

Visuomotor transformations: early cortical mechanisms of reaching

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Recent studies of visually guided reaching in monkeys support the hypothesis that the visuomotor transformations underlying arm movements to spatial targets involve a parallel mechanism that simultaneously engages functionally related frontal and parietal areas linked by reciprocal cortico-cortical connections. The neurons in these areas possess similar combinations of response properties. The multimodal combinatorial properties of these neurons and the gradient architecture of the parieto-frontal network emerge as a potential substrate to link the different sensory and motor signals that arise during reaching behavior into common hybrid reference frames. This convergent combinatorial process is evident at early stages of visual information processing in the occipito-parietal cortex, suggesting the existence of re-entrant motor influences on cortical areas once believed to have only visual functions.

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Abbreviations

AIP	anterior intraparietal area
IPL	inferior parietal lobule
IPS	intraparietal sulcus
LIP	lateral intraparietal area; 7ip
M1	primary motor cortex; F1; area 4
MIP	medial intraparietal area
PE	dorsal part of parietal area 5; area 5d
PEa	part of area 5 of the medial bank of IPS
PEc	posterior part of PE around the edge of the hemisphere
PMd	dorsal premotor cortex
PMdc	caudal part of PMd; F2
PMdr	rostral part of dorsal premotor cortex; F7
PMv	ventral premotor cortex; areas F4 and F5
PO	parieto-occipital cortex
POS	parieto-occipital sulcus
pre-SMA	pre-supplementary motor area; F6
SMA	supplementary motor area; F3
SEF	supplementary eye fields
V6	visual area 6, in the bottom of the rostral bank of the POS
V6A	visual area 6A, in the dorsal part of the rostral bank of the POS

Introduction

Reaching to visual targets requires the solution of a spatial correspondence problem, that between the position of the hand and the position of the target. Even though the direction

of the target is initially coded in retinal co-ordinates, its position in space can be derived by using monocular and binocular cues. Arm and hand position can likewise be mapped in visual space, as well as in the intrinsic co-ordinates signalled by receptors in the muscles, joints, and skin. As coding such information takes place in different co-ordinate systems, a transformation from retinal to body-centred frames is believed to take place as a prerequisite for any successful reaching movement. Many conceptual schemes have been proposed about the nature of the co-ordinate transformations underlying reaching, and inferences have been made on how the reduction to a common hybrid frame can be achieved [1–4,5**,6**]. However, these schemes are mostly derived from psychophysical and motor behavioural studies and bear no direct relationship to the architecture and functional operations of the underlying cortical network. New evidence has provided further insights into the neural mechanisms by which the sensorimotor transformations underlying reaching are performed.

