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RESEARCH ARTICLE

**Michael S. A. Graziano · Dylan F. Cooke ·
Charlotte S. R. Taylor · Tirin Moore**

Distribution of hand location in monkeys during spontaneous behavior

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Abstract Recently it was shown that electrical stimulation of the precentral gyrus of monkeys can evoke complex, coordinated movements. In the forelimb representation, stimulation of each site caused the arm to move to a specific final posture, and thus the hand to move to a location in space. Among these stimulation-evoked hand locations, certain regions of the hand's workspace were more represented than others. We hypothesized that a similar non-uniform distribution of hand location should be present during a monkey's spontaneous behavior. The present study examined the distribution of hand location of monkeys in their home cages. This distribution was similar to that found by stimulation of the precentral gyrus. That is, arm postures that were over-represented in spontaneous behavior were also over-represented in the movements evoked by cortical stimulation.

Keywords Reaching · Grasping · Motor cortex · Posture

Introduction

Primates use their forelimbs with extraordinary versatility to reach, grasp, and manipulate. Their arms and hands can acquire many different postures for different purposes. This versatility is controlled at least partly by primary motor and premotor cortex in the precentral gyrus (e.g., Penfield and Boldrey 1937; Woolsey et al. 1952; Evarts 1968; Georgopoulos et al. 1986; Scott and Kalaska 1997; Rizzolatti and Luppino 2001).

In a recent study of the precentral gyrus in monkeys (Graziano et al. 2002), we electrically stimulated cortical sites using 500-ms stimulation trains, approximating the time scale of the reaching and grasping movements that monkeys normally make (e.g., Georgopoulos et al. 1986; Roy et al. 2000; Reina et al. 2001; Christel and Billard 2002). These stimulation trains evoked complex, coordinated movements that appeared to match common gestures in the monkey's natural repertoire. For example, stimulation of one region of cortex caused the hand to close in a precision grip posture, the wrist and forearm to rotate such that the grip was oriented toward the mouth, the shoulder and elbow to rotate such that the hand moved to the mouth, and the mouth to open. Stimulation of other cortical sites evoked other complex postures of the hand and arm. These electrically evoked postures were arranged across the cortical surface in an apparent, rough map of hand locations in the space around the monkey's body (illustrated in Fig. 1). We also found that the initial convergence of the arm toward the final posture can be evoked by short stimulation trains, for example trains of 100-, 50-, or even 20-ms duration (Graziano et al. 2002; Taylor et al. 2002).

Because these postures are evoked by electrical stimulation, there is some question about their relevance to normal movement. An important initial question is this: does the set of stimulation-evoked postures actually match the normal postures and movements of the monkey? The present paper addresses this question by testing whether the specific proportions found among the stimulation-evoked postures are also found in spontaneous behavior.

The map of electrically evoked postures had two nonuniformities: 1) The map had an expanded representation of hand location in some regions of space, including central space in front of the chest, central space in front of the mouth, and lower space; and 2) Complex configurations of the fingers and wrist were evoked by stimulation in some parts of the map but not in others. These postures of the distal forelimb, including a precision grip, a power grip, a splaying open of the fingers, and pronations and supinations of the wrist, were most commonly evoked from the parts of the map that represented hand locations in front of the chest and in front of the mouth.

We hypothesized that these two types of nonuniformity in the map in motor cortex should also be present in the

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M. S. A. Graziano (✉) · D. F. Cooke · C. S. R. Taylor ·
T. Moore
Department of Psychology, Green Hall, Princeton University,
Princeton, NJ, 08544, USA
e-mail: graziano@princeton.edu
Tel.: +1-609-2587555
Fax: +1-609-2581113

