Perspective

Mapping Behavioral Repertoire onto the Cortex

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A traditional view of the motor cortex in the primate brain is that it contains a map of the body arranged across the cortical surface. This traditional topographic scheme, however, does not capture the actual pattern of overlaps, fractures, re-representations, and multiple areas separated by fuzzy borders. Here, we suggest that the organization of the motor cortex, premotor cortex, supplementary motor cortex, frontal eye field, and supplementary eye field can in principle be understood as a best-fit rendering of the motor repertoire onto the two-dimensional cortical sheet in a manner that optimizes local continuity.

Introduction

One way to describe the topography of the cerebral cortex is that "like attracts like." The cortex is organized to maximize nearest neighbor similarity or local continuity (e.g., Durbin and Mitchison, 1990; Kaas and Catania, 2002; Kohonen, 1982; Rosa and Tweedale, 2005; Saarinen and Kohonen, 1985). This principle can explain the separation of cortex into discrete areas that emphasize different information domains. It can also explain the continuous maps that form within cortical areas.

The reason why the cortex is organized according to proximity is not known, but several plausible explanations can be advanced. One is that it is a side effect of the normal developmental process. During development, axons are guided to their terminations by chemical gradients, and therefore the connectivity from one brain area to another tends to form a topographic continuity (Gierer and Muller, 1995; O'Leary and McLaughlin, 2005). A second possible explanation is that during evolution, information processors that require constant intercommunication tend to be shifted toward each other in cortex in order to minimize wiring length and thus maximize efficiency. A third possible reason is that neurons that are near each other tend to share more synaptic connections and therefore, during Hebbian learning, become tuned to correlated signals. Probably all of these reasons contribute and interact with each other. For example, it has been suggested that primary cortical maps are hard wired, developing according to genetically programmed chemical gradients, and secondary cortical maps grow in a cascade of Hebbian learning from the primary maps (Rosa and Tweedale, 2005). Whatever the cause for the local smoothness constraint, whether ontogenetic, phylogenetic, or some mixture, the cortex seems to be organized along this principle of like attracts like.

For example, adjacent locations on the retina are mapped to adjacent locations in primary visual cortex in a retinotopic map. Conveniently, both the retina and the cortex are two-dimensional sheets and therefore the retina can be mapped onto the cortex in a topologically exact fashion. The mapping becomes more complex, however, when a stimulus space that has more than two dimensions is mapped onto the cortical sheet. Optimizing local continuity then becomes a matter of fitting together disparate pieces in the best compromise possible. For example, at the columnar level, the primary visual cortex represents not only the positions of stimuli on the retina but also the orientations of line segments. Durbin and Mitchison (1990) showed that when this three-dimensional stimulus space is reduced onto a two dimensional sheet, the mathematically optimal configuration in which local continuity is maximized has a pinwheel arrangement that closely resembles the actual arrangement found in the primary visual cortex. This finding that the complex pinwheel arrangement of hypercolumns in primary visual cortex can be explained by means of a dimensionality reduction greatly supported the case for the principle of maximization of local smoothness. The principle was not merely a verbal summary of cortical localization of function; it appeared to be able to make mathematically precise predictions about the details of cortical topography.

Yet after the use of a dimensionality reduction to model the primary visual cortex, little work was done to determine whether the same principle might explain the topographic details of other cortical areas. Probably the reason is that in the primary visual cortex, the relevant parameter spaces are well known and easily defined. The mathematical problem is circumscribed. In other cortical areas, such as high-order visual areas or motor areas, the parameter spaces are less well known, difficult to define precisely, and much more highly dimensional.

In a recent series of experiments, we began to list what we believed to be the relevant information dimensions that shape the organization of the lateral motor cortex in the monkey brain (Graziano et al., 2002, 2004, 2005). These hypothesized dimensions included locations of muscle groups on the body (this aspect of the movement repertoire, if mapped onto the cortex, would tend to produce a somatotopic map of the body), locations in space around the body to which movements are directed (this
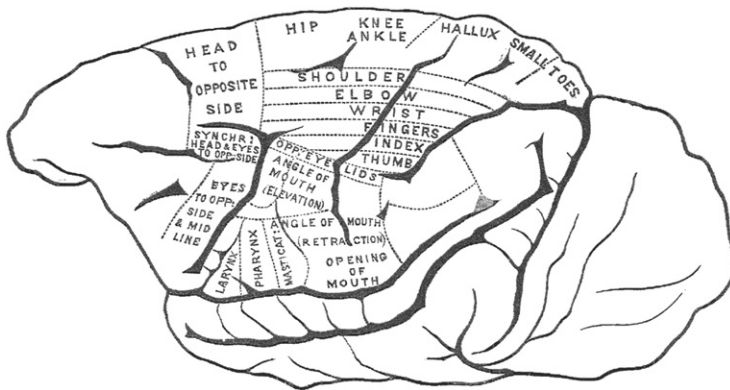
aspect of the movement repertoire, if mapped onto the cortex, would tend to produce a topographic map of space around the body), and the division of the movement repertoire into common, behaviorally useful action types (this aspect of the movement repertoire, if mapped onto the cortex, would tend to produce clusters in cortex that specialize in different common actions). We fed this highly dimensional information domain into a standard dimensionality-reduction engine (Kohonen, 2001) to determine its optimal cortical layout. Though any one of these constraints should have resulted in a simple and orderly map, the simultaneous interaction of the three constraints produced a complex topography (Aflalo and Graziano, 2006). The result included blurred maps of the body, gerrymandered borders, gradients, and pseudo-areas that fit into a larger map in some ways and yet were separate in other ways (Aflalo and Graziano, 2006). The informational space was of such high dimensionality that its reduction onto the cortical sheet did not result in any neatly describable topographic order. Yet this complex topography closely matched the actual pattern observed in the lateral motor cortex of the monkey brain. Quirky features of the motor cortex map emerged as a natural result of the model.

The present article describes an extension of this work outside the boundaries of the lateral motor cortex. The previous work focused on arm and hand movements in the motor repertoire of monkeys. Here, the model was supplied with a broader description of the animal's motor repertoire, including common actions such as eye movements, locomotion, reaching, and chewing. The purpose was to determine the optimal arrangement on the cortex of the animal's movement space, given at least a first-order description of that movement space. The resulting cortical topography generated by the model contained subregions that resembled the primary motor cortex, lateral premotor cortex, supplementary motor area (SMA), frontal eye field (FEF), and supplementary eye field (SEF). The model, therefore, was able to account for the organization of a large sector of cortex comprising about 20% of the cortical mantle.

