

NEUROSCIENCE

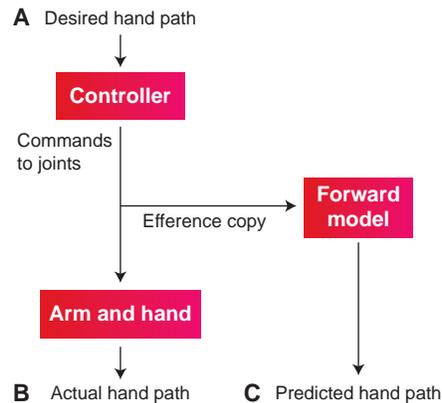
Action, Illusion, and Perception

Jacqueline Gottlieb and Pietro Mazzoni

You are playing soccer and just scored a goal. How aware were you of your action? If asked to do so, how well would you be able to reproduce that successful kick? The question of how humans and other animals perceive their own motor acts has been relatively ignored by neurophysiologists, but is now touched on by Schwartz and his colleagues (1) on page 380 of this issue.

These investigators set out to tease apart the neural processes in the brain that lead to movement versus those related to the perception of that movement. To do this, Schwartz *et al.* used the classical approach of requiring different movements in response to the same visual stimulus—in other words, altering the mapping between visual input and motor output [e.g., (2, 3)]. They asked human subjects to trace, using a hand-controlled cursor, a continuously visible contour that was either circular or ellipsoid. During tracing, subjects saw the cursor and the target contour but had no direct vision of their arm. On some trials, called illusion trials, a mismatch was created between the actual and visible arm trajectories by altering the gain of the cursor along the horizontal dimension only. In these trials, subjects had to perform a circular hand motion in order to trace an elliptical contour, and vice versa they had to perform an elliptical movement in order to trace a circular trajectory. The change in cursor gain occurred gradually across five successive tracing cycles, and subjects seamlessly adapted their arm motion, achieving accurate tracing with no practice. Surprisingly, however, subjects remained unaware of the gain change. When asked to report the trajectory they had traced in the last circuit, all subjects reported the trajectory they had seen and not the one they had actually performed.

To explore the possible neural substrates of this percept, Schwartz *et al.* recorded neural activity in macaque monkeys during the tracing task in two cortical structures known to be closely related to the generation of arm movement: the ventral pre-



Perceiving actions. Visual representations in visually guided limb movements. (A) Motor plan in visual coordinates; (B) visual perception of resulting hand path; (C) predicted hand path. The controller transforms desired hand trajectories (encoded in visual coordinates) into motor commands (encoded in joint coordinates). The forward model simulates the arm (including its musculoskeletal properties) and the external environment (including forces such as friction and viscosity). It takes efference copies of the motor commands and transforms them back into visual space, predicting the expected hand trajectory. The PMv activity reported by Schwartz *et al.* (1) could be involved in A, B, or C.

tor cortex (PMv) and the primary motor cortex (M1). Unlike the human subjects, monkeys were not asked to report what they had just traced; the authors made the assumption that the monkeys' perception was similar to that of humans. All the neurons recorded in PMv and M1 were selective for the instantaneous direction of arm movement. Using a modified population vector analysis (4), the authors reconstructed the trajectory encoded by the population of neurons in each area. They found that the population of M1 neurons traced the path of the actual hand movement, whereas the PMv population of neurons traced the visible path of the cursor.

On the basis of these results, the authors make the provocative suggestion that the visual signal received by PMv neurons directly influences perception—either perception of the external world or perception of one's own actions. As the authors point out, in addition to its connections to M1, PMv is also connected with areas 12 and

46 in the prefrontal cortex, which are considered to be at the top of the hierarchy for object recognition and spatial perception. This is a relatively new view of the PMv, which traditionally has been thought of as a premotor structure of little importance to perception.

The question of the link between early motor areas and perception is an important one and not only from the perspective of the PMv. There are other premotor and parietal areas that are clearly important for movement control but that also contain abundant visual and other sensory signals. Are these visual signals strictly premotor, or do they also influence perception? Indirect evidence suggests that such premotor areas are involved with both perception and visual cognition. For example, the premotor cortex becomes active in tasks of visual imagery (5), and damage to the parietal cortex in humans can have profound consequences for vision and attention independent of movement (6).

Intriguing as the idea is of premotor area involvement in perception, more evidence is needed before this notion can be accepted unequivocally. One problem is that the encoding of sensory signals in a premotor area does not automatically imply that this area is involved in perception. Such signals instead could be used for motor planning. Envisage the neural circuits involved in the generation of a command to move the arm (see the figure). The chain of events starts with a signal of the desired hand trajectory in visual space, which is presumably derived from activity in visual areas specifying the movement target or goal (see the figure, A). This signal could be provided by those PMv neurons with "early" activity in Schwartz *et al.*'s sample, and could be transformed into a motor command (for example, a joint acceleration signal) as it is transmitted to the M1. Thus, the early PMv visual signal could represent an incipient motor command rather than a correlate of perception.