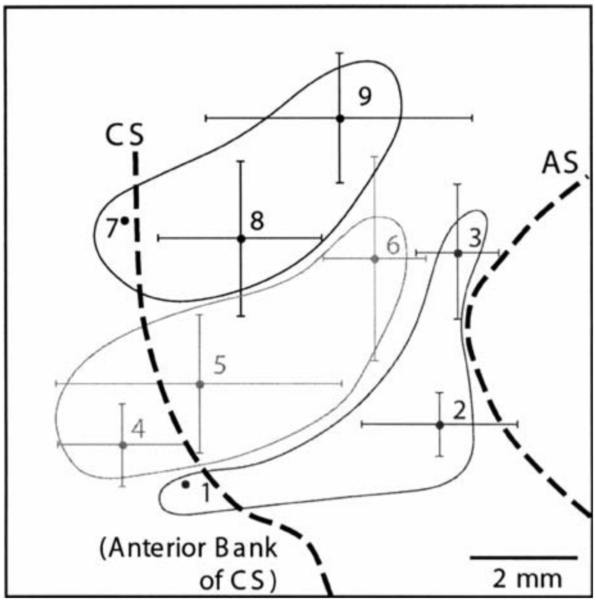

Fig. 1 Map of stimulation-evoked postures in precentral gyrus based on monkey 1 from Graziano et al. (2002). The nine points show the mean location of cortical sites associated with nine spatial zones around the body. For definition of the nine zones, see Fig. 2A. Error bars = x and y standard deviation. For spatial zones represented by three or fewer stimulation sites, no error bars were plotted. These zones include zone 1 (N=1) and zone 7 (N=3). *Dotted lines* show estimated location of lip of central sulcus (CS) and lip of arcuate sulcus (AS). Area behind the lip of the central sulcus represents the anterior bank of the sulcus. These graphs are adapted from data in Graziano et al. 2002, where a more complete explanation is given

spontaneous motor output of monkeys. To test this hypothesis, we studied the movement patterns of monkeys of the same species (Macaca fascicularis) raised in similar laboratory conditions as those used in the stimulation experiments. We recorded the distribution of hand locations during typical daily behavior in the home cage.

Methods

We studied three adult male fascicularis monkeys (3–5 kg, age range 4–6 years) singly housed in a laboratory colony. The cages were equipped with a perch, food (monkey chow and fruit), and a range of toys including rubber chew toys and a plastic mirror hanging by a chain from the ceiling of the cage. The monkeys had a view of other monkeys in nearby cages. The cages were the same as those used to house the monkeys in the previous, electrical stimulation study (Graziano et al. 2002). The living conditions and all other aspects of the experiment were in accordance with NIH guidelines and were approved by the University Animal Care and Use Committee and the attending veterinarian.

The monkeys' behavior was recorded on video at 30 frames/s. The monkeys were first acclimated to the video camera and then taped in 5 to 10-min segments at different times throughout the day ranging from 10:00 a.m. to 5:00 p.m., within the light part of the diurnal cycle.

Videos were analyzed frame by frame. In each frame, the actions of the monkeys' arms and hands were categorized. One category included grasping or manipulating small objects such as food or toys. The second category included supporting the monkey's weight during climbing or sitting. It was often not possible to distinguish whether the hand was actively supporting the weight of the monkey's body or relaxed and supporting only the weight of the arm. Thus, these uses of the arm were combined in this second category. The third category was reaching. During a reach, the video frame in which the hand left the starting location and the video frame in which the hand arrived at the final location were tabulated.

For those segments of video in which the monkey was directly facing the camera, we measured the location of the hand within an imaginary 3×3 grid around the monkey's body; this spatial assessment was made relative to the midpoint of the chest, for each video frame. The nine spatial zones are illustrated in Fig. 2A. Each zone was 12 cm across. The monkeys were often occluded by parts of the cage or facing away from the camera. Only a limited subset of the video showed the monkey clearly in view and directly facing the camera. This subset of the video was composed of 24 segments. The mean duration of the segments was 52.8 s (1,585 frames). The total duration of the segments was 21 min and 4 s (37,918 frames: monkey 1=12,018 frames; monkey 2=10,138 frames; monkey 3=15,762 frames). Did this total time adequately represent the typical distribution of the hands? Several aspects of the data suggest that it did. First, the hands changed spatial zones on a short time scale. Each hand changed spatial zones on average once every 3.45 s. Second, the monkeys' behavior was highly conserved across the analyzed time. When the data were divided into 3-min epochs, we found a similar pattern of hand position for all epochs. That is, any 3 min of video appeared to capture the full range of the

