus, observing an action would activate within the observer the same mechanisms that would be activated were that action intended or imagined by the observer. In turn, this implicit representation in the brain of how movements are generated influences interpretation of observed actions. Hence, there are benefits to

Figure 1



Trials with unconstrained finger positions showing the influence of orientation of opposition axis on (a) the feasibility level and (b) response time. The subjects were seated in front of a horizontally placed 15" monitor. A cylindrical container filled with water (5 cm x 3 cm) was placed at the centre of the monitor screen at a distance of 50 cm from the body plane. Subjects were asked to lift the plastic cylinder and pour the water into another container using a precision grip formed by the thumb and index fingers of their right hand. They were also asked to carefully observe the axis defined by the contact points of the fingers on the cylinder surface, along which the force was applied during the grasp (the opposition axis). After several repetitions of this task, the cylinder was removed and the computer monitor was used to display the target stimuli. In each trial, an image of the upper surface of the cylinder (a circle) was presented for 5 s at the same location where the real cylinder was placed during the preliminary run. Each circle was marked with two contact points, with a defined opposition axis at various orientations with respect to the frontal plane. When shown a stimulus, the subjects were required to answer as quickly as possible whether the previously experienced action of grasping the cylinder full of water and pouring the water would be possible with the fingers placed according to the opposition axis indicated on the circle. No actual movement was allowed. The subjects had to rate the level of feasibility of the grasp using three levels ('easy', 'difficult' and 'impossible') by pressing one of three keys with their left hand. (a) Response times were longer for the grasps judged to be more difficult due to the orientation of opposition axis, as shown in (b). From V Frak, Y Paulignan, M Jeannerod, unpublished data.

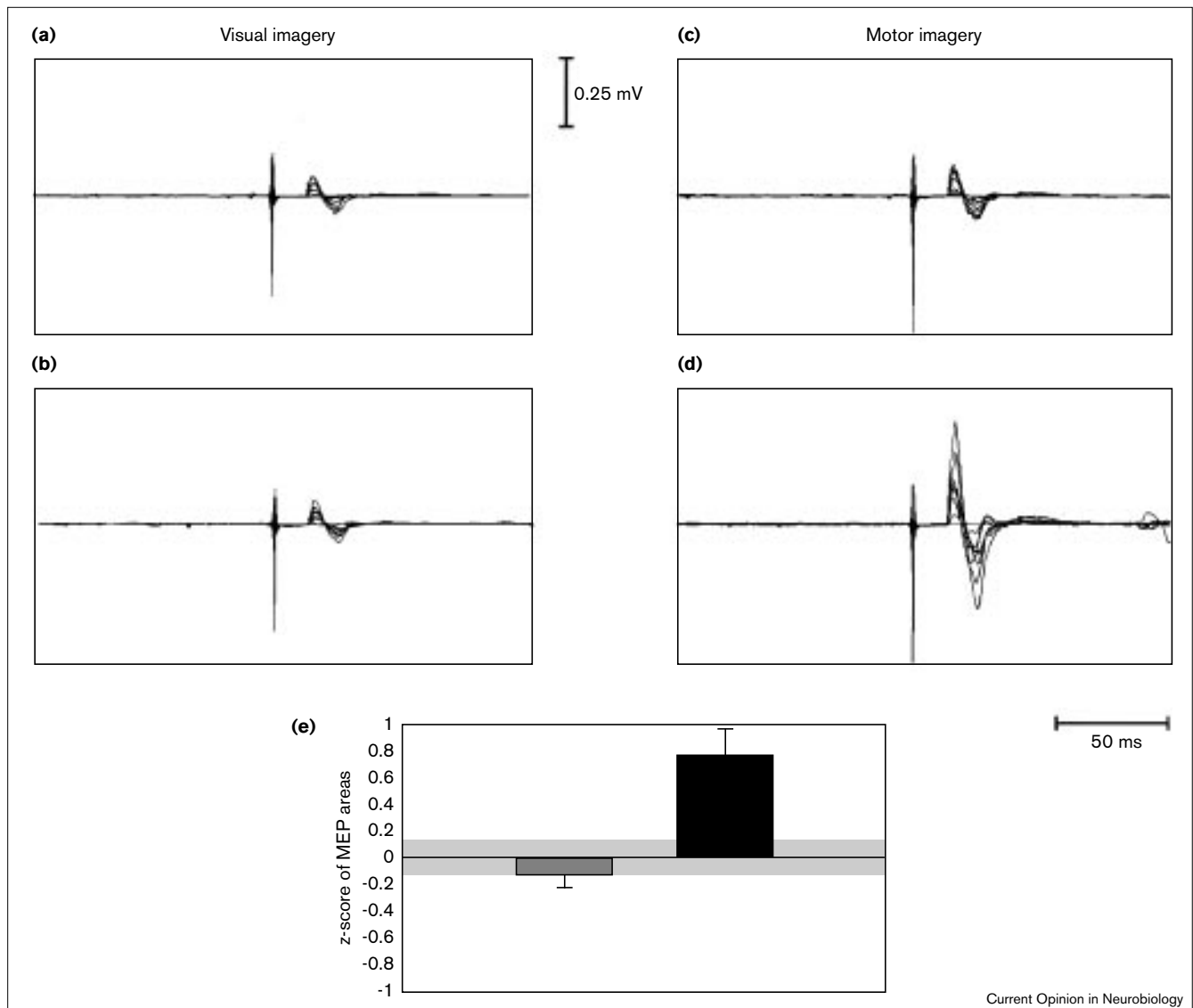
observing actions of others for understanding their behaviour and for learning new motor skills (known as 'observational learning').