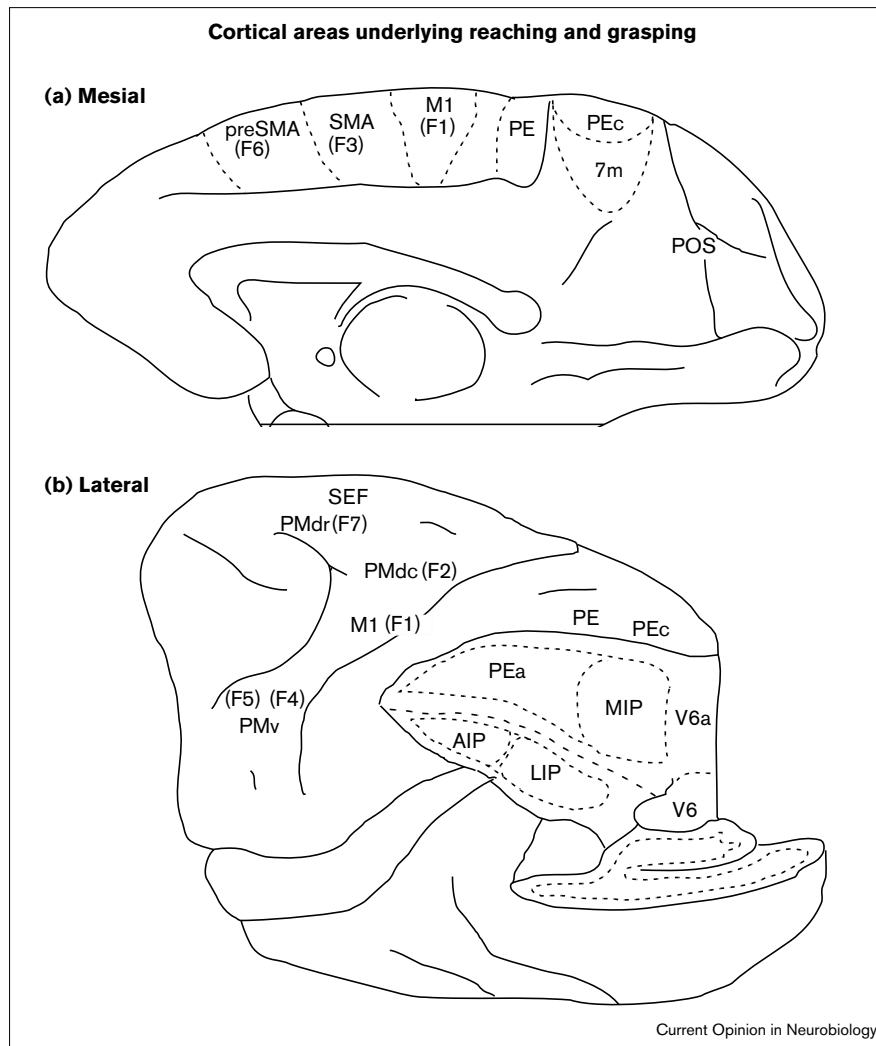
Recent anatomical and physiological data on the functional architecture of the parieto-frontal cortex (Figure 1), have suggested new roles for the posterior areas of the superior parietal lobule — traditionally considered to be higher-order somatosensory centres — and have highlighted the potential motor role of other regions, such as the occipito-parietal cortex, once believed to be purely visual in nature [7]. We will review new information on the sources of visual input to the motor areas of the frontal lobe, the distribution of reaching-related activity across different cytoarchitectonic areas of the cerebral cortex, and the 'early' representations of reaching movements outside of traditional cerebral cortical motor areas.

The functional architecture of the parieto-frontal network for reaching

The cortical sources of the visual input to the frontal motor areas of monkeys were first described by studies [8–10] showing projections to the reach-related zone of the dorsal premotor cortex (PMdc; F2) [11,12] from parietal areas 7m, MIP, and PO [13,14]. Currently, PO is the only visual area in which an expanded representation of the periphery of the visual field has been described. It provides a substrate for those functions included in the broad definition of ambient vision [15] and, therefore, also in the putative processes underlying target localisation that are presumed to be one of the initial stages in the organisation of reaching movements.

A crucial observation of recent studies on the functional properties of reach-related neurons is their capacity to combine different spatial variables, what we have called

Figure 1



Schematic of the cortical areas in monkey involved in reaching to visual targets.

(a) Mesial and (b) lateral views of the cerebral hemisphere. In (b), parts of the parietal and occipital cortices have been removed to show the location of the areas buried within the IPS and POS.

their combinatorial properties [16–19]. Signals about target location on the retina, eye position in the orbit, static posture and orientation of the arm, as well as activity related to the preparation for and execution of combined eye and arm movements, appear to co-exist in many reach-related parietal and frontal neurons, although they influence cell activity to different degrees in different regions. This subject has been treated extensively in recent reviews [16,17,20**]. Briefly, neuronal activity that co-varies systematically with the active static position of the arm and with the direction of arm movement has been observed in M1 [21–25], PMdc [9,26–28], and area 5 [29–32], but has now also been documented in MIP [9], 7m [18,19], and even in the dorsal part of PO [17,33,34] (i.e. in area V6A [35]). Furthermore, the initial position and orientation of the arm modulates the neural activity related to preparation and execution of arm movements in M1 [24,36*], PMd [26,37*] and area 5 [31,37*]. An important new finding is that eye-position signals also influence reaching-related activity in both PMdc [38*] and ventral premotor cortex

(PMv) [39*], as well as in parietal area 7m [18,19]. This suggests that the frontal cortex could contribute to the process leading to target localisation in space and, therefore, to the co-ordinate transformation for reaching. As a consequence, signals about target location from the parietal cortex should be implicit (i.e. resulting from the combination of the retinal co-ordinates of the visual target with eye position in the orbit).