This success of the model provides support for the underlying principle of cortical organization. Even an approximate version of the movement space, when reduced onto a two-dimensional surface according to the principle of like attracts like, resulted in a recognizable sketch of the actual cortical topography.

The following sections first describe some of the principle features of the topography of the cortical motor system and then describe how the present model of a dimensionality reduction operating on the movement space of the animal might account for these previously reported topographic features.

Many Proposed Organizations for Motor Cortex

At least eight types of topographic organization have been proposed for the cortical motor system since its initial discovery.

1. Map of the Body

The first topographic organization to be proposed for the motor cortex was a single map of the body (Ferrier, 1874; Fritsch and Hitzig, 1870). In primates, this map was arranged with the face in a ventral location and the feet in a dorsal location. It was studied in detail over the next several decades (e.g., Beevor and Horsley, 1890; Grunbaum and Sherrington, 1903). Figure 1 shows one of the early, extensive maps of the monkey motor cortex, obtained by applying brief bursts of electrical stimulation to the surface of the brain and observing the evoked muscle twitches (Beevor and Horsley, 1890).

2. Primary Motor and Premotor Cortex

Other researchers proposed a division between a primary motor map that contained a relatively clear separation among body part representations and an adjacent premotor area that contained more overlap among body part representations (Campbell, 1905; Fulton, 1934, 1935; Vogt and Vogt, 1919). Fulton's version of the primary motor and premotor cortex in a monkey brain is shown in Figure 2. Fulton, who more than anyone popularized the concept of a premotor cortex, recognized that the premotor and primary motor cortex were not linked in a simple hierarchical series. The two regions were able to function at least somewhat in parallel. He found that lesions to one or the other did not abolish movement, whereas lesions to both regions permanently abolished all movement (Fulton, 1935).
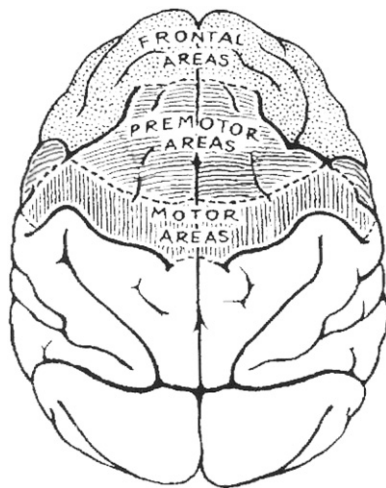
Figure 2. Top View of a Monkey Brain Showing a Division of the Cortex into Motor and Premotor Cortex
Adapted from Fulton (1934).

Figure 3. Two Maps of the Body in the Motor Cortex
The central sulcus is shown opened up, exposing the representation of the fingers and toes in the anterior bank of the sulcus. Adapted from Woolsey et al. (1952).

3. Primary Motor and Supplementary Motor Cortex

Penfield and Welch (1951) and Woolsey et al. (1952) suggested that there was no premotor cortex anterior to the primary motor cortex. Instead they proposed that motor cortex was divisible into two maps of the body arranged at right angles to each other, a lateral motor cortex (M1) and a medial motor cortex (M2 or the supplementary motor area, SMA). The map of the monkey motor areas according to Woolsey et al. is shown in Figure 3. As pointed out by Woolsey et al. in the case of the monkey brain and by Penfield and Welch in the case of the human brain, these two maps of the body are not discretely organized. Each map contains considerable overlap in the representations of body parts. This overlap is especially pronounced in SMA in which stimulation of a single cortical locus can evoke movements that span the entire body.

4. Primary Motor and Many Premotor Areas

Since Woolsey et al. (1952), the divisions commonly recognized in the monkey motor cortex have multiplied. Many researchers now divide the motor cortex into a primary motor cortex and a set of at least six premotor areas (e.g., Dum and Strick, 2002; He et al., 1995; Luppino et al., 1991; Matelli et al., 1985; Matsuzaka et al., 1992; Preuss et al., 1996; Rizzolatti and Luppino, 2001). Some of these premotor areas are shown in Figure 4. No group has done more to uncover the organization of these areas than Rizzolatti and colleagues. Their cytoarchitectonic studies helped to define the areas (Matelli et al., 1985), and their physiological studies helped to establish the functional differences among them (e.g., Gentilucci et al., 1988; Luppino et al., 1991; Rizzolatti et al., 1981, 1988). The work of Rizzolatti and colleagues pointed to an organization in which the premotor areas specialized in tasks of ethological importance. For example, the rostral division of the ventral premotor area (PMVr), termed F5 by Rizzolatti and colleagues, appeared to be involved in the control
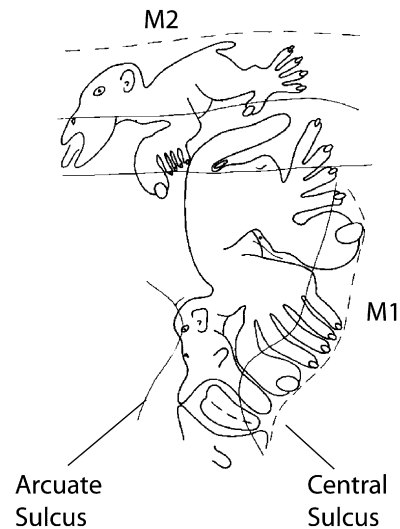
of complex useful hand grasps (Fogassi et al., 2001; Rizzolatti et al., 1988) and in the comprehension of the hand gestures of other individuals (di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004).

Other researchers have attributed more general qualities to the different premotor areas. For example, PMD has been hypothesized to play a role in the preparation for movement (Weinrich et al., 1984). SMA has been hypothesized to play a role in controlling sequences of actions, bimanual coordination, and the internal rehearsal of movement (e.g., Brinkman, 1981; Macpherson et al., 1982; Matsuzaka et al., 1992; Mushiake et al., 1990; Roland et al., 1980a, 1980b). Others have parceled the motor and premotor cortex according to their connectional anatomy. For example, Strick and colleagues described a set of regions in the motor and premotor cortex that project directly to the hand region of the spinal cord (Dum and Strick, 2005).

