

Visuo-motor transformations for arm reaching

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Abstract

Visuomanual co-ordination requires the merging of ocular and arm information in a common frame of reference. Here we consider behavioural evidence in humans for the use of a viewer-centred frame in the specification of end point positions of reaching. We then review anatomical and neurophysiological data in the non-human primate that indicate a prominent role of the parietal cortex in the process of multisensory fusion that leads to egocentric representations of space. Finally, we discuss the functional anatomy of the human parietal cortex in visuomanual co-ordination as revealed by neuroimaging.

Introduction

A long-standing issue in physiology concerns the nature of the neural codes used to store spatial information for reaching movements (cf. Georgopoulos, 1991; Jeannerod, 1991; Paillard, 1991; Caminiti & Johnson, 1992; Kalaska & Crammond, 1992; Soechting & Flanders, 1992; Stein, 1992; Lacquaniti, 1997; Wise *et al.*, 1997). Planning a reach requires the localization of both the target and the arm in three-dimensional (3D) space, and the translation of this spatial information into the appropriate motor commands. Multiple sensory systems (e.g. visual and proprioceptive systems) generally contribute spatial information, and the movement often involves the co-ordination of several body segments, as in orientating the eyes, head and arm together toward the target (Jeannerod, 1988; Lacquaniti, 1997). Multi-systemic sensorimotor co-ordination affords most efficient achievement of the behavioural goal, but it may result in a babel of spatial codes at the level of the nervous system. In fact each peripheral sensory and motor apparatus is endowed with its specific geometry and organization. For instance, the direction of a stationary visual target is mapped topographically on the retina, whereas arm position can be monitored also by proprioception in the intrinsic frame of reference of muscle, joint and skin receptors.

This heterogeneity is mirrored in the diversity of modes of neural processing along the pathways that originate from different sensors or that are directed to different effectors. Ultimately, however, the heterogeneity of the spatial representations needs to be reconciled across different channels at the level of the central nervous system (CNS) by merging multimodal information in a unitary map of space (Simpson & Graf, 1985; Soechting & Flanders, 1992; Lacquaniti, 1997; Knudsen & Brainard, 1995).

In this review, we focus on the case when reaching is performed with visual feedback of the hand, the most common situation in everyday life. We will argue that the end-point positions of reaching are specified by combining visuo-spatial, gaze and arm information in a common egocentric frame of reference. Recent behavioural and

neuroimaging data in humans, as well as anatomical and neurophysiological data in the non-human primate will be reviewed. Special emphasis will be given to the contribution of posterior parietal cortex within the distributed neural network involved in visuomanual coordination.

Psychophysical evidence for multisensory fusion in reaching

In human psychophysics, the frames of reference used by the brain may be revealed by the differences in precision between the neural channels that process spatial information independently (Soechting & Flanders, 1989; Gordon *et al.*, 1994; McIntyre *et al.*, 1997). To this end, the spatial errors made by subjects who point to a visual target after a brief delay following target extinction are analysed statistically. If spatial information is processed in independent neural channels, random noise in one channel should be statistically independent of noise in the other channels (McIntyre *et al.*, 1997). Let us consider the case, for instance, that the level of noise is greater in one channel relative to that in another. This will result in anisotropy of the spatial distribution of the end-points, the direction of maximum and minimum variance corresponding to the spatial orientation of the underlying independent channels.

In the experiment of Figure 1, the subject looked at a small target placed by a robot at a random location in 3D space (McIntyre *et al.*, 1997). The target was lit for a period of 1.4 s, then was extinguished and quickly removed. After a 0.5 s delay, the subject pointed to the remembered target location. Experiments were performed under dim lighting conditions, allowing successive vision of the target and of the finger tip against a uniform, black background. These viewing conditions were designed to test the role of different egocentric signals (visual and proprioceptive) in reconstructing target and hand position, excluding allocentric visual cues from the background. In