An interesting distinction between frontal and parietal cortex is that neural activity in the latter (but not in the former) also reflects eye and arm movements that might be made, as seen in no-go trials of go/no-go tasks in area 5 [40] or during tasks dissociating eye from arm movement in the lateral intraparietal area (LIP) [41,42*]. In this respect, it is interesting that patients with lesion in the right inferior parietal lobule (IPL), in addition to unilateral neglect, also show an impairment of reaching to targets in the left part of space [43*], although it remains to be determined whether this is a motor deficit or a consequence of sensory neglect.

The different types of reach-related activities described above are neither distributed in a random fashion in the cortex nor segregated into individual cortical areas. In contrast, neurons whose activity reflects target location in retinal- and/or head-centered co-ordinates predominate at the intermediate (MIP) [9,14] and caudal (V6A) [35] levels of the superior parietal lobule (SPL), and in the more rostral part of the frontal lobe [8–10,44–46]. Neurons signalling gaze and eye movements can be found in parietal areas V6A [35] and 7m [18,19], and in frontal areas SEF [47•] and PMdc [38•]. Neurons tuned to arm position in space are broadly distributed across the network [9,18,19,33]. Cells whose discharge is coupled predominantly to arm movements are most abundant around the central sulcus, and, therefore, in M1, but are also common in PMd, PMv, MIP, 7m and V6A [17–19,33,34,48]. Furthermore, parietal and frontal regions with similar combinations of neuronal response properties are preferentially linked by reciprocal association connections [9], which are not point-to-point but arranged in a gradient-like fashion. This gradual change of response properties and connectivity patterns across the cortical surface define two symmetrically arranged visual-to-somatic gradients in both frontal and parietal cortices [9].

The origin of visually guided reaching

Evidence exists that coding visually guided reaching requires a multisensory fusion of information ([5•,6•], see [34] for a review). The combinatorial properties of parietal and frontal reach neurons further support this contention. One question that arises is how early in the information-processing flow leading from vision to movement does this convergence of multimodal reach-related signals begin. The study of the ‘early’ mechanisms of reaching is of interest because it can reveal important information about the nature of the underlying visuomotor transformations.

A strictly serial architecture for co-ordinate transformations can only be supported by neuronal mechanisms in which different specific signals are added at different specific processing stages, ideally in different cortical areas. For instance, retinal information about target location, from primary visual areas, would first be transformed into craniotopic [49] or body-centred co-ordinates, and then combined with that concerning arm position and posture; the posterior and intermediate part of the parietal cortex, respectively, could subserve these processes. Once target location and arm position are represented in the same co-ordinates, a hand movement vector can be computed as the difference between hand position and target location [3]. This role could be attributed to motor cortex, as well as to pre-motor areas, especially if arbitrary associations between sensory inputs and motor output are required [16,45,47•]. This serial order of transformations also implies a sequential activation of different areas in time.

In contrast, a distributed and parallel mechanism of co-ordinate transformations could result from multimodal

combinatorial processes occurring simultaneously in functionally similar domains of parietal and frontal cortices, through a recursive mechanism based on reciprocal cortico-cortical connections and supplemented by additional local computations. This parallel scheme is supported by the presence of eye position signals in both superior parietal and frontal motor areas [17–19,38•], which suggests that the putative transformation from gaze-centred visuospatial signals to arm-centred motor co-ordinates is distributed across both regions. It is also supported by studies of the temporal relationships between cell activity and different behavioural events of a reaching task (e.g. target presentation, movement onset, etc.), which have clearly and consistently shown that the distribution of the onset times of cell activity relative to the task events is very similar in frontal and parietal cortices and, furthermore, that these relationships depend on the behavioural context considered [9,30].