Although the motor cortex is clearly heterogeneous and different mixtures of properties can be found in different subdivisions, the precise functions of these many subdivisions are clearly not agreed upon. Adding to the uncertainty, the divisions among these cortical areas are probably not sharp borders, but rather gradients of properties. Most of these areas, including at least the primary motor cortex, PMDc, PMVc, SMA, and the cingulate motor areas, project directly to the spinal cord (Dum and Strick, 1991; He et al., 1993, 1995). It is therefore not entirely clear what hierarchical relationship they have to each other.

5. Integrative Map of the Body in Primary Motor Cortex

From its initial discovery, the map of the body in motor cortex was not described as a discretely organized roster of
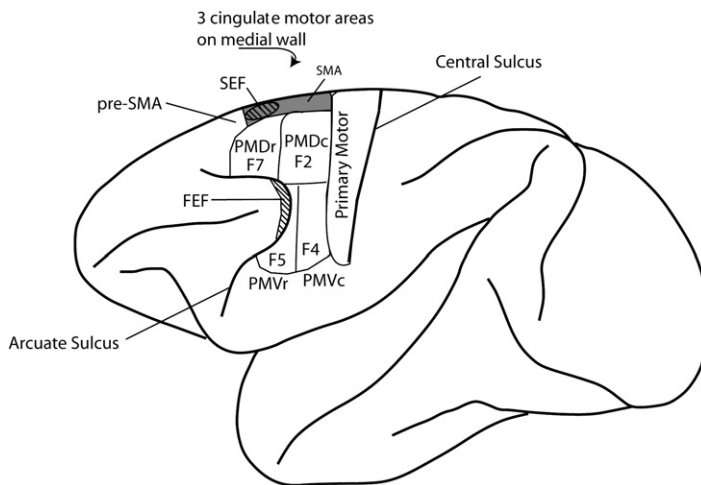
Figure 4. Some Commonly Accepted Divisions of the Cortical Motor System of the Monkey
PMDr = dorsal premotor cortex, rostral division, also sometimes called Field 7 (F7). PMDc = dorsal premotor cortex, caudal division, also sometimes called Field 2 (F2). PMVr = ventral premotor cortex, rostral division, also sometimes called Field 5 (F5). PMVc = ventral premotor cortex, caudal division, also sometimes called Field 4 (F4). SMA = supplementary motor area. SEF = supplementarty eye field, a part of SMA. Pre-SMA = presupplementary motor area. FEF = frontal eye field.

body parts (Ferrier, 1874; Fritsch and Hitzig, 1870). Instead, the representations of body parts apparently overlapped to some extent. This intermingling of representations was frequently confirmed by subsequent researchers (e.g., Woolsey et al., 1952). Asanuma (1975), however, suggested that the intermingling of representations may have been an artifact of a spatially coarse technique and that at a fine grain, such as at the level of individual cortical columns, the motor cortex might have a segregated representation of different muscles or muscle groups. This question was answered rather elegantly by Cheney and Fetz (1985), who showed that the representations of different muscles were intermingled even at the level of individual neurons. Muscles of the fingers, wrist, hand, arm, and shoulder had overlapping representations in the primary motor cortex. The map seemed designed to *integrate* the control of body parts rather than to segregate the control of body parts. This integrative function of the map has been emphasized especially with respect to the fingers in the monkey motor cortex (Schieber and Hibbard, 1993) and the human motor cortex (Sanes et al., 1995). This overlap in the somatotopic map may reflect the integrated use of body parts in the movement repertoire. For example, Nudo et al. (1996) found that a monkey that practices the combined use of two joints in the arm develops greater overlap in the cortical representation of those joints. Martin and colleagues (Chakrabarty and Martin, 2000; Martin et al., 2005) found that in kittens the motor map develops from a segregated representation of joints to an overlapping representation of joints in an experience-dependent manner.

6. Core and Surround Organization in the Primary Motor Cortex

Kwan et al. (1978) first reported a specific violation of the traditional somatotopic order in the primary motor cortex of monkeys. Traditionally, the hand representation was thought to be ventral to the arm representation. Kwan et al. found that the hand representation was instead surrounded by the arm representation on the dorsal, anterior, and ventral sides. This organization in which the hand rep-

resentation forms a core and the arm representation forms a surround was also obtained more recently by Park et al. (2001).

7. Cluster Map of Ethologically Relevant Action Categories

Recently, we electrically stimulated the motor cortex in monkeys (Cooke and Graziano, 2004; Graziano et al., 2002, 2005) and found the often-confirmed map of the body. However, we then extended the electrical stimulation to a duration that was of behavioral relevance. We stimulated for half a second at a time, approximating the duration of a monkey's reaching or grasping, instead of stimulating for the more typical duration of < 50 ms. Neurons in motor cortex are not normally active in 50 ms bursts but instead, to a first approximation, are active throughout the duration of a movement (e.g., Georgopoulos et al., 1982). With this longer stimulation we found that the muscle twitches unfolded into complex actions. Stimulation caused the monkey to perform movements that were common in its normal repertoire. Some of these movements are illustrated in Figure 5, traced from video footage. They included ethologically relevant behaviors such as closing the hand in a grip while bringing the hand to the mouth and opening the mouth; extending the hand away from the body with the grip opened as if in preparation to grasp an object; bringing the hand inward to a region just in front of the chest while shaping the fingers, as if to manipulate an object; squinting the facial muscles while turning the head sharply to one side and flinging up the arm, as if to protect the face from an impending impact; and moving all four limbs as if leaping, climbing, or engaging in other complex acts of locomotion. We found that these different categories of action tended to be evoked from different zones of cortex. The arrangement of action zones in the motor cortex, diagrammed in Figure 5, was consistent across monkeys.