How similar are a simulated and an executed action?

This new approach to motor imagery, which focuses on the vehicle (the brain mechanisms involved) rather than on the content of motor images, was critical for retrieving useful results from experiments where the only data were based on subjective reports. If a motor image bears any relationship to the action it simulates, then properties pertaining to the action should be expressed in the image. This similarity is clearly illustrated by results obtained using the mental chronometry paradigm. It is known, for example, that simulated actions take the same time as executed ones (for a review of earlier work, see [13]). Sirigu *et al.* [14] have reached the same conclusion by instructing subjects to mentally move their index finger between two imaginary targets. Mental movement was paced by a metronome beating at an increasing rate. Subjects had to indicate when they could no longer follow the metronome rate with their mental movement. The metronome frequency at which this occurred was very close to the break frequency for actual movements. In addition, the break frequency was a function of the size of the imaginary targets between which the subject had to move, hence replicating the classical speed/accuracy tradeoff (the so-called Fitts' law) observed with real alternating movements. This result suggests that simulated movements follow the rules that are known to influence motor behavior [15].

Motor simulation thus relies, at least partly, on mechanisms common with those for motor execution. Further evidence supporting this comes from three main experimental sources, which will be detailed in this and the next sections — studies based on brain metabolism, on brain lesioned patients and on changes in brain excitability. Earlier brain mapping experiments using positron emission tomography (PET) had partly answered the questions regarding activation of cortical and subcortical motor structures during motor imagery. Indeed, these experiments were most useful in demonstrating the existence of a consistent cortical network involved in the generation of motor imagery (for a review of work prior to 1995, see [16]). This network involves structures directly concerned with motor execution, such as premotor cortex, lateral cerebellum, basal ganglia; it also involves areas concerned with action planning, such as the dorso-lateral prefrontal cortex, inferior frontal cortex and posterior parietal cortex [7,17,18,19•]. Comparison with motor execution reveals that the cortical zones activated during imagery only partly overlap with execution zones. In SMA, for example, motor imagery involves pre-SMA ([19•]; E Gerardin *et al.*, personal communication), a region anterior to SMA proper to which activation during execution is limited. A similar dissociation also exists in the parietal cortex (E Gerardin *et al.*, personal communication). Finally, the inferior frontal

Figure 2



Subjects were instructed to imagine forearm flexion–extension movements with their right arm. The course of the mental simulation of the movement was paced by a frequency modulated sound. TMS was applied to the motor cortex on one side, and the MEPs were recorded from the contralateral flexor muscle (biceps brachialis). A typical example from one subject is shown. **(a,b)** A control experiment, where TMS was applied during visual imagery of a luminous bar shrinking or

expanding. No change is observed in the flexor MEPs. **(c)** Flexor MEPs recorded following TMS applied during the extension phase of the motor imagery. **(d)** MEPs recorded following TMS during the flexion phase. **(e)** These MEPs are selectively and significantly increased (black bar: z-score for MEP area of flexor muscle during imagined flexion; grey bar, during imagined extension). From [27*], and reproduced with permission.

cortex, which is activated during mental simulation and suppressed during execution, has been suggested to be the site for motor inhibition during mental simulation [19**].

