Coordinate transformations for eye and arm movements in the brain
Lawrence H Snyder

Recent work on the coding of spatial information in the brain has significantly advanced our knowledge of sensory to motor transformations on several fronts. The encoding of information referenced to the retina (eye-centered) but modulated by eye position, called a gain field representation, has proved to be very common throughout parietal and occipital cortex. The use of an eye-centered representation as a working memory of spatial location is problematic if the eyes move during the memory period. Details regarding the manner in which the brain solves this problem are beginning to emerge. Finally, the discovery of eye-centered representations of ongoing or intended arm movements has changed the way we think about the order of operations in the sensory to motor coordinate transformation.

Addresses
McDonnell Center for Higher Brain Function, Department of Anatomy & Neurobiology, Box 8108, Washington University School of Medicine, 660 South Euclid Avenue, St Louis, MO 63110, USA;
e-mail: larry@eye-hand.wustl.edu

Abbreviations

FEF	frontal eye fields
LIP	lateral intraparietal area
PM	premotor cortex
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
PPC	posterior parietal cortex
PRR	parietal reach region
SC	superior colliculus
SEF	supplementary eye fields
V1	visual area 1

Introduction

A major brain function is the manipulation of spatial information. Much of what we do involves extracting spatial information from sensory input and then using that spatial information to direct a motor response. A simple example is reaching for something we have seen. This act requires that spatial information be transformed from a retinal coordinate frame to the coordinate frame of the muscles or joints involved in moving the arm. A major endeavor of systems neuroscience has been to discover the algorithms and the sites at which such transformations are performed [1–4,5•,6•].

This review will focus on several recent issues related to this endeavor. It will consider only transformations of visual information used to drive eye and arm movements in primates, and will focus on the involvement of the parietal cortex. It has long been known that the lateral intraparietal area (LIP) in parietal cortex is involved in coding targets for saccadic eye movements. Recently it has become clear that cortical regions medial to LIP are involved in coding arm movements. The details of how spatial information is represented and manipulated in these regions is of critical importance to our understanding of sensory to motor transformations.

Eye-centered coding and gain fields

Many occipital and parietal areas involved in early processing of visual information do so in an eye-centered frame of reference [7]. In many areas, eye-centered spatial signals are modulated by postural information. Cells in these areas have receptive fields whose locations are fixed with respect to the retina. For example, the receptive field of a particular cell may always lie 10° above the fovea, regardless of the positions of the eyes, head and body. At the same time, however, the magnitude of the activity evoked by any given stimulus depends on eye, head, arm or body position. The original description of this modulation, called a 'gain field', was a monotonic influence of eye position on visually evoked and saccade-related activity in areas 7a and LIP [8]. Since then, gain fields have been described in numerous other brain areas as well.

Effects of eye position have been described in visual area 1 (V1), the cortical area closest to the retinal input and therefore the most likely to be purely eye-centered or retinotopic [9,10,11•,12]. However, these observations are controversial [13•,14]. Elsewhere, the data for eye position gain fields are well established. Spatial responses in areas V3a, MT (middle temporal area), MST (medial superior temporal area), VIP (ventral intraparietal area), V6, V6a, 7m, PMv (ventral premotor cortex [PM]), PMd (dorsal PM) and SEF (supplementary eye fields) have all been shown to be modulated by the position of the eyes in the head [15–22,23•,24•]. Head position gain fields have been reported in both areas LIP and 7a [25]. In LIP, the gain fields are referenced to the body, whereas in 7a they are referenced to the inertial frame, that is, to the fixed world around you. Recently, eye position effects have been identified in V4 [12,26••], demonstrating that eye position gain fields occur even in the ventral ('what') visual pathway.

Several roles for gain fields in coordinate frame transformations have been proposed. Zipser and Andersen [27] first showed that retinotopic signals modulated by eye position could be used as an intermediate stage in computing head-centered location of visual targets. As very few neurons in parietal cortex code in explicit head-centered coordinates [28,29], an alternative proposal is that gain field representations themselves constitute a distributed representation of head-centered spatial information. Consistent with this idea, Bremmer *et al.* [30] recently showed that a network using actual recorded responses could be used to generate a reliable and precise estimate of the head-centered location of a visual stimulus.