8. Map of Spatial Locations to which the Hand Is Directed

We also found that the evoked movements were roughly arranged across the cortex according to the location in
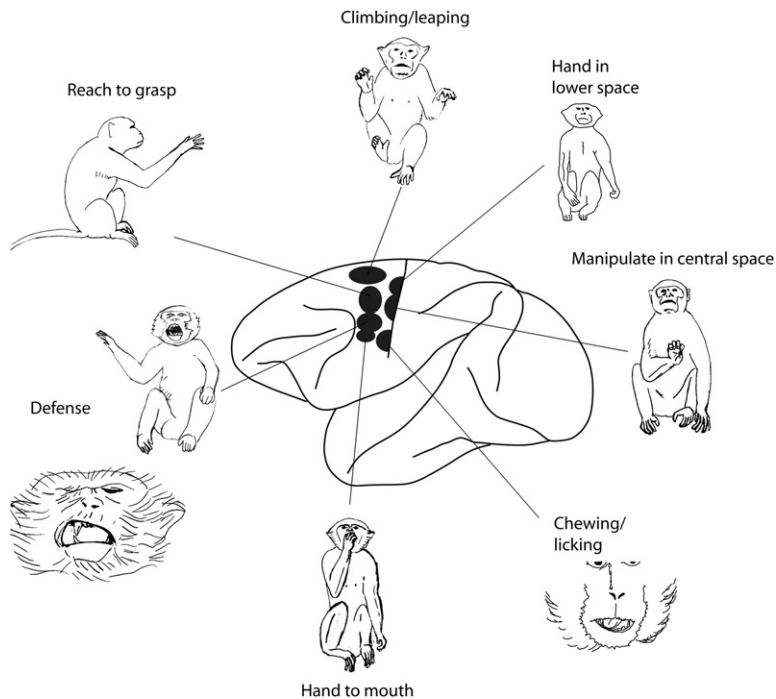
Figure 5. Action Zones in the Motor Cortex of the Monkey

These categories of movement were evoked by electrical stimulation of the cortex on the behaviorally relevant timescale of 0.5 s. Images traced from video frames. Each image represents the final posture obtained at the end of the stimulation-evoked movement. Within each action zone in the motor cortex, movements of similar behavioral category were evoked. Action zones in the motor cortex of the monkey described in Graziano et al. (2002, 2005).

space to which the movement was directed. The height of the hand was most clearly mapped across the cortical surface, as shown in Figure 6. Stimulation of the ventral regions of the arm representation in cortex commonly drove the hand into upper space, such as in the case of the hand-to-mouth movements. Stimulation of dorsal regions of the arm representation commonly drove the hand into lower space. Different hand locations in space were not represented in equal proportion in this map. Instead, those locations in which a monkey tends to place its hand in normal behavior, such as the space just in front of the mouth or just in front of the chest, were also more likely to be evoked by stimulation of motor cortex (Graziano et al., 2004). In this manner, the mapping of hand location in cortex reflected the statistics of the animal's normal behavior. This mapping of hand location was noisy, containing considerable spatial overlap, and broke down entirely in the medial cortex overlapping SMA, where stimulation evoked movements that resembled climbing or leaping.

Each of the above proposed organizations for motor cortex finds support in the data, and yet each is also noisy, blurred, and unable to explain all the variance in the data. This presence of many mapping schemes, each of which partially explains the layout of motor cortex, suggests that a deeper principle of organization may be at work in which a multiplicity of mapping requisites compete for representational space on the two-dimensional sheet of the cortex.

Competition among Mapping Requisites

The following sections describe a model of the topographic organization of the monkey motor cortex. The

model began with a set of movement dimensions hypothesized to be important to the monkey motor repertoire. The model then performed a dimensionality reduction in order to represent those movement dimensions on a two-dimensional cortical sheet. The dimensionality reduction followed the rule of "like attracts like," thus optimizing local topographic continuity. The prediction was that this optimization of local continuity as the guiding principle for arranging the map would result in an organization resembling the actual maps obtained in the monkey brain.

Three types of movement dimension were used to inform the model: somatotopic, ethological action category, and spatial (described more fully below). Each type by itself was of low enough dimensionality that it could have been mapped onto the cortical sheet in a simple and orderly map. The three together, however, presented a more complex optimality problem. To optimize one type of map would be to scramble the other two types of maps. The global optimum therefore required a compromise among the three potential maps. In this sense, the three potential maps competed with each other for the organization of the cortical sheet.

Somatotopy

In the model we defined a set of 12 body parts that could be mapped across the cortical surface. We assigned the model an initial somatotopic organization based on the map of the lateral motor cortex published by Woolsey et al. (1952). This somatotopy is one of the most complete in the literature because it covers most of the precentral gyrus and shows a horizontal (trunk to hand) as well as
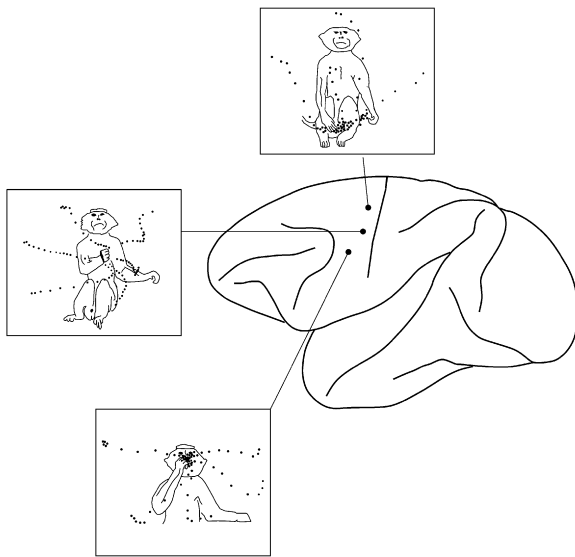
Figure 6. Cortical Mapping of the Spatial Locations to which Hand Movements Are Directed
Within the arm representation of the monkey motor cortex, stimulation in dorsal cortex tended to drive the hand to lower space; stimulation in ventral cortex tended to drive the hand into upper space; stimulation in intermediate cortical locations tended to drive the hand to intermediate heights. Each image is a tracing of the final posture obtained at the end of a stimulation-evoked movement. Each dotted line shows the trajectory of the hand during the 0.5 s stimulation train. Dots show the position of the hand in 30 ms increments. These trajectories show the convergence of the hand from disparate starting locations toward a final location. Adapted from Graziano et al. (2002).

vertical (head to toe) organization. The map of Woolsey et al. is of course a simplification, showing overall somatotopic trends. The monkey motor cortex does not actually have such a cleanly organized somatotopy. The model map began with this simple somatotopic organization, but as described below, in seeking an optimum arrangement, it reorganized into a more complex pattern under the influence of other mapping requisites. The initial state of the map is shown in Figure 7.

