

### 3 A New View of the Motor Cortex and Its Relation to Social Behavior

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#### **Abstract**

Three main views of the primate motor cortex have been proposed over the 140 years of its study. These views are not necessarily incompatible. In the homunculus view, the motor cortex functions as a rough map of the body's musculature. In the population-code view, populations of broadly-tuned neurons combine to specify hand direction or some other parameter of movement. In the recently proposed action map view, common actions in the movement repertoire are emphasized in different regions of cortex. In the action map view, to fully understand the organization of the motor cortex, it is necessary to study the structure and complexity of the movement repertoire and understand how that statistical structure is mapped onto the cortical surface. This chapter discusses the action map in the primate brain and how some of the complex actions represented there may play a role in social behavior.

#### **Introduction**

Since the discovery of motor cortex more than 140 years ago (Fritsch & Hitzig, 1870 [1960]), three prominent views of its function have been proposed. In one view, the motor cortex is a homunculus-like map of muscles, though the map may be partially overlapping and fractured in its somatotopy (e.g. Cheney & Fetz, 1985; Donoghue, Leibovic, & Sanes, 1992; Ferrier, 1874; Foerster, 1936; Fritsch & Hitzig, 1870 [1960]; Fulton, 1938; Gould, Cusick, Pons, & Kaas, 1986; Kwan, MacKay, Murphy, & Wong 1978; Park, Belhaj-Saif, Gordon, & Cheney, 2001; Penfield & Boldrey, 1937; Rathelot & Strick, 2006; Sherrington, 1939; Strick & Preston, 1978; Woolsey, 1952).

In a second view, the motor cortex functions through a population of spatially tuned neurons. These neurons collectively pool or sum their outputs, thereby specifying an arm movement (Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Georgopoulos, Schwartz, & Kettner, 1986). Whether it is hand direction in particular that is specified, or some other parameter of movement

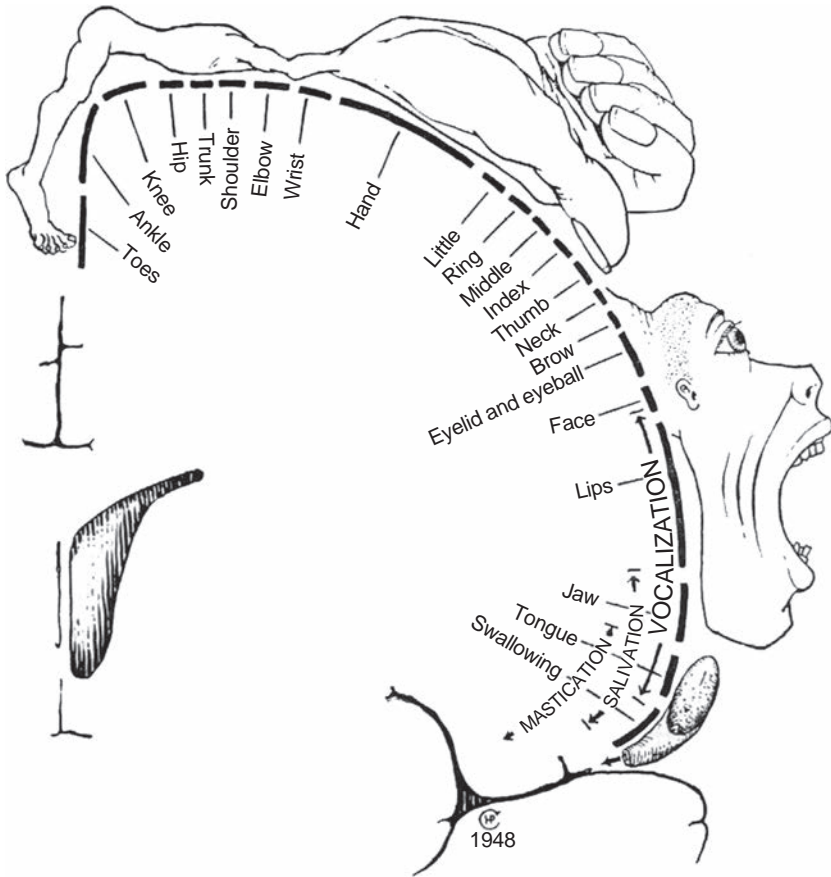
such as speed or force, became controversial and was never fully resolved (e.g. Aflalo & Graziano, 2007; Churchland & Shenoy, 2007; Georgopoulos, Ashe, Smyrnis, & Taira, 1992; Holdefer & Miller, 2002; Kakei, Hoffman, & Strick, 1999; Moran & Schwartz, 1999; Paninski, Fellows, Hatsopoulos, & Donoghue, 2004; Reina, Moran, & Schwartz, 2001; Scott & Kalaska, 1997; Sergio & Kalaska, 2003; Townsend, Paninski, & Lemon, 2006).