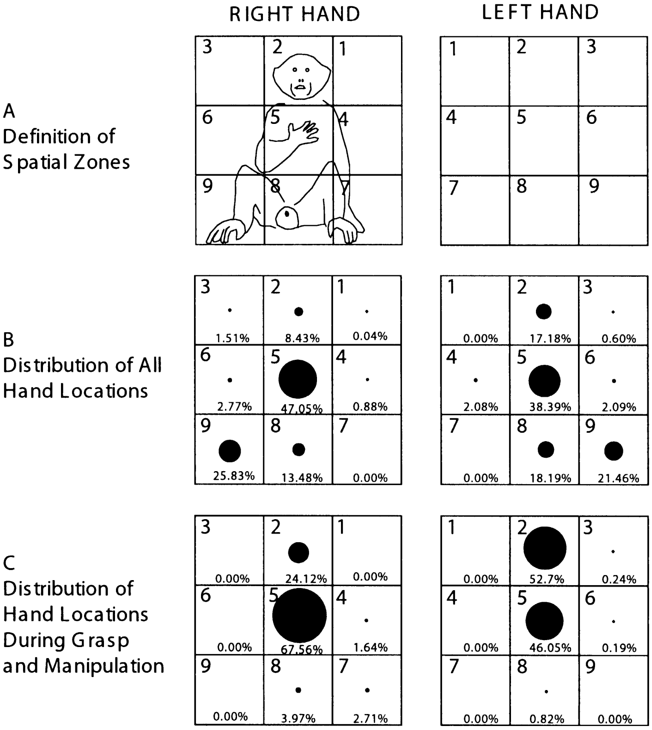

Fig. 2A–C Distribution of hand location during spontaneous behavior. **A** On each video frame, the location of the hand was determined within an imaginary 3×3 grid around the monkey's body. This spatial assessment was made relative to the midpoint of the chest. Each square in the grid was 12 cm across. **B** The distribution of hand locations during all types of activities. Data for three monkeys were combined. The diameter of each circle is proportional to the percentage of time that the hand spent in that spatial zone (time was measured in video frames). The percent is also given beneath each circle. The left and right hands showed a similar pattern. **C** The distribution of hand location during the time that the hand was grasping or manipulating small objects such as food or toys. For right hand, 18.66% of total time was spent grasping or manipulating. For left hand, 29.15% of total time was spent grasping or manipulating monkey's behavior at least at the level studied here. These aspects of the data are described in greater detail in the results section.

Stimulation-evoked postures

We compared the spontaneous behavior measured in the present study with the postures evoked by electrical stimulation of the precentral gyrus in our previous study of two adult male Macaca fascicularis. The stimulation methods and data are described in detail in Graziano et al. (2002) and thus are only briefly described here.

The monkey sat in a primate chair with the head fixed by a head bolt and the limbs and torso free. A hydraulic microdrive was used to lower a tungsten microelectrode (0.1–1.5 Mohms) into the cortex while multineuron activity was monitored on an oscilloscope and over a loud speaker. For most electrode penetrations, we tested 1–3 depths separated by 0.5 or 1.0 mm. To study the anterior bank of the central sulcus, we tested at regular intervals of 0.5 or 1.0 mm until the electrode reached white matter and neurons could no longer be found. Electrical stimulation was applied by means of a Grass stimulator (S88) and two stimulus isolation units (SIU6). The ground lead for the stimulation was in contact with the saline covering the exposed dura and surrounding bone within the recording chamber. Stimulation was triggered by a hand-held button and consisted of a 200-Hz, 500-ms train of biphasic pulses. Each pulse had a negative followed by a positive phase, each phase 0.2 ms in duration. To study the evoked movement, the current was usually set between 25 and 150 microamps. Current was measured via the voltage drop across a 1 Kohm resistor in series with the return lead of the stimulus isolation units.

In order to study the effect of different starting postures, stimulation was applied while the monkey performed a simple reaching task. A small piece of fruit was placed at one of many possible locations around the monkey, and the monkey reached for the fruit. On about half of the trials, stimulation was applied as the hand reached the target location but before the monkey had grasped the fruit. The inter-trial interval was variable between 2 and 10 s. Stimulation was also applied during the monkey's spontaneous movements outside the context of the reaching task, and while the monkey was sitting quietly with the arm stationary. Data were collected by videotaping the monkey's movements from a frontal view. The time of stimulation was recorded on the video by connecting a TTL output from the Grass stimulator to the audio input channel of the video recorder. In this fashion, we could determine the frame in which each stimulation train began and ended. The position of the hand at the end of the stimulation train was categorized by means of the same method used in the present behavioral study, that is, within an imaginary 3×3 grid, each square 12 cm across.

