

Mental motor imagery: a window into the representational stages of action

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The physiological basis of mental states can be effectively studied by combining cognitive psychology with human neuroscience. Recent research has employed mental motor imagery in normal and brain-damaged subjects to decipher the content and the structure of covert processes preceding the execution of action. The mapping of brain activity during motor imagery discloses a pattern of activation similar to that of an executed action.

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Introduction: motor representations

Most of our actions are driven indirectly by internally represented goals, rather than directly by the external environment. Until recently, the existence and structure of such motor representations were inferred from the duration and timing of a reaction, or from the pattern of executed movements [1]. Now, however, a more direct approach has been adopted that exploits the unique ability of human subjects to image and simulate actions consciously [2-4]. Motor imagery is a cognitive state that can be experienced by virtually everyone with minimal training. It corresponds to many situations experienced in everyday life, such as watching somebody's action with the desire to imitate it, anticipating the effects of an action, preparing or intending to move, refraining from moving, or remembering an action [5*,6].

Using motor imagery as a means of analysing covert processes seems justified by previous work on mental imagery in other modalities. Visual imagery engages many of the mechanisms and neural structures employed in visual perception [7,8,9*]. It seems logical, therefore, to look at the motor system for the same direct continuity between mechanisms for the representational stages of action and (action) performance. The experimental arguments reviewed below will demonstrate that a motor image is endowed with the same properties as those of the corresponding (normally covert) motor representation. Namely, it has the same functional relationship to the represented action, the same causal role in the generation of that action, and shares common mechanisms with motor execution.

Physiological correlates of motor imagery

Mental simulation of movement activates motor pathways. During motor imagery, muscular activity often

increases with respect to rest. When this is the case, electromyographic (EMG) activity is limited to those muscles that participate in the simulated action, and tends to be proportional to the amount of imagined effort [10]. The fact that muscular activity is only partially blocked during simulation of movement suggests that motoneurons are close to threshold.

In several other motor imagery experiments, however, EMG is quiescent (e.g. [11]). This does not necessarily contradict the link between motor imagery and muscular activity, as it may merely reflect better inhibition of movement execution under certain conditions or in certain subjects.

This reasoning was confirmed by a recent study of spinal excitability during motor imagery. Bonnet *et al.* (M Bonnet, J Decety, J Requin, M Jeannerod, unpublished data) instructed subjects either to press isometrically on a pedal or to simulate mentally the same action, with two levels of force (weak and strong). Monosynaptic reflexes were increased during mental simulation in the leg involved in the simulated movement, and this increase was more marked for a strong simulated pressure than for a weak one. The increase, which was more marked for tendinous (T)-reflexes than Hoffmann (H)-reflexes, was only slightly less than the reflex facilitation associated with the current performance of the same movement. Whereas both reflexes are conveyed through the same pathways, the effect of the stimulus is significantly different: the H-reflex, which is triggered by the electrical stimulation of Ia fibers, by-passes neuromuscular spindles, whereas the T-reflex is a response to stretching those spindles. A selective increase in excitability of the T-reflex during motor imagery, possibly due to an increase in gamma motoneuron activity, emphasizes the role of spindle afferents, not only during movement execution, but also

Abbreviations

EEG—electroencephalography; EMG—electromyography; fMRI—functional magnetic resonance imaging; H-reflex—Hoffmann reflex; P_{CO2}—CO₂ pressure; PET—positron emission tomography; SMA—supplementary motor area; T-reflex—tendinous reflex.

for organizing the motor output during self-generated actions [12].

Activation of descending motor pathways during mental simulation of movement or related processes is also suggested by experiments measuring cortical responsiveness to transcranial magnetic stimulation. Pascual-Leone *et al.* [13••] found that the size of the area responding to finger movements increases as simulated movements are repeated over training periods, in the same way as when actual movements are repeated. In addition, Gandevia and Rothwell [14] have shown that 'concentrating' on one hand muscle without activating it increases the effect of subthreshold magnetic stimulation of the cortical area corresponding to that specific muscle. Thus, there is a selective enhancement of responsiveness to stimulation of motor cortical areas during motor imagery. A recent experiment supports this notion further. Subjects were requested to observe grasping movements performed by an experimenter. During the observation period, a transcranial magnetic stimulus was applied to their motor cortex. The pattern of muscular response to this stimulus was found to be selectively increased. In addition, Fadiga *et al.* [15••] observed that the set of muscles activated by the stimulus was the same as that used by the subjects when they actually performed the movement. This suggests a common neural basis for imitation, observational learning and motor imagery (see below).

