

neat story told by Jeannerod remains highly underdemonstrated (the use of the conditional mood throughout the paper further reinforces this impression). We will amplify this in connection with three main points.

1. Imagining oneself moving, yet not actually moving, is a specific motor task. Movement usually follows the intention to move, immediately and automatically. By contrast, in Jeannerod's protocol, where subjects are instructed to imagine themselves moving without moving, a specific action is required to inhibit the movement that should normally take place. Jeannerod ignores these active inhibitory processes, assuming that he is studying the pure imagery process. This inhibition is by its nature a central task (with neuronal correlates), one that requires, among other things, verifying the absence of movement. It cannot be ruled out that this inhibitory activity automatically initiates the imagery processes and underlies many of the results obtained or reported by Jeannerod concerning both the neuronal structures involved and the behavioral effects observed (mental training, for example).

In some respects, the problem addressed by Jeannerod is related to the philosophical question famously posed by Wittgenstein (1953): "When I raise my arm, what remains once the fact that my arm raised has been subtracted?" To answer this question, Jeannerod performs the subtraction directly by instructing the subject not to raise his arm. The primary task accordingly becomes remaining motionless; imagining oneself moving is now only the secondary task. This methodology for studying the representing brain seems far from neutral; rather, it transforms the process Jeannerod wishes to investigate.

With this methodology, Jeannerod also touches upon a second philosophical question, this one emphasized by Searle (1983, Ch. 3, "Intention and Action"), concerning the need to dissociate "intentions in action" from "prior intentions." Searle too explicitly considered the task of raising one's arm. Intentions-in-action are present when one raises one's arm spontaneously without any particular intention to move it. Such intentions-in-action cannot be formulated before the action; intimately linked to the motor component of the action, they exist in all intentional action. In addition, "prior intentions" can precede the intentions-in-action. They are present if the subject can formulate his intention to move in advance. Prior intentions are prominently involved in Jeannerod's protocol, where the prior intention ("do not move") is dissociated from the corresponding movement. (Concerning the price of ignoring this distinction, see Searle 1983.) Note that many of our intentional actions are organized only by intentions-in-action, without any prior intentions, especially in sensorimotor behaviors.

2. Imagining oneself moving is different from preparing to move. For Jeannerod to prepare a movement is already to perform it to some extent. We do not share this view. Consider two different tasks: (a) keeping an arm in a fixed position despite variations in external torques and (b) moving the same arm rhythmically. The motor image is very different in these two cases (as different as are the two motor tasks themselves), but there is a great similarity in the preparation of the two tasks. In the first, the greater the expected external torques, the stiffer the arm (Humphrey & Reed 1983); stiffening is realized by an active cocontraction of the agonist and antagonist muscles. In the second task, the same stiffening occurs before the movement begins, but this time in relation to the movement frequency: the higher the frequency, the stiffer the arm (Feldman 1980). The motor preparation is accordingly very similar in both cases. What is observed here is that motor preparation (an anticipatory phenomenon) already has a motor component (even if nothing moves), not just a cognitive component. These discrete tonic and postural components (faintly observable and, in general, slow) are of great importance for the subsequent movement, especially for its timing.