The "late" visual signal that the authors find encoded by PMv neurons—a signal that appears to come after the movement-related signal in M1—may enable the control of movement based on visual feedback. In most natural tasks, the brain relies strongly on visual feedback to produce accurate movement. In the tracing task of the current study, visual feedback (the relative position of the cursor and the target trajectory) was the only source of information that the subjects could have depended on for tracing accuracy during illusion trials. One possibility is that the motor system derives this feedback from the usual visual pathways, which

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gather visual information from the retina and propagate it through a series of visual and ultimately motor areas. However, the delays involved in this pathway could lead to serious instability in the control of movement (7). An alternative possibility, suggested by computational models, is that the brain uses a “forward model” that generates a much faster prediction of the consequences of a given motor command (7). The forward model contains an estimate of the arm’s musculoskeletal properties and of external forces such as friction. The model combines these estimates with a copy of the motor command being sent to the arm from M1 (see the figure) and predicts, with minimal delay, the actual arm trajectory expected to result from that motor command. In

the task set by Schwartz *et al.*, the output of the forward model could be represented by the PMv activity that lags M1 activity and encodes the visible (predicted) path of the cursor. By comparing the predicted movement with the required movement (the target contour) the brain can then make rapid corrections to the ongoing arm trajectory.

The likely contribution of PMv neurons to motor control does not, of course, preclude the possibility that this area also influences perception. Several important questions remain to be answered in this regard. First, it is necessary to determine whether the visual signals encoded in the PMv correlate with visual perception within an individual subject (a macaque monkey). Second, it must be established whether and how in-

activation, lesioning, or other manipulations of premotor areas affect perception. Finally, it must be determined whether different populations of neurons within a single premotor structure contribute differentially to action and perception.

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PSYCHOLOGY

Is Language the Key to Human Intelligence?

David Premack

Humans have acquired six symbol systems: two that evolved—the genetic code and spoken language—and four that we invented: written language, arabic numerals, music notation, and labanotation (a system for coding choreography). Dobzhansky’s quip “All species are unique, but humans are uniquest” raises the question: Is it language, the symbol system that evolved only in humans, that makes humans the “uniquest”? Dobzhansky’s quip raises a more fundamental question: What exactly is the nature of human uniqueness?

The grammar or syntax of human language is certainly unique. Like an onion or Russian doll, it is recursive: One instance of an item is embedded in another instance of the same item. Recursion makes it possible for the words in a sentence to be widely separated and yet dependent on one another. “If-then” is a classic example. In the sentence “If Jack does not turn up the thermostat in his house this winter, then Madge and I are not coming over,” “if” and “then” are dependent on each other even though they are separated by a variable number of words (1–3). Are animals capable of such recursion? In a paper on page 377 of this issue, Fitch and Hauser (4) report that tamarin monkeys are not capable of recursion. Although the monkeys learned a nonrecursive grammar, they failed to learn a grammar

that is recursive. Humans readily learn both. The lack of recursion in tamarins may help to explain why animals did not evolve recursive language, but it leaves open the question of why they did not evolve nonrecursive language. Recursion is not, of course, the only preexisting faculty on which the evolution of language depends, and when we examine some of the other factors (listed in the table), we can see why animals did not evolve language of any kind.

Voluntary Control of Sensory-Motor Systems

A laboratory chimpanzee does not call to attract the attention of its trainer; instead, it pounds on a resonant surface. Similarly, when chimpanzees become separated in the compound, they do not call to one another, as humans would, but search silently until they see one another and then rush together. If, as the evidence suggests, vocalization in the chimpanzee is largely nonvoluntary (reflexive), speech could not have evolved. But then why don’t chimpanzees sign to each other? The chimpanzee has voluntary control of its hands. However, sign language depends on the face as well as the hands, and facial expression in the chimpanzee is evidently as reflexive as vocalization. Facial expressions play linguistic roles in signing, such as denoting the boundaries of clauses. A signer processes emotional facial expression in the right hemisphere, but linguistic facial expression in the left hemisphere (5).

This does not mean, of course, that chimpanzees could not have evolved a language based on pounding on resonant surfaces, arranging stones on the ground, and so on. But it does suggest that they could not have evolved one that is like either speech or sign. (Of course, speech and sign “travel” with the speaker in a way that stones and resonant surfaces do not.)

Imitation

Many species can copy the object (or location) chosen by a role model. This is the first level of imitation. There is, however, a second level of imitation when the individual copies not the model’s choice of object, but rather the model’s motor action. Quite a different kettle of fish. Now the individual must form a mental representation of the visually perceived action and produce an action conforming to the representation (6). Although humans, even as infants, can do this (7), most species cannot, the exception being chimpanzees but they require human training (8–10). Could language evolve in a species in which the young cannot imitate the action of the speaker?

Teaching

Teaching, which is strictly human, reverses the flow of information found in imitation. Unlike imitation, in which the novice observes the expert, the teacher observes the novice—and not only observes, but also judges and modifies (6). Imitation and teaching pair efficiently in humans. Imitation produces a rough copy; teaching smoothens it. A chimpanzee mother could not teach her infant anything because, although the infant watches her problem-solving intently, she never returns the infant’s observation (11). If we asked a chimpanzee mother whose infant was learning to crack nuts with a rock (the chimpanzee’s most complex technology), “Where is he

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