For 270 sites in the precentral cortex (160 sites in monkey 1; 110 in monkey 2), stimulation caused the arm to converge to a final posture and, thus, the hand to move to a final location. These sites spanned the entire forelimb representation, bordered ventrally by a representation of the mouth and face; bordered anteriorly by the arcuate sulcus; bordered posteriorly by primary somatosensory cortex on the floor of the central sulcus; and bordered dorsally by a representation of the leg. The sites were spaced at intervals of 0.5–1.0 mm across the forelimb representation in the precentral gyrus. The scatter of points across cortex can be seen in our previous publication (Graziano et al. 2002). To confirm that the sites were evenly distributed across cortex, the studied area was divided into ten squares, each one 3×3 mm, and the density of sites in each square was calculated. The density was nearly equal in all squares. For monkey 1, the average density was 1.9 sites/mm^2 (SD=0.15; range=1.7–2.1). For monkey 2, the average density was 1.4 sites/mm^2 (SD=0.07; range=1.3–1.6).

To compare the results of the stimulation study with the results of the present study, it was necessary to quantify the amount of cortical representation devoted to each of the nine spatial zones. One possible method would be to estimate the cortical area that, when stimulated, caused the hand to move to each spatial zone. However, it was not possible to draw borders across the cortex that separated the representation of one spatial zone from the next. This was because the representations graded into each other, intermingling with each other at the borders (see Graziano et al. 2002). This intermingling made it impossible to calculate the cortical area devoted to one spatial zone without making a range of uncertain assumptions. Figure 1 (based on data from Graziano et al. 2002) shows the mean position and x and y standard deviation for stimulation sites associated with the nine different spatial zones. While the mean positions are clearly arranged in a topographic order, the overlap is considerable. Also, some spatial zones were represented by few points, in particular the spatial zones on the ipsilateral side of the body. For example, zone 4 included only eight stimulation sites that nonetheless had enough scatter to result in relatively large x and y error bars. Therefore, it is important to note that the size of the error bars is not necessarily related to the amount of cortical representation. Zone 1 (N=1) and zone 7 (N=3), also on the ipsilateral side of the body, were represented by so few points that no error bars were plotted.

To measure the amount of cortical representation devoted to each spatial zone, we calculated the percentage of cortical sites that, when stimulated, caused the hand to move to that spatial zone. The advantage of this method is that the percentage is based directly on the data and does not depend on any assumptions or calculations about cortical area or boundaries. If all nine zones are equally represented, then 11% of the sites should be related to each spatial zone. Any spatial zone with a value larger than 11% is relatively over-represented; any spatial zone with a value less than 11% is relatively under-represented.

Results

Hand location during spontaneous behavior

Figure 2A shows the nine spatial zones that were used to measure hand location relative to the chest. These zones formed a 3×3 grid around the body. In Fig. 2B, the diameter of the circles indicates the percentage of time that the hand spent in each zone during spontaneous behavior. The pattern was similar for the two hands. Each hand spent most time in location 5, directly in front of the chest. This central space was used to manipulate objects, and as a support point against the floor or walls while climbing, walking, or leaning. A second common location for the hand was zone 2, in upper central space. This area of space was most commonly used during the manipulation of objects when the monkey held the object up at eye level to investigate it more closely, or held the object to its mouth to bite it. It was also used when the hand scratched the head or pushed at the cheek pouches. A third common location was zone 8 and 9, the lower space directly in front of and lateral to the body. These areas of space were used mainly to support the body's weight, such as when the monkey leaned to the side while sitting or climbing.

How consistent was this pattern of hand location across time? Figure 3 shows the data divided into epochs of various durations. Figure 3A shows all the data (right and left hands combined). Figure 3B shows the same data divided into 21 epochs, each epoch of 1-min duration. Figure 3C shows the data divided into ten epochs, each epoch of 2-min duration. Figure 3D shows the data divided into seven epochs, each epoch of 3-min duration.