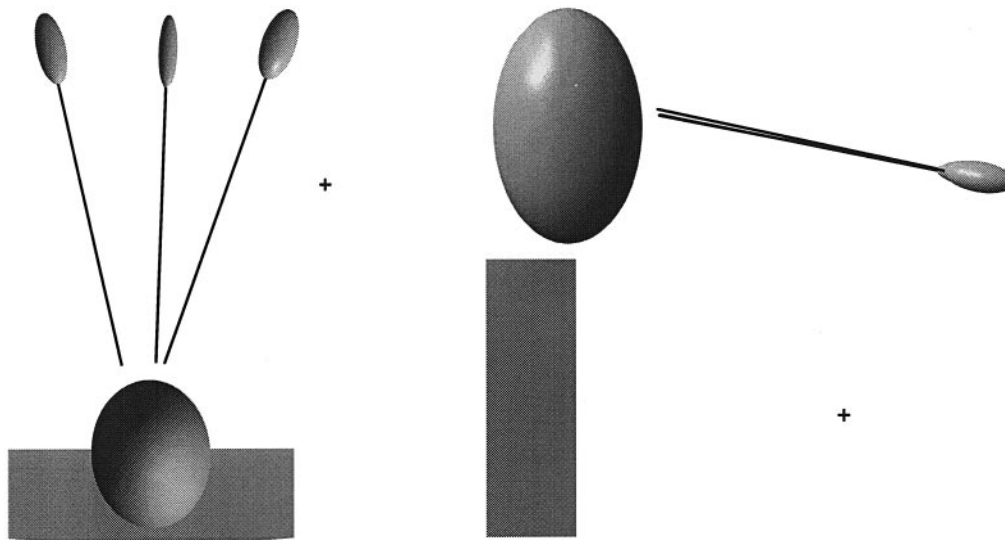


FIG. 1. Variable error for pointing to targets in the left, middle and right workspace regions. Ellipsoids represent the 95% tolerance region for a single target, computed from 180 movements. Lines emanating from each ellipsoid indicate the direction of the primary axis (major eigenvector of the covariance matrix) projected to intersect with the frontal plane through the subject forehead. The '+' indicates the average starting hand position for all movements. A schematic picture of the head and trunk of the subject is shown along with the variable errors in two views: from above (left panel) and from the side (right panel).

Figure 1, '+' denotes the average starting position of the finger for all movements. The final finger positions (end-points) over many repeated trials to the same target locations are scattered within the grey regions (95% tolerance ellipsoids). The lines sticking out of the ellipsoids indicate the axis of maximum variance projected to intersect the frontal plane through the subject forehead.

Under these experimental conditions, the pointing errors of the hand are scattered along the sight-line, the variability of the end-point distance relative to the eyes being consistently greater than the variability of the end point direction relative to the same origin. These results are found independently of the specific location of the target within the 3D workspace (Fig. 1), the hand (left or right) used to perform the movement, the starting position of the hand, and the orientation of the head and eyes during the task (McIntyre *et al.*, 1997). Therefore one can conclude that the specification of the final position of the hand occurs in a viewer-centred reference frame (direction and distance from the eyes), as opposed to shoulder-centred or hand-centred frames (McIntyre *et al.*, 1997).

A multiplicity of cues contribute to localizing both the target and the hand relative to the eyes: these cues include visual intensity, accommodation, retinal topography, stereodisparity, and ocular vergence/version (Collewijn & Erkelens, 1990). A process of fusion of these cues predicts the specific anisotropy of the pointing errors of the arm (McIntyre *et al.*, 1997). Thus visuomanual co-ordination involves the merging of ocular and arm information in a common egocentric binocular frame. The motor commands directed to the arm and the sensory reafference of arm position are initially defined in the intrinsic frames of reference of the arm muscles, joint and skin receptors. As indicated by the experiments reviewed above, arm position is subsequently redefined in viewer-centred coordinates in order to be compared with the location of the remembered target, which is defined in the same coordinates.

In the following we discuss possible neural substrates for the process of multisensory fusion leading to egocentric representations of reaching in a parieto-frontal network.

