

When pliers become fingers in the monkey motor system

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The capacity to use tools is a fundamental evolutionary achievement. Its essence stands in the capacity to transfer a proximal goal (grasp a tool) to a distal goal (e.g., grasp food). Where and how does this goal transfer occur? Here, we show that, in monkeys trained to use tools, cortical motor neurons, active during hand grasping, also become active during grasping with pliers, as if the pliers were now the hand fingers. This motor embodiment occurs both for normal pliers and for “reverse pliers,” an implement that requires finger opening, instead of their closing, to grasp an object. We conclude that the capacity to use tools is based on an inherently goal-centered functional organization of primate cortical motor areas.

neurophysiology | tool use | goal coding | motor act

The capacity to manipulate objects is a sophisticated behavior highly evolved in primates. The basic process underlying it requires coding of the objects' intrinsic properties (size and shape) and their transformation into a specific pattern of finger movements (1).

In primates, the cortical motor area crucially involved in grasping is the rostral sector of the ventral premotor cortex or area F5 (2–6). Neurons in F5 fire in association with specific types of hand shaping (3, 6), and their activity is temporally correlated with different grasping phases. Most neurons discharge in association with the last phase of grasping (“actual grasping”); others start to fire during the phase in which the hand opens and continue to discharge during the phase when the hand closes; finally a few discharge prevalently in the phase in which the hand opens. Hand grasping appears, therefore, to be coded by the joint activity of populations of neurons controlling different temporal phases of the motor act (1).

Primates are able to interact with objects not only by using their natural effectors, but also by using tools. Common tools, such as sticks, stones, and rakes, act basically as functional extensions of natural effectors (7). With practice, they become parts of the agent's body schema (8–10).

To learn tool use, its users have to associate an initial action on an object (e.g., grasp and hold a rake) with subsequent actions that tool possession offers (e.g., reach for an object). Thus, when the use of a tool is learned, a distal goal is coded on the top of the proximal one (11, 12). The aim of the present study was to investigate how the motor cortical system is able to solve this problem.

More specifically, we addressed the following questions: When an object is grasped by a tool instead of the hand, will the cortical motor neurons code the movement of the hand or the distal goal achieved by the tool? And if the distal goal is achieved using an opposite sets of movements, will the neurons still be able to code the distal goal?

To answer these questions we trained monkeys to grasp objects using two types of tools: “normal pliers” and “reverse pliers.” With normal pliers, the object was grasped by opening the hand and then by closing it [Fig. 1A and supporting information (SI) Movies 1 and 2]. With reverse pliers, the object was grasped by using an opposite movement sequence: The hand was first closed and then opened (Fig. 1B and SI Movies 3 and 4). Once the

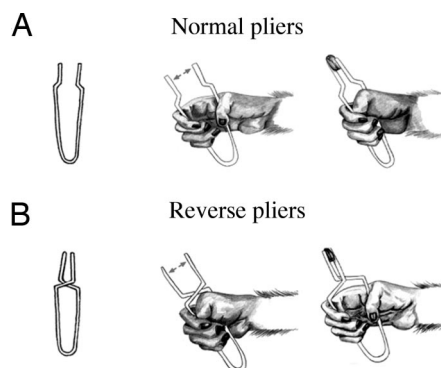


Fig. 1. Schematic illustration of the experimental paradigm used. (A) Normal pliers. (B) Reverse pliers. To grasp the object with normal pliers, the monkey has to close its hand (A), whereas with the reverse pliers, the monkey has to open its hand (B). The arrows indicate the direction of the motion of the pliers tips.

monkeys learned the task, we tested neurons of areas F5 and F1 (primary motor cortex) during grasping performed by using the two types of pliers.