Remarkably, despite 15 years of experimental and theoretical work on gain fields, only circumstantial evidence exists that gain field information is in fact used in a spatial computation: gain fields are ubiquitous, and the distributed representation contains spatial information that is rarely, or never, explicitly represented elsewhere. At one time, an argument could be made that gain field information is not used by the brain. This argument was based on the idea that LIP, one of the first areas in which gain fields were well characterized, serves to identify the location of visual targets for saccadic eye movements and to transfer that spatial information to the superior colliculus (SC). As such, LIP would appear to have no use for the head-centered position information contained in the eye-position gain field. However, recent studies using animals whose heads are not fixed in place now link SC to the control of head as well as eye movements [31,32]; for this purpose, head-centered target location is in fact highly relevant. Thus, the argument that head-centered information in LIP is superfluous is no longer valid. More generally, the investigation of animals that are free to move their heads may well revolutionize our understanding of the role of cortex in localizing targets and directing spatial behavior, much as the data from head-free animals are now revolutionizing ideas about how the vestibular nuclei code information about head movements [33,34].

Updating eye-centered representations

What happens to spatial information encoded in eye-centered coordinates, with or without a gain field, when the eyes move? In area LIP, cells continue to fire in response to remembered task-relevant spatial information. Because LIP response fields are fixed with respect to the eye, a change in eye position would invalidate the information being coded. However, several studies have shown that the working memory signal is transferred to a different population of neurons whenever a saccade occurs during a memory period [35,36]. This remapping of activity is arranged so as to maintain the validity of the (eye-centered) spatial information. As a result, LIP can retain a world-fixed target location despite a change in eye position. It has been suggested that this ability either underlies spatial constancy [35] or else reflects the updating of stored saccade vectors [36]. The remapping of activity usually follows or coincides with a change in eye position. Occasionally, however, remapping can lead the change in eye position, an effect termed 'predictive remapping' [35]. Predictive remapping is consistent with either of the two proposed roles for LIP — the neural substate for spatial constancy, or a buffer which stores target locations for upcoming saccades in an eye-centered frame of reference.

In order to study the mechanism of remapping further, Mushiake and colleagues [37•] compared the effects of colliding visually and electrically evoked saccades in the frontal eye fields (FEF) and LIP [38]. In FEF, an electrically evoked saccade that precedes or coincides with a visually evoked saccade results in an eye position that is independent of the location of the visual stimulus [39]. In other words, a coincident electrically evoked saccade effectively overrides a visually evoked eye movement. If the electrically evoked saccade occurs late (100–200 ms after the visually evoked saccade), then the resulting saccade instead adds to the visually evoked saccade. In LIP, a similar pattern of results occurs, but shifted in time. An electrically evoked saccade must precede a visually evoked saccade by 85 ms in order to completely override it; coincident saccades result in additivity [37•]. Mushiake and colleagues suggest that these data support a role of LIP in remapping upcoming saccade trajectories, and that the 85 ms time shift may be related to the phenomenon of predictive remapping [35]. Unfortunately, as they point out, this time shift does not occur in FEF (or in SC), yet predictive remapping has been reported in both of these areas [40,41].

Relevant to this issue is the fact that activity in LIP is remapped not only in response to intervening saccadic eye movements, but also in response to intervening smooth pursuit eye movements and whole body rotations [42,43]. Interestingly, however, remapping in LIP is dependent upon the expectation that the target will remain fixed in the world. If the animal is led to believe that an extinguished target is not fixed in the world, but instead will move along with the animal's own body, then remapping does not occur [43]. In order to understand what remapping is and why it occurs, it will be important to quantify its occurrence under different behavioral contexts and in different brain areas.

Eye and arm movements

Much work on coordinate frame transformations has focused on studying either eye or arm movements in isolation. Although valuable, this approach has several drawbacks. Eye movements in particular are problematic because the visual and oculomotor reference frames are so similar: a visual target that is 10° above and 5° to the right of fixation, for example, will require an eye movement 10° up and 5° to the right. This confound persists even for targets in depth: the retinal disparity of a visual target correlates with the degree to which the eyes must move disconjugately to foveate it. As a result, it is very difficult to determine whether a given spatial representation codes primarily sensory or motor information, especially in early cortical areas (but see [44•]).

