© Freund & Pettman, U.K. Reviews in the Neurosciences, 12, 175-185 (2001)

Is Reaching Eye-Centered, Body-Centered, Hand-Centered, or a Combination?

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SYNOPSIS

There are currently three main views on the neural basis of visually guided reaching: 1) neurons in the superior parietal lobe guide arm movements in a spatial framework that is centered on the body; 2) neurons in the intraparietal sulcus guide arm movements in a spatial framework that is centered on the eye; 3) neurons in the caudal part of premotor cortex guide arm movements in a spatial framework that is centered on the arm and hand. The three viewpoints are mutually compatible and may fit into a larger pattern. Eye-centered representations of target position, and body-centered representations of arm and hand position, may be integrated to form a hand-centered representation close to the output stage in caudal premotor and primary motor cortex.

KEY WORDS

parietal, premotor, visuomotor, area 5, oculomotor, posture

INTRODUCTION

Primates have an extraordinary ability to reach out with the hand and grasp nearby objects. The action is so commonplace that it is easy to forget how complex a problem the brain must solve. Every time the eyes move, the image of the target moves across the retina. How does the brain reconstruct the external location of the target? Locating the hand in space is no less complex. At least three different types of signals are integrated: proprioceptive information from the joints and muscles, visual information from the sight of the arm, and motor feedback signals. How is all this disparate information put together to guide the hand through space to the target?

There are currently three main views on the neural basis of visually guided reaching. These views are based primarily on single neuron studies in the monkey. The first is that neurons in the superior parietal lobe guide arm movements in a spatial framework that is centered on the body /40/. The second is that neurons in the intraparietal sulcus guide arm movements in a spatial framework that is centered on the eye /2/. The third is that neurons in the caudal part of premotor cortex guide arm movements in a spatial framework that is centered on the arm and hand /29/. In the following sections, I discuss the evidence for each of these viewpoints. In each case, I discuss both strengths and weaknesses of the hypothesis. The three viewpoints are mutually compatible and may all fit into a larger pattern. Eye-centered representations of target position, and body-centered representations of arm and hand position, may be integrated to form a hand-centered representation close to the output stage in caudal premotor and primary motor cortex.

This review also discusses behavioral data from humans. A wide range of experiments shows that humans encode the space on and around the body using many different spatial frameworks, including eye-centered, trunk-centered and arm-centered. In particular, the evidence suggests that reaching is controlled at least partly in a hand or arm-centered coordinate system.

Accepted: 21 April, 2000

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BODY-CENTERED COORDINATES IN PARIETAL AREA 5 OF MONKEYS?

Laquiniti *et al.* /40/ proposed that neurons in area 5 encode the position and movement of the hand in body-centered coordinates. (See Fig. 1 for diagram of brain areas.) In the following sections, I first describe some of the properties of neurons in area 5. These neurons have both sensory and motor properties, and may be involved in representing the locations of body parts. I then describe research into the coordinate system used by area 5 neurons to encode hand position and hand movement.

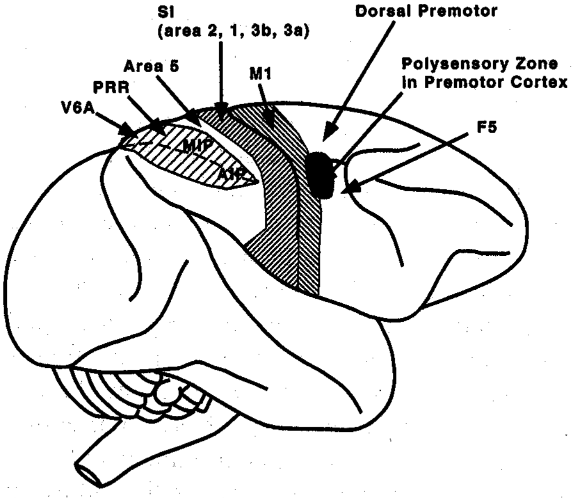

Fig. 1: Side view of the macaque monkey brain showing some of the brain areas discussed in this article. The intraparietal sulcus is opened to show areas V6A, PRR, MIP and AIP.

Somatosensory and motor properties of cortical area 5

Cortical area 5 in the superior parietal lobe receives a direct input from the primary somatosensory cortex /52,54,69/. It in turn projects to primary motor and premotor cortex, as well as to other brain areas /31,32,33,34,66/. Neurons in area 5 respond mainly in relation to limb position, although some neurons also respond to a touch on the skin /11,47,61/. Area 5 neurons often have complex receptive fields that can include several joints and body parts, both sides of the body, and even different somatosensory submodalities combined in a single neuron. In these respects, area 5 appears to represent an elaboration of the more simple response properties found in primary somatosensory cortex.