Results

Recorded Neurons and Histology. The activity of 113 neurons, recorded after monkeys learned to use tools, is the focus of the present report. All of these neurons discharged in association with hand grasping movements. Fifty-five of them were recorded from area F5 and 58 from area F1. Both areas were identified on the basis of their neuron-discharge properties (2, 3, 6) (see also *SI Text*) and of intracortical microstimulation (13–15) (see *Methods*). Histological controls confirmed the location of the recorded sites. The sectors of F5 and F1 from which neurons were recorded in Monkey 1 are shown in *SI Fig. 6A*. The electrode penetrations in Monkey 2 had similar locations. *SI Fig. 6B* illustrates the reconstruction of a series of penetrations in areas F5 and F1 of Monkey 1.

Activity of Area F5 Neurons. All F5 neurons of the present sample discharged during grasping done with normal and reverse pliers.

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As when the grasping was performed by using the hand, the neuron activity during tool grasping correlated with specific temporal grasping phases. With normal pliers, 18 (32.7%) neurons began to discharge during hand opening, reaching their maximum firing rate just before or during hand closure; 28 (50.9%) neurons discharged almost exclusively during hand closure; 7 (12.7%) started to discharge with hand closure and kept firing during the subsequent holding phase. Finally, two (3.6%) neurons fired only during the hand-opening phase.

When the same neurons were tested with the reverse pliers, the temporal discharge pattern remained unchanged relative to the grasping motor act phases: Neurons that with normal pliers discharged when the hand was opening, with the reverse pliers discharged when the hand was closing, the discharge remaining linked to the initial phase of the motor act. Conversely, neurons that with normal pliers discharged when the hand was closing, with the reverse pliers discharged when the hand was opening, the discharge being related to the final phase of the motor act.

It is clear therefore that temporal organization necessary to reach the distal goal, and not the hand movement, was coded in F5 neurons object of the present study.

Examples of two neurons recorded during grasping with the two tools are shown in Fig. 2. As one can see, they both discharged during tool grasping with normal and reverse pliers. Most interestingly, they maintained the same relation to different phases of grasping, regardless of the fact that opposite hand movements were required to reach the distal goal.

Activity of Area F1 Neurons. Two distinct functional categories of neurons were found in F1. The first category was formed by neurons that, as F5 neurons, discharge in relation to the distal goal of the motor act (F1 goal-related neurons, F1g, $n = 26$). The other category consisted of neurons that discharged in relation to hand movements (F1 movement-related neurons, F1m, $n = 32$).

When tested with normal pliers, 12 F1g neurons (46.2%), began to discharge with hand opening, reaching their maximum during hand closure; 13 neurons (50.0%) discharged almost exclusively during hand closure; 1 neuron (3.8%) started to discharge with hand closure and kept firing also during the subsequent holding phase. When the monkeys used the reverse pliers, the temporal discharge pattern remained the same, anchored to a specific grasp phase. (For statistical analysis of the congruence between the temporal courses of neuron activity in the two conditions, see *Methods*). Examples of two F1g neurons are shown in Fig. 3A.

F1m neurons showed a discharge pattern markedly different from that of F5 and F1g neurons. They discharged in strict association with hand movements, regardless of the instrument used. For example, if the maximal discharge was present during hand closure with the normal tool, the same was true with the reverse tool, regardless of the different goals that this movements led to in the two cases. Two examples of F1m neurons are shown in Fig. 3B.

Population Analyses. In addition to single-neuron analysis, four analyses of population activity were carried out, taking as variable the mean discharge frequency of each neuron in the four epochs, that is: background activity (holding pliers), opening of pliers tips, closing of pliers tips, holding.

A first ANOVA with three factors: Population (three levels: F5, F1g, F1m), Condition (three levels: normal pliers, reverse pliers, hand grasping) and Epoch (four levels) showed a significant interaction among all factors ($P < 0.001$). Three separate analyses were then carried out for each of the three populations of neurons, with the following main factors: Condition (three levels) and Epoch (four levels).