A cortical network for visual reaching

Cortical coding of reaching occurs within a distributed parieto-frontal network comprised of many different areas (Fig. 2). It has recently been shown in the monkey that visual signals and eye position signals are combined with arm position signals to generate the motor commands for reaching (see Boussaoud, 1995; Ferraina *et al.*, 1997a, b; Wise *et al.*, 1997). Visuo-proprioceptive integration might occur in a common egocentric frame, realizing a network for the co-ordinate transformations involved in the control of reaching under visual guidance (Lacquaniti, 1997).

Routes of visuo-spatial signals to the parieto-frontal network

These anatomical substrates have been worked out in detail only recently (Johnson *et al.*, 1993; 1996; Tanné *et al.*, 1995). Objects in the visual field are processed within a cortical network of more than 30 visual areas (Felleman & VanEssen, 1991). These areas are organized within two major cortico-cortical pathways or streams, each of which originates in the primary visual cortex (V1). The ventral stream is directed to the inferior temporal cortex and is important for object recognition, whereas the dorsal stream is directed into the posterior parietal cortex and is important for spatial perception and visuomotor performance (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992; Caminiti *et al.*, 1996b; Jeannerod, 1996). Here we are concerned with this dorsal stream.

Spatial visual information flows from V1, V2, V3 to middle temporal area (MT) and medial superior temporal area (MST). Cells in these temporal areas are broadly tuned to the direction and pattern of visual motion (Sakata *et al.*, 1985; Snowden *et al.*, 1992). Visual-tracking neurones in MST receive convergent signals indicating current retinal image motion, eye rotation and head rotation (Thier & Erickson, 1992). Many neurones in MT and MST are selective to different combinations of the optic flow components (translation, dilation, rotation and deformation, Duffy & Wurtz, 1991). In addition, spatial visual signals reach the parieto-occipital area (PO; Covey

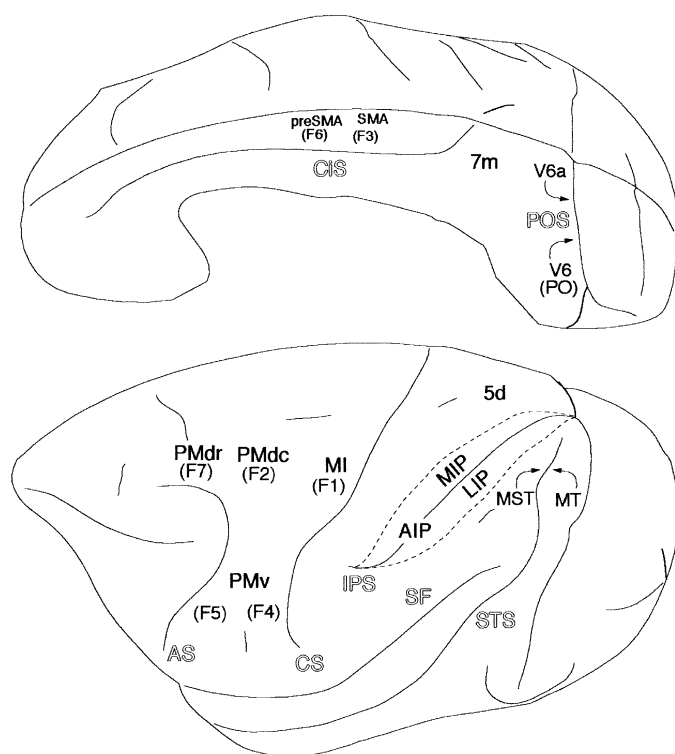


FIG. 2. Brain figurines showing the mesial (top) and lateral (bottom) aspect of the monkey's brain with cortical areas involved in visual reaching. PO (V6) indicates parieto-occipital area, SMA supplementary motor area, MT middle temporal area, MST middle superior temporal area, LIP lateral intraparietal area, MIP medial intraparietal area, AIP anterior intraparietal area, 5d dorsal part of area 5, M1 primary motor cortex, PMdc dorsocaudal premotor cortex, PMdr dorsorostral premotor cortex, PMv ventral premotor cortex; AS, CS, IPS, STS, POS and CiS indicate, respectively, arcuate, central, intraparietal, superior temporal, parieto-occipital and cingulate sulci; SF indicates Sylvian fissure. Arrows indicate approximate location of cortical areas buried within the banks of sulci. The IPS is shown as opened (interrupted lines) to better display the parcellation of intraparietal areas. (Modified from Caminiti *et al.*, 1996a.)