In addition to somatosensory properties, area 5 neurons also respond in association with movement /47/. Even when the sensory nerves from the arm are cut, about 38% of the neurons in area 5 respond just before and during an arm movement /63/. However, the role of area 5 in the control of movement is not yet clear. For example, when the monkey is about to make an arm movement, area 5 neurons began to respond on average 60 ms after the neurons in primary motor cortex /36/. Thus at least some of the motor-related activity in area 5 could be the result of feedback from the primary motor cortex. In another study that compared area 5 to primary motor cortex /21/, neuronal selectivity for the direction of hand movement was greater in primary motor cortex than in area 5; while selectivity to the static position of the hand in space was greater in area 5 than in primary motor cortex. In several studies /37,38/ the monkey was trained to move a handle along specific trajectories while various external force loads were applied to the handle. In this way, the location and direction of hand movement were dissociated from the muscular forces that the monkey used. The results showed that selectivity to the position and trajectory of the hand through space was greater in area 5 than in primary motor cortex; while selectivity to the muscular forces applied by the arm was greater in primary motor cortex than in area 5. Taken together, these studies suggest that although the functions of the two areas may overlap, area 5 may play more of a role in monitoring the position and movement of the arm through space, while primary motor cortex may be more involved in initiating and controlling arm movement. Both these spatial and motor functions are presumably necessary for the accurate guidance of arm movements.

Coding of hand position

Laquiniti *et al.* /40/ studied the effect of hand position on neurons in parietal area 5 by training monkeys to press and hold buttons at various locations. Different neurons preferred different hand positions. The authors presented an example of a neuron that responded best whenever the hand was in an upper position; an example of a neuron that preferred lower positions; and, similarly, examples of neurons that preferred left, right, near or far positions. In addition, the authors found that many neurons appeared to 'anticipate' an upcoming hand position. That is, the firing rate of these neurons was correlated with the position to which the monkey was about to reach.

The authors hypothesized that area 5 neurons encode both the current position and the planned position of the hand with respect to the trunk, in 'body-centered' coordinates. In order to test this hypothesis it would be necessary to rotate the trunk into different positions, independent of the head, the legs, the eyes, or other possible points of reference. A neuron's preferred hand location should then rotate by the same amount, remaining anchored to the trunk, if the trunk-centered hypothesis is correct. An alternative hypothesis is that the neurons encode arm position with respect to the point at which the eyes are looking. As described in below, at least some area 5 neurons in the intraparietal sulcus may use an eye-centered code /2/. When the monkey shifts its point of fixation, the preferred hand position for these neurons shifts by the same amount.

Another possibility is that area 5 neurons do not code the position of the hand in an extrinsic coordinate system, but rather respond in relation to the angle of the joints. For example, a cell that is mainly sensitive to the elevation of the shoulder joint might respond best to upper hand positions. A cell that is sensitive to the extension of the elbow joint might respond better to hand positions that are more distant from the body. A study by Scott *et al.* /62/ suggests that some area 5 cells do code for joint angle and not for hand position in space; in this study, the activity of area 5 neurons during a reaching task depended not only on the position of the hand, but also on the posture of the arm. At least some cells in area 5 respond to complex combinations of joints /11,47,60/ including the position of both arms, the legs and the head. Some area 5 neurons also respond in relation to the position of the eyes /2,18,51/. It would be misleading to describe such a complex cell as coding hand position with respect to the trunk or to any other single reference point.

In summary, area 5 neurons are sensitive to the spatial configuration of the body. They encode the positions of body parts with respect to each other. In that sense, they appear to encode the position of the hand and arm. Whether they code hand position with respect to the trunk, or with respect to some other reference point, or whether different neurons are sensitive to hand position in different ways, is not yet clear. Probably at least some neurons integrate signals from the shoulder and elbow joints, thus specifying the position of the hand with respect to the trunk, exactly as proposed by Laquiniti *et al.* /40/. Other neurons, however, may integrate signals from other combinations of joints.

Coding of hand movement

In addition to examining the code for arm position, Laquiniti *et al.* /40/ and Ferraina and Bianchi /13/ also studied how neurons in area 5 code the trajectory of the arm. These results are more complex and the interpretation less clear. For example, the terms 'shoulder-centered' and 'body-centered' /13/ and the terms 'vector coding', 'motor error', 'variational neurons', and 'difference vector' /40/ sometimes refer to the same thing and roughly match the 'arm-centered' or 'hand-centered' coding described by Graziano *et al.* /29/.

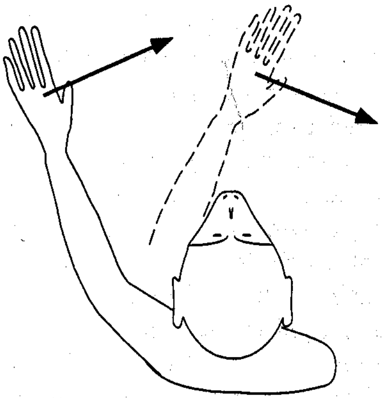

Fig. 2: Hand-centered code for reaching. The arrow represents the preferred direction of reach for a hypothetical neuron. When the initial position of the arm is changed, the preferred direction of reach also changes, maintaining a fixed spatial relationship to the hand.