The study of visually guided arm movements does not suffer from this drawback. The sensory frame of reference imposed by the retina is quite distinct from the motor frame of reference imposed by the joints and muscles of the arm. However, if the arm is studied in isolation and the position of the eyes is not measured, then the sensory frame of reference is indeterminate. This can result in unsuspected artifacts. For example, primates often look to where they are reaching. If a subject begins a trial by reaching for, and looking at, some starting location, then

Figure 1

Two possible orders of operation for early sensory-motor transformations. **(a)** PPC may reflect the output of an early attentional filter through which only salient visual stimuli may pass. These salient locations are then encoded in PPC without regard for whether, or how, they will be used. In this view, activity in PPC is identified with the psychological concept of a locus of spatial attention [80]. A single PPC representation may lead to many different types of motor output. In contrast, representations in PM and in FEF (jointly referred to as PM here) are not generic, but instead reflect committal to a particular motor system. **(b)** The discovery of motor-specific responses in the PPC, coded in retinal (sensory) coordinates, suggests an alternate view. Target selection and response selection occur in tandem, and are largely accomplished within the PPC. Transformations from eye-centered to body-part-centered coordinates are completed later, most likely in PM.
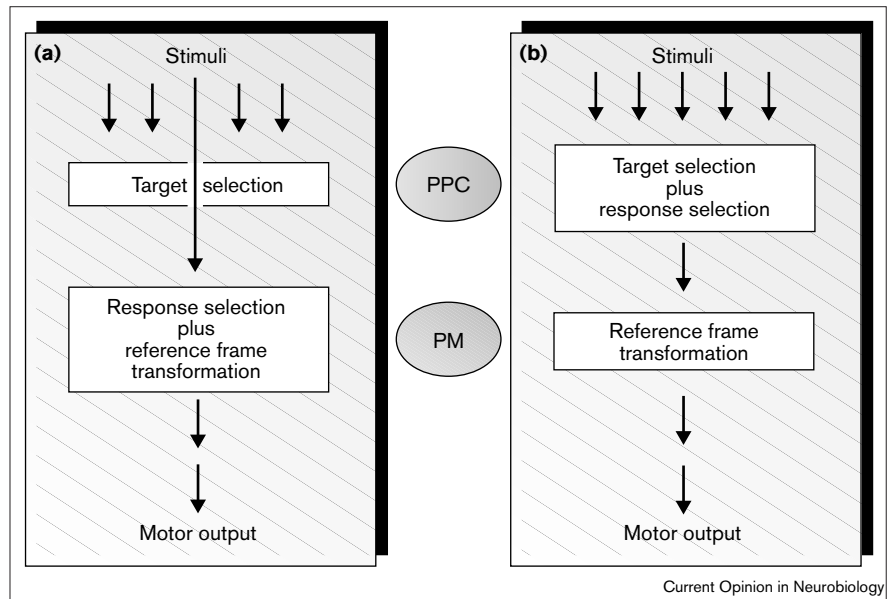
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the arm-centered and eye-centered coordinate frames are brought into alignment. As a result, an eye-centered (sensory) representation can erroneously appear to be arm-centered (motor).

These difficulties can be overcome by controlling (and recording) both eye and arm position. This not only helps to resolve issues related to which reference frame is being used, but also helps to address whether a given spatial representation reflects a generic sensory signal, or whether it is specific to a particular motor system [45]. The study of eye movements alone is insufficient for this purpose. Primates generally look at what interests them. As a result, we might expect that neural activity related to a plan to move the eyes would be closely related to neural activity related to a locus of covert attention and, indeed, this has proved to be the case [46]. The problem is not necessarily limited to eye movements; monkeys and human infants often reach for what interests them. Thus, a salient stimulus in the environment is often also a target for a subsequent movement. As a result, a representation that is in fact linked to a particular motor system may appear to be a generic, general-purpose representation. By careful consideration of both arm and eye movements, this confound can often be eliminated. This approach is not new; Goldberg and colleagues took advantage of it when studying the posterior parietal cortex (PPC) and the FEF in the early 1980s [47]. In these early studies, animals were trained to ignore, attend to, look at, or reach for, a peripheral target. These studies paved the way for two decades of work on attention in the cortex. However, until recently, Goldberg's technique of controlling both eye and arm movements as a means of investigating coordinate frames has been under-utilized.

In the last several years many studies have appeared in which eye and arm movements have been manipulated and monitored. This work has revealed an unexpected and interesting finding: arm movements, and plans for arm movements, are coded in eye-centered coordinates.