The effects of brain lesions are also good indicators of the role of some of these brain sites in controlling motor imagery. Basically, the results show that conditions affecting the motor system leave intact the ability to generate motor imagery. Sirigu *et al.* [20] showed that a patient with hemiparesis, due to cortical degeneration and limited to primary motor cortex, was still able to generate motor imagery with

his affected hand, although the mentally simulated movements were decelerated to the same extent as executed movements. In both conditions, however, the speed/accuracy trade-off was preserved (i.e. movements were faster for easier tasks). Similarly, mentally simulated movements have been shown to be slowed down in Parkinson's patients in the same way as executed movements [21]. Parietal lesions, in contrast, seem to alter the ability to generate imagery. In a patient with a unilateral posterior parietal lesion, Sirigu *et al.* [14] observed a dissociation between execution and simulation of tapping movements with the

contralateral arm. Executed movements, although slower than with the ipsilateral arm, retained the speed/accuracy trade-off, whereas the simulated movements did not.

Motor imagery as a subliminal activation of the motor system

The main debate on neural mechanisms of motor imagery now focuses on the degree of involvement of motor pathways, and particularly, primary motor cortex. The most recent studies used either PET or functional magnetic resonance imaging (fMRI) and relate conflicting results. The extensive PET study by Deiber *et al.* [19**] failed to find a significant activation of primary motor cortex and lateral cerebellum during motor imagery of finger movements. fMRI studies, however, unambiguously demonstrate that pixels activated during contraction of a muscle (an intrinsic hand muscle, for example) are also activated during imagery of a movement involving the same muscle [22]. Porro *et al.* [23] carefully demonstrated this point in comparing fMRI signal intensity during a control task (visual imagery) and two 'motor' tasks, motor performance and imagery of repetitive finger opposition movements. fMRI signals were increased during both motor tasks at the presumed site of the primary motor cortex, in the posterior portion of the precentral gyrus. Porro *et al.* were also able to determine that pixels activated during both motor performance and motor imagery represent a large fraction of the whole population of pixels activated during motor performance (note that the question of whether these pixels contain corticospinal cells cannot be answered using such methods). It remains that primary motor cortex activation reported during motor imagery amounts to only ~30% of the level observed during execution [22,23]. For an indirect confirmation of these results using quantified electroencephalography and neuromagnetic techniques, see [24–26].

The role of primary motor pathways in motor imagery can also be analysed using a more direct measurement of cortico-spinal excitability. Transcranial magnetic stimulation (TMS) of the motor cortex was used to trigger motor-evoked potentials (MEPs) in arm muscles during simulated arm movements. MEPs were found to be increased, but only in those muscles involved in the imagined movements. Accordingly, MEPs were selectively increased in a wrist flexor when the subject mentally simulated wrist flexion, whereas MEPs in the antagonist extensor muscle remained unchanged. In addition, other types of imagery (e.g. visual) did not affect MEPs in any of the recorded muscles (Figure 2) [27*,28*,29].

A logical consequence of increased motor cortex excitability is that it should propagate down to the motoneuron level. This is still a controversial issue, however. Bonnet *et al.* [30] found increased spinal reflexes during a mentally simulated isometric foot pressure. Increase was more marked for the limb used for pressing than for the contralateral limb. In addition, T-reflexes (obtained by a tap on the Achilles

tendon) were more increased than H-reflexes (obtained by electrical stimulation of the soleus muscle). By contrast, Hashimoto and Rothwell [28*] and Yahagi *et al.* [31] found no significant increase in upper limb H-reflexes during simulated wrist movements. The discrepancy between these results could not be due to the EMG (electromyogram) level, which was very low in all these studies. One possible explanation is the broad difference in the sites where spinal reflexes were tested: changes in excitability should be less marked at the upper limb level during a wrist movement than at the lower limb level during a postural activity such as foot pressure.

Conclusions

Future research on motor imagery should follow two main directions. First, it will be important to determine the exact nature of the subliminal activation of the motor pathways involved in this process, and, more specifically, to determine whether it actually corresponds to an 'endogenous' activation of motor structures. This will require a complete description of the state of the motor system, which seems difficult with the presently available techniques. For example, standard EMG recordings may miss the activity of deep muscular fibers; the degree of activity of muscle spindle afferents remains unknown [32]. This approach should bridge the gap between the study of cognitive phenomena such as the covert states of action generation, thought to be possible only in man, and the detailed study of the underlying neural mechanisms accessible only in animals. Recent experimental results in monkeys indicate that this possibility is at hand. Neuron discharges in both parietal and premotor cortices have been shown to map the pattern of an action, even when that action will not be produced by the animal (see [33,34]).

At a more applied level, motor imagery should reveal itself as a potent tool for probing and possibly improving the functioning of the motor system. The fact that the motor pathways are globally activated during motor imagery represents a rationale for rehearsing effects observed during motor learning [35,36] and opens new possibilities for rehabilitating patients with motor impairments.

Acknowledgements

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