Figure 2 (solid-line arm) shows a schematic diagram of a monkey's arm with a vector pointing out of the hand. The vector represents the preferred direction of reach for an area 5 neuron. Most area 5 neurons are broadly tuned, thus this vector represents only the peak of the tuning curve. If the monkey were to reach in that direction, the neuron would respond maximally. What happens if the arm is placed in a different starting position and its preferred direction of reach is tested again? Figure 2 (dotted-line arm) shows a possible result. In this hypothetical example, the preferred vector maintains a fixed spatial relationship to the hand. Such a neuron encodes the reach in hand-centered coordinates. The vector also maintains a fixed spatial relationship to the entire arm, thus can be termed an arm-centered code for movement. It can also be called a motor error signal or a vector code for movement. Because the arm, and therefore the vector of preferred movement, pivots around the shoulder joint, this type of movement coding has also been termed shoulder-centered. According to yet another view, the point around which the vector pivots is not the shoulder, but the center of the trunk; that is, the movement code is trunk- or body-centered.

Note that all of these terms refer to essentially the same phenomenon. Body-centered, trunk-centered, shoulder-centered, arm-centered and hand-centered all refer to a movement vector that has a fixed spatial relationship to the end of the arm. I will refer to it as a hand-centered code.

What is the evidence that neurons in area 5 use a hand-centered code for movement? In the experiment by Ferraina and Bianchi /13/, the monkey was trained to reach from a starting button to a set of surrounding buttons. In this fashion, the preferred direction of reach for a neuron could be determined. Starting buttons in three different locations were used. Therefore, the directional tuning of the cell could be examined at three different locations in the workspace in front of the monkey. For most neurons, the preferred direction of reach changed from one part of the workspace to the next. These changes in preferred direction were variable between neurons. Few single neurons behaved in the simple, hand-centered fashion shown in Figure 2. However, averaged across the sample of neurons, the preferred direction was approximately hand-centered.

Laquiniti *et al.* /40/ used the same experimental paradigm, but analyzed the results differently. For each neuron, they asked whether the activity was best correlated with the initial position of the hand, the final position of the hand, or the hand-centered vector connecting the two. They found that most cells encoded hand position, either initial or final, while only about 30% responded in relation to the hand-centered vector of the reach.

In summary, the evidence suggests that movement of the hand is not well represented in area 5. Most neurons respond in relation to the static position of the hand. Even those neurons that respond before and during a movement are generally anticipating the upcoming position of the hand, not encoding the movement trajectory. Relatively few neurons in area 5 respond in association with the movement vector.

A related finding involves the neuronal code for eye position. In a posterior, medial part of area 5, termed V6A, neurons are sensitive to the position of the eye in the orbit /17/. Different neurons prefer different eye positions. In addition to this sensitivity to static eye position, the neurons also respond in association with saccadic eye movements. Most of these saccade-related responses, however, depend on the final position of the eye; only a small proportion of neurons code the vector of the eye movement /51/. Thus, just as in the case for hand-related neurons, the eye-related neurons in area 5 appear to play a representational role, emphasizing eye position rather than the parameters of the movement. Cortical areas that are closer to the motor output for eye movements, such as the frontal eye fields, use primarily an eye-centered vector code /4/. Perhaps motor areas closer to the output for reaching movements, such as premotor and primary motor cortex, use a hand-centered vector code. This question is discussed in the third section of this review.

EYE-CENTERED COORDINATES IN THE INTRAPARIETAL SULCUS?

Batista *et al.* /2/ proposed that neurons in part of the intraparietal sulcus guide reaching in a coordinate system centered on the eye. In the next section, I review some of the background on this cortical region. I then describe the work on eye-centered coding. Finally, I describe experiments in the superior colliculus and the ventral, anterior premotor cortex that also suggest an eye-centered code for the control of reaching.

Reaching-related neurons in the intraparietal sulcus

The medial bank of the intraparietal sulcus is traditionally part of area 5. Many of the joint-related and reaching-related neurons described in the previous section were probably located in the intraparietal sulcus. However, the medial bank of the intraparietal sulcus has somewhat different connections and response properties from the surface part of area 5, and therefore has been given a separate name, the medial intraparietal area, or MIP /9/. Unlike the surface part of area 5, MIP receives projections from visual areas in the inferior parietal lobe, and at least some neurons in MIP respond to visual stimuli /9/.

Medially, MIP grades into area V6A on the anterior bank of the parieto-occipital sulcus. Area V6a appears to be more involved in representing eye position than arm position, although arm-position signals have been reported in V6A /17,18,51/. Toward the lateral tip of the intraparietal sulcus, MIP grades into an area termed AIP, which may be more involved in the representation of the hand and fingers /60/. Other proposed areas extending on the medial bank of the intraparietal sulcus include the posterior intraparietal area, or PIP /9/ and the parietal reach region, or PRR /64/, but whether these are functionally distinct areas or functionally part of MIP is not yet known. PRR may be located toward the posterior end of the sulcus, near or overlapping area V6A. The next section describes work on reaching-related neurons in PRR.