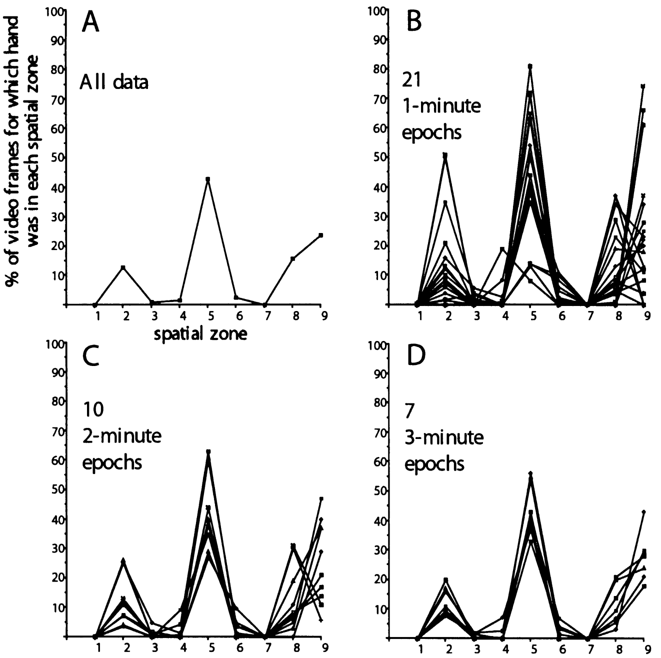

Fig. 3A–D Consistency of hand distribution over time. **A** The distribution of hand locations across the nine spatial zones. This graph shows the same distribution as in Fig. 2B, except that here the data from right and left hands are combined. The data are from three monkeys, totaling 21 min and 4 s of video. Even though the x axis (the nine spatial zones) does not represent a continuous variable, the data points are connected by lines for graphical clarity and to facilitate the comparison to panels B–D. **B** The distribution of hand locations based on the first 21 min of video data, plotted minute-by-minute. **C** The distribution of hand locations based on the first 20 min of video data plotted in 2-min epochs. **D** The distribution of hand locations based on the first 21 min of video data plotted in 3-min epochs. For each 3-min epoch, the pattern was similar to the overall pattern shown in A. Thus, the typical spatial distribution of the hand can be captured in as short a time as 3 min

These graphs show that even a single minute will usually capture the overall pattern of hand location; and that 3 min of data will reliably capture the pattern. That is, the monkeys' behavior is highly consistent and repeats on a short time scale, at least with respect to hand location around the body.

The hand changed spatial zone on average every 3.45 s (SD=6.5 s; minimum=0.03 s, maximum=60.7 s). Thus within a 3-min period, the hand changed zone on average 52 times. This high rate of change in hand position may explain why 3 min of video can capture the overall distribution of hand positions.

The hand spent 23.8% of the total time grasping or manipulating small objects such as food or toys. Figure 2C shows the distribution of hand positions during this subset of the analyzed time. This distribution was significantly different from the overall distribution of hand positions (Chi square=50.37, *p*<0.0001) in that the lower spatial locations were no longer over-represented. Almost all of the grasping and manipulating time was spent in zone 5, directly in front of the chest, and in zone 2, in the central upper space near the mouth. Grasp and manipulation were almost never performed in other parts of the workspace. If the monkey grasped or manipulated an object or a part of the cage that was outside of zone 5 or 2, rather than reach out toward the object, the monkey generally first moved its body until the object was accessible in zone 5 or 2. Even when reaching for food on the ground, the monkey almost always rotated its chest downward until the object on the ground had come into zone 5, in front of the chest.

The arm spent most of its time (88.4%) maintaining a posture, for example for manipulation of an object or for supporting the body during climbing and sitting, and relatively little time (11.6%) actually reaching, that is, in transit from one location to another. Each hand made a reach on average once every 3.9 s (SD=5.8 s; minimum=0.3 s; maximum=31.9 s). The average duration of a reach, from the time the hand left its initial location to the time it touched the final target, was 0.42 s (SD=0.2 s). This time necessarily depended on the distance of the reach. The shortest reach, from the mouth to a piece of food near the mouth, took 0.1 s; the longest, from a hold on the cage to a more distant hold during climbing, took 1.2 s. Reaches included those to a small object for grasping (23.2% of reaches); those to a hand-hold to support the body's weight during climbing and sitting (60.7% of reaches); and those to the monkey's own body for scratching, self grooming, or pushing food out of the cheek pouches (16.1% of reaches).