Eye-centered coding of visually guided arm movements

Eye-centered coding of arm movements has been found in both parietal and premotor cortices. In the parietal reach region (PRR), medial and posterior to LIP, neurons code upcoming or intended arm movements [45,48]. Recently, it was shown that the response fields of these neurons were linked more tightly to the position of the eyes than they were to the position of the hand or of the head and body [49••]. Eye-centered coding of ongoing arm movements had been described in PMv, close to the arcuate spur [50]. This activity was time-locked to the arm movement, yet 40% of neurons were modulated by the direction of gaze. Of these gaze-sensitive cells, many were reported to reflect the position of the target relative to the eye.

These findings have important consequences for how we think about the order of operations in the sensory to motor transformation. Prior to these reports, the frame of reference used for spatial coding was taken to indicate the type of information being coded. Thus, cells using an arm-centered frame of reference were considered to code arm movements [17,51,52,53•], whereas cells which used a non-motor (e.g. eye-centered) frame of reference were believed to code information without regard for a particular motor effector [7,47]. As a result, the properties of coding arm movements and coding in an arm-centered frame of reference appeared to be inseparable. This in turn suggested a general organizational principle: the process of

transforming the frame of reference for spatial information and the process of deciding how to respond to a particular target are inseparable and occur together at the same locus in the brain.

This view of brain organization is schematized in Figure 1a. Salient stimuli are selected for representation in the PPC ('target selection') [47,54,55•]. Next, a decision is made concerning how the salient target will be acquired ('response selection'), and the results of this decision are then manifest as spatial signals in premotor cortex (reaching movements) and in the FEF (eye movements). The key point is that, in these frontal areas, spatial signals are coded in body-part-centered (motor) coordinates. Thus, the transformation from retinal (sensory) coordinates to body-part-centered (motor) coordinates ('reference frame transformation') appears to be inseparable from the process of response selection.

The finding of neurons coding arm movements in an eye-centered frame of reference shows that, in fact, the processes of response selection and reference frame transformation are separable. Integrating this new information requires a revision in the scheme of Figure 1a. The existence of an eye-centered reach representation in PRR is evidence that parts of PPC reflect not only target selection, but also response selection (Figure 1b). This suggests (but does not prove) that response selection precedes coordinate transformation. The coding in PPC is not purely eye-centered. Initial arm position has some effect in PRR, V6a and 7m [22,49••,56••]. Similarly, eye and head position gain fields in LIP and elsewhere represent an influence of other non-retinal frames of reference [57]. Furthermore, just as the coding in PPC is not purely retinotopic, the coding in premotor cortex is not purely arm-centered; Mushiake's [50] data suggest that eye-centered coding may persist all the way into some premotor regions.

An alternative view is that the eye- and arm-centered representations we find in the brain are not mere stages in a serial process, but rather that each is a useful representation in its own right. In this view, the fact that PPC contains primarily eye-centered codes whereas PM contains primarily arm-centered codes does not reflect a progressive transformation. Instead, both eye- and arm-centered representations co-exist at the same time in two different places, each to be used for a different purpose.

Eye-centered coding of ongoing arm movements has also been described in SC [58••]. Arm-movement-related discharge in a structure believed to code eye movements was surprising when first described in 1993 [59], but is now well documented. These responses suggest that SC plays a role not only in eye and head orientation, but also in bringing the arms to a target. A recent report shows that the responses of 40% of arm-related SC cells are independent of arm position but dependent on gaze direction [58••]. The dependence is consistent with eye-centered coding of target location. Most of these cells lie at the same anatomical depth as the more typical saccade neurons. (The remaining reach-related cells, including an overwhelming majority of those lying deep to the saccade-related cells, are independent of eye position but are dependent on arm position.) The interleaving of eye-centered saccade-related and eye-centered reach-related cells suggests a role for the SC in the coordination of eye and arm movements, although at this time this is highly speculative.

In all three areas, PRR, PMv and SC, cells exist that code arm movements but are strongly influenced by eye position, consistent with the coding of targets for arm movements in an eye-centered frame of reference. This might simply be the representation of choice for storing targets for upcoming arm movements, or it might be used for some aspect of eye–hand coordination [60•]. There are differences between the patterns of activity seen in PRR compared with PMv and SC. PRR most probably includes parts of V6a, and V6a is known to project to both SC and PMv [61]. Yet in PRR, activity is associated with both planned as well as ongoing arm movements, whereas in SC and PMv, activity is associated only with ongoing movements. Nearly one third of reach-related PRR cells also discharge during saccades [62], and cells in V6a fire immediately after saccades in an eye-position-dependent manner [63•]. In contrast, only 14% of reach-related SC cells fire during saccades [58••,64]. Further information about differences in these eye-centered representations may provide clues as to their roles in generating visually guided arm movements.