Ethologically Relevant Action Category
In the model, in addition to defining a set of body parts that could be mapped across the cortical surface, we also defined a set of eight action categories. In seeking local continuity, the model tended to form clusters for each action category. These action categories were based on the actions commonly evoked by electrical stimulation from the monkey motor cortex: hand-to-mouth movements, manipulation of objects in central space, reaching to grasp, defensive movements (including both arm withdrawal and facial defensive movements), chewing, bracing the hand in lower space, exploratory gaze shifts, and complex locomotion such as climbing. Each action category combined more than one body part. A hand-to-mouth action, for example, combined the hand, arm, neck, jaw, and lips. As a result, to create a local cluster
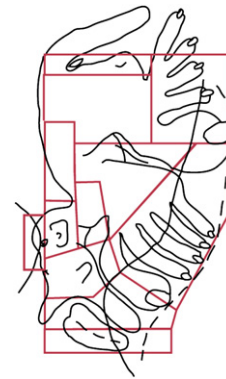

Figure 7. The Initial State of the Map Model
The map of the monkey body in the lateral motor cortex according to Woolsey et al. (1952) is shown, with an overlay showing the simplified, blocked arrangement of 12 body parts defined as the initial state of the motor cortex model.

in cortex that represented a hand-to-mouth action necessarily conflicted with any simple or exact somatotopic map of the body. Therefore, a cluster map of action categories and a somatotopic map of the body were partially opposed forces shaping the topography.

Hand Location
In the model, those movements that involved the arm were also assigned a hand position in space. During optimization, the map sought continuity in this representation of hand location. Any possible hand location map, however, was necessarily constrained by the simultaneous mapping of action categories. The reason is that each action category was associated with a characteristic set of hand locations (Figure 8). For example, hand-to-mouth movements were associated with hand locations in a small region of space around the mouth, climbing-like movements were associated with hand locations generally distant from the body and distributed in the frontal and lateral space, and so on. A cluster map of action categories and a spatial map of hand location were therefore interacting forces shaping the topography.

Optimization of the Map Model
The cortical map was optimized according to the method of Kohonen (2001). The Kohonen method is a standard tool for solving the problem of dimensionality reduction, or the problem of representing a multidimensional space on a lower dimensional space such that neighbor relationships are optimized. For the present purpose, the Kohonen method was not meant to model the specific neuronal interactions or learning algorithms of the brain. Rather, the method was merely an analytic tool that optimized topographic continuity. The manner in which the Kohonen method was adapted to a model of motor cortex, and the manner in which the movement repertoire was codified as a multidimensional space, is described in detail in Aflalo and Graziano (2006). Only the final result of the
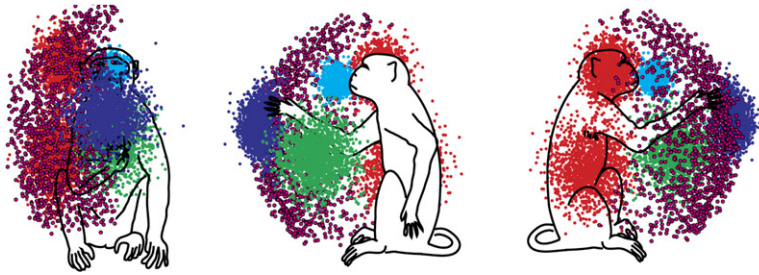
Figure 8. Hand Locations Associated with Categories of Movement in the Model
Three views of a schematized monkey showing the distribution of hand locations allowed for hand-to-mouth movements (light blue), reaching (dark blue), defense (red), central space/manipulation (green), and climbing (pink with black border).

model, after the dimensionality reduction was performed, is described below.

Similarities between the Model Motor Cortex and the Monkey Motor Cortex

Figure 9 shows the final state of the model, after the dimensionality reduction had settled on a solution that optimized local continuity. For consistency with the spatial arrangement found in the monkey brain, in the following discussion "posterior" refers to nodes on the right of the map, "anterior" to nodes on the left, "dorsal" and "medial" to nodes toward the top, and "ventral" and "lateral" to nodes toward the bottom of the map. Each panel shows the final state of the map with a different aspect of the representation highlighted. For example, panel (A) shows the representation of the tongue, mainly in the ventral part of the map. Panels (B)–(L) show the representations of the other body parts. Panel (M) shows the representations of the eight explicitly defined ethological action categories. Panels (N)–(P) show the representations of hand position across the map model. Panel (Q) shows a hypothetical demarcation on the model of some commonly accepted divisions in the monkey motor cortex.

The topography generated by the artificial model of motor cortex is similar to the actual motor cortex of the monkey in the following ways.

1. As a result of the dimensionality reduction, the initially discrete somatotopy was turned into a blurred somatotopy, much more similar to the actual maps obtained in physiological experiments (e.g., Donoghue et al., 1992; Gould et al., 1986; Park et al., 2001, 2004; Sessle and Wiesendanger, 1982). The reason for the somatotopic overlap is straightforward. Most of the movements incorporated into the model involved combinations of body parts. Therefore, in developing representations of those actions, the map was forced to develop overlapping representations of body parts.

2. The model developed a distinction between a posterior strip of the map and an anterior strip. Along the posterior strip (the right edge of the array), a relatively discrete progression can be seen. This progression includes a mouth representation at the bottom, then a region that emphasizes the hand but also weakly represents the arm, then a region that emphasizes the arm but also weakly represents the hand, then a region that represents the foot and leg. A classical motor somatotopy is displayed. Along the anterior strip of the map (the left edge

of the array), the somatotopy is much more overlapping and fractured, and a classical motor somatotopy is not as evident, consistent with the overlapping topography typical of the monkey premotor cortex.

The reason for this trend in the self-organizing map is clear. Some of the movements in our model required coordination among major segments of the body. These movements involved the axial musculature, because the trunk and neck form the connecting links between different body segments. The initial somatotopy was arranged with the axial musculature in an anterior region and the distal musculature in a posterior region. As a result, during map optimization, the complex movements that link more than one body segment gravitated to the anterior regions of the map. For example, reaching involved not only the arm and hand but also the torso and thus emerged in an anterior location; hand-to-mouth movements involved the neck to coordinate between the arm and the mouth, and thus emerged in an anterior location; climbing-like movements involved the neck and torso as the connecting links between head, arms, and legs, and therefore emerged in an anterior location. Thus, in our model, in its final state, one can distinguish a posterior strip that is "primary-like" in that it contains a relatively discrete somatotopy, representing body segments in a partially separate manner; and an anterior strip that is "premotor-like" in that it contains a more integrated, blurred somatotopy and represents movements of greater intersegment complexity. However, no processing hierarchy is implied by the map. The anterior strip does not necessarily control the posterior strip. Rather, it represents different kinds of movements.

