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MENTAL IMAGERY IN THE MOTOR CONTEXT

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Abstract—The working hypothesis of the paper is that motor images are endowed with the same properties as those of the (corresponding) motor representations, and therefore have the same functional relationship to the imagined or represented movement and the same causal role in the generation of this movement. The fact that the timing of simulated movements follows the same constraints as that of actually executed movements is consistent with this hypothesis. Accordingly, many neural mechanisms are activated during motor imagery, as revealed by a sharp increase in tendinous reflexes in the limb imagined to move, and by vegetative changes which correlate with the level of mental effort. At the cortical level, a specific pattern of activation, that closely resembles that of action execution, is observed in areas devoted to motor control. This activation might be the substrate for the effects of mental training. A hierarchical model of the organization of action is proposed: this model implies a short-term memory storage of a 'copy' of the various representational steps. These memories are erased when an action corresponding to the represented goal takes place. By contrast, if the action is incompletely or not executed, the whole system remains activated, and the content of the representation is rehearsed. This mechanism would be the substrate for conscious access to this content during motor imagery and mental training.

Key Words: mental imagery; learning; motor control.

INTRODUCTION

The aim of this paper is to investigate the concept of mental imagery in the context of motor actions. The general idea is that motor imagery is part of a broader phenomenon (the motor representation) related to intending and preparing movements. The process of motor representation, a normally non-conscious process, can be accessed consciously under certain conditions: a motor image is a conscious motor representation. According to this definition, motor images are endowed with the same properties as those of the (corresponding) motor representation, that is, they have the same functional relationship to the imagined or represented movement and the same causal role in the generation of this movement. This idea has been fully developed elsewhere [39]. The aim of the present paper is to examine its implications for a model of action generation.

A possible way of differentiating motor images from other, better known, types of imagery (e.g. visual) is to determine the subjective 'distance' between the self and his own imaginal experience. Mental images can be experienced by the self as a spectator watching a visual scene in which an action is performed by the representing subject himself (the so-called 'external' imagery of sport psychologists, see [45]). Images can also be experienced from within, as the result of the 'first person' process involving mostly a kinesthetic representation of the action ('internal' imagery [45]). Motor imagery would thus belong to the latter type. It would imply that the subject feels himself executing a given action,

whether it involves the whole body (e.g. running), or it is limited to a body part (e.g. writing, pointing to a target or holding pressure against an obstacle). Motor imagery, therefore, requires a representation of the body as the generator of acting forces, and not only of the effects of these forces on the external world. A number of everyday situations correspond to this definition: watching somebody's action with the desire to do it, anticipating the effects of an action, preparing or intending to move, refraining from moving, remembering an action, etc., can be considered as putative motor images. These situations have been extensively used in the context of mental practice (this point will be developed in a later section).

There are at least two ways of dealing with motor images. One is the cognitive approach, using psychological methodology for disclosing the structure and content of the mental phenomenon. The other one is more physiological, based on observation of bodily correlates of motor imagery and eventually on inferring its structure and content from these observations. These approaches will be described in the next two sections.

ACCESSING THE CONTENT OF MOTOR IMAGES

An influential theory (the dual coding theory [50]) concerning the cognitive status of mental imagery consists of splitting the cognitive apparatus into two different modes of generation, the verbal and the non-verbal modes. Imagery would pertain to the latter mode. Hence, images would be generated using modality-specific units (Paivio's *imagens*). *Imagens* correspond to natural objects or object parts, or groupings of objects, which can become simultaneously available to build a mental image (of somebody's face, of my living room, of an action, etc.).

This theory implies that the verbal and the non-verbal (imagery) systems are functionally independent, in the sense that they can be activated separately: yet they remain interconnected, so that it is possible to generate mental images through verbal instructions, and to describe mental images verbally. I would like to argue that one of the differences between motor and other types of imagery lies in the strength of this connection between the verbal and the non-verbal systems. Common experience shows that visual images are easily described verbally. Shape, color, size of represented objects can be described in great detail. In contrast, motor images are difficult to transfer into a verbal code. It is difficult, if not impossible to describe the coordination of movements needed for swimming, for example. In spite of being poorly coded verbally, however, motor representations are cognitively accessible, using indirect methods such as matching the imaged movement with a real movement or measuring mental movement time. As an example of this approach, Klatzky and her colleagues have nicely demonstrated that some aspects of movements performed during interactions with objects are consciously accessible, and that such knowledge is reflected in motor performance. Subjects can reliably indicate which hand shape they would use when interacting with a given object and, conversely, when a hand shape is designated, which category of objects would elicit it [41]. More recently, Klatzky *et al.* [42] studied how functional interactions with objects are represented. They found that subjects can determine cognitively which actions are effected by proximal effectors (the arm) or distal effectors (the hand), or which hand configuration would have to be used for a given action. These representational distinctions correspond to the motor pattern which is observed when real object-oriented actions are performed (e.g. [36]).