Comparison of spontaneous behavior and stimulation-evoked behavior

The *gray bars* in Fig. 4A show the proportion of time that the hand spent in each of the nine spatial zones during spontaneous behavior. The *black bars* show the distribution of hand locations evoked by electrical stimulation of the precentral gyrus (based on data from Graziano et al. 2002). Stimulation of a high percentage of sites caused the hand to move to zone 5, the central space in front of the chest; zone 2, the upper central space mainly near the mouth; and zone 8 and 9, the lower space in front of the monkey and lateral to the body. This distribution of stimulation-evoked hand locations was similar to the distribution of hand locations observed during spontaneous behavior. The two data sets were highly correlated (r=0.92). A regression analysis showed that the two patterns matched significantly. The linear relationship between the two data sets was significant (F=39.777, *p*=0.0004).

In the above analysis, to quantify the distribution of hand locations during spontaneous behavior, we focused on the amount of time that the hand spent in each spatial zone. For much of this time the arm was actively maintaining a posture such as during manipulation of objects in zone 5, holding of objects at the mouth in zone 2, and supporting the body's weight in zones 8 and 9. However, as described in the methods section, it was sometimes difficult to distinguish when the arm was actively maintaining a posture and when it was passively resting. This was especially true of zones 8 and 9, when

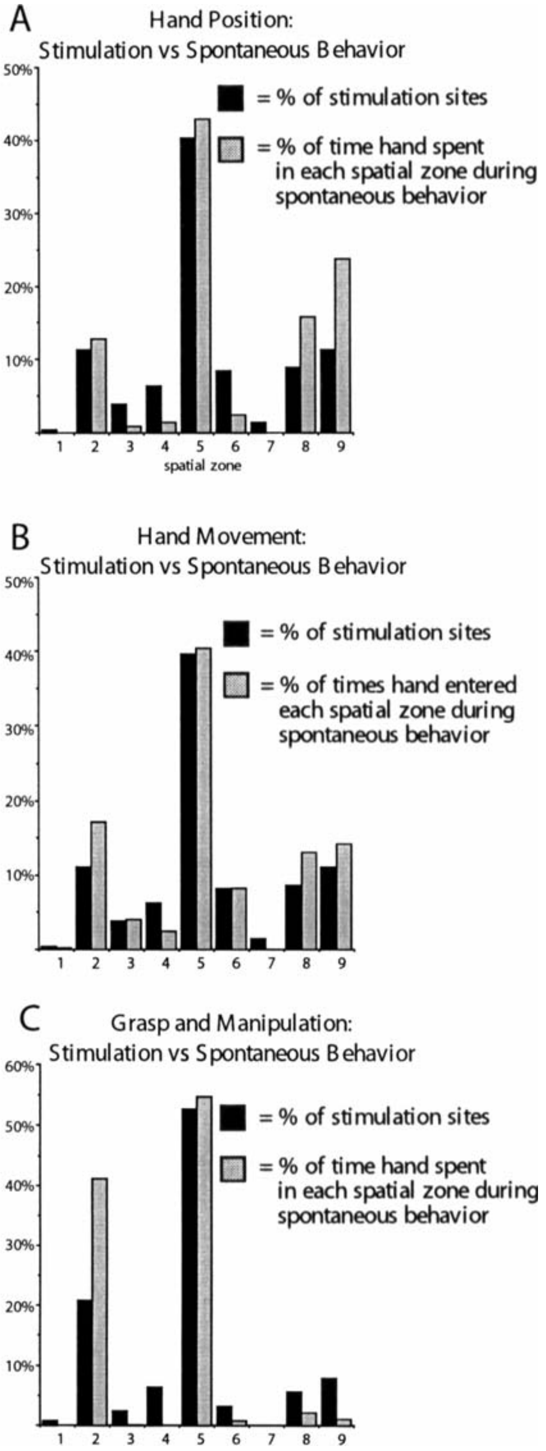

Fig. 4A–C Comparison of spontaneous behavior and stimulation-evoked behavior. **A** *Gray bars* show the distribution of hand locations during spontaneous behavior observed in the present experiment. This distribution is the same as that shown in Fig. 3A. The height of each gray bar shows the proportion of time that the hand spent in that spatial zone. The *black bars* show the distribution of hand locations evoked by stimulation of sites in precentral cortex (Graziano et al. 2002). The height of each black bar indicates the percentage of sites (of 270 total sites) for which stimulation caused the hand to move into that spatial zone. The two distributions are significantly correlated (regression analysis, F=39.777, *p*=0.0004). **B** *Gray bars* show the proportion of times that the hand entered each spatial zone during spontaneous behavior. *Black bars* show the proportion of cortical sites for which stimulation caused the hand to move into each spatial zone (same as in A). The two distributions are significantly correlated (regression analysis, F=119.13, *p*<0.0001). **C** *Gray bars* show the time spent within each spatial zone, during spontaneous behavior, for the subset of time during which the hands were grasping or manipulating. *Black bars* show the proportion of cortical sites for which stimulation caused the hand to move into each spatial zone, for the subset of sites (125 sites) at which stimulation also evoked a posture of the fingers or wrist. The two distributions are significantly correlated (regression analysis, F=47.576, *p*=0.0002)

the hand was typically braced against the floor. Another possible approach to quantifying hand position is to consider the proportion of times that the hand entered each spatial zone. This analysis does not take into account the amount of time that the hand stayed at a position once it had entered a spatial zone, but rather focuses on active changes of position. This alternative analysis is shown in Fig. 4B. The *gray bars* show the proportion of times that the hand moved into each spatial zone during spontaneous behavior. The *black bars* show the distribution of hand locations evoked by electrical stimulation of the precentral gyrus. Just as in Fig. 4A, these two distributions were highly correlated (r=0.97). A regression analysis showed that the two patterns matched significantly (F=119.13, *p*<0.0001).