These results raise the problem of the mechanism and the locus of motor inhibition during motor imagery. During motor preparation, the movement is blocked by a massive inhibition acting at the spinal level to protect motoneurons against a premature triggering of action—hence the decrease of spinal reflexes during the preparatory period and their re-increase shortly before the movement starts [16]. During mental simulation, it is likely that the excitatory motor output generated for executing the action is counterbalanced by another, parallel, inhibitory output. The competition between two opposite outputs would account for the partial block of the motoneurons, as shown by residual EMG recordings and increased reflex excitability. It is not yet possible to identify whether this inhibitory output originates in the cortex or elsewhere.

The autonomic system, normally not submitted to voluntary control, is also activated during motor imagery. Heart rate, respiration rate and end-tidal P_{CO_2} (CO_2 pressure) were measured in subjects actually performing or mentally simulating a leg exercise [17,18]. After only a few seconds of actual or mental exercise, heart rate began to increase up to about 50% and 32% over the resting value, respectively. Respiration rate also increased almost without delay during actual effort and during mental simulation [19•]. These results confirm that a large fraction of the fast increase in heart and respiration rates at the onset of exercise (both real and mental) is due to central factors rather than metabolic changes [20]. Vegetative activation during preparation for effort

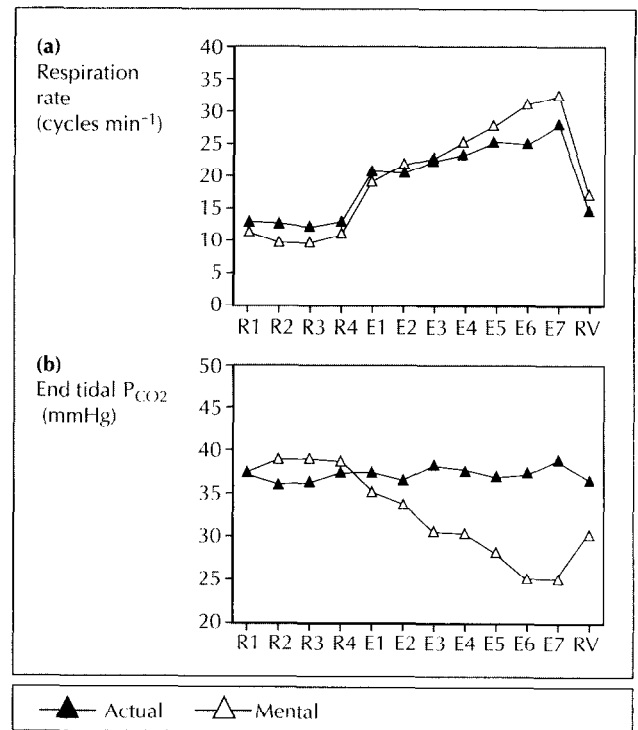


Fig. 1. Ventilatory effects of mental motor imagery. In this experiment, subjects ($n = 10$) were requested to produce a physical effort (pedalling with the right foot against a 15 kg load) for 2 min, and then mentally simulate the same exercise for the same duration. Instructions were to start pedalling at a rate of ~ 1 Hz and then to increase the frequency up to submaximal effort. The noise of the ergometer while the subject performed the actual effort was tape-recorded and played back to the subject during the mental session. (a) Respiration rate and (b) end-tidal P_{CO_2} were sampled every 17.5 s. R1–R4, rest; E1–E7, effort; RV, recovery. Note the sharp increase in ventilation at the onset of effort, and the graded increase during exercise, both actual and mental. Also note the drop in P_{CO_2} during mental effort as a result of increased ventilation in the absence of metabolic demands. Adapted from [18].

is thus part of motor programming. It is timed to begin when motor activity starts, which represents an optimal mechanism for anticipating the forthcoming metabolic changes and shortening the intrinsic delay needed for heart and respiration to adapt to effort (reviewed in [21]).