The possibility of accessing the content of motor images through a chronometric analysis of mentally simulated actions has been investigated by using a reaction time paradigm. Georgopoulos and Massey [26] measured reaction time in subjects who were asked to move a manipulandum at a given angle from the direction shown by a visual target. The duration of the reaction time was found to increase with respect to the movements normally directed at the visual target. Furthermore, this increase in reaction time was a function of the amplitude of the angle. The authors interpreted this finding by hypothesizing that subjects mentally rotated the movement vector until it reached the desired angle, and that the time taken for this rotation was greater for larger angles. Reaction time, considered as mental movement time, in fact correlated linearly with mental movement difficulty (calculated from the amplitude of the angles). This behavior conforms to the classical Fitts' law, which accounts for the duration of movements under accuracy constraints [18]. Hence Georgopoulos and Massey's conclusion that, because Fitts' law holds in this condition, "both real and imagined movements might be governed by similar amplitude-accuracy relations" ([26], p. 361). This finding substantiates the way parameters of movement execution (in this case, direction) are coded centrally during motor preparation, and provides a physiological rationale for the expression of such a universal motor rule as Fitts' law.

Attempts were made in our laboratory to measure the duration of a purely mentally performed action. Two main results were obtained in these experiments. First, the duration of a mentally performed action (e.g. walking mentally to a previously memorized target) was found to be similar to that of the same executed action [12]. Second, the duration also increased as a function of the 'difficulty' of the task. Subjects were instructed either to actually walk or imagine themselves walking on beams that had the same length but varied in width. The beam width was assumed to be a factor of difficulty, i.e. the narrower the beams, the more difficult the task. A clear effect of task difficulty was found in both actual and mental movement times [13]. This result can be interpreted within the above framework of the speed-accuracy trade-off.

A new experiment was undertaken to verify the validity of Fitts' law in purely mental actions. Normal subjects were instructed to walk mentally through gates of a given apparent width positioned at different apparent distances. The gates were presented to the subject with a 3-D visual display (a virtual reality helmet) which involved no calibration with external cues and no possibility for the subject to refer to a known environment. Subjects had to indicate the time they started walking, and the time they passed through the gate. Again, mental walking time was found to increase with increasing gate distance and decreasing gate width. Thus, it took the subjects longer to walk mentally through a narrow gate than to walk through a larger gate placed at the same distance [10].

The question raised by these experiments is to understand at which level of action generation the description of the representation is made. One of the current interpretations given to Fitts law holds that the increase in movement duration is due to an increase in the amount of feedback information to be processed for higher accuracy demands. If this interpretation were correct, it would imply that the subject imagines movement execution and that he uses some implicit knowledge about performing movements of the same degree of difficulty [54], for example, that one has to slow down when going through a narrow door. Thus, it would not be surprising to observe similar timing in both execution and simulation. Although the issue of implicit knowledge cannot be ruled out completely, another interpretation would be that Fitts' law governs not only the execution, but also

the planning of actions, so that movement execution can be adjusted to the requirements of the goal. Consider, for example, an everyday life situation where the same behavior arises, e.g. driving a car through gates of different widths. As the gates get narrower, the driver, even if he is aware that the car fits the gate width, will spontaneously slow down and nearly stop the car before getting through the gate. In other terms, the driver tends to adjust the velocity of his car to the accuracy requirement of the path: the greater the accuracy needed to drive the car safely through the obstacles, the slower the velocity. This example suggests that the driver's behavior, as well as that of the subjects passing mentally through the gates, is determined by his representation of the action, rather than by constraints arising during execution. This justifies the use of motor imagery as a tool for understanding the content of motor representations.