Reaching toward targets while eye position is controlled

In a study by Batista *et al.* /2/, monkeys were trained to foveate a target and then, while maintaining the same eye position, to reach toward other positions. Neurons in PRR responded while the monkey was preparing to reach. The preferred direction of reach for many cells was anchored, not with respect to the trunk or the initial position of the arm, but with respect to the foveal target. For example, a cell might prefer reaching to the left of the point of fixation. If the point of fixation were moved, then the preferred direction of reach would move with it. These cells therefore encoded the direction of reach in eye-centered coordinates.

This result suggests that PRR is involved in coordinating between the eye and the hand. Area V6A, which is near PRR and may partly overlap it, contains a high proportion of neurons that respond in relation to eye movement, but also many that respond in relation to arm movement /17,18,51/. Thus perhaps this general region of the intraparietal sulcus, including both PRR and V6A, contributes to the integration of eye movement and hand movement /73/.

Does PRR initiate arm movements, or does it monitor the changing position of the arm? That is, does it play a dynamic role or a representational role? As described in previous sections, neurons in area 5 appear to play a part in both roles, but are more involved in representing the spatial configuration of the body than in actively guiding movement. Perhaps PRR, a part of area 5, follows the same trend. However, this remains to be tested.

Eye-centered coding of reach in other brain areas

The superior colliculus is traditionally an eye-movement structure, but at least some collicular neurons respond in relation to reaching /71/. Stuphorn *et al.* /67/ found that these reaching-related neurons had a preferred direction of reach, and that this preferred direction was fixed with respect to the point at which the monkey was looking. Thus the superior colliculus also appears to code reaching in eye-centered coordinates.

Mushiake *et al.* /50/ studied reaching-related neurons in a part of premotor cortex, and found that about 40% coded hand movement in an eye-centered reference frame. The remaining 60% were unaffected by eye position. This recording sight was in the ventral and anterior part of premotor cortex, just behind the lower limb of the arcuate sulcus, roughly in the area termed F5 by Matelli *et al.* /43/. Area F5 neurons are known to respond during grasping and manipulation of objects, to the sight of objects that the monkey is about to grasp, and even to the sight of other monkeys or humans grasping objects /16,19,49/. One possibility is that the processing of hand and finger movements during grasping requires some degree of retinal, and especially foveal, spatial representation.

Is reaching controlled in an eye-centered reference frame?

Eye position and limb position are tightly coupled. We tend to look at where we are reaching. If we hold out a finger in the dark, we can fixate its position and even track it with smooth pursuit eye movements /35/. The neurons in PRR, the superior colliculus and premotor cortex that combine eye position with hand position may underlie this type of integration. But is reaching toward a target with the hand controlled in a coordinate system fixed to the eye? Reaching must be controlled at least partly separately from the eye, since it is possible to pursue one target with the eyes while reaching toward another target. Try throwing a coin across the room and pursuing it with your eyes while reaching toward a pencil on your desk. It is surprisingly easy. Though eye position and hand position often interact, and though some brain areas may monitor and control them in tandem, other brain areas must be able to control them separately. Targets for reaching, even visual targets, must ultimately be encoded relative to a reference point other than the eye.

ARM CENTERED COORDINATES IN CAUDAL PREMOTOR CORTEX?

Graziano *et al.* /29/ proposed that neurons in part of the premotor cortex locate nearby objects and guide reaching in multiple coordinate systems fixed to different parts of the body. In the following sections I first review the properties of neurons in premotor cortex and how they encode the space near the body. I then describe the hypothesis that a subset of neurons encodes the space around the hand and also guides movements of the hand in hand-centered coordinates. Finally, I describe experiments in humans that suggest that reaching is controlled in hand-centered coordinates.

Multimodal representation of space around the body

Premotor area 6, just anterior to the primary motor cortex, has long been known to play a role in the control of movement /72/. It receives projections from several parietal areas including 5, MIP, VIP and 7b /6,7,31,32,34,39,42,46/. The parietal neurons described above, those that code hand position in area 5 and those that code reach direction in PRR, probably project to premotor area 6. This in turn projects to primary motor cortex, and also directly to the spinal cord /1,12,23,30,41, 42,44,48/. The premotor cortex is therefore in a position to receive sensory information and influence motor structures.

The premotor cortex is not a uniform area. Neurons in the most caudal part of the premotor cortex, adjacent to the primary motor cortex, often respond to passively presented tactile, visual and auditory stimuli /15,19,27,29,58/. That is, these neurons have sensory receptive fields in addition to their motor properties. The tactile receptive fields are arranged to form a rough somatotopic map, though in some monkeys the map is less clearly segregated than in others. In the face and arm part of this map, and especially the region of overlap between the face and arm, about 40% of the neurons also respond to visual stimuli /15,19,27, 58/. A small percentage of neurons are trimodal, responding to tactile, visual and auditory stimuli /28/.