Recent studies of cell activity in arm-reaching tasks have shown that neurons in areas 7m and V6A [17–19,34] combine information about arm position and arm movement with eye-movement, retinal, and gaze signals. These combinatorial properties only become evident when neurons are studied through a variety of behavioural tasks aimed at dissociating the different signals influencing neuronal activity. Figure 2 displays the activity of a prototypical neuron of V6A. This neuron’s activity shows directional tuning as a function not only of hand position and arm movement, but also of (saccadic) eye movement and eye position. In addition, the cell’s activity is modulated by visual stimuli, mainly if these move across the retina along paths that converge on the fovea. The activity related to arm position and arm movement is sustained when the monkey maintains constant fixation or is still modulated in darkness, and therefore in the absence of visual feedback of limb position and movement trajectory. This indicates that the cell’s activity carries genuine arm-position- and movement-related signals, which are modulated by the angle of gaze. In areas 7m and V6A, other neurons display profound changes in activity when reaching is performed in darkness; they participate in the control of hand position and movement trajectory in the visual field.

These results indicate that many variables related to visually guided reaching, including visual stimuli and oculomotor and arm motor behavior, can influence single-cell activity at an early stage in visuomotor processing (i.e. in the occipitoparietal and mesial parietal cortices). The early motor influences on cell activity of areas 7m and V6A — the latter has, so far, been regarded as purely visual in function — are probably dependent on re-entrant signals from parietal and frontal cortices. Reciprocal association connections could be the substrate for this re-entrant mechanisms [50,51•,52•].

Considered together, these recent observations render untenable any hypothesis that the visuomotor transformations underlying reaching are organised in a simple serial manner, and also refute the implicit identification of the parietal cortex as the only cortical site in which the

Figure 2 legend

Combinatorial properties of a reach-related neuron in the parietal-occipito cortex (specifically, area V6A). Six behavioral tasks were used to dissociate the different signals influencing this neuron's activity. **(a)** Displays cell activity in the form of polar plots (PPs; upper) and directional tuning curves (TCs; lower) while the monkey made arm movements to eight different targets (subtending 30° visual angle; located at 45° angular intervals) during a standard reaching task to foveal targets (SR, red) and during reaching to extra-foveal targets while keeping constant fixation at the center of the workspace (SRf, blue). Activity is shown during reaction-movement time (RMT), in which the eyes saccade to the target and shortly after the arm reaches toward it, and during target-holding time (THT), in which both the eyes and hand (SR) or only the hand (SRf) remains immobile on the different spatial targets. The circles in the PPs and the horizontal lines in the TCs indicate the activity during control time. This neuron's activity is modulated in a directional way during reaching (RMT) to both foveal and extra-foveal targets, although the directional tuning changes under these conditions, suggesting that the signal relating to direction of arm movement is modulated by eye position. In addition, neural activity is also modulated during THT under both task conditions, with a significant difference between SR and SRf. This suggests the existence of a genuine arm position signal that is

modulated by eye position. **(b)** In the EPO task, the monkey made saccades to the same targets used in the previous tasks. Here, cell activity changes with the direction of saccadic eye movements and with static eye position on different targets. **(c)** In the SDR task, a cue signal instructed the animal about the direction of the next arm movement (Arm RMT) to be performed on the change of color of the cue (go-signal), after a variable delay time (DT3). The animal made a saccade to the cue (Eye RMT), then the eyes remained immobile on the target while the arm was preparing to move and finally moved toward it. This task was performed under normal light conditions (SDRI; red) and in total darkness (SDRd; blue) – that is, in the absence of visual feedback about hand movement trajectory. The task confirms the cell's directional modulation with saccadic eye movements, but also displays significant directional suppression of activity during preparation and execution of arm movement (DT3, RMT), as well as during THT. This is so both in light and darkness, with significant changes in activity across task conditions during eye RMT, DT3, THT, but not RMT. **(d)** Finally, in the visual fixation task, this cell displays a large receptive field that includes the fovea and extends up to 30° in the periphery of the contralateral lower quadrant of the visual field. Activity is maximal (red) for visual stimuli moving inward (In) toward the fovea than in the opposite way (Out).

transformation from visuospatial to motor co-ordinates occurs. Instead, they support a parallel mechanism based on simultaneous processing of reach-related variables along the representational continuum of the distributed parieto-frontal system.

This parallel processing does not appear to be unique to reaching or to the frontal and parietal operations underlying it. A distributed system involving the inferior parietal lobule and prefrontal cortex appears to obey similar rules, as shown recently in a study using a spatial working memory task in macaque monkeys [53*].