The possibility that these autonomic changes are a consequence of muscular activity can be ruled out by the spectroscopic analysis performed by Decety *et al.* [18], which shows no change in muscular metabolism during mental simulation. In fact, the combination of increased respiration rate and unchanged muscular metabolism during mental simulation results in a progressive drop of P_{CO_2} in this condition (Fig. 1): this never happens during physical effort, where ventilation eliminates CO_2 at about the same rate as it is produced, and where P_{CO_2} remains constant. Recent work by Gandevia *et al.* [22] also supports this explanation: they observed graded cardiovascular changes in curarized subjects attempting muscular contractions, a situation close to motor imagery. As paralysis was complete, the changes could not be due to residual muscular activity and had to be of a central origin.

Brain activity mapping during motor imagery

Pioneering studies using two-dimensional regional cerebral blood flow (2-D rCBF) mapping or single photon emission computed tomography (SPECT) have emphasized the activity of several brain areas during motor imagery [23–26]. Prefrontal areas, supplementary motor area (SMA), cerebellum and basal ganglia are the main activated areas. Recent positron emission tomography (PET) studies reveal that brain activity is in fact influenced by the nature of the imaginal task. Decety *et al.* [27] instructed subjects to imagine themselves grasping visually presented three-dimensional objects with their right hand. This strongly activated Brodmann area 6 in the inferior part of the frontal gyrus on both sides as well as area 40 in the contralateral inferior parietal lobule. Subcortically, the caudate nucleus was found to be activated on both sides and the cerebellum on the left side. Another focus of activity was observed in left prefrontal areas, extending to the dorsolateral frontal cortex (areas 9 and 46). Finally, the anterior cingulate cortex (areas 24 and 32) was bilaterally activated.

In other studies, where the task consisted of repetitive, internally generated eye [28] or hand [29••] movements, an additional activation of SMA was observed. Interestingly, comparison of externally and internally generated movements in the same subjects showed that SMA activation during simulated movements was more rostral than commonly observed during executed movements [29••,30]. This finding reinforces the notion that SMA is divided into areas of different hierarchical status with different functional implications: the posterior zone is purely executive (the SMA proper) [31], whereas the more anterior zone is more related to representational stages of action and to motor imagery [29••].

Consciously representing an action thus involves a pattern of brain activation that resembles that of an intentionally executed action (Fig. 2; see e.g. [32•]). Whether primary motor cortex is also activated during imagery still remains uncertain. Georgopoulos *et al.* [33] found that the activity of cortical cells in monkey primary motor cortex was modified during the preparatory period of a reaching movement directed toward a memorized target. In humans, however, in spite of the clear activation of descending corticospinal pathways described above, most researchers found no activity in caudal area 4 during imagined movements when using PET [27,29••,34•] or functional magnetic resonance imaging (fMRI) [35,36]. (For an exception, see Pascual-Leone *et al.* [13••], who reported fMRI primary motor cortex activation in this condition, although the level of activation was less than during execution.)

Taken together, the results on the neural correlates of motor imagery provide a good basis for explaining the effects of 'mental practice', now commonly used by sportsmen for mentally rehearsing motor performance [37]. Motor imagery and related states, such as observation of actions performed by others, produce