In the past decade, a new, third view has been proposed, the action map view of the motor cortex (Graziano, 2006, 2008; Graziano, Taylor, & Moore, 2002). In the action map hypothesis, the motor cortex is organized around the common, useful behaviors performed by the animal. These behaviors extend far beyond the simple reaching and grasping actions typically studied. Different categories of action, such as hand-to-mouth actions, manipulation of objects in central space, reaching, defensive actions, or complex interactions among all four limbs useful for leaping or climbing, are emphasized in different regions in the cortex. In this view, to understand the motor cortex it is necessary to study more than the musculature of the animal's body and more than a few movement parameters such as direction or force. One must study the structure and complexity of the movement repertoire and how that statistical structure is mapped onto the cortical surface.

These three views are not necessarily incompatible. All three could be correct. Certainly the motor cortex contains a rough somatotopy, neurons in it are indeed broadly tuned and would require a population to specify the output, and different highly complex actions tend to be evoked by activity in different subregions of the motor cortex as though the network has become organized around common components of behavior. The following sections describe these three views of motor cortex, emphasizing the most recent action map hypothesis.

### **The Homunculus**

In 1870, Fritsch and Hitzig electrically stimulated the surface of the dog brain and obtained muscle twitches. They noted that these movements could be evoked from a small number of sites or 'centers' in the anterior half of the brain. Shortly after, Ferrier (1874) obtained the first true motor map in monkeys, establishing a systematic map of the body along the precentral gyrus with the legs at the top of the brain and the mouth near the bottom. These early reports emphasized the overlapping and complex nature of the map and the many muscles activated by stimulation of a single site in cortex. Subsequent work, however, emphasized the view of the motor cortex as a roster of muscles laid out in topographic order. A particularly influential report was published by Penfield & Boldrey (1937), nearly 70 years after the initial discovery of motor cortex. Penfield first drew a little distorted man stretched across the surface of



**Figure 3.1** The motor homunculus of the human brain, from Penfield and Rasmussen (1950).

*Notes:* A coronal slice through the motor cortex is shown. Each point in motor cortex was electrically stimulated and the evoked muscle twitch was noted. Although each cortical point could activate many muscles, a rough body plan could be discerned.

the human brain and used the term ‘homunculus’ to describe it (Penfield & Rasmussen, 1950). Penfield’s map is shown in Figure 3.1.

Most researchers who studied the motor map, including Penfield, noted that the map is not precise. It is blurred and overlapping. The organization is not a simple segregation of muscles (e.g. Cheney & Fetz, 1985; Donoghue et al., 1992; Ferrier, 1874; Foerster, 1936; Fritsch & Hitzig 1870 [1960]; Fulton, 1938; Gould et al., 1986; Kwan et al., 1978; Park et al., 2001; Penfield &

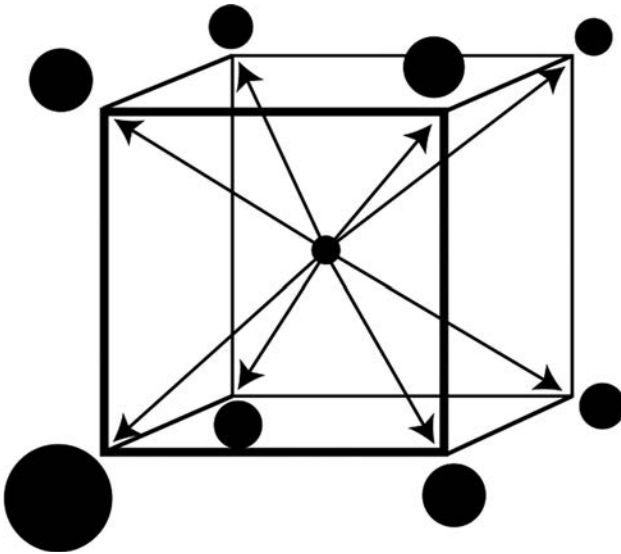
Boldrey, 1937; Rathelot & Strick, 2006; Sherrington, 1939; Strick & Preston, 1978; Woolsey, 1952). The argument that a single site in the cortex controls a single muscle, or perhaps a small number of muscles that cross a single joint, was promoted by a few researchers, notably Asanuma (1975). But according to most reports, each cortical locus, and even each cortical neuron, contributes to the activity of a range of muscles that cross a range of joints. This intermingling has been tested most extensively in the case of the arm and hand muscles (e.g. Cheney & Fetz, 1985; Donoghue et al., 1992; Meier, Aflalo, Kastner, & Graziano, 2008; Park et al., 2001; Rathelot & Strick, 2006; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995; Schieber & Hibbard, 1993).