PHYSIOLOGICAL CORRELATES OF MENTAL SIMULATION OF MOVEMENT

What is the situation of motor images among the other motor phenomena, such as motor intention, preparation, or execution? Again, there are several possible ways of dealing with this problem. A first hypothesis states that simulating a movement is the same thing as actually performing it, except that execution is blocked. An alternative hypothesis states that mental simulation is limited to rehearsing early stages of action, well ahead of execution. Whereas the first hypothesis generates specific predictions (e.g. one should expect finding in motor imagery physiological correlates similar to those measured during real action), the second one is mostly a default hypothesis. It would only become plausible if sufficient convincing evidence for the first one could not be shown. In this and the following sections, some of these arguments will be discussed under two main headings, the physiological changes occurring during mental simulation of movements, and the effects of mental training.

Physiological correlates have been recorded in many experiments involving mental motor imagery. Electromyographic activity (EMG) was frequently found to increase with respect to rest during motor simulation. Jacobson [35] found micromovements and increased EMG in those limbs involved in imaginal movements, but not in the contralateral ones. These discharges were related to the requirements of the imagined task (e.g. rhythm). Shaw [61] found EMG increase to be proportional to the amount of imagined effort. Hence the common claim that the kinesthetic image of a motion pattern is accompanied by the same innervation pattern as during the motion itself (see also [28] and [30]). Wehner *et al.* [65] looked for a possible relationship between the amplitude course of the mental (ideomotor) EMG and processual task characteristics. They found frequency characteristics in the mental training EMGs similar to those in the active training EMGs, which shows that there are task-specific frequencies in the EMG of the relaxed arm during mental training. The fact that EMG was found to be quiescent in several experiments (e.g. [66]) also involving motor imagery does not contradict the above idea. It may only reflect better inhibition of movement execution under certain conditions. Conversely, the fact that muscular activity is sometimes only partially blocked during motor simulation (as shown by residual EMG) emphasizes the delicate equilibrium between excitatory and inhibitory influences at the motoneuron level and suggests that motoneurons are close to threshold (see below).

The fact that mental simulation of movement activates motor output was confirmed by a recent study of spinal excitability during motor imagery. Bonnet *et al.* [5] instructed

subjects either to press isometrically on a pedal, or to simulate mentally the same action. Two levels of strength (weak and strong) were used. The main result of this experiment was that motoneuron excitability, as tested by the amplitude of spinal monosynaptic reflexes, was increased during mental simulation. This increase was only slightly less than the reflex facilitation associated with the current performance of the same movement. Tendonous-reflex (T-reflex) amplitude was more increased than H-reflex amplitude. In addition, the change of reflexes in the leg imagined to be involved in the movement was larger for a strong than for a weak simulated pressure. In accordance with some of the foregoing results, a weak EMG activity was found during mental imagery, which was modulated by the lateralization and intensity of the imagined movement.

The fact that the T-reflexes were more facilitated than H-reflexes is important to consider. Both reflexes are conveyed via the same monosynaptic neuronal pathways but the H-reflex, which is triggered by the electrical stimulation of the fibers, short-cuts neuromuscular spindles, while the T-reflex, which is triggered by a tendon tap, is a response to stretching these spindles. Insofar as the sensitivity of neuromuscular spindles to muscular stretch is under the control of gamma motoneurons, an increase in excitability of the T-reflex, but not of the H-reflex, would result from a selective increase in gamma motoneuron activity. The possibility of a spindle activation during mental simulation of a movement is an interesting one. Spindle afferents are known to play a role not only during movement execution, but also for organizing the motor output during self-generated actions [31, 53]. For example, passively executed movements or vibrations of the corresponding tendon strongly facilitate, via spindle activation, the initiation of voluntary movements when such an initiation has become difficult, or even impossible, after either a lasting immobilization or a cerebral lesion [7].

