THE REPRESENTING BRAIN: NEURAL CORRELATES OF MOTOR INTENTION AND IMAGERY

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Abstract

This target article concerns how motor actions are neurally represented and coded. Action planning and motor preparation can be studied using motor imagery. A close functional equivalence between motor imagery and motor preparation is suggested by the positive effects of imagining movements on motor learning, the similarity between the neural structures involved, and the similar physiological correlates observed in both imagining and preparing. The content of motor representations can be inferred from motor images at a macroscopic level: from global aspects of the action (the duration and amount of effort involved) and from the motor rules and constraints which predict the spatial path and kinematics of movements. A microscopic neural account of the representation of object-oriented action is described. Object attributes are processed in different neural pathways depending on the kind of task the subject is performing. During object-oriented action, a pragmatic representation is activated in which object affordances are transformed into specific motor schemata independently of other tasks such as object recognition. Animal as well as clinical data implicate posterior parietal and premotor cortical areas in schema instantiation. A mechanism is proposed that is able to encode the desired goal of the action and is applicable to different levels of representational organization.

1. Introduction

This paper starts with a neurophysiologist's dream: It became possible to study a representing brain. The experimenter was able to contemplate the core of brain activity, an activity uncontaminated by ingoing or outgoing events. He had full access to the endogenous functionning of the brain and could watch internal representations getting organized and ultimately steering behaviour! Reality is less bright: the experimenter interested in neural representations must accept to rely on paradigms elaborated by
psychologists, on mental chronometry, even on introspection. He must accept to infer the realm of cognitive brain functions from measurements of remote physiological correlates or from comparisons with animal studies.

The general idea of this paper is that actions are driven by a represented goal rather than directly by the external world. Representations may be built from the environment, they may rely, at least partly, on knowledge acquired from the outside. Yet, their vehicle is a genuine apparatus which pertains to the structure of the brain itself and constrains their expression and modalities of functioning. This conception will be illustrated by studying representations in the domain of motor actions. It will be postulated that the generation of actions involves a representational step operating with fixed rules and relying on identifiable building blocks. Alternative conceptions, implying mechanisms such as direct transformation of ingoing activity into outgoing activity or self-organization of endogenous activity for producing movements, will be only briefly discussed and, in fact, largely ignored.

It will also be proposed that the representational step of action generation processes information in a particular way (it will eventually be called the "pragmatic" mode of representation), which contrasts with other modes of representation operating on the "semantic" mode. The content of semantic representations can be readily accessed consciously; images of visual scenes, faces, words can be generated and verbally described. This is not the case for the content of pragmatic representations. Although everyone can generate, spontaneously or with minimal training, vivid motor images, these images are difficult to describe verbally. Motor representations are not objects of contemplation, they are normally rapidly transformed into movements. Yet, the idea will be defended that motor imagery, when properly defined and used, can be a key phenomenon for understanding motor representations, and studying the cognitive content of actions.

2. The imagery debate.

Modern work on the relations of mental imagery to brain functions is faced with opposite conceptions. According to one of these conceptions, mental imagery can be considered as an amodal process, unseparable from other types of propositional activity. This position reflects the idea that all knowledge, regardless of its source modality, can be expressed in a single uniform, abstract, type of representation relying on formal symbol-manipulating operations: thus, there would be no fundamental difference in how perceptually-based and verbally-based information is represented in memory (e.g., Pylyshyn, 1984). An alternative conception is that there are in fact at least two codes for mental activity, such that the code for representing mental images would be different from that for linguistic propositions (see Paivio, 1986).

The coexistence of distinct verbal and nonverbal symbolic neural systems is clearly compatible with the current neuropsychological model of functional localization, whereas on the contrary, there is no clear evidence for a unitary amodal representational system.

The nature of the code involved in each type of representation is another matter of discussion. It has been suggested that mental images are analog, or pictorial (Kosslyn et al, 1979) representations of objects or events, as opposed to the discrete symbolic nature of linguistic representations. This hypothesis implies that mental images should bear a definite relationship to the actual object or event that is internally represented; or, in other words, that "the information in mental representations and the operations that can be performed on them are related in a nonarbitrary and continuous fashion to their perceptual-motor counterparts" (Paivio, 1986, p. 177; for review, see Pinker, 1984). The issue that mental imagery might not be a genuine phenomenon but, rather, pertains to the same class of representational mechanisms as those which are involved in processing ingoing or outgoing information will be developed with examples drawn from research on visual and motor images.

2.1. A brief look at visual imagery

In the domain of ingoing information, arguments in favor of this hypothesis arise from a large body of data obtained with visual imagery, suggesting that mental representation retains the metric spatial properties of the represented scenes or objects. First, the time needed to mentally "scan" a memorized
visual object has been found to be proportional to the actual extent of this object. This point was clearly demonstrated by Kosslyn et al in an experiment where subjects were instructed to mentally scan between landmarks located on a memorized map. The mental scanning time was a direct function of the distance between the landmarks on the map (Kosslyn et al, 1978). In addition, when mental scanning time was compared to actual scanning time, it was found that it takes about the same time to scan between two landmarks on the memorized map as it takes to scan between the same landmarks on the actual map (Denis and Cocude, 1990).

One possible explanation for this striking property of visual imagery of preserving the metric properties of represented objects is that the image is generated within brain areas which are spatially mapped. In primary visual cortex, not only do the right and left halves of the visual field project to left and right hemispheres, respectively, but also the topographical organization of retinal projections is in definite concordance with external space. If this explanation were correct (as indeed it seems to be, see below), the apparent distance between represented objects would simply reflect the distance between parts of the activated cortical surface, themselves corresponding to the projection of different parts of the visual field. Obviously, because the primary visual areas only encode the retinocentric position of objects (not their egocentric position), this mechanism would require the participation of visual areas beyond striate cortex.

This reasoning is supported by a large number of clinical and experimental findings. First, in the clinical domain, it has been observed that congenitally blind adults retain a spatial organization of their mental imagery (Kerr, 1983). If one assumes that spatial images in blind people also correlate with activity of visual cortex, then the spatially ordered character of these representations is a logical finding. Spatial imagery processing ability need not depend on visual perceptual experience, it would depend on the spatial properties of the brain areas which are involved in generating the images. Other arguments in the same direction can be drawn from observations in brain damaged patients. It may be conjectured that, if part of the representation of the visual field were missing (as in the case of an occipital lesion, for example), then the size of the mental visual field should be reduced. Farah et al (1992) tested this hypothesis in a patient before and after unilateral occipital lobectomy, using a paradigm designed by Kosslyn (1978). Kosslyn had shown that subjects instructed to imagine familiar objects moving slowly toward them, were able to indicate at which distance these objects would begin to overflow the size of their mental visual field. In the lobectomized patient, Farah et al found that this distance had doubled with respect to that indicated before the operation. This result suggests that the size of the mental visual field was reduced by the occipital lobectomy, to the same extent as the actual visual field. In addition, this reduction was found only for the horizontal dimension, not the vertical dimension, which is consistent with the anatomical damage suffered by the patient. Further observations in brain-damaged subjects show that the preserved and impaired aspects of visual perception are similarly preserved and impaired in visual imagery. One of the most striking examples was described by Bisiach and Luzzatti (1978). They found that patients with hemispatial neglect, who were unaware of visual stimuli from one side of space as a consequence of a posterior parietal lesion, also presented the same neglect in imagined space: the patients failed to report items from the neglected side when they imagined a familiar visual scene.

Finally, another set of experimental data in normal subjects also tend to support the same idea of a common neural substrate for visual imagery and perception. The pattern of cortical activation during visual imagery seems to match, at least in part, that observed during visual perception. Roland and Friberg (1985) and Goldenberg et al (1989 a, b) using regional cerebral blood flow analysis, showed activation of occipital and inferior temporal regions to occur in subjects performing visual perceptual tasks or tasks requiring the use of visual imagery. Tasks requiring a different sort of imagery (e.g., motor) or tasks involving non-imaginal thinking did not activate the same areas. Very similar findings were also reported using electrical brain activity mapping during visual perception and imagery (for a review, see Farah, 1989).

The above observations stress the fact that mental images, at least in the visual modality, rely on the same neural substrate as the perceptual images that are generated during normal perception. The precise relations between the two phenomena, however, need to be better understood. At least one clinical case of
complete loss of visual imagery with preservation of normal visual perception has been reported (Charcot et Bernard, 1883). Much more recently, the reverse situation has been observed by Behrmann et al (1992). They reported the case of one agnosic patient who was unable to recognize visual objects (face recognition, however, was preserved), but had intact visual imagery ability. Such cases are not against the idea of a commonality of neural structures for perception and imagery if one postulates the existence of a hierarchical organization of the mechanisms for processing visual representations. The step of image generation would be distinct for images built with perceptual or with memorized material; subsequently the two types of images would converge on the same structure. The posterior part of the left hemisphere could be one of the possible areas where this convergence would take place (Farah et al, 1992, Goldenberg, 1992).

2.2. The case of motor imagery

The above framework used in the context of visual imagery can also be tentatively generalized to mental representations in other modalities, and specifically, to motor imagery. Such a generalization implies that motor imagery pertains to motor physiology in the same way as visual imagery pertains to visual physiology. Accordingly, motor imagery would be part of a broader phenomenon (the motor representation) related to intending and preparing movements. This hypothesis will be explored by comparing motor imagery with motor preparation: the structure and the contents of these two processes will be analyzed for searching differences and similarities, and new experiments will be proposed for clarifying their mutual relations. A few specifications are in order before the hypothesis can be further elaborated.