In a recent experiment mapping the precentral gyrus, these multimodal neurons were found in a relatively restricted zone just posterior to the bend in the arcuate sulcus /25/. This area was termed the polysensory zone. In earlier studies, the polysensory neurons were described as being located in ventral premotor cortex, or area PMv /15,19,27,58/. While this description is strictly correct, it has caused some confusion. The polysensory zone is mainly in the caudal and dorsal part of PMv, as shown in Figure 1. Its location and size varies somewhat among monkeys. Other experimenters who investigated the neuronal coding of space in PMv recorded from a region that is more ventral and anterior, and found somewhat different results /3,50/. Anatomical and mapping studies /19,48/ suggest that there are two arm fields in premotor cortex, one that is ventral and anterior, in area F5, apparently specialized for the control of the fingers and hand; and one that is more caudal and dorsal, apparently specialized for the control of the arm. The polysensory zone overlaps this caudal and dorsal representation of the arm.

For the bimodal, visual-tactile neurons, the visual receptive fields are usually adjacent to the tactile ones and extend outward from the skin a limited distance /58,15,27/. This distance varies among neurons. Some neurons respond to stimuli only within a few cm, others respond within about 20 cm, and a minority respond to stimuli as far away as a meter. Just like the visual receptive fields, the auditory receptive fields emphasize the space near the body. Most of the auditory neurons respond best to nearby sounds, regardless of the intensity of the stimulus /28/. The polysensory zone therefore contains a representation of the space on and near the body. One suggestion is that the purpose of this representation is to guide movement of the head and limbs toward, away from, and around the objects that surround the body /26/.

For most bimodal cells, the visual receptive field is anchored to the site of the tactile receptive field on the body /14,15,20,27,29/. When the monkey's eyes move, the visual response may change magnitude, but the location of the visual receptive field does not change. If the tactile receptive field is on the head, then rotating the head will cause the visual receptive field to move in tandem with the head. If the tactile receptive field is on the arm, placing the arm in different positions will cause the visual receptive field to move with the part of the arm that contains the tactile response. Some neurons have a tactile receptive field on the upper arm, and for these cells, the adjacent visual receptive field moves as the upper arm moves. Other cells have a tactile receptive field on the forearm, and the adjacent visual receptive fields appear to move with the forearm. Thus the bimodal neurons encode visual space in body-part-centered coordinates. This type of spatial coding would be especially useful for the control of movement. A set of visual receptive fields anchored to the hand, for example, would be able to locate nearby stimuli with respect to the hand, providing a hand-centered signal for guiding reach.

Possible relationship between bimodal neurons and the control of movement

Premotor neurons help to guide movement. Electrical stimulation of premotor cortex causes muscle movements, lesions of premotor cortex impair movement, and premotor neurons respond before and during movement /19,53,55,70/. However, only about 40% of the neurons in the polysensory zone have visual receptive fields. Do these visually responsive neurons contribute to the control of movement? If so, how do their visual receptive fields interact with their movement properties?

Graziano et al. /27/ studied the motor properties of neurons with a tactile receptive field on the head and a visual receptive field near the face. About 60% of these face-related bimodal neurons responded during one direction of head movement. This response was usually reduced or eliminated if the head was turned passively. That is, these neurons with sensory properties also had motor properties that corresponded to the same body part.

The data are less clear for neurons related to the arm. Cells with a tactile receptive field on the arm and a visual receptive field near the arm often respond during arm movements /19/, but these movement-related responses have not been systematically studied. It is unknown whether the motor properties match the visual properties. A cell that prefers visual stimuli to the left of the hand might also respond to movements of the hand to the left. Such a cell would code both the target of the reach and the movement itself in hand-centered coordinates. A cell that prefers visual stimuli near the medial surface of the arm might respond when the monkey reaches around an object. These possibilities have yet to be tested.

Mushiake *et al.* /50/ studied neurons in an area of the precentral gyrus that they termed primary motor cortex. However, based on the results of a recent mapping study /25/, this region probably also overlapped the polysensory zone. In this study, the monkey reached toward various targets while the eyes fixated one of two possible locations. None of the neurons was influenced by the position of the eyes. The neurons therefore did not code reaching in an eye-centered coordinate system. Caminiti *et al.* /5/ studied neurons in the arm representation in both primary motor and caudal premotor cortex. They found that, averaged across neurons, the preferred direction of reach was approximately hand centered.

In summary, the evidence suggests that neurons in caudal premotor cortex participate in controlling movements of the arm and hand. A subgroup of neurons, the bimodal neurons, responds to the sight of nearby objects, and encodes the location of those objects in body-part-centered coordinates. In particular, neurons related to the arm and hand encode visual stimuli in arm- and hand-centered coordinates. It remains to be tested whether the same bimodal neurons also guide reaching in a hand-centered coordinate system. The evidence suggests that this part of the brain does not encode reaching in an eye-centered reference frame. Instead, on the population level, the neurons use a hand-centered code for reaching.