Combinatorial coding of arm movements

A large number of parietal areas code arm movements. Reach-related responses have been described in areas 7a, 7b, 5, MIP (medial intraparietal), MDP (medial dorsal parietal), 7m and V6a [2,65,66]. PRR also contains reach-related responses and appears to overlap with areas MIP, MDP and V6a. Caminiti and colleagues have pointed out that the activity in 7m and V6a does not fit neatly into a single coordinate frame [22,56••]. Instead, activity is influenced by varying combinations of visual input [67•], eye position, eye movements, arm position and arm movement. Because they do not find explicit eye-centered, head-centered, body-centered or arm-centered coding, they reject the idea of simple serial coordinate frame transformations. Instead, they view the sensory-motor transformation as a process in which a densely interconnected network of areas generates motor commands [68•]. This approach places organizational principles at the level of networks of areas, rather than at the level of single cells. Their most recent work, however, demonstrates a small amount of organization at the single-cell level [56••]. In V6a, the preferred directions for visual, eye and arm-related signals tend to be aligned at the level of the single cell. Although the elucidation of organizational principles at the level of small networks is extremely valuable, it is perhaps too early to abandon the search for organizational principles at the level of the single neuron, even in complex areas such as V6a.

Connectivity

The work of Caminiti and colleagues in understanding sensory-motor transformations at the level of networks of areas underscores the importance of studying inter-areal connectivity. Much excellent work focusing on parietal and premotor connectivity (e.g. [69,70•]) has been recently reviewed [71,72]. The resulting data, especially when paired with neurophysiological results, are absolutely essential to understanding how sensory signals are converted into actions.

One way to pair anatomical and neurophysiological information is to characterize the responses of cells which project from one cortical area to another. Within any area there is a wide range of cell types. It seems likely that much of this range reflects local (within-area) processing, and that only a subset of cell types, representing the result of the local computations, would project out to other areas. Surprisingly, this does not seem to be the case. In a series of heroic studies from the Wurtz laboratory, cells projecting from LIP and FEF to SC were antidromically identified. The responses of projection cells were then compared to the general population of cells. These and other studies failed to show major differences between responses in the projecting neurons and the general population of neurons [73,74,75•]. A related issue is how responses from neurons within each of these three areas differ from one another. As might be predicted from the antidromic activation data, patterns of activity in FEF and LIP [76] and in LIP and SC [77] are not too dissimilar. Furthermore, reversible lesion experiments in FEF and LIP [78•] do not support a serial processing model, but instead show that memory activity in these two areas is interdependent.

The picture that emerges from these studies of inter-areal connectivity and function is that areas LIP, FEF and SC behave as an interconnected network, and that hierarchical or serial processing is minimal. This is in line with the theories of Caminiti and colleagues, in which processing units are at the level of small networks of areas rather than at the level of individual areas or single neurons. However, these data are at odds with the previously described microstimulation data showing clear differences between activity in areas LIP and FEF [37•], and with previously described differences in single unit activity recorded during go/no-go tasks [47,79]. (In both of these cases, the data being compared were collected within a single laboratory and therefore the differences cannot be explained on the basis of differences in technique or neuronal sampling.) Resolving this paradox is an important issue for future studies. It is possible that simple tasks engage multiple areas in a similar manner. If this is true, then as more complex tasks are introduced — for example, tasks involving coordinated eye and arm movements — clear differences may emerge.

Conclusions

Recent findings have significantly advanced our understanding of how sensory signals are transformed into motor actions.

Visual spatial information is obtained in a retinal or eye-centered frame of reference. Eye-centered frames of reference that are modulated by eye, head or arm signals (gain fields) are proving to be very common across the cortex. Working memory signals that are stored in gain field representations can be updated when the direction of gaze changes; a fuller description of the circumstances under which this remapping occurs, and some insights into the mechanism, are beginning to appear. While some work has aimed at categorizing and classifying the responses of individual areas in parietal and premotor cortex, other computationally inspired work is making progress by considering how sensory-motor transformations are performed by networks of areas. Finally, a major advance in understanding sensory-motor transformations has occurred with the renewed use of paradigms in which the movements of two effectors (e.g. the arm and the eye) are independently controlled. These paradigms have revealed motor programs encoded in sensory frames of reference, which probably reflect early manifestations of motor plans in the cortex. A critical issue for future work is the extent to which these early manifestations of motor plans may reflect not the normal behavior of the system, but instead the overtraining that takes place before single-neuron recording ever begins. Although extremely difficult to address in an awake behaving monkey preparation, this issue is critical for our understanding of how the brain performs sensory-motor transformations.