One possible explanation for the overlapping nature of the map is that the function of the motor cortex may be to coordinate among muscles and joints that are commonly used together. In support of this view, when cats and monkeys are infants, prior to extensive movement experience, their motor maps have little overlap in the representations of different joints. As the animals gain experience with movement, especially movement that combines the action of more than one joint, the muscle map develops an adult-like pattern of overlap (Chakrabarty & Martin, 2000; Martin, Engber, & Meng, 2005; Nudo, Milliken, Jenkins, & Merzenich, 1996). These results suggest that the complexity and overlap in the cortical map are related to the complexity and overlap in the movement repertoire. While there is clearly a rough somatotopic map in the motor cortex, it is also clear that the motor cortex does not function as a look-up table of muscles or small groups of muscles. Something much more complex is occurring that emerges from the statistics of the animal's natural movement repertoire.

### **The Population Code**

In an attempt to study some of the complexity of natural movement, Georgopoulos and colleagues pioneered the directional reaching paradigm (1982, 1986). In this paradigm, a monkey is trained to reach in many possible directions from an initial central location. During the reach, the activity of motor cortex neurons is recorded. In a now-classic finding, most neurons in the arm region of the motor cortex are active during the reach and are broadly tuned, showing more activity for one preferred direction of reach and progressively less activity for directions that are progressively different from the preferred. These authors noted that a population of such neurons could in effect 'vote', each one voting for its own preferred direction, and once the votes were summed, the result would correspond to a highly specified hand path. Figure 3.2 illustrates the responses of a neuron broadly tuned to the direction of reach.

Over the past 30 years, this account of a population code for the direction of reach has encountered controversy. Motor cortex neurons do not necessarily



**Figure 3.2** Direction tuning of a motor cortex neuron similar to that described in Georgopoulos et al. (1986).

*Notes:* A monkey was trained to make hand movements from a central location to eight possible surrounding locations forming the vertices of an imaginary cube. Many neurons in motor cortex were broadly tuned to the direction of the reach, firing more during one direction and less during neighboring directions. Here, the size of each black dot represents the firing rate of a hypothetical motor cortex neuron during each direction of reach. This neuron prefers a lower, left direction of reach.

maintain the same preferred direction when different muscle activations or different joint rotations are required to move the hand along the same paths (Scott & Kalaska, 1997). It may be, therefore, that the neurons do not encode the ‘extrinsic’ variable of hand direction, but instead ‘intrinsic’ variables such as muscle force or joint rotation. It has been suggested that many motor cortex neurons are better tuned to velocity, joint angle, joint configuration, force or the muscle output itself (e.g. Afshar & Graziano, 2007; Churchland & Shenoy, 2007; Georgopoulos et al., 1992; Holdefer & Miller, 2002; Kakei et al., 1999; Moran & Schwartz, 1999; Paninski et al., 2004; Reina et al., 2001; Scott & Kalaska, 1997; Sergio & Kalaska, 2003; Todorov, 2000; Townsend et al., 2006). The many hundreds of papers and many thousands of person-hours over 30 years have not resulted in a consensus.

Two general conclusions may be useful to draw from this literature. First, motor cortex neurons are indeed broadly tuned to different movements.

Consistent with the initial insight of Georgopoulos and colleagues, populations of broadly tuned neurons in the motor cortex are likely to control movement.

Second, it is not really correct to think of neurons in motor cortex as ‘coding’ for movement variables. The concept of ‘coding’ of specific parameters may have been unwisely borrowed from the domain of sensory physiology, where neurons code for specific stimulus attributes. Neurons in the motor cortex become active and thereby cause movements. Their activity must necessarily ultimately control many aspects of movement such as direction, speed, posture and force, since normal movements vary in those respects. The details of how that control is accomplished remain unclear, arguably because the experiments have focused on correlational methods. Those methods can reveal only so much. Correlation does not imply causation, whereas the fundamental truth of neuronal activity in the motor cortex is that it causes movement.

### **Box 3.1** Stimulation on a behavioral timescale

The first century of experiments on the motor cortex, from Fritsch and Hitzig’s discovery of motor cortex in the dog brain (1870 [1960]) to Woolsey’s mapping of the monkey motor cortex (1956), was dominated by the use of electrical stimulation applied to the surface of the brain. Asanuma (1975) and colleagues moved to a more refined method involving small currents (microamps) in brief pulse trains (often less than 10 ms) applied through microelectrodes, sometimes directly to layer 5 of cortex, the output layer. The assumption seems to have been that this punctate stimulation could serve as a method of anatomical tract tracing. It could reveal the pathway of interest from cortex to muscles with a relay in the spinal cord, while avoiding the complication of signals spreading through other connectivity. In retrospect, given the rich, network-like connectivity within the motor system, this hope of picking out a single descending pathway by activating small groups of neurons for short durations seems naïve.