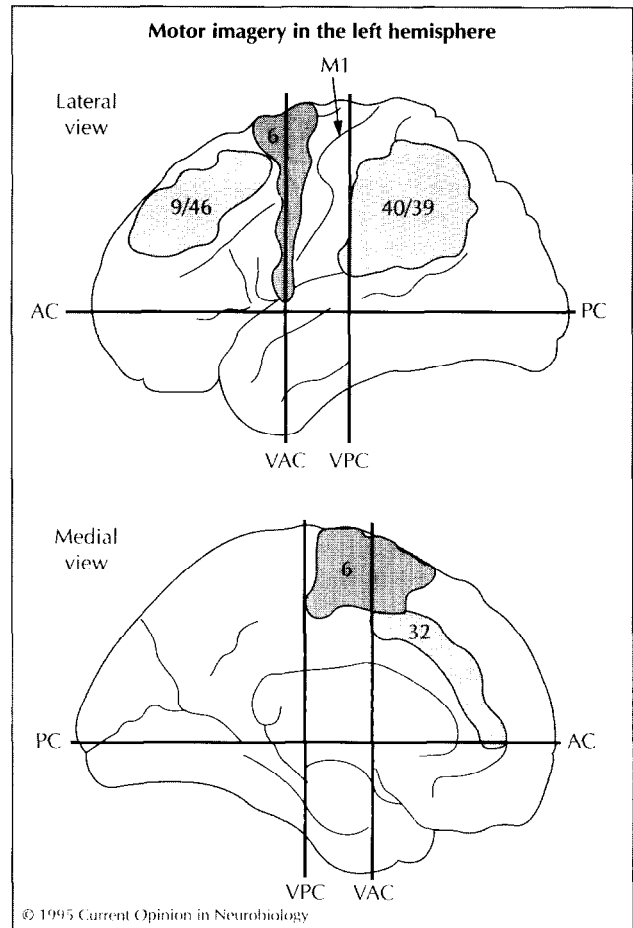


Fig. 2. Pattern of cortical activation during mental motor imagery in normal subjects. The main Brodmann areas activated during motor imagery have been outlined on schematic views of a left hemisphere. Note the consistent involvement of pre-motor area 6, without involvement of primary motor cortex (M1). The AC-PC (anterior commissure to posterior commissure) line defines the horizontal reference plane in the magnetic resonance imaging (MRI) scan. The vertical line passing through the AC (VAC) defines a verticofrontal plane. VPC is the vertical line passing through the PC. Data taken from [27,29••,34•].

a selective enhancement of neural activity in those motor pathways concerned with the simulated action. This leads to an increase in muscle strength [11] and a decrease in the variability of movements [38••]. These results have important implications for the mechanisms of motor learning. As selective improvements in motor performance can be obtained in the absence of an increase in muscular activity (and therefore without re-afferent input from the muscle), they suggest that learning could be due to a purely central shaping of motor output.

Motor imagery in motor disorders

A prediction arising from the close relationship between mental simulation of movement and motor execution is that motor imagery should be affected by motor impairments. The finding that, in normal subjects, mental movement times and real movement times are

closely similar [2] provides a means for verifying this prediction. Accordingly, a pathological condition that slows movements, for example, should also increase mental movement time for simulating the same movements.

Mental movement times were compared in normal subjects and Parkinsonian patients by Dominey *et al.* [39••]. Patients were selected at the early stage of their disease, when they had a predominantly akinetic syndrome and presented essentially unilateral signs (on the right side). Normal subjects and patients were instructed to perform, with either hand, a sequential finger movement (touching the pad of the thumb with the pad of the other four fingers) in conditions of motor execution and motor imagery. Parkinsonian patients were slower than normals in all conditions; during motor execution, their movements were slower than normals in both hands, although this effect was more marked in the right (primarily affected) hand. The same slowness and asymmetry was observed for mental movements. The degrees of asymmetry in both motor execution and mental imagery were significantly correlated (Fig. 3). This result stresses the problem that Parkinsonian patients have in controlling their internal states and, particularly, in using internal cues for shifting between states, as this is required for execution of a sequential task.