Other effectors normally not submitted to voluntary control, such as the autonomic effectors, are also likely to be activated during motor imagery. This possibility was tested by instructing subjects to either actually perform or mentally simulate a leg exercise at two levels of work. Heart rate, respiration rate and end-tidal P_{CO_2} were measured in both conditions. After a few seconds of actual exercise, respiration and heart rates began to increase. The heart rate increased about 50% over the resting level value. In the mental condition where no work was produced, this increase was about 32% [11]. The difference between the two situations might reflect the contribution of the reflex regulation of respiration and heart rates in response to peripheral factors. It remains that a large fraction of this immediate increase at the onset of exercise (both real and mental) would be due to the effect of motor preparation, not to the metabolic changes. This point confirms earlier experiments of Adams *et al.* [2] who showed that heart rate and cardiac output already increase notably within about 5 beats after exercise was started. Respiration changes within one breathing cycle. These findings suggest that vegetative activation during preparation to effort would be timed to begin when motor activity starts. This would represent an optimal mechanism for anticipating the forthcoming metabolic changes and shortening the intrinsic delay needed for heart and respiration to adapt to effort (for a review, see [56]). Autonomic activation during imagined action thus pertains to the same phenomenon of preparation to action and appears as a mandatory consequence of motor simulation.

The possibility that these autonomic changes were a consequence of muscular activity can be ruled out. The spectroscopic analysis performed by Decety *et al.* [11], showing no change in muscular metabolism during mental simulation, is against this possibility. In

addition, Gandevia *et al.* [23] observed graded cardiovascular changes in paralyzed subjects attempting muscular contractions. As paralysis was complete, these changes could not be due to residual muscular activity.

The issue of physiological correlates of motor simulation has also been investigated using brain activity mapping techniques. Roland *et al.* [57] asked normal subjects to imagine a rapid and skilled sequence of digit movements. They found a significant and localized rCBF change mainly in the supplementary motor area (SMA). Decety *et al.* [15] studied normal subjects imagining a graphic movement (writing 'one, two, three', etc.). The subjects were instructed to imagine the movement at the 'first person perspective' and to try to 'feel their writing hand'. Regions corresponding to the prefrontal cortex, SMA, and also the cerebellum were activated significantly, as well as in the basal ganglia (see also [58]).

A recent confirmation of the pioneering studies of Roland *et al.* [57] was provided by the PET data obtained by Fox *et al.* [19] and Stephan *et al.* [62]. They showed that imagined finger movements activate the supplementary motor area (SMA) and parietal areas bilaterally. Actual movement activates contralateral sensorimotor cortex, as well as SMA and parietal areas on both sides. Stephan *et al.* also noticed that during imagination the SMA foci were located more anteriorly than during execution. Confirmatory data were also obtained by the functional Magnetic Resonance Imaging (fMRI) technique. Sanes *et al.* [60], in studying fMRI activation during both executed and imagined finger movements, found that, whereas anterior motor areas (such as SMA) are activated in both conditions, M1 is activated only during execution. Hallett *et al.* [29], also using fMRI, reported that some activation occurred in primary motor cortex during imagined movements. The level of activation was less during imagination than during execution.

Finally this problem was reinvestigated recently by Decety *et al.* [14], using PET. Three-dimensional graspable objects (cylinders and spheres of different sizes, colors and orientations) were presented to subjects who were instructed to 'imagine themselves grasping the objects with their right hand'. A significant rCBF increase was observed in areas concerned with motor behavior. At the cortical level, area 6 in the inferior part of the frontal gyrus was strongly activated on both sides. Activity also increased in left prefrontal areas, extending to the dorsolateral frontal cortex (areas 9 and 46), and in the parietal lobule (area 40). Finally, the anterior cingulate cortex (areas 24 and 32) was bilaterally activated. At the subcortical level, the caudate nucleus was found to be strongly activated on both sides and the cerebellum was involved only on the left side. The absence of labelling in the SMA proper in this experiment can be explained by the type of movement simulated by the subjects. In the present case, simulated movements were visually guided reach and grasp movements directed at external objects, whereas in previous studies where SMA was found to be activated, simulated movements were rapid sequential and purposeless internally generated finger movements.

Consciously representing an action thus involves a pattern of cortical activation which resembles that of an intentionally executed action [20, 52]. At the moment, most of the available evidence shows that the primary motor cortex is silent when no execution occurs. But, as the above Hallett *et al.*'s experiment [29] suggests, the use of more sensitive techniques might not confirm this conclusion. Other recent observations using transcranial stimulation of primary motor cortex go in the same direction in showing an increase in motor responses during mental simulation of movement or related activities ([25, 29], see below). Activation of motor cortex, however, is not the sole explanation for this

enhancement of cortical responsiveness. The corticofugal volley produced by cortical stimulation could be more efficient, simply because of the increase in reflex excitability at the spinal level. Similar discussions have been raised by experiments in other types of mental imagery, such as visual imagery [43] or internal speech [32].