In other neural systems, the use of microstimulation developed along a different tradition. Microstimulation was applied on a longer timescale thereby evoking some aspects of normal behavior. The technique was used successfully in the superior colliculus and frontal eye fields to study saccadic eye movements, in the middle temporal visual area and primary somatosensory area to study perceptual decisions, and in the hypothalamus to study motivated states such as hunger and rage, among other aspects of brain function (e.g. Bruce, Goldberg, Bushnell, & Stanton, 1985; Caggiula & Hoebel, 1966; Hess, 1957; Hoebel, 1969; King & Hoebel, 1968; Robinson, 1972; Robinson & Fuchs, 1969; Romo, Hernandez, Zainos, & Salinas, 1998; Salzman, Britten, & Newsome, 1990; Schiller & Stryker,

1972). None of these experiments involved any assumption about activating one 'correct' pathway while avoiding signal spread through collateral pathways. Instead, the assumption was that the signal, injected in one place in the system would spread according to the natural connectivity, influence related networks and alter behavior in a revealing manner.

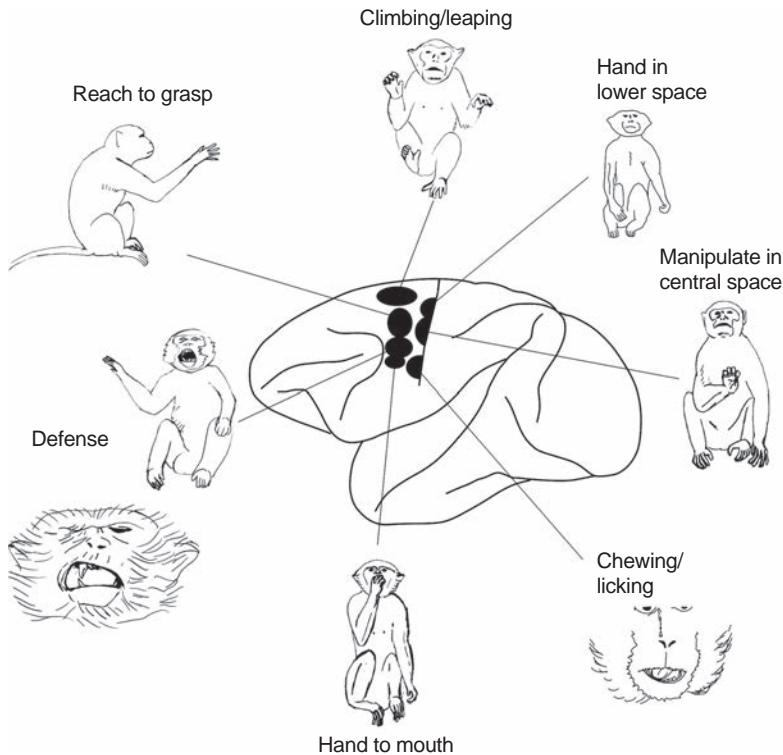
Microstimulation on a behavioral timescale was not systematically studied in the motor cortex until recently. Taking a method common in the study of other brain areas and transplanting it into the motor cortex resulted in a new picture radically different from anything that had been described before. Stimulation of the monkey motor cortex on a behavioral timescale, such as for the half-second of a typical reaching movement, evoked complex movements that resembled components of the animal's normal repertoire (Graziano, 2008; Graziano, Aflalo, & Cooke 2005; Graziano et al., 2002). Different movements were evoked from different sites in an 'action map'.

### **An Action Map in the Motor Cortex**

In the past decade, a new view of the motor cortex has begun to emerge. In this view, the function of the motor cortex is not to decompose movement into constituent muscles and joints or into elemental movement parameters such as direction and speed, but instead to help produce some of the most complex components of the movement repertoire. The initial studies to point toward an action map involved applying microstimulation to the motor cortex of monkeys (Graziano et al., 2002). Instead of stimulating on a short timescale, such as for 50 ms or less, as had become traditional in the study of the motor cortex, these experiments involved stimulation for half a second, roughly matching the timescale of a monkey's normal arm movements (see Box 3.1). Figure 3.3 summarizes the results.

Stimulation in different regions of the cortical map evoked different movements that closely resembled common categories of action from the monkey's normal repertoire. For example, when sites within one region of the map were stimulated, a hand-to-mouth movement was evoked (Graziano et al., 2002, 2005). The movement included a closure of the hand into an apparent grip, a turning of the wrist and forearm to direct the hand toward the mouth, a rotation of the elbow and shoulder bringing the hand through space to the mouth, an opening of the mouth, and a turning of the head to align the front of the mouth with the hand. The movement occurred reliably on each stimulation trial and could be replicated even when the monkey was anesthetized. If a lead weight was hung on the hand, the movement compensated and pulled the hand to the correct height to reach the mouth. Yet the movement was in some ways stereotyped. For example, if a barrier was placed between the hand and the mouth,





**Figure 3.3** Action zones in the motor cortex of the monkey.

*Notes:* These categories of movement were evoked by electrical stimulation of the cortex on the behaviorally relevant timescale of 0.5 seconds. Images are traced from video frames and each image represents the final posture obtained at the end of the stimulation-evoked movement. Within each action zone in the motor cortex, movements in similar behavioral categories were evoked.