3. What becomes of motor imagery if motor programs do not exist? The way Jeannerod "imagines" motor representation is

not at all independent of his conception of motor organization (fortunately!). Generally speaking, he subscribes to motor programming theories: before movement is initiated, a motor program is chosen (for example, prehension) and its parameters (grasping hand, direction, amplitude, duration, etc.) are specified. This prescribes the movement to be performed. For Jeannerod, motor representation is so closely associated with movement programming that both encode the same parameters. The motor programming theory, however, is far from being the only available theory of movement organization. Jeannerod knows there are alternative theories, but he has elected to ignore them: "alternative mechanisms . . . such as self-organization of endogenous activity for producing movement will be discussed only briefly [very briefly really!] and otherwise largely ignored." In one rival theory (motor self-organization theory), stable solutions emerge at the behavioral level (that of the movement) from interactions occurring at more elementary levels, among others the nervous system, the musculoskeletal system, and external forces (see Taga et al. 1991 for a locomotor example). Here the nervous system deals only with the production of the muscular forces to be combined with the external forces to produce the desired movement, given both the intrinsic dynamics and the morphology of the effector system (with the biomechanical system best described as neither "constraining" – as Jeannerod believes – nor "helping," but as simply "contributing," as one component in the emergence of movement). All the elementary systems interact to shape the movement. As demonstrated by Bernstein (1967a), there are no unique links between motor command and movement (an idea that Jeannerod has transposed directly into the principle that there is no direct relation between motor representation and movement).

According to the motor self-organization theory, it is imagining the *goal* that determines the way the elementary components must interact. Spatiotemporal parameters (such as the duration, amplitude, force, etc., of the movement) would arise a posteriori, as an emergent consequence of the dynamic behavior of the system (Kelso et al. 1981). There would accordingly be no need to represent duration, force, and kinematics to perform a movement even if one took Jeannerod's findings as a demonstration that this was possible. Moreover, Jeannerod does not state that the motor image plays a role during an overt movement; he says only that it is revelatory of processes that are normally concealed from both the subject's consciousness and the investigator's instruments during the overt movement. This dual revelation, seen as neither artefact nor epiphenomenon, has given us abundant food for thought. We especially appreciate Jeannerod's ubiquitous use of the conditional mood, leaving room as it does for our own dream of a brain nonisolated, and, dare we say, at one with its body.

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Representations of movement and representations in movement

Giuseppe Pellizzer and Apostolos P. Georgopoulos
pell001@maroon.tc.umn.edu; Brain Sciences Center, Veterans Affairs
Medical Center, Minneapolis, MN 55417; Department of Physiology,
University of Minnesota Medical School, Minneapolis, MN 55455

Marc Jeannerod champions the cognitive approach to motor control from an innovative perspective. In his target article he appraises the role of mental representations in the preparation and control of movement by considering studies on mental imagery. Although this may seem odd at first, this strategy

provides significant advances into the understanding of the role of mental representations in the control of movement. In recent work we applied a strategy akin to the one advocated by Jeannerod, namely, we used mental imagery paradigms to study properties of representations of movement (Pellizzer & Georgopoulos 1993a). In this commentary we would like to present some studies on mental transformations of the intended direction of movement. Moreover, we would like to show that this strategy can give information on properties of motor representations not only at a "macroscopic" level (e.g., movement time), as in the examples presented in the target article, but also at a "microscopic" level (e.g., kinematics).

Neural coding of the intended direction of movement. If the brain is capable of representing movement parameters then one should be able to observe neural activity related to these parameters when the movement is intended. One of the movement parameters that has been reliably related to neural activity in the motor cortex and other brain structures is the direction of movement. Typically the activity of neurons in the motor cortex is broadly tuned to the direction of movement (Georgopoulos et al. 1983; 1984; 1986). That is, the activity of these neurons is most intense for a particular direction (the so-called neuron's preferred direction) and decreases for movements made farther away from this direction. This means that a given neuron fires during movements in various directions, and conversely, that during a movement in a given direction a large population of neurons is engaged. Movement direction can therefore be uniquely defined only at the level of the neuronal population. One hypothesis is that the ensemble of directionally tuned neurons can be regarded as an ensemble of vectors (Georgopoulos et al. 1983). A particular vector points in the direction of the neuron's preferred direction and its length is a function of the change in activity of the neuron. The vector sum of these vectors (the neuronal population vector) points at or near the direction of the movement, even when calculated at successive short time intervals (Georgopoulos et al. 1984). Hence the neuronal population vector provides a tool to monitor in time the processing of the directional information when the movement is intended.