Visuomotor transformation underlying grasping

The cortical network underlying the control of hand movement includes, at the very least, the anterior intraparietal area (AIP), ventral premotor area F5 and their sets of cortico-cortical connections [54]. Instead of the broad directional tuning properties displayed by cells linked to movement of more proximal parts of the arm, hand-movement-related neurons in these areas display 'sharp' tuning to particular hand actions or to specific object shapes (see [55,56**,57*,58,59*] for recent reviews). The issue of how limited sets of neuronal populations preferentially related to different specific hand actions can cope with the infinite variety of hand movements has been addressed, at the theoretical level, through the so-called 'schema' approach developed by Arbib ([60]; see [54] for a review). The schema model proposes that populations of neurons form a series of separate networks to define specific categories of hand movements, hand geometries during grasping, and the temporal fractionation of actions. Neuronal populations in areas AIP and F5 would store a 'vocabulary' of different motor schemas in the form of multiple parallel frontoparietal cell assemblies.

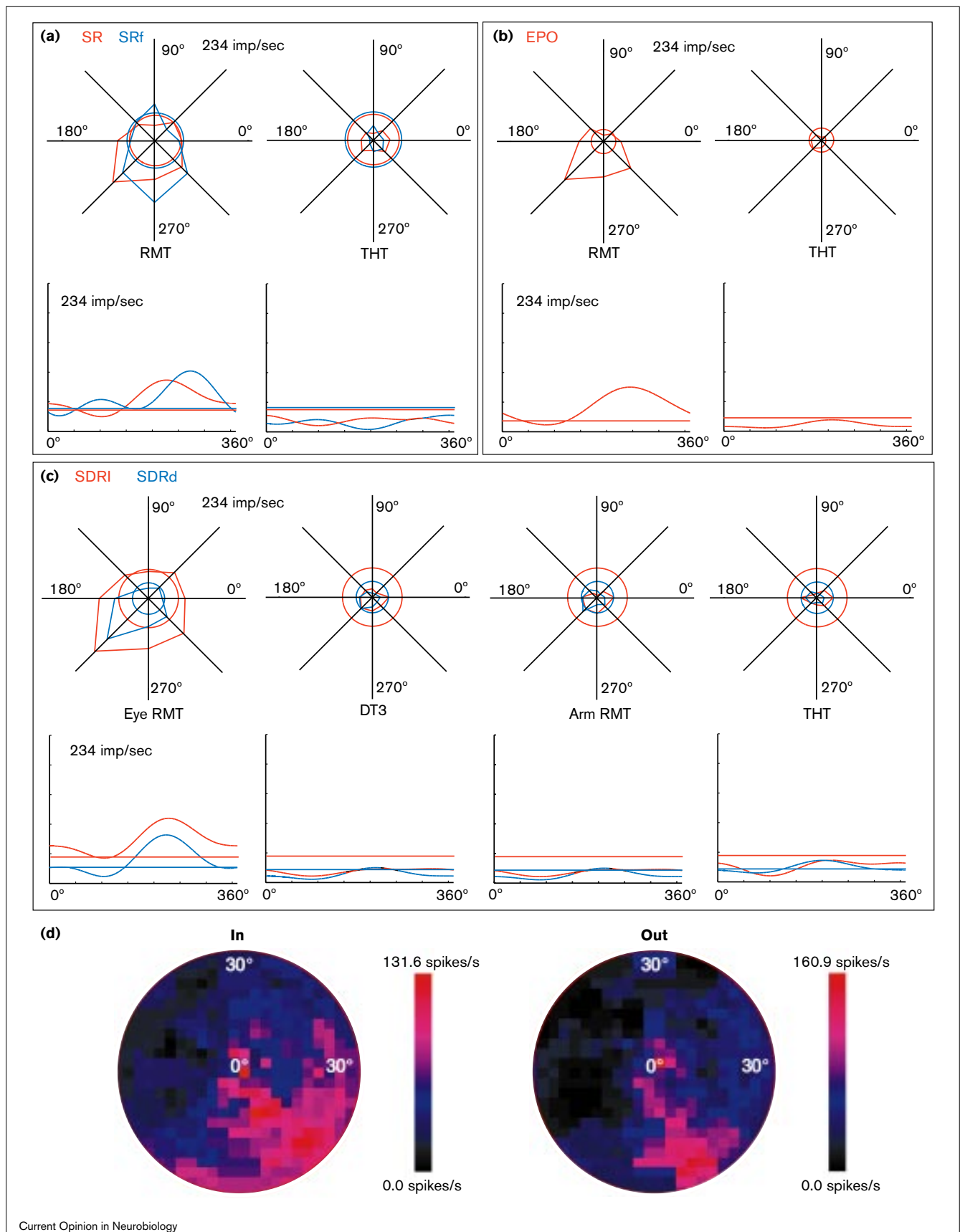
This conceptual approach suggests that the participation of each category of AIP and PMv neurons in a broad range of different motor tasks would be unlikely and undesirable because the different schemas to which they contribute serve to control conflicting hand actions. In contrast, it implies that successful hand grasping and manipulation of objects requires the preferential activation of the most appropriate frontoparietal cell network (schema). Thus, the visuomotor mechanisms underlying grasping appear quite different from those underlying reaching. However, it is also possible that this vocabulary of hand motor action in AIP and F5 possesses the potential to specify various basic 'primitives' of the full motor repertoire of the hand, and that population mechanisms still to be described determine the infinite variety of hand actions. The issue of the redundancy of degrees of freedom of hand movement has been addressed by the 'virtual finger' model [61], in which the control of hand configuration is achieved through a set of 'virtual fingers' working as a functional ensemble. A recent study of hand kinematics under different conditions [62**], however, does not fully support this model, because it appears that all the degrees of freedom of the hand are controlled as a unit. Further work is required to uncover the principles of hand movement control and their underlying neural basis.