*Source:* Adapted from Graziano et al. (2002, 2005).

the hand did not move intelligently around the barrier as in normal, motivated behavior. Instead, it crashed into the barrier and remained pressing against it until the stimulation current stopped. Electrical stimulation in this region of the map therefore appeared to generate a stereotyped, average version of a common movement. A large part of a monkey's spontaneous repertoire is composed of complex interactions between the hand and the mouth (Graziano, 2008; Graziano, Cooke, Taylor, & Moore, 2004).

A specific zone in the motor cortex, sometimes called the polysensory zone, contains a high proportion of neurons that respond to tactile and visual stimuli



(Fogassi et al., 1996; Gentilucci et al., 1988; Graziano, Hu, & Gross, 1997; Graziano, Yap, & Gross, 1994, Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Each multimodal neuron has a tactile receptive field on the skin and also responds to visual stimuli in the space near the tactile receptive field. Some neurons also have auditory responses that are strongest to sounds near the body. Electrical stimulation of these cortical sites typically evokes a movement that appears to protect the body surface in the area of the tactile receptive field (Cooke & Graziano, 2004a; Graziano et al., 2002, 2005). For example, if a site in the cortex responds to touching the left cheek and to visual stimuli near or approaching the left cheek, then stimulation of that site evokes a squint, a folding back of the left ear, a rightward turning of the head, a lifting of the left shoulder, and a rapid lifting and lateral movement of the left arm as if to block a threat. The movement is fast, reliable across trials, and can be evoked even when the animal is anesthetized. Chemical inhibition of this cortical region results in a temporary reduction of a normal defensive reaction such as to an air puff, and chemical disinhibition results in a hypersensitivity to threats to the face and an exaggerated defensive reaction (Cooke & Graziano, 2004b). In the case of the defensive movements, therefore, the evidence shows corroboration among four different sources of data: the response properties of the neurons, the effect of electrical stimulation, the effect of chemical manipulation, and the animal's natural movement repertoire.

Another region of the map, when stimulated, resulted in reaching movements of the arm into distal space with the palm facing outward and the hand shaped as if to grasp something (Graziano et al., 2005). To compare the effects of electrical stimulation with the response profiles of neurons, we conducted a study in which the monkey was restrained in a chair but free to move its arm spontaneously, grabbing, reaching, scratching and so forth (Aflalo & Graziano 2006a, 2007). These movements of the arm were tracked in three dimensions at high resolution by a set of lights fixed to key points on the arm. Using regression analysis, each neuron could be matched to a preferred posture of the arm, defined not by hand position in space, but by an 8-dimensional joint space. If the arm moved toward that preferred posture, the neuron became more active during that movement. If the arm moved toward other postures, the neuron was less active. The preferred postures obtained at a site in the cortex tended to match the joint configuration of the arm evoked by stimulation of that same site. Although other tuning models were tested, a tuning for preferred posture explained more of the variance in neuronal activity (36 percent) than did direction tuning (8 percent) or speed tuning (3 percent). These results do not in any way discredit the direction-tuning or speed-tuning hypotheses. The neurons did show a significant degree of direction and speed tuning. But the results do suggest that tuning to a single movement variable is unlikely to account for

the full pattern of activity in these neurons. Most complex movements require the control of many movement variables simultaneously. Perhaps that is why the neurons that control movement are tuned to so many variables at the same time. Moreover, many common actions of the arm, such as reaching or hand-to-mouth, depend on adjustments or variations round an underlying stabilizing posture, perhaps accounting for why a tuning to posture accounts for so much of the variance in neuronal activity.

Other complex movements, evoked from other regions of the map, included bringing the hand into central space with the fingers gripped or otherwise shaped as if to manipulate an object; putting the hand down into lower lateral space as though bracing the weight of the body on it; and bilateral movements of all four limbs in a pattern that resembled complex locomotion such as climbing or leaping (Graziano et al., 2002, 2005).