The intention of movement can be studied in several tasks. The most common case is when a pointing movement toward a visual target has to be produced as soon as the target is presented. The time elapsed between the onset of the target and the onset of the movement (i.e., the reaction time [RT]) can be regarded as the time during which the movement is intended. In other cases, a delay can be imposed before the movement is initiated. During this delay the visual stimulus can either be present (instructed delay task), or absent (memorized delay task). In all these cases the neuronal population vector points in the direction of the intended movement during the RT, or the instructed or memorized delay period (Georgopoulos et al. 1986; 1989a; Smyrnis et al. 1992). These results indicate that the direction of the intended movement is represented in a dynamic form at the neuronal population level in the presence or absence of an immediate motor output.

Transformation of the intended direction of movement. The monitoring of the neural activity related to the intended direction of movement can be applied to conditions in which a mental transformation of the direction of the movement must be performed before the movement is produced. Monkeys were trained to move a handle either toward a visual stimulus (direct task) or 90 degrees counterclockwise from the stimulus (transformation task) depending on the brightness of the stimulus. The activity of motor cortical neurons in the direct task was as described above. Concerning the transformation task, there were no neurons whose activity changed only in the transformation task, which suggests that the representation of the direction of movement during this task does not involve a separate neuronal population in the motor cortex. The analysis of the population vector as a function of time during the RT revealed an

orderly counterclockwise rotation of the neuronal population vector from the direction of the stimulus to the direction of the movement (Georgopoulos et al. 1989b). Based on the simple hypothesis that the motor cortex is involved only in the production of the movement, one would have expected the population vector to point only in the direction of the upcoming movement. Instead, these results indicate that the motor cortex also participates in mental transformations occurring before the execution of the movement. Moreover, they show that during the RT the direction of the intended movement is progressively transformed, passing through intermediate directions (Lurito et al. 1991).

These results agree with the hypothesis of Shepard and Metzler (1971) concerning mental rotation of visual images and extend its domain to motor processes. Do mental rotations of the direction of the intended movement and of mental images share common aspects or are they independent processes? To answer this question, we compared the performance of human subjects in a visuomotor mental rotation task and a visual mental rotation task (Pellizzer & Georgopoulos 1993b). We took advantage of the fact that the processing rates can vary appreciably among subjects. We found that the processing rates were correlated between those tasks, but neither correlated significantly with the processing rate in a visuomotor memory scanning task. These results suggest that visuomotor and visual mental rotations share common processing constraints that cannot be ascribed to general processing performances. Several hypotheses can be made to explain these results. One is that a common brain structure is accessed jointly by the visual and motor systems during the mental rotation and that this structure forms the basis of the common constraints observed. Another hypothesis is that the mental rotation involves different systems, visual or motor, depending on the task, but that the neural implementation of the rotation itself would obey the same rules.

Do these studies of mental transformations provide some insights concerning the control of movement? This is what we would like to show in the next section.

Mental rotation and control of continuous motor trajectories. The results of the experiments on mental rotation indicate that the brain takes time to change the direction of the upcoming movement and that this time is proportional to the angle of change of direction. One can therefore hypothesize that during movements that require changes of direction (e.g., drawing, handwriting) some time is spent during the movement to define the change of direction (Pellizzer et al. 1993). Moreover, the larger the angle of change of direction, the longer the time to complete it. This hypothesis leads to the prediction that the more curved a segment of the trajectory, the slower the speed will be to trace it. This is indeed what has been observed in many different experiments on drawing and handwriting (e.g., Pellizzer et al. 1993; Viviani & Terzuolo 1982). The relation between speed and curvature exists also when no movement is produced and the trajectory is defined in the isometric force space (Massey et al. 1992). This finding suggests that the relation between speed and curvature results from central constraints and not from biomechanical factors related to the motion of the inertial load of the arm. Mental rotation studies discussed above indicate that these central constraints involve the process of changing the direction of the upcoming movement. This is a time-consuming process whose duration is proportional to the angle of directional change.

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