First, the fact that motor imagery and motor preparation are both assigned to the same motor representation vehicle has a strong logical consequence, namely that motor images cannot be considered as an epiphenomenon of the process of motor generation. Instead, in continuity with the claim made in the Introduction section, which attributed the motor representation a causal role in the generation of movements, motor images must also be considered to be functionally related to the imagined movement. This point will be extensively discussed in Section 3.

Second, some difficulties concerning the notion of motor imagery itself must be examined. The first difficulty is to draw a clear distinction between motor and other types of imagery, including visual imagery. Motor imagery bears some resemblance with situations involving mental manipulation of visual images, like mental rotation (Shepard and Metzler, 1971) or mental scanning (Kosslyn et al, 1978). This resemblance, however, does not mean that mental scanning, for example, belongs to the same category as motor imagery. A clear difference can be drawn between the "dynamic" subtype of visual imagery whereby we are able to imagine scenes in which objects or people (including ourselves) are seen in motion (see Paivio, 1986) and motor imagery. Indeed, in the Kosslyn et al situation subjects were instructed to scan the imagined displacement of a small speck moving between two points on the memorized visual map, not to imagine themselves locomoting between these points. A source of confusion, however, may be that motor imagery often relates to actions that take place within represented visual space, and, for this reason, cannot be entirely segregated from visual imagery.

A possible way of conceptualizing the specificity of motor images is to distinguish between "internal" and "external" imagery. According to sport psychologists, internal imagery is a first person process involving mostly a kinesthetic representation of the action, whereas external imagery is a third person process involving a visual representation of that action or of the space where it takes place (see Mahoney and Avener, 1977). Motor imagery would thus belong to the former type. It would relate to the representation of the self in action, and would imply that the subject feels himself executing a given action, whether it involves the whole body (as in running for example) or it is limited to a body part (as in writing, pointing to a target or holding pressure against an obstacle, for example). Representation of the self in movement, 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 (most of them ill-defined) correspond to this definition: imitating somebody's movements, anticipating the effects of an action,
feeling kinesthetic or bodily sensations (muscle contractions, heart beats), etc, can be considered as putative motor images. The difficulty of verbalizing such situations, in agreement with the implicit nature of motor preparation, contrasts with the more accessible visual imagery.

An example can be used to illustrate this point. Consider for example the teacher and pupil situation during the action of learning a motor skill like playing a music instrument. The pupil watches the teacher demonstrating an action, with the instruction of later imitating and reproducing that action. Although the pupil remains immobile during the teacher's demonstration, he must image in his mind the teacher's action. Conversely, when the teacher watches the pupil's repetition, in spite of not performing the action himself, he will experience a strong feeling of what should be done and how this could be done. Similar feelings may be experienced by sport addicts watching a football game on television. They must play in their mind the appropriate action to catch the ball (and indeed, they express their frustration when the ball has been missed by the player). The vividness of the imagined action can be such as to induce in the watchers changes in heart and respiration rates related to the degree of their mental effort (see Section 3.3).

One could speculate that, while the pupil watches the teacher, neurons located in the areas of his brain relevant to motor preparation and planning will fire as if he were actually preparing the action he watches. Similarly, the teacher's feelings when he watches the pupil's performance would be based on the discharge of the same neurons, in his own brain, as those which were firing while he was himself preparing and executing the correct movements. The speculation therefore implies that these "representation" neurons are the same as those which are activated during preparation to actual action. The existence of such representation neurons could possibly be demonstrated by monitoring brain metabolism (using imaging techniques) of the teacher and his pupil while watching each other. Before this experiment becomes possible, however, one might consider analogous situations in the monkey. Rizzolatti and his group have described a class of neurons in the rostral part of the inferior premotor cortex, which fire prior to and during specific actions performed by the animal (e.g., picking up a food morsel with a precision grip). Neurone discharge is usually not conditional to the hand used, nor to the orientation of the grip, it relates to the fact that the monkey performs that particular action (Rizzolatt et al, 1988; see below). Recently, these authors noticed that the same neurons also fire while the monkey observes the experimenter performing the same action (di Pellegrino et al, 1992). According to the authors, "there is always a clear link between the effective observed movement and that executed by the monkey and, often, only movements of the experimenter identical to those controlled by a given neuron are able to activate it." This very striking result supports the idea of representation neurons as a common substrate for motor preparation and imagery.

2.3. Relevance to the motor theory of perception.

Although this is not the central theme of the paper, it is appropriate to have a brief look at one of the major theories dealing with image generation, the so-called motor theory of perception. This theory is a broad framework for integrating data from many sources and dealing with many aspects of the perception/action domain.

Its main claim is that mental states such as perception or imagery may arise from movement or, more precisely, from "innervation" (centripetal as well as centrifugal) associated with movements. There are many variants to this theory, particularly for what concerns the neural correlates which are potentially associated with or involved in, the generation of these mental states. The "peripheral" variant would hold that, in the same way as the perceived image of an object arises from the muscular discharges produced during the movements for exploring it, the mental image of that object is produced by covert muscular discharges in the related muscles. This idea was extensively developed by W. James in the chapter on "Imagination" in his "Principles of Psychology" (James, 1890) and was later exploited by Jacobson (e.g., Jacobson, 1930). Lieberman's hypothesis for the perception of speech would be in the same vein (e.g., Lieberman and Mattingly, 1985). (For a review of the historical and epistemological roots of the motor theory, see Scheerer, 1984).
Several of the data reported below are potentially interpretable within this framework. This, however, does not mean endorsement of the detailed mechanisms for generating motor representations postulated by the motor theory, especially when it claims that motor images are generated by peripheral mechanisms that propagate to central levels. Existence of muscle discharges during a mental state does not imply a bottom-up influence of these discharges (via proprioception, for example) on the mental state. The idea which is developed here is quite the reverse and is closer from what would be a "central" version of the motor theory. The key phenomenon in this conception is the motor intention, which is thought to be largely endogenous. Motor imagery would represent the result of conscious access to the content of the intention, and the content of the intention would constrain the expression of the image. In neurophysiological terms, the corollary discharge model (e.g., Teuber, 1960), which postulates that neural discharges arising from motor centers during intention to move can influence centers involved in perception, would be in agreement with this conception, as it does not require activation of peripheral mechanisms to generate the image.

3. Functional equivalence of motor imagery and motor preparation

Motor images and motor preparation processes have different subjective contents. Motor preparation is an entirely non-conscious process, which escapes the subject's awareness. Only the final result is under the subject's judgement, so that the action, once executed, can be recognized by him to correspond (or not) to his intent. By contrast, the content of motor images can be accessed consciously by the imaginer.

This difference between the two situations, however, may be one of degree, not of nature. This assumption implies that, if motor preparation, which normally lasts for a very brief period of time, could be prolonged, then the intention to act would become progressively a motor image of the same action. If this were the case, then the non-conscious to conscious transition would be only determined by the time allowed for the preparation processes to access awareness and to become conscious. Actions which fail or which are cancelled at the last moment may be situations where a non-conscious program is transformed into a conscious image. This idea that motor representations (intentions) become known to the subject when they are not followed by execution is supported by a number of clinical observations which have in common that action is prepared but cannot be executed. Amputated subjects, for example, report feeling movements of their phantom limb, and seem to have a clear image of their intended action (for complete description, see Schilder, 1935). Similar feelings are reported by patients with deafferented limbs (due to peripheral deafferentation or other causes). They may describe their intended action in great detail while no actual movements can be observed from the outside (e.g., Duchenne de Boulogne, 1855; Jeannerod et al, 1984). These data suggest that, in the condition of executed action, the content of the motor representation would not reach consciousness because it would be cancelled as soon as the corresponding movement is executed (perhaps by the incoming signals generated by execution itself). By contrast, in the condition of motor imagery, where execution is purposively blocked or delayed, the representation would be protected from cancellation and would become accessible to conscious processing.

The hypothesis of a continuum between motor preparation and motor imagery sharply contrasts with the classical idea (borrowed from studies of language) of a unitary symbolic representation for the different types of mental activities, including motor representation. In a representative survey of this trend, Requin (1992) proposed that "At the highest level., motor actions would be represented in a non-motoric, holistic and symbolic mode and could give rise to a conscious experience" (p 161). Admittedly, it is probably always possible, in examining the biological underpinnings of mental activities, to find a level "higher" than the one under study. The rest of this paper, however, through a detailed analysis of arguments suggesting that "conscious" (imagined) and "non- conscious" (prepared in view of execution) actions share common mechanisms and show functional equivalence, will show that a similar framework can be applied to different levels of organization, including the most mental ones. This analysis will be conducted along three main lines: the effects of motor imagery on subsequent motor performance; the mapping of brain areas involved in motor imagery and preparation, respectively; and the physiological correlates of motor imagery and preparation.
3.1. Effects of motor imagery on motor learning and training.