Acknowledgements

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38. Mays LE, Sparks DL: **Saccades are spatially, not retinocentrically, coded.** *Science* 1980, **208**:1163-1165.

39. Schlag J, Schlag-Rey M: **Colliding saccades may reveal the secret of their marching orders.** *Trends Neurosci* 1990, **13**:410-415.

40. Umeno MM, Goldberg ME: **Spatial processing in the monkey frontal eye field. I. Predictive visual responses.** *J Neurophysiol* 1997, **78**:1373-1383.

41. Walker MF, Fitzgibbon EJ, Goldberg ME: **Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements.** *J Neurophysiol* 1995, **73**:1988-2003.

42. Powell KD, Goldberg ME: **Remapping of visual responses in primate parietal cortex during smooth changes in gaze.** *Soc Neurosci Abstr* 1997, **23**:17.

43. Snyder LH, Harper TM: **The representation of spatial information in monkey lateral intraparietal area (LIP) depends on the task being performed.** *Soc Neurosci Abstr* 1999, **25**:1547.

44. Gottlieb J, Goldberg ME: **Activity of neurons in the lateral**
• **intraparietal area of the monkey during an antisaccade task.** *Nat Neurosci* 1999, **2**:906-912.
Monkeys were trained to make saccades either towards or away from a peripheral visual target. LIP activity was found to correlate much more strongly with target location than with saccade direction. The authors sug-gest that LIP codes target locations, not intended movements. An alternative interpretation is that LIP may not be involved in generating saccades to non-visual targets, but rather is responsible for encoding salient positions in space (see annotation to [55•]).

45. Snyder L H, Batista AP, Andersen RA: **Coding of intention in the posterior parietal cortex.** *Nature* 1997, **386**:167-170.

46. Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL: **A common network of functional areas for attention and eye movements.** *Neuron* 1998, **21**:761-773.

47. Bushnell MC, Goldberg ME, Robinson DL: **Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention.** *J Neurophysiol* 1981, **46**:755-772.

48. Snyder LH, Batista AP, Andersen RA: **Intention-related activity in the posterior parietal cortex: a review.** *Vision Res* 2000, **40**:1433-1441.

49. Batista AP, Buneo CA, Snyder LH, Andersen RA: **Reach plans in**
•• **eye-centered coordinates.** *Science* 1999, **285**:257-260.
Monkeys were trained to plan and execute reaches without moving the eyes. A range of initial eye and arm positions were tested. Many cells in the medial part of the PPC coded upcoming arm movements in an eye-centered frame of reference. This suggests that the decision to respond to a stimulus using a particular effector precedes rather than accompanies the sensory to motor coordinate frame transformation.

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 Neurophysiol* 1997, **78**:567-571.

51. Graziano MS, Hu XT, Gross CG: **Visuospatial properties of ventral premotor cortex.** *J Neurophysiol* 1997, **77**:2268-2292.

52. Graziano MS, Gross CG: **Visual responses with and without fixation: neurons in premotor cortex encode spatial locations independently of eye position.** *Exp Brain Res* 1998, **118**:373-380.

53. Graziano MS: **Where is my arm? The relative role of vision and**
• **proprioception in the neuronal representation of limb position.** *Proc Natl Acad Sci USA* 1999, **96**:10418-10421.
Visual responses in premotor cortex were mapped when animals viewed their own arm or a prosthetic arm in different positions. The similar effects on receptive field location observed in the two conditions indicate that arm-centered responses in premotor cortex are partially dependent on visual cues regarding arm position.

54. Gottlieb JP, Kusunoki M, Goldberg ME: **The representation of visual salience in monkey parietal cortex.** *Nature* 1998, **391**:481-484.