Some of the results presented in this section raise the problem of the mechanism and the locus of motor inhibition during motor simulation. We know that during preparation inhibition occurs at the segmental spinal level: hence the decrease of spinal reflexes during the preparatory period and their reincrease shortly before the movement starts [6]. The pattern of spinal excitability during motor simulation, with a marked increase in T-reflex, is thus closer to that of real action than that of preparation. The mechanisms by which the motor command is actively inhibited should thus differ for preparation and simulation. In the former case, the movement would be blocked by a massive inhibition acting at the spinal level to protect motoneurons against a premature triggering of action [55]. In the latter case, the excitatory motor output would be counterbalanced by another, parallel, output from other (non-primary) motor cortical areas, which would only partially polarize the motoneurons.

THE EFFECTS OF MENTAL TRAINING

If one considers the strong relationships of motor imagery to the neural substrate, it is logical to expect that the central changes produced during imagery will affect subsequent motor performance. Conversely, the observed changes might represent an explanation for those effects known to arise as a result of mental training.

The influence of mental training using motor imagery on motor performance has been recently reassessed and confirmed by several experiments [17]. It has been shown that mental training affects not only global motor performance (e.g. muscular strength, [66]), but also aspects of the performance normally thought to be more specific outcomes of training, such as reduction of variability and increase in temporal consistency. This was shown by Vogt *et al.* [64]. They examined how subjects learned to replicate a periodic movement pattern displayed visually. Training was either physical (replicate the visual pattern by flexion-extension of the elbow), mental (form a mental image of the movement needed to replicate the pattern), or observational. Physical test blocks were performed (without visual feedback) after the training period in each modality. Physical and non-physical types of practice were found to exert similar effects on replication of movement form, spatial scaling, consistency of movement tempo, and consistency of relative timing.

How can the benefit of motor images on motor execution be explained? As no movement occurs, the first explanation is that of a purely central effect. Increased traffic in neural circuits could be responsible for improving synaptic efficacy in critical parts of the system, such as, for example, in the cerebellum or basal ganglia. This would result in increasing the capacity of the system for tuning motoneuronal populations or sharpening coordination between agonist and antagonist muscle groups. Yue and Cole [66] came to the conclusion that the increase in muscle strength following mental training did not primarily result from neural changes at the execution level, but at higher planning and programming levels of the motor system. The altered programs in turn would achieve strength gains by acting on the spinal circuitry.

This central explanation seems to be supported by the effects of magnetic transcranial stimulation of motor cortex. The size of the excitable area devoted to finger movements

was found to increase as movements were repeated over training periods (a fact reported in animal experiments by Grunbaum and Sherrington as early as 1903, see [27]). Interestingly, this increase was observed for imaginal training as well [29]. A relevant observation was made by Gandevia and Rothwell [25]: they showed that 'concentrating' on one hand muscle without activating it increased the effect of subthreshold magnetic stimulation of the cortical area corresponding to that muscle (and not of other muscles). Thus, there is a selective enhancement of cortical responsiveness during imagery or related processes.

The central explanation is an interesting one, as it has implications for the process of learning in general. Thus, there would be an inner regulation of external performance without recourse to actual movement and to the related sensory feedback and knowledge of results. This explanation is compatible with a hierarchical model of action generation where an internal representation of the action releases efferent signals in lower level mechanisms, and where a comparison of the efferent discharges with the internal representation of the action is performed (see [40] and [44]). A similar model will be developed in the next section.