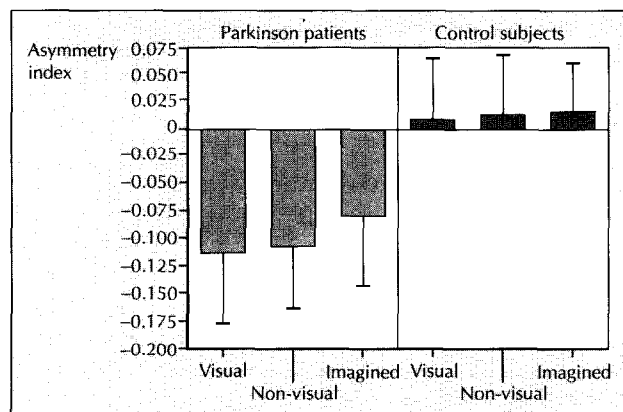


Fig. 3. Histogram demonstrating the slower of motor execution and motor imagery in Parkinson disease patients. Movement time was measured in right-sided hemi-Parkinson patients ($n=7$) and right-handed normal controls ($n=7$), during a sequential motor task (touching the tip of the thumb with the tip of the other fingers, five times in a row) in three different conditions: actual performance under visual control (Visual) and without visual control (Non-visual), and mental performance (Imagined). Measurements were taken between a verbal 'go' signal preceded by a 'ready' signal, given by the experimenter, and a verbal 'stop' signal given by the subject. Both hands were tested, and an 'asymmetry index' was calculated, with positive values indicating faster performance with the right hand, and negative values indicating faster performance with the left hand. Note a rightward (non-significant) bias in control subjects. Parkinson patients, by contrast, showed a much faster performance with the left (unimpaired) hand. The same variation was observed under all three conditions. Adapted from [39••].

Impaired motor imagery in patients with Parkinson disease could, however, have resulted from a general difficulty in generating mental images. In order to

control for this, Dominey *et al.* [39••] compared patients' performance during two mental rotation tasks: letter rotation, where the time to decide whether the letter was normal or mirror-oriented was measured; and hand rotation, where the response depended on whether the hand shown was right or left. Chronometric studies suggest that the latter task is resolved by the subjects mentally making an implicit movement with their own hand until it matches the presented hand [40]. Parkinson patients were slower for hand rotations than for letter rotations, and their performance in hand rotation correlated with their poor imagery performance in the sequential finger movement task.

Hemiplegic patients are also mentally slower with their impaired arm [41]. Recently, a patient with progressive hemiparesis in the left arm due to a right rolandic lesion was tested for her ability to reproduce, both physically and mentally, finger, wrist, elbow and shoulder movements displayed by the experimenter. The left arm was slower in executing motor tasks with the fingers and elbow, but not with the shoulder. The same difference, with the same effectors, was observed for mentally simulated movements [42]. It thus appears that although a motor cortical lesion does not affect the ability to generate motor imagery, it impairs mentally performed actions to the same extent as real movements.

A perspective on apraxia

Apraxic patients become impaired when they have to imitate actions, reproduce actions from memory or pantomime symbolic gestures (the so-called ideomotor apraxia) [43,44]. They also have difficulties in recognizing gestures and discriminating between gestures performed by another person [45]. A patient (LL) with a bilateral posterior parietal lesion described by Sirigu *et al.* [46•] illustrates these points. Hand and finger movements were inadequate when LL was instructed to use an object out of context, such as to perform the gesture of eating soup with a spoon. The spoon was grabbed incorrectly and was turned several times in the fingers. LL's problem was not a pure hand-shaping deficit, as finger posture was correct when she took the object, not for demonstrating its use, but for handing it over to the examiner. The deficit also extended to recognition of correctness or incorrectness of hand postures during object use by the examiner. Finally, LL was equally poor at verbally describing hand postures in relation to unseen objects.

These findings support the notion that the motor impairments observed in apraxic patients result from a specific alteration in their ability to mentally evoke actions, or to use stored motor representations for forming mental images of actions. Thus, the deficit arises when the patient shifts from a strategy where object-oriented actions are processed automatically, to when the content of these actions has to be explicitly represented. A further logical step would be to examine apraxic patients for their ability to generate motor

imagery, with the idea that their deficit in selecting and organizing motor 'memory' will also be revealed when evoking actions mentally [47].

The same could be true for a related disorder, constructional apraxia, also frequently observed following parietal lesions. Patients have no problem recognizing, identifying or naming objects. Yet, they cannot reproduce the same objects by drawing, especially when requested to perform three dimensional drawings for complex objects or geometrical figures. Patients seem to have lost the ability to process visual information for interacting with objects [48], or to identify correctly the object attributes needed for object-oriented actions [3]. Accordingly, it can be predicted that these patients should have no problem in evoking visual images of objects, whereas they should be unable to simulate object-oriented actions mentally.

Conclusions

We have shown converging evidence for a similarity of neural processes involved in central representation of actions and motor imagery. This points to motor imagery as a direct means of accessing the mechanisms of action preparation and imitation.

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