55. Kusunoki M, Gottlieb J, Goldberg ME: **The lateral intraparietal area**
• **as a salience map: the representation of abrupt onset, stimulus motion, and task relevance.** *Vision Res* 2000, **40**:1459-1468.
Data from [54] are presented in order to argue that activity in LIP represents salient locations in space, and is unrelated to saccades *per se*. The critical control test involves repeated saccades made to a single location in the absence of a target. Under these conditions, activity in many (but not all) LIP cells is greatly reduced. The authors conclude that LIP therefore does not encode saccadic intention. However, the data also imply that the endpoint of the control saccades must no longer be a salient spatial location (otherwise it would be represented in LIP). This suggests, in turn, that the saccades have become automatized and are no longer goal-directed. Thus, an alternative interpretation of the data is that LIP codes goal-directed saccade endpoints; automatized movements performed in the absence of a goal would require different circuits.

56. Battaglia-Mayer A, Ferraina S, Mitsuda T, Marconi B, Genovesio A,
•• Onorati P, Lacquaniti F, Caminiti R: **Early coding of reaching in the parietooccipital cortex.** *J Neurophysiol* 2000, **83**:2374-2391.
Monkeys were trained to perform a battery of tasks involving combinations of eye and arm movements. Visual motion, eye position, arm position and arm movement were shown to modulate the responses of many V6a neurons. For any given cell, the best directions for these factors tended to align with one another. However, the modulations produced were complex and task-specific. The authors note that such properties are ideal for generating the commands necessary to guide reaching movements.

57. Pouget A, Snyder LH: **Computational approaches to sensorimotor transformations.** *Nat Neurosci Suppl* 2000, **3**:1192-1198.

58. Stuphorn V, Bauswein E, Hoffmann KP: **Neurons in the primate**
•• **superior colliculus coding for arm movements in gaze-related coordinates.** *J Neurophysiol* 2000, **83**:1283-1299.
Neurons in SC were characterized by motor preference, frame of reference, and anatomical depth while monkeys made arm and eye movements. Nearly half of the neurons that fired during arm movements showed a significant influence of gaze. Most of these were located at similar depths as eye-movement-related neurons, yet fewer than 10% were modulated during saccades. Most fired with movements of either arm. The discovery of gaze-related arm-movement neurons in SC completely changed our view of that structure.

59. 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.

60. Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE,
• Grafton ST: **Role of the posterior parietal cortex in updating reaching movements to a visual target.** *Nat Neurosci* 1999, **2**:563-567.
A fascinating study that uses transcranial magnetic stimulation to selectively disrupt corrective arm movements when reaching to a visual target. Humans reached for targets which sometimes were displaced slightly at around the time of movement initiation. These displacements were normally corrected for, but the correction was abolished when stimulation disrupted activity in parietal cortex on the side contralateral to the target. This indicates that the stimulated area plays a role either in estimating current hand position, in transmitting relevant information to other brain areas, or in computing motor error. The authors suggest the latter: they propose that PPC is the site at which visual information and current arm position are compared in order to generate a motor error signal.

61. Shipp S, Blanton M, Zeki S: **A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: cortical connections of areas V6 and V6A.** *Eur J Neurosci* 1998, **10**:3171-3193.

62. Snyder LH, Batista AP, Andersen RA: **Saccade-related activity in the parietal reach region.** *J Neurophysiol* 2000, **83**:1099-1102.

63. Nakamura K, Chung HH, Graziano MS, Gross CG: **Dynamic**
• **representation of eye position in the parieto-occipital sulcus.** *J Neurophysiol* 1999, **81**:2374-2385.
Within the parieto-occipital sulcus, neurons were found to encode information about eye position immediately after a saccade. Firing rate was modulated by post-saccadic eye position. This modulation was distinct from modulation related to the direction of the saccade. However, the eye position modulation was transient, persisting only several hundreds of milliseconds after the end of each saccade.

64. Werner W, Hoffmann KP, Dannenberg S: **Anatomical distribution of arm-movement-related neurons in the primate superior colliculus and underlying reticular formation in comparison with visual and saccadic cells.** *Exp Brain Res* 1997, **115**:206-216.

65. Galletti C, Fattori P, Kutz DF, Battaglini PP: **Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule.** *Eur J Neurosci* 1997, **9**:410-413.

66. Battaglia Mayer A, Ferraina S, Marconi B, Bullis JB, Lacquaniti F, Burnod Y, Baraduc P, Caminiti R: **Early motor influences on visuomotor transformations for reaching: a positive image of optic ataxia.** *Exp Brain Res* 1998, **123**:172-189.