In the above hypothesis, the EMG activity observed during mental training would have to be considered more as an effect than a cause of the processes taking place during learning. The recent findings on spinal reflexes during motor imagery reported in the previous section, however, suggest an alternative—albeit complementary—interpretation. A tonic afferent discharge arising from the muscular spindles during imagery (possibly due to increased gamma motoneuron activity) could have implications for subsequent shaping of motor performance and improvement in learning. Note that this interpretation is compatible with the 'central' explanation above, as it also involves the activity of a central generator for triggering the spindle activity. A similar explanation would hold for changes in the motor system during motor preparation. Mellah *et al.*'s [46] experiments in the monkey showed that a small proportion of biceps motor units were active during the preparation period preceding the instruction to make a flexion of the arm. These units, which had a low threshold and a low discharge rate, stopped firing shortly before the movement began. This preparatory muscular activity, it was suggested, played an important role in a subsequent movement, increasing the stiffness of the muscle and reducing its time constant in responding to the phasic command. It could also have provided afferent information to facilitate the central neurons responsible for generating the phasic command. Disentangling the 'central' and 'peripheral' sources of information for mental practice would require studies in deafferented patients. This would involve testing the ability to generate an imagined movement in a deafferented limb (in patients suffering peripheral neuropathy, for example). If vivid imagery persisted in these patients and if gains in subsequent performance were obtained, this would rule out a role of spindle afferents, even if EMG discharges were recorded.

A MODEL FOR SELF-GENERATED ACTIONS

The final section will deal with an attempt at designing a simple model of generation and control of goal-directed action compatible with the occurrence and the effects of mental imagery. A testable hypothesis will be proposed, implying that motor representations for acting and for imaging are one and the same thing, and that the two modes of representations are only distinguishable by the circumstances in which they are generated.

This hypothesis obviously rejects the notion of motor images as an epiphenomenon unrelated to the generation of actions (for a discussion of this point, see [39]).

Motor representations are conceived here as 'internal models' of the goal of an action. The goal of an action, however, can be specified at several different levels which represent different aspects of the same action [59]. It can be defined as the final result at which the action is intended. It can also be defined as a sequence of intermediate actions needed to achieve the final result; or as a program of coordinated joint movements; or as a set of motor commands, etc. (see [37]).

The first assumption of the model is that these functional (and possibly, anatomical) levels of representation are organized hierarchically. This hierarchy can be conceived as a sequence of different modules (Fig. 1): The complete internal model of the action to be performed is stored at the higher level. Activation of the modules has to follow a precise order, such that the global internal model of the action activates an appropriate plan, which in turn activates motor programs, etc. This conception of action generation is in agreement with previous models. Hierarchical architectures similar to those of computer programs were often used to conceptualize action plans where actions were represented as sequences of steps involving tests and operations (see [48]). Norman and Shallice [49], for instance, assumed that specification of the components of actions was carried out "by means of numerous memory schemas, some organized into hierarchical or sequential patterns, others in heterarchical or independent parallel (but cooperating) patterns" ([49], p. 5). In this conception, any given action sequence was represented by an organized set of schemas, with one—the source schema—serving as the highest order control and activating the other component-schemas for the individual movements of that action. When a given source-schema had been selected, component-schemas were controlled by horizontal and vertical processing threads. Horizontal threads determined the order of activation of the component-schemas and thus specified the structure for the desired action sequence, although vertical threads determined activation values for these schemas. Activation values involved attentional control, motivational factors, etc. The notion of schema, which is a convenient one for accounting for the way representations are stored at intermediate and lower levels (see, e.g. [4]) is probably too restrictive for higher representational levels. Intentions, by definition, do not always correspond to preexisting schemas and may represent newly built mental structures.

The other important feature of the proposed model is that it involves control mechanisms which are activated in parallel with the main stream of information (Fig. 1). These control mechanisms imply a storage of operations performed at each level in as many motor memories as there are levels. These memories are used as a comparator for controlling the unfolding of the action. Reafferences picked up at the periphery and documenting the current state of the action are fed into the motor memories and can be used to signal its degree of completion. If the desired action has been completed, the reafferences and the content of the memories will coincide, and the latter will be erased. If the action is incomplete, residual activity will persist in the memories: this will reactivate the corresponding module and generate corrections. Finally, if the desired action does not take place, memories will remain fully activated, which in turn will maintain the whole system activated.