If motor preparation and motor imagery are related processes, they must interfere at some level: for example, imagining a movement should influence the subsequent performance of that movement. The sport psychology literature in the early 1960s offers a large number of studies reporting the effects of mental imagery on subsequent motor performance. Comparison of the performances of subjects who had received "mental practice" to those of control groups who had not received mental instructions led to the conclusion that mental practice facilitates performance (for a review, see Feltz and Landers, 1983). The interpretation of this effect, however, differs widely among authors. According to Paivio (1986), the improvement in motor performance following mental practice might be due to motivational factors which increase the physiological arousal of the performer. According to others, mental imagery could have a beneficial influence on neural mechanisms involved in performing the subsequent action. Finke (1979) reported that subjects imagining pointing at visual targets during wearing laterally displacing prisms showed the same after-effects as if they had actually pointed with the prisms. This result, which involves a directional bias in executing the adapted movements, could hardly be explained by motivational factors. Similarly, Johnson (1982) studied the effects of imagined movements on the recall of a learned motor task. Prior experimental data had been reported (e.g., by Stelmach and Walsh, 1973), showing that the recall of a learned movement was distorted if another movement was interpolated between acquisition and recall. The distortion was a bias of the to-be-recalled movement in the direction of the interpolated movement. Johnson conjectured that, if imagined and actual movements were functionnally equivalent, then the same effect on recall should be obtained by interpolating an imagined movement instead of an actual one. This hypothesis proved correct in that the imagined and the actually produced movements led to the same direction error during recall.

The neural basis for these effects remains hypothetical. There is a possibility that efferent discharges generated during the imagining process, could represent the substrate for subsequent facilitation of motor performance through priming of the motor pathways by descending volleys. A number of data suggest that mental imagery is accompanied by subthreshold motor activation and even small movements. Eye movements have been recorded during recall of visual scenes (e.g., Jeannerod and Mouret, 1962). The work of Jacobson (1930) first suggested that muscles were selectively activated during imagined action. Shaw (1940) reported that, during imaginal weight lifting, EMG activity of forearm muscles increased linearly with the magnitude of the weight. The same author, however, also showed that increased EMG activity during imaging was largely distributed across muscle groups, including those not related to the imaginal action (Shaw, 1938). More recently, EMG activity was found to vary as a function of the type of imagery: it increased more during internal imagery than during external imagery (Harris and Robinson, 1986).

Although these data could be interpreted in support to the peripheral version of the motor theory, this is not the only possible explanation. It could also be argued that the centrally generated image "leaks" into executive mechanisms which are held under (incomplete) inhibition and that the observed effects of training are due to purely central changes. This view is supported by recent work on mental muscular "training". Yue and Cole (1992) compared the increase in muscular strength produced by actual training (repeated maximal isometric contractions) and by mental training (imagining the same effortful contractions). In both conditions, the maximal force produced by the trained muscles increased significantly (by 30% and 22%, respectively). EMG recordings during the training sessions showed that, whereas high levels of contraction were produced during actual training, the muscle was quiescent during mental training. Lack of muscular activity during mental exercise was also observed by Decety et al (1993) in a study using NMR spectroscopy of the muscles involved in the imagined effort. No change in muscular metabolic indices were observed. Yue and Cole (1992) came to the logical conclusion that the increase in muscle strength following mental training did not occur primarily as the result of changes at the execution level of the motor system. They suggested instead that neural changes occurred at higher (programming and planning) levels, and that the altered programs in turn achieved strength gains via actions on spinal circuitry.
There are only a few data concerning changes arising in the motor system during motor preparation. Experiments in the monkey by Mellah et al (1990) showed that a small proportion of biceps motor units were active during the preparation period for a flexion of the arm preceding the instruction to move. These units, which had a low threshold and a low discharge rate, stopped firing shortly before the movement began. This preparatory muscular activity was suggested to have an important role on a subsequent movement by increasing the stiffness of the muscle and reducing its time constant in responding to the phasic command. It could also be a source of information (via alpha-gamma coactivation) for facilitating the central neurons responsible for generating the phasic command.

The results of Mellah et al (1990), showing the existence of "covert" muscular discharges during motor preparation seem to be in agreement with the Jacobson type of observations on motor imagery, where muscle discharges were also observed, but not with those of Yue and Cole (1992) and Decety et al (1993) showing muscular quiescence. In fact, the two sets of data can still be reconciled: according to Mellah et al (1990), the muscle fibers which fire during preparation belong to deep muscles, the activity of which escapes surface EMG. In addition, they are likely to be of the slow tonic group, a type of fibers which have a low metabolic rate, undetected by NMR. It is therefore possible that similar muscular activity could be observed also during motor imagery if the appropriate recording technique was used. It remains, however, that an incomplete inhibition (occurring as a consequence of instructions or of a subject's bias) would still be a valid explanation for accounting for these muscular discharges.

Determining unambiguously the type of the relationship of the EMG activity during motor preparation and motor imagery to the representational process would require a reexamination of these phenomena in deafferented patients. This would involve testing the ability of generating an imagined movement with a deafferented limb (in patients suffering peripheral neuropathy, for example). Persistence of vivid imagery in these patients, which is likely to be the case according to the observations mentioned earlier in this Section, would rule out the peripheral origin of the image, even if EMG discharges were recorded.

3.2. Neural structures involved in motor imagery and preparation.

If motor imagery and motor preparation are related phenomena, then they should share the same neural mechanisms. The commonality of involved structures already found for visual perception and imagery is an indication that this should also be the case in the motor domain. Studies of brain activity during mental simulation of movement were first published by Ingvar and Philipson (1977) using regional cerebral blood flow (rCBF) measurements. They showed that the rCBF pattern differed whether unilateral hand movements were actually executed or mentally simulated. In the latter case, an increase in frontal lobe activity was observed, whereas actual execution also led to activation of the rolandic area. Decety et al (1990) using an improved version of the same technique confirmed this early finding. In addition, they showed a bilateral increase in metabolic activity of the cerebellum during mentally simulated movements. According to Roland et al (1980), mere planning of an aimless finger movement sequence (without execution) activated the supplementary motor area (SMA), whereas planning of the same sequence followed by execution activated both the SMA and the primary motor area (see also Roland, 1984). SMA was also found to be activated during both imaging and executing a motor task (Decety et al, 1990).

The facts that the rolandic region was activated only during executed movements, and that SMA was activated during both imagined and executed movements were confirmed by Fox et al (1987). These authors, in addition, found that a limited part of premotor cortex, the posterior inferior premotor area, was involved preferentially during imagined movement. In fact, comparison of cortical activation during motor preparation and motor imagery is rendered difficult by the lack of a clear definition of the tasks used by the different authors. For example, does the execution of movements in a fixed, no choice, condition involve the same amount of "preparation" as movements executed on the basis of prior instructions and relying on the selection of one out of several alternative responses? Deiber et al (1991) found a bilateral activation of SMA and anterior premotor cortex in both cases. However, the level of activation was higher in the multiple choice than in the no choice condition. These results do not represent a definite confirmation of the above prediction, neither do they rule it out. Further experiments are needed, where
tasks involving different degrees of preparation, different levels of complexity of stimuli, etc., will be performed by the same subjects in both the mental and the actual movement conditions. A direct comparison of the two conditions (e.g., using ET image subtraction methods) should then become possible and provide a clearer answer to this query.

3.3. Physiological correlates of motor imagery and preparation.

Preparation to action involves several different types of phenomena. Some of these phenomena can be purposively inhibited (albeit incompletely) by the subject: the production of the prepared or intended movement can be blocked, for example in the motor imagery situation. Other phenomena, however, escape voluntary control. This is the case for activation of vegetative functions normally associated with muscular activity, such as adaptation of heart and ventilatory rates to effort. Monitoring these functions during motor preparation and imagery is thus an interesting way for comparing the two situations.

Fine grain analysis of cardiac and respiratory rate changes at the onset of voluntary effort has shown that these changes tend to anticipate muscular activity. Krogh and Lindhard (1913) found an abrupt rise in pulmonary ventilation and heart rate during the first few seconds following work onset. As this effect was too fast to be due to an excess in CO2 produced by the muscles, they concluded that its origin was an increase in excitability of respiratory centers by "irradiation of cortical impulses". These early changes in heart and respiration rates during preparation were confirmed in more recent experiments. Adams et al. (1987) have shown that heart rate and cardiac output already show a noticeable increase within about 5 beats after exercise is started. Respiration changes follow one breathing cycle. These effects can hardly be explained by metabolic factors, since a reflex increase in heart rate based on CO2 increase in venous blood should take a longer time. A plausible explanation is that vegetative activation during preparation to effort would be timed to begin slightly prior to the time when motor activity starts. This would represent an optimal mechanism for anticipating the forthcoming metabolic changes (by increasing perfusion of muscles with oxygenated blood) and shortening the intrinsic delays needed for heart and respiration to adapt to effort (for a complete review, see Requin et al, 1991).