3. The model developed a blurred, secondary map of the body that resembled the SMA body map found in the monkey brain (e.g., Macpherson et al., 1982; Mitz and Wise, 1987; Woolsey et al., 1952). This secondary map in the model was located along the medial edge, progressing from a representation of the foot in a posterior location, through a representation of the trunk and arm, to a representation of the head and eye in an anterior location. The reason for the emergence of this secondary somatotopy in the model is clear. It is a mapping of the action category related to complex locomotion. Locomotion in a complex environment strewn with obstacles, in which the hands and feet need to be placed on disparate opportune surfaces, includes all limbs, the head, the eye, the torso, and the tail as a balancing device. Not all body parts are moved simultaneously; instead, the actions form
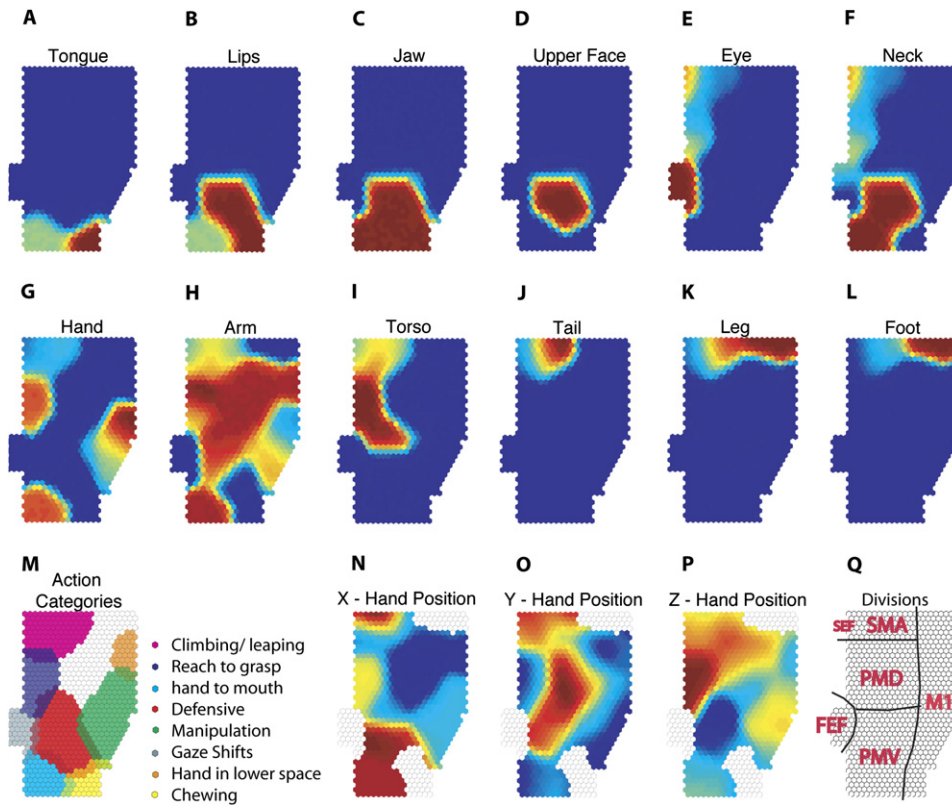
Figure 9. Final State of the Map Model
(A–L) Representations of the 12 body parts after map reorganization. Warm colors = map locations in which the body part is more strongly represented.
(M) Arrangement of the eight ethological categories of movement after reorganization. A dorsal region of the map represented movements of the arm, leg, and foot that did not fit into any of the eight specifically defined action categories.
(N–P) Maps of hand location after reorganization. Only those nodes that had a non-zero magnitude of arm representation are colored, as only these nodes had a defined hand position. X = hand height, warm colors = greater height; Y = lateral location of hand, warm colors = more lateral locations; Z = distance of hand from body along line of sight, warm colors = more distant locations.
(Q) Some common divisions of the monkey motor cortex drawn onto the map model.

an overlapping distribution, some movements weighted more toward the upper body and some weighed more toward the lower body. This highly overlapping distribution of movements, incorporated into the model, resulted in an overlapping map of the body that emerged adjacent to the original leg and foot representation.

4. The hand representation became divided into three main regions (Figure 9G). One hand representation was located in the posterior part of the array, as if corresponding to the primary motor hand area; the second hand representation was located in an anterior region within the dorsal half of the array, as if corresponding to the dorsal premotor hand area; and the third hand representation was located in an anterior region at the ventral edge of the array, as if corresponding to the ventral premotor hand area. These three hand areas also resemble the three lateral hand areas described by Dum and Strick (2005) on the basis of projections from cortex to the spinal cord. The reason why the model developed three distinct hand areas is that it was trained on three distinct categories of action that emphasized the hand: manipulation

in central space (represented in the posterior region), reaching to grasp (in the dorsal anterior region), and hand-to-mouth movement (represented in the ventral anterior region).

5. The posterior hand representation in the model was partially surrounded by a region of greater arm representation (Figures 9G and 9H). The core and surround organization resembles the organization found in the monkey primary motor cortex (Kwan et al., 1978; Park et al., 2001). The reason for this organization in the model is that there is a range of actions involving different relative contributions of the arm and hand. The actions that emphasize the hand tend to cluster, as the map seeks to optimize nearest-neighbor relationships. The actions that emphasize the arm, however, have a greater diversity, including a range of arm positions in space around the animal, and therefore do not cluster to the same extent. The cortex just dorsal to the core hand area emphasizes arm locations in lower space. The cortex just ventral to the core hand area emphasizes arm locations in more elevated space. The core-surround organization in the

model is therefore a result of a complex interaction among several mapping requisites.

6. The eight ethological categories of movement became focused into eight cortical zones that were relatively discrete, with minimal overlap (Figure 9M). The topographic arrangement of the zones in the self-organizing map closely resembled the arrangement observed in the actual monkey brain. This arrangement of ethological zones resulted from the initial somatotopy and the subsequent attempt of the model to optimize nearest-neighbor relationships. For example, the hand-to-mouth movements converged on a ventral location where the mouth, hand, and arm representations could most easily develop a region of overlap. The climbing movements converged on a dorsal location where the arm, leg, and torso representations could develop a region of overlap. The reaching movements converged on a region where the arm, hand, and torso could most easily develop a region of overlap. In this manner, the topography of these action zones on the cortex was highly constrained.