Electrical stimulation of sites in the precentral gyrus sometimes evoked a complex posture of the fingers and wrist, in addition to causing the hand to move to a location in space. These finger and wrist movements included a precision grip, a power grip, a splaying open of the fingers, and pronations and supinations of the wrist. Such complex postures of the distal forelimb were found for 125 stimulation sites. As shown in Fig. 4C (*black bars*), most of these 125 sites also involved a movement of the hand to zones 5 or 2. This distribution of stimulation-evoked movements resembled the distribution found for grasping and manipulating during spontaneous movements (Fig. 4C, *gray bars*). The two distributions were highly correlated (r=0.93). A regression analysis showed that the two patterns matched significantly (F=47.576, *p*=0.0002). There were, however, some differences between the two distributions. During spontaneous behavior, 95.9% of the grasp and manipulation was performed in zones 2 and 5; only 4.1% of grasp and manipulation was performed in other regions of space. In the stimulation map, this bias toward zones 2 and 5 was less pronounced. Of the sites at which stimulation evoked complex postures of the fingers and wrist, 73.6% involved movement of the hand to zones 2 or 5; while 26.4% involved movement of the hand to other spatial zones.

Is the "stimulation-evoked behavior" actually spontaneous?

One alternative interpretation is that the movements obtained during electrical stimulation were not caused by the stimulation, but instead were merely spontaneous movements that sometimes happened to occur during the time of the stimulation. In this view, the reason why the distribution of hand locations is similar for both the electrical stimulation results and the spontaneous behavior is that the so-called stimulation results represent spontaneous behavior. This explanation, however, cannot account for the results. If this were the case, then for each stimulation site, we should have obtained the full distribution of normal spontaneous hand locations. Instead, for each stimulation site, we obtained movement toward one and only one location in space around the monkey, as documented in Graziano et al. (2002). For example, for one typical cortical site, stimulation for 500 ms at 50 microamps and 200 Hz always caused the hand to close in a precision grip posture, the wrist and forearm to rotate such that the grip was oriented toward the mouth, the shoulder and elbow to rotate such that the hand moved to the mouth, and the mouth to open. On each of 45 recorded trials, the movement of the hand toward the mouth began within one video frame of the onset of stimulation, that is, within 33 ms. The movement continued through the entire stimulation train. After studying the site in this fashion, we injected the monkey with a mixture of ketamine (10 mg/kg) and acepromazine (0.1 mg/kg) and waited until the monkey was fully tranquilized with eyes closed and no longer emitting spontaneous behavior. We then stimulated the same cortical site for another 35 trials and obtained a similar opening of the mouth accompanied by a movement of the hand toward the mouth. Again, on every trial, the movement of the hand toward the mouth began within one video frame or 33 ms of the onset of the stimulation train. These and other tests are discussed in Graziano et al. (2002).