Hand-centered coordinates for reaching in humans

When we reach toward a target, we normally have proprioceptive feedback from the arm, a continuous view of the hand, and a continuous view of the target. According to the hand-centered hypothesis, all of these sources of information should be important for the control of reaching. It is not enough to know where the target is; that is, it is not enough to know the end-point of the reach. It is also important to know where the hand is, and to determine the difference between hand location and target location. A number of experiments have investigated the effect of removing one or another of these sources of information. If the hand-centered hypothesis is correct, then reaching should be compromised if any one of these sources of information is removed. This is the case. For example, when subjects view a target only briefly at the beginning of the reach, the movement is less accurate than when the target is visible throughout the entire reach /57/. This result indicates that the reach is not preprogrammed, but depends on the continuous adjustment of the position of the hand relative to the target. Likewise, vision of the hand throughout the reach improves accuracy /10,56/. If the subject wears a displacing prism and is given a brief initial view of the hand, the subsequent reach is misdirected /59/. The importance of the view of the hand is especially clear in patients who have lost proprioceptive sense in their arms due to nerve degeneration. These patients have no other sense of arm position than vision. If these patients reach toward a target without the sight of their limbs, they make large errors in both direction and extent /22/. Together, these studies show that information about both the location of the target and the location of the hand are continuously monitored and integrated during the reach.

In several studies, the pattern of errors during reaching was analyzed in order to determine whether there is any spatial coordinate system that underlies the motor planning. Soechting and Flanders /65/ found that the errors were most systematic when plotted in a coordinate system whose origin was located roughly at the shoulder. This origin was somewhat variable between tests, ranging in location from the eye to the upper arm. How does this result relate to the suggestion that the target for reaching is represented with respect to the hand?

It is important to note that visual information first enters the brain in retinal, or eye-centered, coordinates, and is presumably transformed through many intermediate stages before arriving at hand- or arm-centered coordinates near the motor output stage. Therefore, any errors in reaching toward a target may reflect an accumulation across many different coordinate frames. The exact parameters of the reaching task may bias which processing stage and therefore which coordinate system contributes most to the errors. For example, McIntyre *et al.* /45/ found that errors in reaching were arranged in a manner centered on the point between the eyes, suggesting that the largest source of error was binocular depth perception. Two other groups /8,24/ found that errors during reaching were mainly overreaches or underreaches along a line connecting the hand and the target. This pattern of errors suggests a hand-centered code for the reach. Tipper *et al.* found a hand-centered effect of distractor objects in a reaching task /68/.

In summary, the psychophysical evidence from humans suggests that reaching is controlled at least partly in a hand-centered coordinate system. Both the location of the target and the initial location of the hand are used to guide a reach; and the pattern of errors suggests that one signal used by the brain is the location of the target relative to the hand.

What are the coordinates for reaching?

Is reaching controlled by neurons in area 5 in body-centered coordinates; by neurons in PRR and other brain areas in eye-centered coordinates; or by neurons in caudal premotor and primary motor cortex in hand-centered coordinates? Perhaps all these areas participate in reaching. Area 5 may be especially important in monitoring the position of the limb. PRR may contribute to the coordination and spatial integration between limb and eye movements. These areas project to premotor and primary motor cortex, where the neurons may use predominantly a hand-centered reference frame to control the reach. In this scheme, many different coordinate frames are used to guide reaching, and a hand-centered one is the final step in cortical processing.

ACKNOWLEDGEMENTS

I thank C. Gross, D. Cooke and L. Snyder for their helpful comments.