7. The defensive zone developed an internal topography in which arm-related defensive movements were represented in the dorsal part of the defensive zone and purely face-related defensive movements were represented in the ventral part of the defensive zone (compare Figures 9D, 9H, and 9M). This arrangement emerged because, in the initial somatotopy, the face was represented in a more ventral location than the arm, biasing the final configuration. The arrangement matched the results from the monkey brain (e.g., Graziano et al., 1997, 2002). In the corresponding zone in the monkey brain, some neurons have tactile responses on the arm and visual responses near the arm, and stimulation of these neurons evokes arm retraction. These neurons tend to be located in the dorsal part of the defensive zone. Other neurons have tactile responses on the face and visual responses near the face, and stimulation of these neurons evokes face-related defensive movements. These neurons tend to be located in the ventral part of the defensive zone. The model therefore correctly captured this detail of the monkey motor cortex.

8. The model developed noisy maps of hand location that approximated the findings in the monkey motor cortex. The height of the hand (Figure 9N) was most consistently mapped, with upper hand positions in a ventral location in the map and lower hand positions in a dorsal location. A dorsal, anterior region of the map, overlapping the representation of climbing-like movements, represented a range of hand locations again roughly matching our findings in the monkey brain. The lateral position of the hand (Figure 9O) was less clearly ordered, and the forward distance of the hand along the line of sight (Figure 9P) showed little consistent topography.

9. The model developed two hot spots for eye movement, resembling the locations of FEF and SEF in the monkey brain (Figure 9E). The FEF-like area was in an anterior, lateral location. This area resulted from the initial somatotopic arrangement in which the eye was represented in

that location. The SEF-like area was in an anterior, medial location, in the most anterior part of the SMA-like region of the map. This SEF-like area developed because of the inclusion of gaze shifts in the complex locomotor action category. In these respects, the model converged on an arrangement essentially identical to that in the monkey brain.

The model did not incorporate any dimensions related to the vectors of eye movements. Nonetheless, one feature of topography can be discerned in the FEF-like area in the model. The model placed the pure eye-movement representation in the ventral part of the FEF and the combined eye and head movements in the dorsal part of the FEF. This can be seen by comparing the distribution of the eye and the neck representations in Figures 9E and 9F. A topography of this type is also present in the actual monkey FEF. Indeed, the main organizational feature of the FEF in the monkey, and the only topographic feature that has been consistently found, is a tendency for long-amplitude gaze shifts that require both eye and head movements to be represented in dorsal FEF, and small-amplitude saccades that do not require head movements to be represented in ventral FEF (Bruce et al., 1985; Knight and Fuchs, 2007). The model therefore correctly reconstructed this detail of topography within the FEF.

In a similar manner, within the SEF-like area in the model, combined eye and head movements were represented preferentially in the anterior part. In the actual monkey brain, long saccades that recruit both the eye and the head are preferentially represented in the anterior part of SEF (Chen and Walton, 2005; Tehovnik and Lee, 1993).

Thus, the model correctly reconstructed the essential features of the topography in both eye movement areas.

10. Although the representation of eye movement in the model became focused on an FEF-like and SEF-like area, some representation of eye movement also developed in the cortex between these two areas, in the PMD-like region of the map. In the actual monkey brain, eye movement is indeed represented to some degree in PMD, and this eye movement representation is stronger in the more anterior part of PMD (Boussaoud, 1995; Bruce et al., 1985; Fujii et al., 2000). The reason why the model developed an eye representation in this region is because of the representation of reaching in the same region of the map. It has been reported that reaching to grasp an object and gaze movements are often integrated (Mennie et al., 2007). Therefore, in the definition of movements supplied to the model, the reaching-to-grasp category was composed of a range of arm and hand movements, some of which were associated with eye movement.

11. The organization of the cortical motor areas is essentially consistent among monkeys. An important question is whether the topography produced by the present model, which closely matches many of the features of the real topography, is robust or whether it changes radically with a small change in the input parameters. We therefore tested variants of the model, including alterations in the size and shape of the cortical sheet used as

a basis for the model, variations in the proportions of different movements supplied to the model, modifications to the hand locations assigned to different movements, and variations in the proportions of different body parts combined within each movement. Every parameter that was used as input to the model was varied, while preserving the same general description of the movement space. These changes in the information used to seed the model resulted in small changes in the final result in the exact size and exact locations of functional regions. The overall pattern, however, remained robust. The arrangement of functional zones in the model converged on more or less the same optimal configuration. This robustness of the model despite changes in the input parameters is described in greater detail in Aflalo and Graziano (2006).

Limitations of the Model

1. A set of little understood motor areas in the monkey cortex lies in the cingulate sulcus on the medial wall of the hemisphere (He et al., 1995). These areas, labeled in Figure 4, are absent from the model. The reason is that there is not yet any known functionality for those areas to supply to the model. If the cingulate motor areas were electrically stimulated, what movements would be produced, and would those movements be recognizably part of the animal's normal repertoire? This experiment has not yet been done, nor have single-neuron experiments explored the specific functions of those areas. The model does not, of course, create or discover functionality; its intended goal is to explain why known functions are arranged as they are on the cortex.

2. In the actual monkey motor cortex, the oral representation is larger and extends more ventrally than the corresponding representation in the model. The probable reason for the model's inaccuracy is its impoverished description of oral movements. In reality, in addition to chewing, oral behaviors include spatially precise and complex movements of the tongue within the mouth, swallowing, vocalization, food pouch storage, and probably other behaviors. A more inclusive description of the motor repertoire in this case would probably lead to a larger and more diverse mouth and tongue representation in the model. Comparing the model to reality, however, would be difficult because little is known about the organization of the mouth and tongue representation (but see Huang et al., 1989).

3. The model contains a coarse, first-order description of the movement repertoire. Forelimb movements, for example, are composed of movements of the hand and of the arm, ignoring the details of fingers, wrist, forearm, elbow, and shoulder. Manipulation of objects is described as a single category of action, without differentiation of specific grips or wrist rotations within that category. Whereas this rough description of large segments of the movement repertoire appears to be sufficient to capture the large-scale organization of the cortical motor areas, it ignores the possibility of a more fine-grained structure such as at the columnar level for the representation of

movement details. With more specific information about the statistics of a monkey's movement repertoire, it may be possible to extend the model in this direction to determine if it can correctly predict columnar organization.