A first attempt at testing the validity of this model can be made by describing the functioning of the lower levels. Hence, the program module sends commands to the execution level (e.g. direction and extent of a movement). If an external perturbation arises

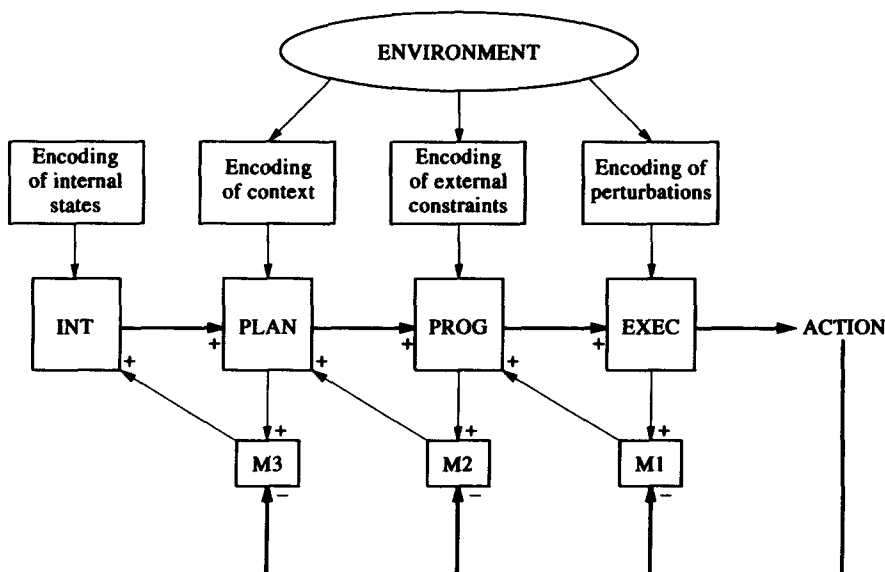


Fig. 1. A functional chart for self-generated actions. The main flow of information goes through the cognitive steps of action (e.g. intending, planning, programming and executing). Each of these levels can be influenced by level-specific environmental cues, which define the context or the constraints of a given action, or which arise from perturbations during execution. The higher level (intending) is supposed to be less influenced by environmental cues and more by internalized cues. The lower row depicts level-specific short-term memories which are activated by changes occurring at each of the cognitive steps, and deactivated by reafferences arising from movement execution.

For details see text.

during execution and the correct effect is not obtained, the reafferences (e.g. visual, proprioceptive) arising from the periphery will not correspond to the representation of the desired state stored in the memory, and the memory will not be cancelled. An error signal will be transferred to the program level which will change its specification until execution is finally correct. This comparison process can be very fast (see examples below): this is a prerequisite for preventing the error signal from propagating to higher levels. If, however, the alteration of the program is not sufficient to obtain the desired effect, the program level will remain activated and the error signal will propagate to the plan, etc.

This mechanism, classically known in neurophysiology as the 'corollary discharge' or 'efference copy' mechanism [34, 63], postulates that signals generated by the motor centers provide information about future movements before they have reached the effector. This mode of regulation (also termed "internal feedback" by Miles and Evarts [47]) has a major advantage in minimizing correction delays when a perturbation occurs during execution of a movement. For example, when the visual target of a reaching movement is suddenly displaced during the movement a correction can be generated within 100 msec or less, so that the target is correctly acquired with only little increase in movement time. This correction is achieved through a kinematic rearrangement during the early phase of the movement (see [51]). There are also examples of fast corrections in other types of movements. Abbs and Gracco [1] have described rapid compensation (within 50 msec or less) of perturbations applied to articulators during speech (see also [9] for a similar result with mechanical perturbations applied to fingers during rapid grasps). This type of correction implies a dynamic comparison between the internally generated signals which

represent the desired movement, and incoming signals which monitor the current state of execution. Since the reafferent signals are delayed with respect to the command signal, the comparator must look ahead in time and produce an estimate of the movement velocity corresponding to the command. The image of this estimated velocity is used at the input level for computing the actual position of the effector with respect to the target. The movement stops when the two signals correspond. Simulation experiments showed that accurate corrections can be generated when target position is perturbed, without notable increase in movement duration, which is compatible with the observed data [33].