The comparison of the coding mechanisms for reaching and grasping will be an interesting challenge for future research.

Temporal coding of movement

An important mechanism by which behaviorally relevant information could be represented in the instantaneous discharge patterns of cell assemblies is illustrated by recent studies of the motor cortex [63**]. These studies report shifting patterns of synchronous unitary activity within sets of simultaneously recorded neurons during

Figure 2



preparation for reaching to a previously cued visual target (i.e. during a purely cognitive motor process). Synchronization linked, at different times, different elements of the discrete cell assembly studied, without any change in average firing frequency.

That these synchronized cell assemblies are functionally significant is supported by the finding that the composition of the assemblies varies systematically as a function of stimulus events, stimulus expectancy, level of motivation and behavioral reaction times. Time-dependent changes in synchronization of activity among members of a network may serve not only to establish functional links necessary for the composition of motor commands, but also to represent certain spatial parameters of movement, such as direction [64•].

How the information embedded in these patterns of synchrony can be used to increase the capacity of a network of cells to encode multiple parameters of motor events, however, remains to be determined. When binding visual, somatic, and motor information necessary for reaching during the coordinate transformations linking sensory and motor processes, transient synchronization of neuronal activity must presumably take place across many different parietal and frontal nodes of the distributed system. Furthermore, a read-out mechanism that is capable of detecting the occurrence of synchronous activity in the network and of linking their specific patterns to specific sensory events, central cognitive processes, and forms of motor behaviour may exist. The study of the variable and time-dependent recruitment of neurons into a given network (for a review, see [65••]) under different task conditions emerges as a central issue for future research on the neural basis of motor behavior.

Conclusions

The behavioral act of visually guided reaching probably originates at the moment retinal, gaze, arm position and movement signals first coverage. There is no unique cortical locus for this event. The entire parieto-frontal networks is involved from the very onset. The parietal cortex should not be regarded as the only area in the cortex in which coordinate transformations are performed, because the process most probably involves frontal cortex as well. Frontal cortical neurons combine not only arm position and movement signals, but also visuospatial and gaze information. Similarly, parietal neurons integrate, from very early stages, not only visual and gaze signals, but also arm position and movement information. This combinatorial computation mechanism takes place along a visuomotor continuum of properties that confers a gradient architecture to the parieto-frontal network. The smooth transition of information coded in different dimensions is the essence of the co-ordinate transformation underlying reaching. No single cortical area encodes reach-related information in an explicit unimodal coordinate framework (for a review, see [66••]).