Based on these results, we proposed a new hypothesis about the organization of the motor cortex. The complex map might reflect a complex movement repertoire that is flattened onto the cortical sheet. Computational studies showed that, indeed, when a statistical description of a monkey's typical movement repertoire is flattened onto a model of the cortical sheet, subject to a local smoothness constraint in which similar movements are mapped near each other, the resulting map is a close approximation to the actual map obtained by physiology (Aflalo & Graziano, 2006b; Graziano & Aflalo, 2007). In this method, the map begins with an initial state that resembles the discrete somatotopic map imposed on the motor cortex at the outset of development. The map then re-organizes to reflect the complexity of the movement repertoire. The computational method reproduces the standard map of the body, complete with many of its otherwise-puzzling reversals, fractures and overlaps. It also reproduces the arrangement of actions in the action map. Actions that involve coordination among many body parts, such as hand-to-mouth actions or climbing-like actions, tend to gravitate to the anterior edge of the map where the axial muscles are also emphasized, since the axial muscles are necessary to link up different body segments. Actions that focus mainly on individual body parts, such as chewing, or manipulation of an object with the fingers, tend to gravitate to the posterior edge of the map. Actions of the hand tend to cluster in three cortical zones because they play a prominent role in three different types of behavior: manipulation of objects in central space, interactions between the hand and the mouth, and reaching to acquire an object. In these and other ways, the topography predicted by the model closely matched the actual topography in the motor cortex. The model provided a potential explanation for the functional topography spanning a large swath of cortex, including the primary motor cortex, the caudal parts of the premotor cortex, the supplementary motor map, the frontal eye field and the supplementary eye field. A relatively simple

underlying principle, a flattening or rendering of the movement repertoire onto the cortical surface, may help explain the seemingly complex organization of the cortical motor system.

### **Further Studies of Cortical Action Maps**

The findings described in the previous section have been corroborated by a range of studies in the primate brain. Stepniewska, Fang, and Kaas (2005, 2009) used electrical stimulation to extensively map the parietal cortex and motor cortex of monkeys and prosimians and found action categories in distinct cortical zones. Overduin, d'Avella, Carmena, and Bizzi (2012) found that stimulation in the motor cortex evoked natural synergistic activations of the hand muscles, and that different synergies were emphasized in different adjacent regions of cortex. Van Acker et al. (2013) obtained complex movements of the limbs, including hand-to-mouth movements, on stimulation of the monkey motor cortex. Caruana, Jezzini, Sbriscia-Fioretti, Rizzolatti, and Gallese (2011) evoked complex social gestures by stimulating the insular cortex of monkeys and found different categories of gesture in adjacent regions of the cortex. Desmurget, Song, Mottolese, and Sirigu (2013) obtained complex, behaviorally relevant movements on stimulation of the human motor cortex.

The rodent motor cortex may share a similar organization. Haiss and Schwarz (2005) evoked different behaviorally relevant whisking actions on stimulating different regions of the rat motor cortex, including exploratory whisking from one cortical region and defensive-like whisker retraction and squinting from another cortical region. Ramanathan, Conner, and Tuszynski (2006) found that stimulation of the rat motor cortex evoked different kinds of forepaw movements from different zones in the cortex. When the reaching zone was lesioned, the rats lost the ability to reach. The ability quickly recovered. When the recovered rats were mapped again, their cortex showed a new zone, near the lesioned site, from which reaching movements could be evoked, and the size of the new reaching zone correlated with the extent of the rat's behavioral recovery. Harrison, Ayling, and Murphy (2012) studied the mouse motor cortex. In order to determine whether the effect of electrical stimulation was somehow artifactual, they compared it to the effect of optogenetic stimulation, which is more precise because it specifically induces action potentials in cell bodies in a small target area. They obtained complex, multi-joint movements of the limbs to specific postures. The more precise optogenetic stimulation matched the results of electrical stimulation at the same sites. Bonazzi et al. (2013) systematically mapped the rat motor cortex using long-train electrical stimulation and found complex, multi-joint movements of the limbs that matched the rat's behavioral repertoire and that were arranged across the cortical surface in an apparent action map.

The evidence is therefore strong and increasing: the motor cortex is organized at least partly as an action map. The bulk of the evidence thus far comes from microstimulation studies, but those studies are now corroborated by optogenetic stimulation, single neuron physiology, chemical inhibition and disinhibition, lesions and recovery from lesions, studies of the natural movement repertoire, and computational studies.

The homunculus – the textbook account of the motor cortex – is not complete and is probably not the fundamental principle of organization. The slightly more subtle, common view of a ‘noisy’ homunculus is simply a classical homunculus plus the admission that there must be some other, unknown principle influencing the organization. What is that principle? To understand the organization and function of the motor cortex, it may be necessary to understand the movement repertoire of the animal. The movement repertoire is complex and multidimensional. Actions vary in terms of body parts involved, location in space to which actions are directed, broad behavioral significance such as defending the body surface or acquiring objects, and probably many other aspects of movement. Added to that, the cortex tends to self-organize in a manner that optimizes local similarity. It tends to form two-dimensional maps. The squeezing of the multidimensional movement repertoire onto the two-dimensional cortical surface, with an initial bias toward a somatotopic map, appears to result in a complex, but ultimately understandable organization. Many of the quirky details of that organization can be understood through a mathematical analysis, as shown in modeling studies (Graziano & Aflalo, 2007). It is not a simple map in the sense of a map of visual space or a well-ordered map of the body, because the dimensionality of the movement repertoire is too high to be laid out simply on the cortical surface. But it can be understood in a principled manner.