REFERENCES

1. Barbas H, Pandya DN. Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey. J Comp Neurol 1987; 256: 211-228.
2. Batista AP, Buneo CA, Snyder LH, Andersen RA. Reach plans in eye-centered coordinates. Science 1999; 285: 257-260.
3. Boussaoud D, Barth TM, Wise SP. Effects of gaze on apparent visual responses of frontal cortex neurons. Exp Brain Res 1983; 93: 423-443.
4. Bruce CJ, Goldberg ME. Primate frontal eye fields: I. Single neurons discharging before saccades. J Neurophys 1985; 53: 606-635.
5. Caminiti R, Johnson PB, Galli C, Ferraina S, Burnod Y. Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets. J Neurosci 1991; 11: 1182-1197.
6. Cavada C, Goldman-Rakic PS. Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. J Comp Neurol 1989; 287: 393-421.
7. Cavada C, Goldman-Rakic PS. Posterior parietal cortex in rhesus monkey: II: Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. J Comp Neurol 1989; 287: 422-445.
8. Chieffi S, Allport DA, Woodin M. Hand-centered coding of target location in visuo-spatial working memory. Neuropsychologia 1999; 37: 495-502.
9. Colby CL, Duhamel JR. Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. Neuropsychologia 1991; 29: 517-538.
10. Desmurget M, Rossetti Y, Prablanc C, Stelmach GE, Jeannerod, M. Representation of hand position prior to movement and motor variability. Can J Physiol Pharmacol 1995; 73: 262-272.
11. Duffy FH, Burchfiel JL. Somatosensory system: organizational hierarchy from single units in monkey area 5. Science 1971; 172: 273-275.
12. Dum RP, Strick PL. The origin of corticospinal projections from the premotor areas in the frontal lobe. J Neurosci 1991; 11: 667-689.
13. Ferraina S, Bianchi L. Posterior parietal cortex: functional properties of neurons in area 5 during an instructed-delay reaching task within different parts of space. Exp Brain Res 1994; 99: 175-178.
14. Fogassi L, Gallese V, di Pellegrino G, Fadiga L, Gentilucci M, Luppino M, Pedotti A, Rizzolatti G. Space coding by premotor cortex. Exp Brain Res 1992; 89: 686-690.
15. Fogassi L, Gallese V, Fadiga L, Luppino G, Matelli M, Rizzolatti G. Coding of peripersonal space in inferior premotor cortex (area F4). J Neurophys 1996; 76: 141-157.
16. Gallese V, Fadiga L, Fogassi L, Rizzolatti G. Action recognition in the premotor cortex. Brain 1996; 119: 593-609.
17. Galletti C, Battaglini PP, Fattori P. Eye position influence on the parieto-occipital area PO (V6) of the macaque monkey. Eur J Neurosci 1995; 7: 2486-2501.
18. Galletti C, Fattori P, Kutz DF, Battaglini PP. Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobe. Eur J Neurosci 1997; 9: 410-413.
19. Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. Exp Brain Res 1988; 71: 475-490.
20. Gentilucci M, Scandolara C, Pigarev IN, Rizzolatti G. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. Exp Brain Res 1993; 50: 464-468.
21. Georgopoulos AP, Massey JT. Static versus dynamic effects in motor cortex and area 5: comparison during movement time. Dev Brain Res 1985; 18: 159-166.
22. Ghez C, Gordon J, Ghilardi MF. Impairments of reaching movements in patients without proprioception.

II. Effects of visual information on accuracy. J Neurophys 1995; 73: 361-372.
23. Godschalk M, Lemon RN, Kuypers HGJM, Ronday HK. Cortical afferents and efferents of monkey postarcuate area: an anatomical and electrophysiological study. Exp Brain Res 1984; 56: 410-424.
24. Gordon J, Ghilardi MF, Ghez C. Accuracy of planar reaching movements. I. Independence of direction and extent variability. Exp Brain Res 1994; 99: 97-111.
25. Graziano MSA, Gandhi S. Location of the polysensory zone in the precentral gyrus of monkeys. Exp Brain Res 2000; 135: 259-266.
26. Graziano MSA, Gross CG. Spatial maps for the control of movement. Curr Opin Neurobiol 1998; 8: 195-201.
27. Graziano MSA, Hu X, Gross CG. Visuo-spatial properties of ventral premotor cortex. J Neurophys 1997; 77: 2268-2292.
28. Graziano MSA, Reiss LAJ, Gross CG. A neuronal representation of the location of nearby sounds. Nature 1999; 397: 428-430.
29. Graziano MSA, Yap GS, Gross CG. Coding of visual space by premotor neurons. Science 1994; 266: 1054-1057.
30. He S, Dum RP, Strick PL. Topographic organization of corticospinal projections from the frontal lobe: motor areas on the lateral surface of the hemisphere. J Neurosci 1993; 13: 952-980.
31. Johnson PB, Ferraina S, Bianchi L, Caminiti R. Cortical networks for visual reaching: physiological and anatomical organization of the frontal and parietal lobe arm regions. Cereb Cortex 1996; 6: 102-119.
32. Johnson PB, Ferraina S, Caminiti R. Cortical networks for visual reaching. Exp Brain Res 1993; 97: 361-365.
33. Jones EG, Coulter JD, Hendry SHC. Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. J Comp Neurol 1978; 181: 291-348.
34. Jones EG, Powell TPS. An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 1970; 93: 793-820.
35. Jordan S. Ocular pursuit movement as a function of vision and proprioceptive feedback. Vis Res 1970; 10: 775-780.
36. Kalaska JF, Caminiti R, Georgopoulos AP. Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. Exp Brain Res 1983; 51: 247-260.
37. Kalaska JF, Cohen DAD, Prud'homme M, Hyde ML. Parietal area 5 neuonal activity encodes movement kinematics, not movement dynamics. Exp Brain Res 1990; 80: 351-364.
38. Kalaska JF, Hyde ML. Area 4 and 5: differences between the load-dependent discharge variability of cells during active postural fixation. Exp Brain Res 1985; 59: 197-202.
39. Kunzle H. An autoradiographic analysis of the efferent connections from premotor and adjacent prefrontal regions (areas 6 and 8) in *Macaca fascicularis*. Brain Behav Evol 1978; 15: 185-236.
40. Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R. Representing spatial information for limb movement: role of area 5 in the monkey. Cereb Cortex 1995; 5: 391-409.
41. Leichnetz GR. Afferent and efferent connections of the dorsolateral precentral gyrus (area 4, hand/arm region) in the macaque monkey, with comparison to area 8. J Comp Neurol 1986; 254: 460-492.
42. Matelli M, Camarda R, Glickstein M, Rizzolatti G. Afferent and efferent projections of the inferior area 6 in the macaque monkey. J Comp Neurol 1986; 255: 281-298.
43. Matelli M, Luppino G, Rizzolatti G. Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. Behav Brain Res 1985; 18: 125-136.
44. Matsumura M, Kubota K. Cortical projection to hand-arm motor area from post-arcuate area in macaque monkeys: a histological study of retrograde transport of horseradish peroxidase. Neurosci Lett 1979; 11: 241-246.
45. McIntyre J, Stratta F, Lacquaniti F. Short-term memory for reaching to visual targets: psychophysical evidence for body-centered reference frames. J Neurosci 1998; 18: 8423-8435.
46. Mesulam M-M, Van Hoesen GW, Pandya DN, Geschwind N. Limbic and sensory connection of the inferior parietal lobule (area PG) in the rhesus monkey: a study with a new method for horseradish peroxidase histochemistry. Brain Res 1977; 136: 393-414.
47. Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C. Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. J Neurophys 1975; 38: 871-908.
48. Muakkassa KF, Strick PL. Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized 'premotor' areas. Brain Res 1979; 177: 176-182.
49. Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G. Object representation in the ventral premotor cortex (area F5) of the monkey. J Neurophys 1997; 78: 2226-2230.
50. Mushiake H, Tanatsugu Y, Tanji J. Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze. J Neurophys 1997; 78: 567-571.
51. Nakamura K, Chung HH, Graziano MSA, Gross CG. A dynamic representation of eye position in the parieto-occipital sulcus. J Neurophys 1999; 81: 2374-2385.
52. Pandya DN, Kuypers HGJM. Cortico-cortical connections in the rhesus monkey. Brain Res 1969; 13: 13-36.
53. Passingham RE. The Frontal Lobes and Voluntary Action. Oxford: Oxford University Press, 1993.