The hypotheses outlined in this review share with other proposals [67••] the idea that the posterior parietal cortex creates implicit representations by combining multimodal and corollary signals. Re-entrant signaling [68] through cortico-cortical reciprocal parieto-frontal connections can play a crucial role in the combinatorial process leading to visually guided reaching. It is worth stressing that similar concepts have inspired different models of sensorimotor transformations [69–71] based on multiplicative interaction between inputs within recurrently connected populations of neurons.

To decipher the link between theoretical concepts — such as reference frames, co-ordinate systems and sensorimotor transformations — and the underlying causal neural mechanisms will require further understanding of the dynamical properties of interacting neuronal populations distributed across wide expanses of the nervous system, and not confined to any anatomical border.

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- of special interest
- of outstanding interest

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The spatial errors made during pointing to memorized target locations in space were analyzed in experiments in which subjects could see their fingertip against a uniform background. This set-up made it possible to test the role of diverse signals, such as vision and proprioception, in providing a central image of target and hand position, while excluding allocentric visual cues. Movement endpoints were quantified in terms of constant and variable errors, and their orientation expressed as a function of workspace location, to reveal the underlying frames of reference. The pointing errors of the hand were scattered along the line of sight, independent of the target location in the three-dimensional workspace, the hand used, its starting position, the eye and head orientation. When the duration of the memory delay was increased, an increase of the size but not of the orientation of the variable-error ellipsoids was observed. The authors conclude that these results support a viewer-centered reference frame specifying direction and distance from the eyes, as opposed to a shoulder- or hand-centered reference frame. Fusion of cues about visual intensity, accommodation, retinal topography, stereodisparity and ocular vergence/version can predict the observed anisotropy of pointing errors. This implies that ocular and arm information merge into an egocentric binocular frame of reference, where they can be compared. This is a superb study.

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- **to visual targets: psychophysical evidence for body-centered reference frames.** *J Neurosci* 1998, **18**:8423-8435.

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between target presentation and reaching to memorized target locations. To characterize the acquisition, transformation and storage of sensori-motor information, the authors used constant and variable errors and a newly introduced measure of local distortion, which refers to the fidelity with which the relative spatial organization of targets is maintained in the configuration of final pointing positions. Experiments were performed in dim light, total darkness, variable delay duration, and different effector hand and workspace locations. The results show that the orientation of the variable errors differs between light and dark conditions, because the axes of maximum variability converged toward the head in the light and to different origins in the dark. Increasing the memory delay resulted in a change in the magnitude of the viewer-centered variability in the light, but in its reorientation in the dark. Local distortion measures revealed a contraction of endpoint positions for both light and dark along an axis intermediate between the eyes and the arm. The magnitude of the contraction increased only for the longer delays in the dark. Simulations performed to identify the origin of the coordinate system in the dark show how a cascade of eye- and shoulder-centered local contractions predict the experimental data. The authors proposed a coordinate system linked to the eyes and the effector hand, with an independent storage of direction and distance within short-term memory. This is another excellent study (see also [5**]).

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 • In this study, monkeys had to make reaching movements with similar hand trajectories but different arm orientations. This task dissociated extrinsic variables such as target location and hand trajectory, which remained constant across task conditions, from intrinsic variables related to arm geometry and limb dynamics. Many M1 cells showed significant changes of directional properties, including orientation of preferred directions and sharpness of tuning curves. The authors describe a mathematical model that shows how neuronal activity encoding intrinsic parameters would undergo similar changes across task conditions. This is an interesting study of the controversy on the variables encoded in M1 neuronal activity.
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 • A welcome extension of an earlier paper by these authors [36*]. In this study, they included analysis of PMd and area 5, where neurons also showed significant changes in directional properties when reaching movements were made with different arm orientations. These effects were greater in M1 than in PMd.
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eye position on the directional tuning of neurons were not investigated at the population level; furthermore, the effects on cell activity of initial arm position were not studied while keeping constant fixation. Therefore, the evidence presented, with together the findings of previous studies on PMd [26,28] and of recent experiments on areas cortico-cortically connected to it, such as 7m [18,19], make it more plausible that PMd encodes arm movement direction within a hybrid co-ordinate system that combines signals regarding, at the very least, arm-movement direction, arm position and gaze direction.

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