The brevity of motor preparation, however, makes it difficult to observe its effects on vegetative effectors. More specific experimental designs are required, where the effects of central commands can be prolonged in time or dissociated from those of the normally concomitant metabolic changes. One example of such a design is given by the experiment of Goodwin et al (1972). These authors used tendon vibration during voluntary sustained muscular contraction to modulate the level of central command. When vibration is applied to the tendon of a muscle, the Ia afferent volley arising from this muscle tends to reflexly decrease the activity in the antagonist. If the antagonist is voluntarily contracted, the amount of central command needed to maintain the same degree of contraction increases. The reverse occurs (i.e., central command decreases when vibration is applied to the contracted muscle itself. Goodwin et al measured cardiovascular (heart rate and blood pressure) and respiratory changes during tendon vibration. They found that these changes mapped the level of central commands. As muscular exercise was maintained constant throughout the experiment, these vegetative effects had to be attributed to the modulation of the central commands produced by vibration. This result provides a qualitative evidence for a graded vegetative response in relation to central command for action.

Similar effects should logically be observed during attempts to move in pathologically or experimentally paralysed subjects. Although this remains to be verified, animal experiments strongly suggest that this is indeed the case. In paralyzed animals, electrical stimulation of brainstem areas which provokes fictive locomotion also produces concomitant activation of vegetative effectors (Eldridge et al, 1981, 1985). This coupling of motor preparation and cardiac activation in fact seems to rely on a very primitive mechanism, which can already be demonstrated in invertebrates (Arshavsky et al, 1990).

Motor imagery is another situation where action-related brain activity can be dissociated from the effects of execution. Decety et al (1991) monitored activity of vegetative effectors in normal subjects during mental simulation of actions like running on a treadmill at several different speeds or pedalling at different rates. They reported that both heart rate and total ventilation increased with respect to the resting level,
and that this increase was proportional to the intensity of simulated exercise (for a confirmation of this result, see Wang and Morgan, 1992). The absence of overt muscular activity during mental simulation of exercise was ascertained by using NMR spectroscopy (Decety et al., 1993; see discussion of this point in Section 3.1. above). Such an autonomic response in a situation where no muscular work was produced can only be attributed to a central influence similar to that observed during motor preparation. As the autonomic system by definition escapes voluntary control and cannot be held under inhibition, the central influences on this system become recordable at the periphery. The precise neural pathways for this central regulation of vegetative effectors during motor preparation and mental simulation remain to be determined.

4. The content of motor representations.

The preceding sections were devoted to understanding the role of the motor representation phenomenon as a vehicle for mediating motor behaviour. In the present and the following sections, the problem of the content of these representations will be addressed. The main issues to be discussed will be: What are the parameters which are coded in motor representations? Can these parameters be accessed experimentally? Is it possible to identify within motor images, parameters that are normally encoded in motor programs? If the two processes of preparation and imagery represent different degrees or different aspects of the same phenomenon, and if they address the same objectives, then they should contain the same informations. In other words, parameters that are relevant to describing actual movements, and which are likely to be represented during motor preparation, should also be represented in imagined movements. Conversely, the consciously accessible content of motor images should provide information as to which parameters are represented during motor preparation.

One has to draw first a distinction between what is represented and how this is implemented. Obviously, any represented aspect of a movement has to be ultimately transformed into a set of neural command pulses for muscle contractions. This is not to say that muscle contractions are represented. One should expect that the represented aspects of movements integrate lower levels of execution. One of the historical landmarks illustrating this problem is the controversy which arose at the end of the last century among motor physiologists, about whether electrical stimulation of motor cortex evoked simple muscular contractions or pre-organized movements (see Jeannerod, 1983). The issue will therefore be to determine the level of complexity at which movements are actually represented, among the wide variety of possible representations. Are they represented as the activation of a set of muscles, or as kinematic contours, or as an ensemble of functional synergies, or as a set of motor "rules" (see Saltzman, 1979, Gottlieb et al., 1989)? In the following Sections a number of possibilities will be reviewed, including the representation of relatively global parameters of movements like their duration and force, as well as more specific kinematic rules. Duration and force have not been chosen arbitrarily: those are the parameters of motor preparation which are the most directly experienced by subjects during the motor imagery process and have directly explorable introspective counterparts.

4.1. Is there a representation of the duration of an action?

A number of experimental data point to the similarity of the time duration needed for mentally and actually performing the same action. Already in 1962, Landauer compared the time taken by a subject for speaking the alphabet or series of numbers aloud and for thinking them to himself. He found that overt and implicit recitations took almost the same time. Landauer concluded that "it seems that one does not think words and numbers appreciably faster than one can say them aloud, suggesting that the two behaviours may involve much the same central processes". Decety and Michel (1989) reached the same conclusion in comparing actual and mental movement times in a graphic task. The time taken by right-handed subjects to write their signature or a piece of text was found to be the same whether the task was executed actually or mentally. The same temporal invariance was found, although movement duration was globally increased, when subjects used their left hand. Another interesting finding was that it took the subjects the same time, both actually and mentally, whether they wrote the text in large letters or in small letters. This behaviour conforms to the so-called "isochrony principle" previously described for actually
performed learned motor skills like writing or drawing (see Viviani and McCollum, 1983).

Further results suggest that the similarity of duration for actually and mentally performed actions can be generalized beyond the category of learned skills. Decety et al (1989) compared the duration of actually walking at targets placed at different distances with that of mental simulation of walking at the same targets. Blindfolded subjects were asked either to walk, or to imagine themselves walking, at previously inspected targets located at 5, 10 or 15 meters. Walking times were read on a stopwatch that the subjects held in their right hand, and that they switched on when they started to walk (actually or mentally) and off when they stopped. In the actual walking condition, walking times were found to increase with the distance covered. The same effect was observed in the mental walking condition. Moreover, and most importantly, mental walking times were found to be closely similar to those measured in the actual walking condition for the same subjects and for corresponding distances.

The fact that walking times were invariant across actual and mental conditions in such a basic task as walking to targets raises an interesting discussion. Several authors (e.g., Pylyshyn, 1973; see also Richman et al., 1979, Mitchell and Richman, 1980) would argue that the subjects had tacit knowledge of what should happen when they walked mentally for longer distances, namely, that duration of the action should increase. If this were actually the case, the observed temporal invariance would be simply due to a strategy of the subjects of replicating in the mental condition the temporal sequence registered in the actual condition. It is not clear, however, if and how the duration of movements is coded centrally. No simple answer can be given to the question of what are the cues used by subjects to determine the duration of a mental event. One has first to bear in mind some of the theoretical reservations raised by classical XIXth century philosophers on representation of time. According to W. James (1890), we have no sense of empty time, we can only judge the duration of sensations or of mental states. Because a succession of feelings is not a feeling of succession, we do not perceive time as such (see Debru, 1992).

The duration of a movement is a combined variable, which arises from the unfolding of the movement itself: it depends on the force-mass relations involved in the action (for a complete treatment of this point, see Gottlieb et al, 1989). There is a common observation showing that duration of a simple movement (single joint, constant mass, no strong accuracy requirements) is a function of its extent, that is, of the distance to be covered. In order to produce movements of a greater extent in this condition, the command system has just to increase the amount of muscular force. Accordingly, maximum acceleration and maximum velocity tend to increase linearly (within limits) with extent of the movement. However, the fact that greater force is associated with greater distance and with longer duration cannot be considered as a general rule 1. For example, if the load of the moving limb increases, the same distance can still be covered within the same time, provided force is increased and additional energy is spent, which means that in this case, greater force will no longer be associated either with greater extent or with longer duration of the movement. In addition, in actions involving small displacements and high accuracy requirements, the force, but not the duration, increases with distance covered (the above mentioned isochrony principle). The level of force programmed in the motor commands is thus associated with greater duration of the movement only in a restricted number of situations, and therefore cannot be used as a cue for determining movement duration.

One possible way to further document this point is to compare the durations of actual and mental movements performed against an external load. If the duration required for performing the movement is encoded centrally within the motor representation, the external load should not affect the perceived duration of the imagined action. If, on the other hand, duration is represented as a function of other variables, like muscular force, then the durations of the imagined and the actually executed movements should differ, because the load would exert its effect only in the actual condition and not in the mental condition. This possibility was tested in a further experiment by Decety et al (1990) using the same subjects and the same setup as in the previous one. Blindfolded subjects loaded with a 25 kg weight placed in a rucksack were positioned on the track and were instructed to walk or to imagine themselves walking at previously inspected targets. Walking times in the actual walking condition with the 25 kg load were in the same range as those measured in the same subjects in the first experiment without the load. By
contrast, in the mental walking condition with the load, durations were significantly increased (by 30% or more) in all subjects and for all target distances.

The results of this second experiment, in showing a clear dissociation between actual and mental walking times, first demonstrate that subjects were not merely replicating in the mental condition the estimation of the durations they had experienced in the actual walking condition. Even more importantly, they suggest that force, rather than duration, is the encoded variable, and that estimated duration is merely derived from the level of centrally represented force. When the subjects carried the load, they centrally programmed a greater force to overcome the resistance. In the actual walking task, this increase in force resulted in maintaining the same speed as without load, whereas in the mental walking task, the increase in encoded force was not used to overcome any resistance, because subjects did not actually walk. This interpretation does not yet account for the increase in subjective movement duration when the load was present: the link between encoded force and experienced time is still missing. It may simply be that subjects "read" the increase in felt force as an increase in felt movement duration, according to their common experience.

This shows that duration is not encoded in itself, but, instead, that force must be the most used cue for evaluating movement duration. Finally, it is interesting to note that subjects spontaneously reported in this condition a strong sensation of effort which they felt to increase with the distance of targets. This sensation may have been the subjective correlate of the increased level of force specified by the program.