Fig. 4*Top* shows the average of the normalized mean discharge frequency of F5 neurons during grasping with normal pliers,

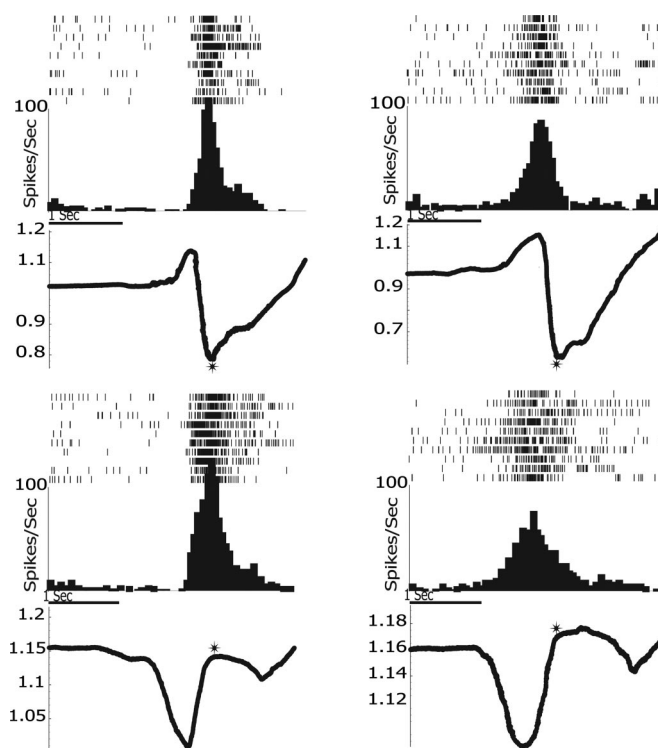


Fig. 2. Activity of two neurons recorded in area F5. Rasters and histograms (10 trials) illustrate the neurons' discharge recorded during grasping with normal pliers (*Upper*) and reverse pliers (*Lower*). Both rasters and histograms are aligned with the end of the grasping closure phase (asterisks). The traces below each histogram indicate the instantaneous hand position (average of the voltage changes values occurred during neuronal recording) recorded with the potentiometer and expressed as a function of the distance between the pliers handles. Trace down indicates that the hand closes, and the distance between handles decreases, whereas trace up indicates that the hand opens, and the distance between handles increases. The values shown on the vertical axes indicate the potentiometer-measured voltage. With normal pliers (*Upper*), Unit 210 (*Left*) began to fire during hand closure (trace down), reaching the maximum at approximately the moment in which the food was grasped; with the reverse pliers (*Lower*), this unit started to fire with the hand opening (trace up), also reaching its maximum when the food was grasped. Unit 199 (*Right*) started to fire in normal pliers (*Upper*) condition during hand opening (trace up), reaching its maximum at the beginning of the hand closure. With reverse pliers (*Lower*), the neuron started to fire during the hand closure (trace down), reaching its maximum during hand opening. Unit 210: peak force, averaged across 10 trials, 2.8 N and 10.2 N with normal and reverse pliers, respectively. Unit 199: peak force, averaged across 10 trials, 3.9 N and 9.3 N with normal and reverse pliers, respectively.

reverse pliers, and with the hand. ANOVA showed that both factors were significant at $P < 0.001$, whereas the interaction between them was not significant. In all conditions, Epoch 3 (closing of pliers tips) was the epoch with the highest discharge ($P < 0.001$).

The results of the same analysis, performed on F1g population (Fig. 4 *Middle*) showed that all factors ($P < 0.001$) and the interaction between them were significant ($P < 0.001$). A post hoc analysis showed that Epoch 3 was the Epoch with the highest discharge in all conditions ($P < 0.001$). This analysis also showed that during the use of normal pliers, the activity in Epoch 3 was higher than in the other two conditions ($P < 0.001$).

Finally, the analysis of F1m neurons showed that the behavior of this category of neurons radically differed from that of F1g and F5 neurons (Fig. 4 *Bottom*). The ANOVA revealed that the two main factors and the interaction were significant ($P < 0.001$). The post hoc analysis showed that, for this category of neurons,