67. Galletti C, Fattori P, Kutz DF, Gamberini M: **Brain location and visual**
• **topography of cortical area V6A in the macaque monkey.** *Eur J Neurosci* 1999, **11**:575-582.
Over half of V6a neurons are visually responsive, with many tuned to orientation and motion direction. More than one quarter of neurons have receptive fields in the inferior contralateral quadrant, and these receptive fields are smaller than the receptive fields located in the other three quadrants. As in area LIP, topography is weak − adjacent neurons often do not have adjacent receptive fields. The authors suggest that this organization is compatible with a role in visually guided reaching.

68. Burnod Y, Baraduc P, Battaglia-Mayer A, Guigon E, Koechlin E,
• Ferraina S, Lacquaniti F, Caminiti R: **Parieto-frontal coding of reaching: an integrated framework.** *Exp Brain Res* 1999, **129**:325-346.
Relevant monkey anatomy and physiology are reviewed, but the main point of this paper is to propose a novel brain architecture. In this architecture, motor plans are elaborated not by the sequential passage of information from area to area, but instead by diffuse networks that span multiple areas. To implement this, neurons in parietal and premotor cortex are envisioned to possess properties that vary continuously across cortex without regard for areal boundaries, in a way similar to previous hypotheses concerning the premotor and motor cortex. A neural network model is described that instantiates this idea. The model is ambitious and well conceived, and represents an intriguing hypothesis about brain organization and function.

69. Matelli M, Govoni P, Galletti C, Kutz DF, Luppino G: **Superior area 6 afferents from the superior parietal lobule in the macaque monkey.** *J Comp Neurol* 1998, **402**:327-352.

70. Caminiti R, Genovesio A, Marconi B, Mayer AB, Onorati P, Ferraina S,
• Mitsuda T, Giannetti S, Squatrito S, Maioli MG, Molinari M: **Early coding of reaching: frontal and parietal association connections of parieto-occipital cortex.** *Eur J Neurosci* 1999, **11**:3339-3345.
An anatomical study of parietal−parietal and parietal−frontal connectivity, interpreted in the context of a review of neurophysiological data.

71. Wise SP, Boussaoud D, Johnson PB, Caminiti R: **Premotor and parietal cortex: corticocortical connectivity and combinatorial computations.** *Annu Rev Neurosci* 1997, **20**:25-42.

72. Caminiti R, Ferraina S, Mayer AB: **Visuomotor transformations: early cortical mechanisms of reaching.** *Curr Opin Neurobiol* 1998, **8**:753-761.

73. Pare M, Wurtz RH: **Monkey posterior parietal cortex neurons antidromically activated from superior colliculus.** *J Neurophysiol* 1997, **78**:3493-3497.

74. Gnadt JW, Beyer J: **Eye movements in depth: what does the monkey's parietal cortex tell the superior colliculus?** *Neuroreport* 1998, **9**:233-238.

75. Sommer MA, Wurtz RH: **Composition and topographic**
•   **organization of signals sent from the frontal eye field to the superior colliculus.** *J Neurophysiol* 2000, **83**:1979-2001.
FEF neurons projecting to SC were identified and characterized during various saccade tasks, and their responses compared to those of the general population of FEF responses. Despite meticulous analysis, there was no evidence that any particular subtypes of FEF neurons were more or less likely to project to SC than any other subtypes.

76. Chafee MV, Goldman-Rakic PS: **Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task.** *J Neurophysiol* 1998, **79**:2919-2940.

77. Pare M, Wurtz RH: **Discharge properties of monkey superior colliculus neurons orthodromically activated by lateral intraparietal sulcus stimulation.** *Soc Neurosci Abstr* 1998, **24**:1498.

78. Chafee MV, Goldman-Rakic PS: **Inactivation of parietal and**
•   **prefrontal cortex reveals interdependence of neural activity during memory-guided saccades.** *J Neurophysiol* 2000, **83**:1550-1566.
Monkeys performed a memory-guided saccade task. A visual target was flashed and then, a short while later, a trigger signal released the movement to the memorized location. Memory period activity was recorded in either area LIP or FEF while the other area was cooled using a cryoprobe. These are technically difficult experiments in non-lissencephalic animals (possessing sulci and gyri). However, the authors provide convincing data that cooling either area has comparable effects on visual, mnemonic and saccadic responses in the other area. This suggests that LIP and FEF act in concert rather than in a serial fashion.

79. Goldberg ME, Bushnell MC: **Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades.** *J Neurophysiol* 1981, **46**:773-787.

80. Goldberg ME, Segraves MA: **Visuospatial and motor attention in the monkey.** *Neuropyschologia* 1987, **25**:107-118.