4.2. The representation of force and effort.

The previous section has emphasized the idea that the amount of force required to produce the desired motor effect pertains to motor preparation. Indeed, at the physiological level the firing of neurons in the primary motor area has been shown to correlate with muscular force (Evarts, 1968; Hepp-Reymond et al., 1978; Wannier et al., 1991; But see Footnote 2). The working hypothesis in this section will be that the programming of force has a subjective correlate, the sensation of effort, which can become perceivable by the actor independently of actual movement execution, and can be monitored experimentally.

Research on sensations of effort and their physiological correlates (Sperry, 1950; von Holst and Mittelstaedt, 1950) has been continuing almost without interruption since their description by von Helmholtz in the last century (see Scheerer, 1987, Jeannerod, in press). These sensations have been recently studied both in patients with complete or partially recovered paralysis, and in normal subjects during transient neuromuscular block or during fatigue. Studies in patients with paralysis of central or peripheral origin (see Gandevia, 1982) replicated some of the classical self-observations of Mach (1906). In conformity with these earlier findings, hemiplegic patients reported that attempts to move their completely paralysed limbs produced no feeling of effort. When their ability to move began to return, they reported that their attempts were accompanied by a feeling of intense heaviness of the plegic limb. Eventually, their sensations of heaviness decreased as their movements became easier and regained strength. By contrast, in patients with paralysis of peripheral origin, attempts to move the paralysed limbs were always associated with sensations of heaviness.

Experiments involving transient paralysis in volunteer subjects have led to more ambiguous results. Several authors using ischemic block or local injection of curarizing agents to produce paralysis of one hand, failed to observe overt sensations of effort during their attempts to move (Laszlo, 1966; McCloskey and Torda, 1975). However, another less direct, but more objective, method for measuring the central level of effort is to ask the subjects to indicate the quantity of force that they have to generate for achieving a given task. Gandevia and McCloskey (1977) instructed subjects to press a lever with one thumb (the reference thumb) in order to produce a reference tension, displayed visually on an oscilloscope screen. With the other thumb, they had to press another lever so as to match, without visual control, the muscular force produced by the reference thumb. During partial curarization on the side of the reference thumb, the subjects could still produce the reference tension by pressing the lever by putting more force into the action in order to overcome the partial neuromuscular block. Accordingly, with their other thumb, they indicated a much larger muscular force than normally required to produce the same tension. The same authors (Gandevia and McCloskey, 1977) also used the perceived heaviness of weights as a measure
of effort. The same matching technique as above was used, i.e., subjects chose weights with one arm until the heaviness perceived with that arm matched the reference weight lifted by the other arm. During partial paralysis, the subjects chose exaggerated weights, hence indicating an increase of the heaviness perceived with the weakened arm. These results replicated earlier results obtained with muscular fatigue instead of partial paralysis. McCloskey et al. (1974) had shown that after the reference arm supported the weight for some minutes and became fatigued, weights heavier than the reference weight were chosen to match it. These results fit the Holmes statement, that forces exerted by weakened muscles tend to be overestimated (Holmes, 1922; Holmes observed this fact in patients with unilateral cerebellar lesion and found consistent overestimation of weights by the asthenic cerebellar arm). The explanation for this fact is that subjects have to produce more force centrally to overcome the muscle weakness. If judgement about force (the sensation of effort) relied only on information directly related to the actual muscular tension (such as proprioceptive discharge), then no overestimation should occur: on the contrary, subjects should underestimate the generated force.

Other aspects of sensations of innervation (their temporal organization) can also be measured by using purely introspective methods. These aspects can be inferred from judgements subjects make about when they release the command to move a limb. In the McCloskey et al. (1983) experiment, subjects were instructed to perform a test movement at will. The instructions also implied that they should disregard the movement, and concentrate on their issuing of the command to the limb ("think about when you tell it to move"). Finally, they were given a reference stimulus which occurred at a variable delay with respect to the onset of their movement (as judged from EMG onset). It was found that the reference stimulus had to be given about 100 ms prior to EMG onset in order to be judged by the subject coincident with onset of the motor command. In order to avoid possible cues arising from contracting muscles, the same experiment was repeated under ischemic block of the arm: in that case, where no muscle contraction occurred, the efferent volleys were recorded from the nerve upstream with respect to the block. Again, the reference stimulus had to precede significantly the nerve volleys to be felt coincident with the subjective central command. This experiment therefore demonstrates that subjects can in some way identify the neural signals related to their central commands, and that they can distinguish these signals from those arising from muscles at the time of the movement itself. Several arguments demonstrate that the command-related sensations are unlikely to have arisen from the muscle. The sensations are in advance with respect to EMG; they persist under ischemic block; in addition, muscle spindles, which might represent a possible source of signals for these sensations, do not seem to discharge during isometric muscle contraction prior to the movement (Vallbo, 1973).

The problem that remains to be solved is the precise nature of these "sensations". Gandevia (1982) proposed an interpretation which could account for the sensations of effort reported by subjects attempting to move against weakened muscles (by neuromuscular blockade, fatigue, or other ways), as well as for their perception of increased heaviness. He suggested that neural traffic in motor corticofugal pathways might be read off 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 cases of distal paralysis, where corticofugal pathways are not altered. In a more recent paper, however, the same author (Gandevia, 1987) 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. This observation conforms with Penfield's observations during direct electrical stimulation of the cerebral hemispheres in conscious patients: when such stimulations produced a movement, the patient invariably experienced having been moved passively by the experimenter, and had no sensation of having been the author of his/her movement (Penfield and Boldrey, 1937). It can therefore be suggested that the relevant discharges for the sensations of innervation arise from structures such as premotor cortex or basal ganglia, which subsequently impinge upon primary motor cortex and on the descending pathways. This interpretation would be consistent with the fact that premotor cortex and basal ganglia are both activated during motor imagery, although this is not the case.
for motor cortex proper (see above).

It is thus likely that mental images related to a movement should contain indication, accessible to the subject, related to the amount of force which is being prepared. Sensations of effort have been measured (using subjective scaling) during simulated exercise (e.g., Decety et al, 1993), and have been found to increase with the degree of mental exercise. It is difficult at the moment to determine which cues are used by the subjects to detect the amount of programmed force.

4.3. The representation of motor rules.

Is it possible to study mental kinematics? Though this may seem a bizarre question, it is an important one. The previous sections, in showing a close similarity of neural processes for preparing and imagining movements, implied that at least some of the kinematic rules that have been described for actually executed movements (i.e., those which do not pertain to the interaction with the external force field) should already be present at the representation level. This prediction can be verified using experimental data with several different categories of goal-directed motor behaviour.

4.3.1. Representation of kinematic regularities.

Skilled movements like writing or drawing obey well defined kinematic regularities. A temporal structure exists in those movements, which cannot be ascribed to biomechanical factors alone and which, therefore testifies to the intervention of central coding. First, as already mentioned, because tangential velocity of these movements is scaled to their amplitude, movements of different amplitudes tend to have the same duration (see Viviani and McCollum, 1983). This kinematic principle seems to be maintained in mentally simulated movements: to take an example already reported in Section 3, subjects take the same amount of time to mentally write a small or a large signature (Decety and Michel, 1989).

A second principle is that the tangential velocity of the moving limb is a function of the radius of curvature of the movement, i.e., it is minimum when the curvature is maximum (Lacquaniti et al, 1983, Massey et al, 1992). Tracking experiments show that subjects cannot depart from this relation between geometry and kinematics. When instructed to track a target moving with a different spatiotemporal pattern (e.g., accelerating rather than decelerating in the curves), their performance deteriorates. Subjects' movements during the attempts to track the target "continue to bear the imprint of the general principle of organization for spontaneous movements, even though this is in contrast with the specifications of the target" (Viviani, 1990). The main point of relevance here is that the same relation between velocity and curvature is also present in subjects' perceptual estimation of the regularity of the trajectory of a luminous target. A target moving at a uniform velocity is paradoxically seen moving in a non-uniform way and, conversely, the condition for perceived uniform velocity is that the movement has a kinematic structure which respects the above velocity/curvature relation (Viviani and Stucchi, 1992a). According to Viviani and Stucchi (1992b), the explanation for this fact would be that perception is constrained by motor schemas, that is, by the implicit knowledge that "the central nervous system has concerning the movements that it is capable of producing". This experiment clearly shows that there is a central representation of what a uniform movement should be, and that this representation influences visual perception. If this interpretation (based on the "central" version of the motor theory) is correct, then the kinematic structure of mentally produced movements should also follow the same rule. This remains to be tested.

Another relevant set of data comes from studies dealing with Fitts law. The classical conception of Fitts law, namely that the increase in duration of a goal-directed movement when this movement becomes more difficult, is due to the time needed to process visual feedback, has been recently questioned. Fitts law seems to pertain, not to the execution stage of movements (as this classical explanation would hold), but to the preparation stage. Indeed, the difficulty/duration relation (or its corollary, the duration/accuracy relation) exists in movements executed without visual feedback (Prablanc et al, 1979). The "correction" submovements, which occur in accuracy demanding tasks and which partly account for th increased duration, are observed independently from the presence of visual feedback, hence suggesting that they
pertain to the motor plan. The relation between duration and accuracy would thus be the result of neural coding of the movement during the preparatory stage (e.g., Jeannerod, 1986a. For a general review of this problem, see Meyer et al, 1990).