### **Social Implications of Defensive Movements**

Primates, like most animals, have an elaborate set of coordinated behaviors that protect the body surface from damage. We studied these reactions in macaque monkeys, comparing the defensive-like movements evoked from the action map to naturally occurring defensive movements (Cooke & Graziano, 2003, 2004a, 2004b; Cooke, Taylor, Moore, & Graziano, 2003). As these experiments progressed, we noticed a similarity between standard primate defensive movements and many of the actions in human social communication (Graziano, 2008; Graziano & Cooke, 2006).

Evolution works with what it has and as a result follows strange and quirky paths – such as from fish fins to human hands, or from jawbones to inner ear bones. Could many of the social gestures and expressions we consider to be fundamental to human nature, such as smiling, laughing and crying, have evolved

from something as specific as defense of the body surface from impending collision? The hypothesis that defensive reactions gave rise to many social displays was proposed by Darwin (1872) and elaborated by Andrew (1962). In this final section, I discuss some speculations based on my own observations of defensive movements in primates.

Three key properties of defensive reactions make them especially likely to evolve into social displays. First, defensive reactions communicate something about the internal state of an animal. Large magnitude defensive reactions suggest stress or a recent startle. More subdued defensive reactions suggest a state of confidence and calm. An animal that is cringing and glancing over its left shoulder broadcasts that it expects a threat from that particular direction. A male and female that allow close body contact with minimal defensive reactions communicate a willingness to mate with each other. Defensive movements are therefore informative.

Second, defensive movements are easily visible to other animals. These actions not only contain information about inner state but also telegraph it to anyone nearby and watching.

Third, an animal cannot safely suppress its defensive reactions or it would expose itself to risk of injury. It therefore cannot help leaking information about its inner state to anyone watching its defensive actions.

Given these properties, animals might evolve brain mechanisms for detecting and taking advantage of the defensive reactions of others. If you can observe and interpret those behaviors, you gain predictive power over other animals. At the same time, animals might evolve mechanisms for modifying their defensive reactions or deploying them in non-defensive situations in order to manipulate the behavior of whoever is watching. In this way, a large and related subset of social signals might have emerged from the more basic need to defend the body from intrusion or attack.

For example, the human smile is thought to have evolved from the 'fear grimace' or 'silent bared teeth display' of non-human primates such as macaques (Andrew, 1962; van Hooff, 1972; Preuschoft, 1992). It may be tempting to think of the silent bared teeth display as solely a facial action. However, that is not correct. In macaque monkeys, it is part of a whole-body display that includes wrinkling the skin around the eyes, lifting the upper lip, folding the ears back against the skull, pulling the head down, hunching the shoulders, curling the body forward, and pulling the arms across the front of the torso. All of these actions are also part of a standard startle and defensive stance. If animal A looms aggressively toward animal B, animal B should engage in a defensive posture to protect itself. The defensive posture, however, accomplishes more than physical protection. As a side effect, it broadcasts information about the degree of submission of animal B. From there, according to the hypothesis, evolution shaped the behavior into a social adaptation, from which

humans derive the smile, a signal that says, 'I am not aggressive'. The human smile also sometimes communicates submission. The cringing, servile posture that people use to communicate submission could also be considered a modification of the same original defensive reaction.

A similar story could be constructed about laughter. Human laughter is thought to be homologous to the open-mouthed play display of chimpanzees (van Hooff, 1962, 1972; Preuschoft, 1992; Ross, Owren, & Zimmermann, 2010). Just as for the smile, it may be that too much emphasis in the literature is placed on a limited part of the behavior, in this case the mouth and the voice. Laughter may be much more than just a matter of mouth and voice, and the whole-body context may be useful to consider. Play fighting, a behavior common in mammals, involves attack and defense including all the normal reactions that protect the body and maintain a margin of safety. I previously suggested (Graziano, 2008) that human laughter may have evolved from a ritualized modification of that defensive behavioral set. Consider tickle-evoked laughter. It is caused by intrusions into normally defended personal space. The components go far beyond the mouth and voice. It includes a contraction of musculature around the eye and sometimes eye closure; sometimes tear production; a raising of the upper lip accompanied by a bunching of the cheeks upward toward the eyes; a ducking downward of the head and a shrugging upward of the shoulders; a hunching or forward curving of the torso; a pulling of the arms inward across the vulnerable abdomen; and a series of vocal calls. Point for point, it resembles a ritualized defensive reaction with alarm calls. By hypothesis, the normal defensive behavioral set during a play fight was modified into a social signal. The laughter is effectively a touché signal. It communicates that the tickler has gotten into the most heavily defended parts of the ticklee's personal space. The tickler has won a point in the play fight.