4. The hypothesis tested here is that information is arranged across the cortex according to the same like-attracts-like optimality principle used by the model. The model, however, does not address how that optimization occurs in the brain. The cortex presumably finds this optimal organization through a combination of evolution and experience-dependent fine-tuning. Through this process, a region of the cortex comes to emphasize eye movements, another region emphasizes reaching, and so on. These cortical zones take on the cytoarchitecture and connections useful for their specific information domains. The major cytoarchitectural and connectional properties that define cortical zones are presumably the result of optimization through evolution. Smaller fine-tuning of cytoarchitecture and connections is presumably possible through experience. These issues of evolution versus learning, and of cytoarchitecture and connections, however, are not directly addressed by the model. Instead, the model directly addresses only the mapping of information across the cortex and assumes that the physical properties of cortex, such as cytoarchitecture and connections, follow the functionality.

5. The model as it stands does not encompass all cortical motor areas. Rather, it encompasses a set of areas that directly control movement through their output to subcortical motor nuclei and the spinal cord. Other cortical regions such as the parietal motor areas and rostral premotor areas, outside the perimeter of the present model, may play other roles in the control of movement. Some of these possible cortical interrelationships are discussed in the next section.

Hierarchy

Figure 10 shows a hierarchical diagram for the cortical motor system. This diagram contains three general classes of cortical motor area. First is a mosaic of output areas. These cortical "action zones" are organized around the broad categories of action that make up the animal's behavioral repertoire. They correspond to the traditional primary motor cortex, caudal premotor cortex, SMA, possibly the cingulate motor areas, the FEF, and the SEF, all of which, in the present scheme, are at approximately the same hierarchical level. Second, a set of parietal areas provides a liaison between sensory processing and the motor output areas (e.g., Matelli and Luppino, 2001; Wise et al., 1997). Third, a set of rostral premotor areas provides a liaison between the prefrontal areas and the output areas (e.g., Lu et al., 1994; Takada et al., 2004).

The difference between the scheme proposed here and a more traditional scheme lies mainly in the cortical output areas. In the traditional view, the main cortical output is a single map of muscles within the primary motor cortex. That map represents individually meaningless movements that higher-order areas can combine into meaningful
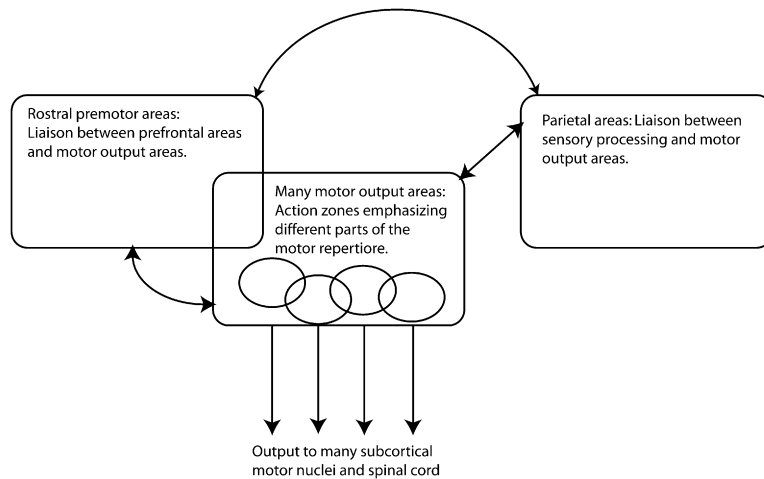
Figure 10. Possible Hierarchical Organization of the Cortical Motor System

actions. In the modified scheme described here, many output zones exist, each one emphasizing a different meaningful type of action. Some actions may involve the independent control of joints, others may involve integration among joints, and therefore these output zones are diverse in their properties.

These proposed cortical action zones are not strictly separate areas. For this reason, they are drawn schematically as overlapping ovals in Figure 10. They are more like clusters. They are hills that emerge with different movement emphases.

These output zones are also not strictly on the same hierarchical level. For this reason they are depicted at different heights in the schematic in Figure 10. Broadly speaking, they are part of the cortical output, projecting to subcortical motor nuclei and to the spinal cord, thus directly controlling movement. Yet they emphasize movements with a diversity of control requirements. It is likely that among the output zones are differences in complexity, in the level of abstraction of the information that is processed, and in the manner in which information flows laterally from one zone to another as they recruit each other to optimize their functions. For these reasons, it is probably not correct to think in terms of rigid hierarchies with absolute stages.

Cortical Output Zones May Participate in a Variety of Higher-Order Functions

Different actions in the motor repertoire of monkeys may be more or less associated with different higher-order functions. For example, reaching presumably requires some degree of advanced planning, as it involves a delay before a goal is reached. It also presumably involves at least some control of external spatial variables to guide the hand. Manipulation of objects that are already in grasp, in contrast, may require less planning, less control of spatial variables, and more control of muscle forces and individual joint rotations in the fingers, wrist, and forearm. Defensive movements require processing of sensory events near the body. They are typically reactive and

presumably therefore involve little planning, yet they require a processing of spatial locations and trajectories. Complex locomotion such as climbing that negotiates obstacles in the environment along a desired path might rely especially on an internally generated sequencing of events, and certainly on coordination across the two sides of the body.

Perhaps these kinds of associations can explain some of the suggestions of higher-order functions relatively emphasized in different cortical zones. For example, motor preparation signals are particularly common and robust in the PMD where reaching is emphasized (e.g., Weinrich et al., 1984). Visuospatial information is more prevalent in PMV, where defense of the body surface is emphasized (Graziano et al., 1997, 2002; Rizzolatti et al., 1981). In the SMA, where we obtained movements that resembled complex locomotion, such as climbing, various studies have suggested a relative emphasis on sequences of actions, bimanual coordination, and internal rehearsal of movement (e.g., Brinkman, 1981; Macpherson et al., 1982; Matsuzaka et al., 1992; Mushiake et al., 1990; Roland et al., 1980a, 1980b). Neurons in the primary motor hand area are relatively more correlated with joint rotations and muscle forces, such as might be useful for manipulation of objects, whereas neurons in premotor cortex are relatively more correlated with direction in space (Kakei et al., 1999, 2001).

These findings have generally been interpreted in the traditional framework of a set of premotor areas that specialize in higher-order aspects of movement and a primary motor cortex that implements movement through a direct projection to the spinal cord. Yet this strictly hierarchical view is problematical as reviewed above, as most of these areas project in parallel to the spinal cord, and correlations both with higher-order functions and with motor output can be found to some degree in all of these areas. In the view proposed here, the nonhomogeneous distribution of properties across the motor output regions of cortex emerges as a natural result of the varied control requirements of different parts of the animal's motor repertoire.

The organization, in this view, is best described as a mapping of the highly dimensional space of the motor repertoire onto the two-dimensional space of the cortex.

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