If the idea that the above temporal relationships may already exist at the central stage of the motor process and are not determined at the execution level is correct, then the same temporal relations should also be found in situations where the action would be planned but not executed. There are no experimental data which could fulfill the criterion for a purely mental Fitts law. However, the results of an experiment carried out by Georgopoulos and Massey (1987) are interesting to consider under this respect. They instructed subjects to move a lever in a direction different from that indicated by a visual stimulus. The instruction was that they moved at a given angle (randomly selected by the experimenter on each trial) from the direction shown by the target. Georgopoulos and Massey showed that the duration of the reaction time for these movements was increased with respect to those of movements normally directed at the visual target. Furthermore, this increase in reaction time was a function of the amplitude of the angle. The authors' explanation for this finding was that subjects had to mentally rotate the movement vector until it reached the desired angle, hence the increase in reaction time as a function of the angle.

Georgopoulos and Massey thus explicitly interpreted their findings within the Fitts law's framework. Reaction times, which they considered as a "mental movement time", were correlated with mental movement "difficulty" (calculated from the amplitude of the angles) as classically found for the duration of executed movements. Hence their conclusion that, because Fitts law hold in this condition, "both real and imagined movements might be governed by similar amplitude-accuracy relations" (1987, p 361). Further support for this interpretation was obtained by Georgopoulos et al (1989) by transposing the same paradigm to monkeys trained to move a handle at given angles with respect to the direction of a target light. During the animal's performance, they recorded from neurons located within primary motor areas, coding for movements in a given direction. Georgopoulos et al computed the population vector (by summing the individual vectors encoded by several individual neurons) in relation to movements directed at visual targets, including in the condition where the monkey had to make movements in a direction different from that of the visual target. In the latter condition, they found that the direction of the population vector changed during the reaction time of the movement. The vector progressively rotated from the direction indicated by the visual target, to the direction of the intended movement. 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 an universal motor rule as Fitts law 3.

A simple experiment in human subjects can be proposed for verifying the validity of this rule in purely mental actions. In this experiment, the subjects would receive the instruction to walk mentally through a gate of a given width (previously shown on a screen). They would have to indicate the times when they started walking, and when they passed through the gate. Trials would be repeated with gates of different widths. If the above predictions are correct, the mental walking time should (at least within limits) correlate with the gate width, the narrower the gate, the longer the time.

4.3.2. Representation of motor constraints and potentialities.

Other experiments reveal that the representation of an action takes into account the biomechanical constraints of the represented movement. Stelmach et al (in press) examined the act of prehension when subjects were asked to grasp, with their thumb and index finger pads, an elongated object placed at different angles of orientation with respect to the sagittal body axis. Grasp preferences were documented with respect to whether a forearm rotation was needed or not for grasping the object placed at each orientation angle. Remarkably stable grasp preferences were noted across the different angles. For angles 90. or less, no rotations were observed; however, for angles 110. or greater, rotations were employed to reorient the finger opposition space during the transport phase of the movement. Only one angle, 100., produced any evidence of grasp ambiguity in how to approach the object. As the movements were fast and forearm rotation (when present) occurred early in the trajectory, the angle of the object at which an
unproned hand posture would become uncomfortable had to be determined at the representation level and did not relate to a control exerted during the movement. The same interpretation can be given to the results of Rosenbaum et al (1990) and Rosenbaum and Jorgensen (1992). They found that the decision to make a given type of grip (e.g., underhand vs overhand) for grasping an object is taken according to the subsequent use of the object, in order to avoid awkward or uncomfortable hand postures and to minimize times in extreme joint angles. They used a horizontally positioned cylindrical bar and counted the number of times subjects would use an overhand or underhand grip to take the bar when its left or its right end had to be placed on a horizontal surface. Subjects using their right hand were found to consistently make overhand grasps when they had to place the bar vertically with the right end on the surface. Rosenbaum et al's hypothesis for explaining these results was that the representation does not specify which actions are allowed in which situations, but rather, which actions are not allowed. This is somewhat contradictory to other facts reported below (see Section 5.1.2) about preshaping of the hand, indicating that object affordances are indeed centrally represented. The use of motor imagery would be one way of testing this point in examining whether subjects are able to image "impossible" movements, i.e., escaping anatomical and biomechanical limitations. Although it has been reported that, under conditions of perturbed proprioceptive input (e.g., by tendon vibration, Roll et al, 1990), subjects may perceive their limbs in abnormal positions, it is unlikely that during imagery in normal conditions they would be able to simulate these positions. Experimental results by Shiffrar and Freyd (1990) showed that the perceived motion of human limbs (extrapolated by subjects from rapidly alternating pictures) tends to respect the biomechanical constraints and do not violate the laws of biological motion.

5. Representation of goals for actions.

It becomes progressively clear throughout this paper that the representation of an action cannot be limited to the parameters and constraints dictated by execution of the action by the motor system. The goal of the action also must be encoded. In this section, the idea will be developed that the goal of an action includes an internal representation of both the external object toward which the action is directed, and the final state of the organism when this object has been reached. This conception has a long history in the literature, under the heading of the "schema" theory. Head (1920) first used this concept to account for maintenance and regulation of posture. It was later developed by others as an internal model of the body in action built from sensations and previous responses to external stimuli (for a critical account, see Oldfield and Zangwill, 1942. See also Schilder, 1935 and Lasheley, 1951).

More recently, Schmidt (1975) proposed that the motor response schema arises as a representation of the information elements that are present within the context of executing a movement (e.g., initial condition of the musculature, specification of the muscular commands, sensory consequences of the movement, and response outcome). Some of these entities, the monitoring of initial state and the specification of the commands for example, are independent from the movement itself, while some others are consequences of it. Motor control and learning would thus be the result of an interplay between central and peripheral events, until the actual outcome of the movement would correspond to the desired (represented) outcome. The notion of the representation of a goal therefore implies that the organism is looking ahead toward a new state, the representation of which steers the transformation until its completion. In the present section, this aspect of motor representations will be studied at two levels, that of the visuomotor transformation, and that of action planning.

5.1. The lower level: Objects as goals.

It will be first shown that, when objects are goals for actions, their visual attributes are represented in a specific way (the pragmatic mode), used for the selection of appropriate movements, and distinct from other possible modalities of representation used for other aspects of object-oriented behaviour (one of them being the semantic mode). This description of object processing is in continuity with previous attempts, as it has long been recognized that the same object or event can be processed in different ways, according to the task in which the subject is engaged. The distinction between different modes of processing, however, was usually grounded on the amount of overt cognitive content involved: hence the
distinctions between conscious/non-conscious, explicit/implicit or automatic/controlled modes of processing (Bridgeman, 1989). Consciousness, however, is not at issue here, as it does not discriminate between semantic operations and motor or sensorimotor operations: both can be achieved without explicit awareness (see Holender, 1986).

The nature of the dichotomy proposed here would be closer to the distinction made by the Mishkin group on neuroanatomical grounds (e.g., Mishkin et al, 1983), between object vision and spatial vision, epitomized as the now classical distinction between "What?" and "Where?". At variance with Mishkin, however, it is postulated that the motor representation includes much more than the spatial aspects of movements. During object-oriented action, objects are not only located in space and reached; they are grasped, manipulated and used. For this reason, it seems preferable to classify object attributes, not with regard to putative anatomical or functional channels, but rather with regard to the observed interactions between the subject and the objects during a given action: object attributes would thus be classified only on the basis of their inclusion in one or the other aspect of object-oriented behaviour.

If it is the relevance of a given attribute to a particular task that governs its inclusion within a given type of representation, a large set of attributes are relevant to both: this would be the case for those contributing to shape, size, compliance, texture, etc. Others, by contrast, are probably irrelevant to the pragmatic representation (e.g., color) or are of little or no relevance to semantic processing (e.g., weight). This is the reason why the classification based on a distinction between spatial vision and object vision may be incomplete or even misleading. According to Kosslyn et al (1990), parameters related to object size should be specified at the same level as location or orientation, and should therefore pertain to the process of "spatiotopic mapping". Size, however, is not merely a spatial attribute: although phenomenal size depends on distance, this is not true for represented size which remains invariant with respect to distance. Represented size, not phenomenal size, is thus part of object identity. The same could be said of shape, which obviously changes as a function of the relative positions of the object and the perceiver, though it remains representationally constant. The Marr distinction between viewer-centered and object-centered descriptions of objects may be useful in this context (Marr, 1982). Operations which require a viewer-centered description (localizing, reaching) activate a spatial ("Where?") system. Those which require an object-centered description (identifying, grasping, manipulating) activate other systems: One is the system for semantic processing (the "What?" system), and the other one, which is under discussion here, is the system for pragmatic processing. This again stresses the fact that the same attribute can belong in theory to several representational categories according to the task which has to be performed.

5.1.1. Neuroanatomical evidence for multiple representations of objects.

Research in this field already has a long history, which can be followed across the various interpretations of the duality (in fact, the multiplicity) of central visual pathways. In spite of the above critiques, one of the most useful interpretations was that of Ungerleider and Mishkin (1982) who proposed that projections arising from primary visual areas follow two distinct pathways: the ventral route involving the occipito-temporal pathway with its main relay in infero-temporal cortex; the dorsal route involving the occipito-parietal pathway ending in posterior parietal cortex (see also Morel and Bullier, 1990, Baleydiere and Morel, 1992). The functional value of this anatomical duality is supported by the effects of lesion of each pathway on monkey behaviour. Lesions of the ventral system primarily affect object recognition, whereas lesions of the dorsal system produce disturbances in object localization (Pohl, 1973).