But note how complicated the evolutionary dynamics can become. Each person has control of a social reward, the touché signal that can be dispensed to others to shape their behavior. When you laugh at someone else's joke, could it be that you are providing a signal in response to a display of mental agility? Has the other person gotten the better of you in a mental play fight, and effectively won a point, for which you are providing a social reward? Or suppose someone wins a point by causing discomfort to someone else, and bystanders laugh to reward the win. Is this how ridiculing laughter emerged? In this speculation, laughter is transformed from a defensive reaction, to a component of a play fight, to a touché signal, to a branching bush of quirky social uses, until the behavior is modified into a bizarre and idiosyncratic multiplicity of human behaviors.

Could a similar story be constructed for crying? Again, many previous attempts to understand crying from an evolutionary perspective, such as Darwin's (1872) or Andrew's (1962), focus on the most obvious facial aspects

of it, the tear production. But crying may be better understood in the context of a whole-body action. The similarity between crying and laughing was noted 3,000 years ago by Homer, who famously compared the laughter of men at a banquet to the crying they were about to do when Odysseus walked in and killed them all. Crying can include a squinting of the eyes, an excretion of tears, a lifting of the upper lip that results in an upward bunching of the cheeks toward the eyes, a ducking of the head, a shrugging of the shoulders, a forward curving of the torso, a flexion of the hips and knees, a pulling of the arms across the torso or upward over the face, and a series of vocalizations. These components point-for-point resemble or are exaggerations of a defensive reaction, including the copious tear production that normally protects the eyes from dust or other contaminants. Perhaps crying, like laughing, is a modified defensive reaction, but in this case used to solicit help. Other animals give distress cries, such as kittens that cry for their mothers, but as far as I know only humans combine the distress cry with the physical signs of defending the body and especially the eyes against intrusion. Human crying illustrates just how idiosyncratic social signals can become.

Consider the phenomenon of personal space. The zoo curator Hediger (1955) was the first to describe a protective flight zone around animals. When a threatening predator enters this margin of safety, the animal escapes. Other researchers soon noted that humans also have an invisible bubble of protective space surrounding the body, generally larger around the head, extending farthest in the direction of sight (e.g. Dosey & Meisels, 1969; Hall, 1966; Horowitz, Duff, & Stratton, 1964; Sommer, 1959). When that personal space is violated, the person steps away to reinstate the margin of safety. Personal space is fundamentally a protective space that people maintain with respect to each other. It is one of the most basic and obvious ways in which defensive actions intersect with social behavior.

But we cannot always maintain a personal space. The mechanisms that defend personal space must be adjusted in some way to allow for social touching. Not only must the defensive reactions be turned down and personal space shrunk up, but that alteration in the defensive reaction can itself turn into a social signal. A dog rolls on its back and exposes its stomach, a normally heavily defended part of the body, as a gesture of submission and trust. Humans allow themselves to be kissed on the parts of the body that are normally most heavily defended – the face, the neck, the hands – to communicate trust and willingness. Women in fashion magazines tilt their heads and expose their necks, as if offering to let the viewer's teeth onto the one body part most vulnerable to predation. All of these examples show how an overt dropping of your defensive reactions toward somebody else can act as a social signal.

The speculations in this final section may seem far removed from the action map of the motor cortex. Yet the action map as shown in Figure 3.3 has a large



zone related to defensive behavior. Neurons in that zone monitor the space around the body using their sensory receptive fields, and that monitored space shares a notable resemblance to personal space (Fogassi et al., 1996; Gentilucci et al., 1988; Graziano & Gandhi, 2000; Graziano et al., 1994, 1997; Rizzolatti et al., 1981). Several other anatomically connected brain regions, such as the ventral intraparietal area, have similar properties and may be part of a larger network that helps to maintain a margin of safety (Graziano & Cooke, 2006). Could this network of brain areas also contribute to social behavior? As unexpected and *non sequitur* as it may seem, could it be that actions that defend the body surface from injury and collision form the evolutionary basis of a great part of our standard social repertoire?

Recent studies suggest that these specific brain areas may indeed play a role in social interaction. Socially relevant stimuli such as faces have an especially strong influence on these neuronal mechanisms, and the same mechanisms may be involved in judging the margins of safety around other people's bodies (Brozzoli et al., 2013; Holt et al., 2014; Sambo & Iannetti, 2013; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). The emerging story shows how three seemingly unrelated topics – social behavior, defensive reactions and the action map in motor cortex – may overlap in a meaningful way.

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