54. Pearson RCA, Powell TPS. The projections of the primary somatosensory cortex upon area 5 in the monkey. Brain Res Rev 1985; 9: 89-107.
55. Petrides M. Motor conditional associative-learning after selective prefrontal lesions in the monkey. Behav Brain Res 1982; 5: 407-413.
56. Prablanc C, Echallier JE, Jeannerod M, Komilis E. Optimal response of eye and hand motor systems in pointing at a visual target. II. Static and dynamic visual cues in the control of hand movement. Biol Cybern 1979; 35: 183-187.
57. Prablanc C, Pelisson D, Goodale MA. Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. Exp Brain Res 1986; 62: 293-302.
58. Rizzolatti G, Scandolara C, Matelli M, Gentilucci M. Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. Behav Brain Res 1981; 2: 147-163.
59. Rossetti Y, Desmurget M, Prablanc C. Vectorial coding of movement: vision, proprioception, or both? J Neurophys 1995; 74: 457-463.
60. Sakata H, Taira M. Parietal control of hand action. Curr Opin Neurobiol 1994; 4: 847-856.
61. Sakata H, Takaoka Y, Kawarasaki A, Shibutani H. Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. Brain Res 1973; 64: 85-102.
62. Scott SH, Sergio LE, Kalaska JF. Reaching movements with similar hand paths but different arm orientations. II. Activity of indivisual cells in dorsal premotor cortex and parietal area 5. J Neurophys 1977; 78: 2413-2426.
63. Seal J, Gross C, Bioulac B. Activity of neurons in area 5 during a simple arm movement in monkeys before and after deafferentation of the trained limb. Brain Res 1982; 250: 229-243.
64. Snyder LH, Batista AP, Andersen RA. Coding of intention in the posterior parietal cortex. Nature 1997; 386: 167-170.
65. Soechting JF, Flanders M. Sensorimotor representations for pointing to targets in three-dimensional space. J Neurophys 1989; 62: 582-594.
66. Strick PL, Kim CC. Input to primate motor cortex from posterior parietal cortex (area 5). I. Demonstration by retrograde transport. Brain Res 1978; 157: 325-330.
67. Stuphorn V, Bauswein E, Hoffmann K-P. Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. J Neurophys 2000; 83: 1283-1299.
68. Tipper SP, Lortie C, Baylis GC. Selective reaching: evidence for action-centered attention. J Exp Psychol-Hum Percep Perf 1992; 18: 891-905.
69. Vogt BA, Pandya DN. Cortico-cortical connections of somatic sensory cortex (areas 3, 1 and 2) in the rhesus monkey. J Comp Neurol 1978; 177: 179-192.
70. Weinrich M, Wise SP, Mauritz K-H. A neurophysiological study of the premotor cortex in the rhesus monkey. Brain 1984; 107: 385-414.
71. Werner W. Neurons in the primate superior colliculus are active before and during arm movements to visual targets. Eur J Neurosci 1993; 5: 335-340.
72. Wise SP. The primate premotor cortex: past, present, and preparatory. Annu Rev Neurosci 1985; 8: 1-19.
73. Wise SP, Boussaoud D, Johnson PB, Caminiti R. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. Annu Rev Neurosci 1997; 20: 25-42.