Clinical observations, following the lead of Poppelreuter (1917), indicate that a similar duality in cortical functions also exists in man. More recent observations, however, pointed to a division of labour between the two pathways, different from what was initially suggested by the Mishkin group. Goodale et al (1991; see Milner and Goodale, 1991) reported the case of a patient who was unable to recognize objects (the classical picture of visual object agnosia). The patient was also unable to purposively size her fingers according to the size of visually inspected target objects (an easy task for normal subjects, see Jeannerod and Decety, 1990). In contrast, when instructed to take these target objects by performing prehension movements, the patient was quite accurate. Not only was she able to reach the object location, but she also
preshaped her hand accurately according to the object size and shape. The lesion in this patient was likely to have interrupted the occipito-temporal (ventral) pathway. In fact, this observation fits into the broader framework of the preservation of object use in patients presenting semantic processing deficits. In these patients, lesions predominate in the temporal lobes and are usually more marked on the left side (Saffran and Schwartz, in press).

At variance with occipito-temporal lesions, posterior parietal lesions do not impair object recognition. Instead, they alter arm movements during reaching (the typical optic ataxia symptom) and also finger movements during preshaping and grasping. Patients misplace their fingers when they have to visually guide their hand to a slit at different orientations (Perenin and Vighetto, 1988). Duringprehension of objects, they open their finger grip too widely with no or poor preshaping, and close it when they come in contact with the object (Jeannerod, 1986b. See also Jakobson et al, 1992). These clinical observations, in showing that lesions can create a "double dissociation" between different types of deficits in object-oriented behaviour, confirm the hypothesis of selective semantic and pragmatic representation mechanisms. The prediction can therefore be made that, if this hypothesis is correct, motor images of object-oriented actions (e.g., grasping) and visual images of the same objects should be processed by different cortical areas. Recent results showing preferential activation of posterior parietal cortex (using a brain imaging technique) during visually guided finger movements (Grafton et al, 1992) partly support this prediction. It can also be predicted that the pattern of brain activation could be changed, by only changing the requirement of the task in which the subject would be engaged (e.g., imagine manipulating vs imagine classifying the same objects).

These neuroanatomical data thus provide a framework for describing the neurophysiological substrate of the pragmatic representation. The function of the representation neurons postulated earlier in this paper stands in between a "sensory" role (to extract from the external world the attributes of objects or situations that are relevant to a given action) and a "motor" role (to encode some aspects of that action). A population of neurons located in the monkey posterior parietal cortex (area 7a) and studied by Taira et al (1990) might fulfill this criterion of a visuomotor representation. These neurons are selectively activated during manipulation by the animal of visual objects of a given configuration (e.g., a push-button, a handle, etc). Neither presentation of the preferred object, nor movements aimed at this object in the dark are sufficient alone to activate them. Because they involve both a sensory and a motor counterpart, these neurons thus relate to a given type of action, rather than to a given motor pattern of the hand or to a given visual configuration. It is thus not surprising that lesions of this posterior parietal area in the monkey affect the ability to shape the hand to object size or orientation, in the same way as it does in man (Haaxma and Kuyper, 1975, Faugier-Grimaud et al, 1978).

Another population of neurons, located in premotor cortex (area 6), also pertain to the same category: indeed, they seem to be complementary to those recorded in area 7. Their discharge relates to preparation of distal movements and is influenced by the way the acting hand is shaped prior to and during the action directed toward a target object: precision grip neurons, whole hand prehension neurons, etc., can be identified. In many cases, the hand used for the action is irrelevant, so that neuron discharge is altered in relation with movements of either hand. Finally, they are poorly responsive to visual objects presented outside the context of an action oriented toward them (Rizzolatti et al, 1988). The fact that a significant proportion of these premotor neurons have been found to be also activated during observation, by the animal, of their preferred object-oriented action performed by an actor (Di Pellegrino et al, 1992, see above) is of critical importance for their representational role. It is likely that, if properly examined, the parietal neurons described by Taira et al would also show a similar property. Mutual exchange between these parietal and premotor neuronal groups (granted by extensive anatomical linkage between the two areas, see Morel and Bullier, 1990) seems a highly plausible substrate for pragmatic representation.

5.1.2. Predetermined motor patterns.

Actions like grasping relate to the object as a goal for the action. The object attributes are represented therein as affordances, that is, to the extent that they afford specific motor patterns, not as cues for a given
perceptual category. This function does not imply binding of object attributes into a single entity, as this would be the case in a semantic type of representation. Instead, each attribute contributes to the motor configuration of the hand by selecting the relevant degrees of freedom. In addition, as already suggested, this process is effected within an object-centered system of coordinates, as shown by the fact that the hand configuration for grasping an object is not affected by its location with respect to the body and that, conversely, the opposition space tends to remain invariant with respect to the object. There are limitations to this assertion, however, because the arm geometry creates constraints that may require changes in hand configurations for extreme positions of the object. Examples of such constraints were shown in the experiments of Stelmach et al (In press) and Rosenbaum et al (1990).

It can be proposed that the motor patterns corresponding to the object affordances, which unfold during the movement, are predetermined within the pragmatic representation. Indeed, none of the aspects of prehension movements can be shown to depend on direct visual control of the hand. The coordination of reaching and grasping, the biphasic pattern of grip formation, the covariation of maximum grip size with object size, etc., can all be achieved in situations where the hand remains invisible to the subject (Jeannerod, 1981, 1984). In addition, the level of muscular force involved in prehension is largely specified during the preshaping phase, in anticipation to contact with the object. Lifting an object implies a sequence of coordinated events where the grip force (to grasp the object) and the load force (to lift it) vary in parallel (see Johansson and Westling, 1988). Several experiments have shown that available information about object weight (e.g., based on visual size cues) can accurately determine grip and load forces in advance with respect to the grasp itself (Gordon et al, 1991).

These results point to the fact that actions are driven by implicit knowledge of object attributes. To account for this fact, Arbib has proposed a simplified form of representation, the "motor schema" (Arbib, 1985; Iberall et al, 1986; Iberall and Arbib,1990). Arbib's conception is that motor representations are composed of elementary schemas which are activated by object affordances and can adjust to visual input. During the action of prehension, motor schemas for the subactions of "reach", "preshape", "enclose", "rotate forearm", or for the selection of a the number of fingers involved, etc., would be available and would be automatically selected when required by object affordances. Those are functional units which can be assembled into a limited number of postures: the posture selected during the preshape defines the optimal opposition space for applying the required forces to the object (Iberall et al, 1986). Finally, it is specially interesting in the present context that Arbib recently included in his schema model a "look-ahead" device, whereby a given schema would remain activated until completion of the corresponding action (Hoff and Arbib, 1992). This notion has been introduced in physiology already some time ago (see Jeannerod, 1990). Robinson (1975), for example, in his model for the generation of saccadic eye movements, specifically proposed that the spatiotemporal course of saccades is obtained by substracting a signal related to the actual position of the eyes from a signal related to their intended position, thereby driving the eyes at the target until the difference between the two signals becomes zero.

This idea of a central coding of the "desired" position of an effector system has been proposed for the control of various kinds of movements, e.g., speech movements (MacNeilage 1970, Abbs and Gracco 1984), arm movements (Pelisson et al, 1986) or finger movements (Cole and Abbs 1987, Paulignan et al, 1991a, b). Most of the above authors drew their conclusion from experiments involving sudden perturbations occurring during movement execution. The corrections in movement trajectory and/or kinematics in response to these perturbation can be so fast (usually within less than 100 ms) that they cannot be due to programming another movement based on feedback error detection. Instead, they have to rely on an open-loop adjustment of the ongoing program. This suggests that the central representation must be a "dynamic" structure, in the sense that it permanently monitors movement-related signals (e.g., proprioceptive) and compares them with the ongoing efferent commands. Any deviation arising from this comparison would immediately trigger corrections (see Prablanc et al. 1979; Jeannerod 1990; and for a computer model using the same principle, Bulock and Grossberg 1988). This property of the pragmatic representation of steering the action toward a goal-state will be further developed in the final section.

The level at which motor schemas are implemented neurally is obviously quite hypothetical. The neurons
recorded by the Sakata group in area 7a and the Rizzolatti group in area 6 would fulfill the requirements for "schema neurons". They would compare to neurons which have been recorded in the other representational system (the ventral system for semantic or iconic representation of objects). Those are not mere feature detectors, they are endowed with high- order visual properties: they are selective for complex visual stimuli (e.g., faces) and generalize their response across different modes of presentation of the same stimuli (see Perrett et al, 1982).