A possible anatomical substrate for these mechanisms can be found in the many collaterals arising from the pyramidal tract, and distributing to subcortical structures involved in motor control, such as the striatum, the ventral lateral nucleus and the ventrobasal complex of the thalamus. At the brainstem level, pyramidal collaterals contribute to the dorsal column nuclei (see [47]). These collaterals could carry information concerning the 'desired' movement, to be compared with reafferent proprioceptive information concerning the actually performed movement. A similar organization seems to exist in the spinal cord. The cervical propriospinal neurons, which receive a copy of the motor commands and where visual and proprioceptive reafferent signals have been shown to converge, could play the role of a comparator (e.g. [3]).

The next point to be discussed is the relevance of this model to motor images. It is noteworthy that, in conditions of normal execution (i.e. when the executed and the represented actions coincide), there is usually no awareness of the content of the representation at any level and no image is experienced. This is explained by the fact that motor imagery and execution have different time constants. Because imagery, unlike execution, implies subjective awareness, it takes longer to appear. If imagery actually occurred in conditions of normal execution, it would be delayed with respect to the corresponding action. This effect would be even more pronounced in cases of fast movements or during the occurrence of corrections (see [8] and [38]). By contrast, awareness is a common experience in conditions where the action is delayed, incompletely executed or blocked. According to the above model, those are conditions where the motor memories are not or incompletely erased, and where the representational levels are kept activated: this persisting activation would thus be the substrate for (conscious) motor images. In addition, because activation persists at all levels of the system when action is not performed, there is a possibility that the content of the motor image reflects activity of any of these levels. The actually experienced image would depend on the level which would be probed (e.g. by the experimenter) with the proviso that this level would be consciously accessible. The content of higher levels of the system should in principle be more accessible to subjective experience than that of the lower ones.

Observations made in experimentally paralysed subjects are interesting to consider in this context, as the situation created by paralysis bears some analogy with mental simulation: in both cases, action is represented, not executed, even though the level at which motor output is blocked is clearly different in the two conditions. Subjects with experimental paralysis of one limb experience strong sensations of effort when they attempt to move that limb. Totally curarized subjects are able to feel and to describe their intended movements [24]. Gandevia [21] proposed an interpretation for the sensations of effort reported by subjects with weakened muscles on their attempts to move. He suggested that neural traffic in motor corticofugal paths might be read off by the subjects and used as the relevant signal for the observed illusions. Indeed, complete paralysis

following pyramidal lesions at the cortical level is not accompanied by sensations of increased effort or heaviness, precisely because no traffic occurs in the motor pathways after such lesions. Sensations reappear during partial recovery of movements, when neural traffic reestablishes. The same hypothesis would account for permanence of sensations of effort in all cases of distal paralysis, where corticofugal pathways are not altered. In a more recent paper, the same author proposed that the discharge responsible for these sensations does not arise directly from the corticofugal pathway, because transcranial electrical stimulation of this pathway does not produce a sensation of effort. Instead, the subject experiences a passive movement [22]. He therefore suggested that the relevant discharges for these sensations arise from structures such as premotor cortex or basal ganglia.

It is interesting to note in this context that basal ganglia have been found to be activated during mental simulation of movement [14]. In addition, motor imagery has been found to be considerably slowed in patients with Parkinson's disease, whereas in the same subjects a normal imagery ability for other types of images (e.g. visual) is preserved [16].

The above speculation bears some relevance to the role of motor imagery and mental simulation of movement in motor learning (the so-called mental practice). As already stressed earlier in this paper, the postulated persisting activation of central loops during motor imagery represents a possible substrate for improving synaptic efficacy in the circuits which are rehearsed. Another explanation is represented by the possible gamma activation during motor imagery. This explanation deserves careful consideration, because the resulting spindle discharge would be very different from that produced during real movement. During real movement, discharges arise from spindles in the muscle antagonist to the movement, whereas, during simulated movement discharges arise from the agonist muscle. This difference is a critical one in the present model: spindle discharge during movement execution is one of the reafferent signals by which completion is signalled to the system, whereas spindle discharge during movement simulation would in fact reinforce the activity of the motor memory and contribute to the activity of the central loop.

Finally, the model also predicts a similar explanation for other types of learning, such as learning obtained by repeating the to-be-learned movement. Because at the early stages of learning actions are performed very slowly, large error signals arise from the periphery, due to inaccurate performance. These conditions create a situation where the central loops remain activated and can be rehearsed. This suggests that learning by performing would not be substantially different from learning by imaging, as the neurophysiological substrate would be the same in both cases.

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