Latency was calculated by frame-by-frame analysis of the video record for 44 stimulation sites based on at least ten trials per site. Twenty-six sites had a consistent latency within one video frame, that is, within 33 ms. Fourteen sites had a latency between one and two video frames, or between 33 and 66 ms. Four sites had a latency between two and three video frames, or between 66 and 99 ms. No sites had a movement latency longer than three video frames.

Since at each site we obtained a movement closely time-locked to each stimulation train, since at each site the movements were consistent in their terminal position, since the movement changed systematically when the electrode was moved to a new cortical site, and since on control tests we obtained similar movements in anesthetized monkeys, the movements were apparently caused by the stimulation and were not spontaneous movements.

Discussion

We examined the spatial distribution of hand locations during spontaneous behavior in monkeys. This distribution was nonuniform in two ways: 1) The hand was most often in central space in front of the chest, central space in front of the mouth, and lower space both in front of and lateral to the body. This distribution was consistent across the sampled time and could be observed by averaging over a time period as short as 3 min; and 2) When we analyzed the subset of the data during which the hand was engaged in manipulation and grasp of small objects, we found a different spatial distribution. Grasp and manipulation were performed almost exclusively in central space in front of the chest and mouth. We compared these patterns of hand use with the distribution of hand and arm postures that were evoked from the precentral gyrus in our previous study. The distributions showed a significant match, confirming the hypothesis of the study. That is, the stimulation-evoked postures in the precentral gyrus matched the statistics of the monkeys' normal behavior.

It is important to note that these results are correlative. The correlation is suggestive. It shows that the map of postures, obtained with electrical stimulation, at least matches the statistics of normal behavior. This study is thus a first step in evaluating the stimulation-evoked map of postures. However, to determine whether normal movement is actually controlled by means of a map of postures will require further experiments, such as single-neuron recording studies and deactivation studies.

One possibility is that monkeys raised in different environments, with different motor experiences, may develop different motor cortex maps (e.g., Qi et al. 2000). Our electrical stimulation study was performed in monkeys raised and housed in laboratory cages. In the present study, therefore, we examined the behavior of monkeys in the same laboratory environment. The present results might not extend to monkeys in the wild or in other environments. There is currently little data on the typical spatial distribution of the hand, or on any metrics of the motor system other than handedness, in wild monkeys.

The motor homunculus

The map of the body in motor cortex was first described by Fritsch and Hitzig (1870) and popularized by Penfield, in the case of humans (Penfield and Boldrey 1937), and Woolsey, in the case of monkeys (Woolsey et al. 1952). Both Penfield and Woolsey warned that their drawings of body parts across the motor cortex were approximate and did not capture the complexity of overlapping and fractured representations. While motor cortex clearly contains some somatotopy, there does not appear to be a fine-grained homunculus with separate representations for each joint or muscle (e.g., Cheney et al. 1985; Gould et al. 1986; Donoghue et al. 1992; Sanes and Schieber 2001).

The map of arm and hand postures that we obtained with electrical stimulation may represent a level of organization existing within the larger, crude somatotopic map of the body. The map that we obtained within the arm representation appears to be organized according to the location in space to which the hand moves. This type of organization may help to explain the apparent disorganization and intermingling in the muscle map. Bringing the hand to a location in space, for example to grasp an object, requires muscles from the hand, arm, shoulder, and torso acting together. Such a map is consistent with the view that motor cortex does not specify the activity of individual muscles, but rather specifies complex muscle synergies that underlie behaviorally useful postures and movements. The present study shows that these postures may be represented in a way that is roughly proportional to their use during daily behavior. That is, rather than viewing the homunculus as a man with big lips and fingers, it may be more accurate to view the homunculus as a collection of useful movements and postures, some more represented than others.

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