A more global approach to this problem has also been developed, contributing to the same notion that preshaping, manipulation and tactile exploration of objects are based on predetermined schemas. Klatsky et al (1987) showed that subjects tend to classify usual objects into broad categories, the boundaries of which are determined by the pattern of hand movements these objects elicit when they are to be grasped, used and manipulated. Four main prototypical hand shapes (e.g., poke, pinch, clench or palm) seemed to be sufficient for defining the interaction between the hand and most usual objects. Conversely, when subjects were shown unfamiliar forms, and were asked to indicate which hand shape was the most appropriate, they generated highly regular responses, which could be predicted from the geometrical parameters of the forms (e.g., the area of their projecting surface in the frontal plane). This differentiation of hand shapes according to the form of objects was retained in preshaping during actual reaching (see also Pellegrino et al, 1989). Finally, the same authors trained subjects to produce the various hand shapes in response to visual presentation of these shapes. They showed that, in the trained subjects, presentation of a hand shape subsequently facilitated the judgements they made about the feasibility of interactions with objects. The same was not true if the cue was presented verbally (Klatsky et al, 1989). These results, which demonstrate that representation of a motor configuration of the hand influences knowledge about manual interactions with objects (and conversely), are reminiscent of the effects of motor imagery on motor performance, described in section 3-1.

5.2. The higher level: Long-term action planning.

The lower level of representation of actions, as tentatively described in the foregoing sections, is only one of the possible levels where representation mechanisms might operate. Object oriented actions are embedded into broader representations where longer term plans are encoded. It is beyond the scope of this paper to attempt a full description of this upper level, because it would involve consideration of the many processes underlying selective attention, motivation and decision (see Butter, 1987 and Heilman et al, 1987, for reviews). Only a few suggestions can be made, showing that the same general framework which has been used for the lower level may also tentatively be applied.

One has first to conceive the existence of higher-level schemas controlling the selection, the activation or the inhibition of those processed at the lower level. These higher-level schemas are action plans where, in addition, the serial order of the movements needed to achieve the action is represented (Lashley, 1951; for a review, see Keele et al, 1990). Human neuropsychology provides indications as to the reality of such a hierarchical organization for the supervisory control of action (see Noran and Shallice, 1980, Shallice, 1988). One of these indications comes from observation of a group of patients with prefrontal lesions, who present the so-called "utilization behaviour" (Lhermitte, 1983). These patients will compulsively imitate gestures or even complex actions performed in front of them by an experimenter. Similarly, when faced with usual objects (e.g., a glass and a bottle of water) they will not be able to refrain from using these objects in a compulsive way (pouring water in the glass and drinking large quantities of water, etc). This striking behaviour can be explained by an impairment of the inhibitory control normally exerted on the elementary motor schemas. In addition, it stresses the role of prefrontal cortex in organizing behavioural inhibition. One possible consequence of this impairment is that frontal patients presenting this syndrome should be unable to generate motor imagery without immediately transferring the imagined action into motor output.

Whereas utilization behaviour seems to represent an exaggerated expression of the activity of high-level representation neurons, another pathological situation, ideomotor apraxia, provides the opposite picture. Apraxic patients have difficulties imitating movements, they cannot perform symbolic gestures (those
which require the use of a stored representation). They often cannot reconstruct the sequence of movements which are needed to achieve a complex action. Lehmkühl et al. (1981) showed that this deficit was not due to a memory problem in the usual sense, but rather reflected an impairment of the representational stage of sequencing: their apraxic patients were not able to correctly order cards depicting the successive steps of actions like preparing tea, for example. As the elementary schemas are usually preserved in such patients, their deficit should be in selecting and organizing schemas into a purposive action. 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 schemas would also reflect in a deficit in evoking actions mentally. This possibility was explicitly considered by Roy and Hall (1992), their hypothesis (even more radical than ours) being that, "if an impairment in image generation does underlay apraxia, one might predict a coincidence between the severity of the image generation deficit and the severity of apraxia" (p 276). Clinical observations indicate that this hypothesis might be correct. Heilman et al. (1982) identified one type of ideomotor apraxia following left posterior parietal lesions, where patients were impaired in recognizing gestures: their interpretation was that the patients had lost the "visuokinesthetic engrams" needed for building up a representation of these gestures. The parietal neurons involved in these lesions obviously should have a higher hierarchical status than those underlying the low-level pragmatic representation.

In fact, it should be possible to study the higher level using simple experiments similar to those described for the lower one. The Rosenbaum et al. (1990) situation, for example, stresses that hand shapes seem to be planned in anticipation of movements to be performed at a later stage in the sequence, that is beyond the movement which is currently prepared. A similar result was reported by Marteniuk et al. (1987). Subjects had to reach for a small disc, and then to either fit the disc into a tightly fitting well (fit condition), or to throw it in a larger container (throw condition). Marteniuk et al. found that the kinematics of the initial reach, which was common to the two conditions, differed according to whether the instruction was to fit or to throw. In the fit condition, the peak velocity of the reach was lower and a larger proportion of movement time was spent decelerating. These results clearly indicate that the motor representations, including those during motor preparation, expand in time far beyond the movement which is actually prepared.

The higher level is more difficult to describe in neurophysiological terms. The functional operations underlying motor planning, preparation and imagery must involve large neuronal ensembles, which are likely to be widely distributed. In addition, high-order representation neurons should encode complex goals, not only affordances. For this reason, their discharge should reflect the temporal contingency of the action required for reaching the goal. In other words, they should not be influenced by completion of the intermediate steps of the action (e.g., by activation of elementary schemas), but should rather continue firing until the final goal has been reached. One possibility would be that these neurons encode final configurations (of the environment, of the body, of the moving segments, etc) as they should arise at the end of the action, and that they remain active until the requested configuration has been obtained. This sustained activity would represent the reference (the goal) to which the current state of execution of the action would be compared (Jeannerod, 1990). Accordingly, these neurons would remain activated as long as the represented action would not be completed, including in situations where the execution would be blocked. In this case, where the action would not take place, the sustained discharge would be interpreted centrally as a pure representational activity and would give rise to mental imagery. At the moment, only a few experimental results suggest that neurons in the monkey prefrontal cortex might have properties relevant to this function (Fuster, 1985; Barone and Joseph, 1989). Interestingly, the prefrontal areas where these neurons are located are reciprocally connected with abundant projections to and from the posterior parietal cortex, particularly the inferior parietal lobule (see Petrides and Pandya, 1984) and, in addition, project on the premotor area. It is thus possible that the elementary schemas available in the posterior parietal and the premotor areas can be gated by the prefrontal cortex for achieving the selected action plan. New experimental designs will be needed for a more complete demonstration of this mechanism.

6. Conclusion.
Any study dealing with motor behaviour must take into account the fact that the overt aspect (the movement) is only part of the entire phenomenon. The hidden part (the representation) exists in its own right. The two are equally important to study, because, as Bernstein (1967) conjectured, they do not map entirely onto each other. Describing the overt movement does not give full access to the representation; and conversely, fully describing the representation (if this were at all possible) would not tell what the corresponding movement would be. The reason for this discrepancy is that execution involves biomechanical constraints related to implementation by the musculoskeletal apparatus, and distortion by external forces, which are not necessarily represented centrally. In addition, representations are likely to be endowed with properties (partly built on experience from previous actions) which may not be apparent in their eventual motor counterpart. They seem to be structured with different levels of organization; they use cognitive rules for establishing the serial order of action parts, for assembling programs, etc. To be provocative, the overt movement is not a reliable source of information on its own representation.

One of the aims of this paper was to show that motor representations can indeed be observed and described in themselves, due to our strange ability of exploring our own minds and displaying our mental states. A specific methodology has to be used, because imagined or represented movements are not easy to describe verbally (as opposed to other types of representations), a property which limits the impact of paradigms derived from cognitive psychology. In addition, methods exclusively based on subjective verbal reports or on observation of behavioural responses would overemphasize the "macroscopic" aspects of motor representations, those for which it is difficult to find precise neural correlates. An attempt was therefore made into description of more "microscopic" aspects, by infering the content of the representation from recordable physiological correlates. This attempt leads to the operational definition of a pragmatic representation, specific for the different levels at which an action is imagined, planned and prepared. Observation of autonomic changes during imagined action, psychophysical analysis of motor "sensations", effects of brain lesions, etc. are potential windows into its hidden part. More and more direct measures will become available, particularly with improvement of brain imaging techniques in man, and with extension of the representation paradigm in monkeys. The real challenge will be to be able to directly observe a representing brain and to record therein the activity of neuron populations fitting the criteria for representation neurons.

One of the most stringent criteria is that once the proper neurons have been selected, the resulting network must remain active as long as action is not performed: This enduring activity is the basis for the central representation of a goal to which execution can be compared. The comparison mechanism simultaneously takes place at several levels, for controlling execution of the whole action as well as its basic elements. Combination of this framework of interlocked schemas with the concept of enduring activation will provide a basis for further experimental description of the pragmatic representation.

**Notes.**

1. The relation between force and duration may also vary according to the task. Gottlieb et al (1989) made it clear that in time- constrained tasks, subjects control the amplitude parameter of force impulses, whereas in spatially-constrained tasks, the duration of the force impulse is affected by the accuracy demands.

2. Recent work by Georgopoulos et al (1992) suggests that primary motor cortex might code dynamic force (or the change in force) rather than static force. This would be congruent with the fact that the same neurons also code movement direction.

3. In the strict sense, Fitts law defines movement duration as a function of task difficulty. In view of the recent evolution of the theory, however, it seems reasonable to look at the duration of the reaction time as a mental movement time (see Meyer et al, 1990).
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