et al. 1982; Gattass *et al.*, 1985; Colby *et al.*, 1988), which receives direct projections from V1, V2, V3, MT and MST. PO has a quasi-uniform representation of the retina without foveal magnification. As one moves from V1, V2, V3 to MT, MST and PO, the receptive field size of individual neurones increases. Large receptive fields may contribute to localizing objects over retinal translation.

Visual information is relayed from PO to the medial intraparietal area (MIP) and to area 7m. Area 7m receives also from areas 7a and lateral intraparietal area (LIP) of the inferior parietal cortex and projects to dorsal area 5 and MIP in the superior parietal cortex. Both MIP and 7m are connected with the dorsal premotor cortex (area PMd), and its boundary with primary motor cortex (M1). Short cortico-cortical connections may quickly transfer visuospatial information to M1. This step-wise progression of information from visual to motor cortices is paralleled by a direct projection from PO to the rostral part of dorsal premotor cortex (PMdr, Tanné *et al.*, 1995; Johnson *et al.*, 1996). Furthermore, the connections between 7a and 7m (Cavada & Goldman-Rakic, 1989) can offer a route to frontal motor areas to the signals coming from the population of reaching neurones of the inferior parietal lobule (Mountcastle *et al.*, 1975; MacKay, 1992; Snyder *et al.*, 1997). In addition, MST projects to areas of the inferior parietal lobule and of the lateral bank of the intraparietal

sulcus (area 7a, LIP, ventral intraparietal area (VIP), Cavada & Goldman-Rakic, 1989; Andersen *et al.*, 1990; Boussaoud *et al.*, 1990). These parietal areas in turn send information to the ventral premotor area (PMv, areas F4 and F5 of Matelli *et al.*, 1986). The network involving inferior parietal and ventral premotor areas plays a special role in the control of hand preshaping and grasping (see Jeannerod *et al.*, 1995). This anatomical layout of the distributed cortical system indicates that both parallel and hierarchical mechanisms are set in operation when a visual stimulus is presented which serves as a target for a reaching movement.

Gaze-position signals

The visual receptive fields of neurones in different cortical regions are modulated by the position of the eye in the orbit. This was originally shown by Andersen & Mountcastle (1983) in the inferior parietal cortex and has been later extended to V1 (Trotter *et al.*, 1992), V3a (Galletti & Battaglini, 1989), PO (Galletti *et al.*, 1993), MT and MST (Squatrito & Maioli, 1996; Bremmer *et al.*, 1997a), 7a and LIP (Andersen *et al.*, 1990b; Bremmer *et al.*, 1997b), PMv and dorsolateral prefrontal cortex (Boussaoud *et al.*, 1993).

It has been suggested that the combination of retinotopic receptive fields with eye position signals may result in a distributed code of target location relative to the viewer (Andersen *et al.*, 1985; Galletti *et al.*, 1993). The receptive fields of the neurones do not appear to shift their retinal locations when eye position changes, but the visual and eye position signals interact with one another to form gain fields in which the amplitude of the visual response is modulated by eye position (Andersen *et al.*, 1985). Thus these parietal neurones are tuned to a particular location in head-centred space, but only over a limited range of eye positions. Generating a signal, then, for location in head-centred space independent of eye position requires the activity of not one but a subset of parietal neurones (Andersen, 1995).

In addition, eye-position signals can modulate arm movement related activity in area 7m (Ferraina *et al.*, 1997a), and PMd (Boussaoud, 1995). Thus, there exists ample evidence for the kind of neural integration of visual, eye-position and arm-position signals that would be required to generate the egocentric representations described by psychophysicists.

Somatosensory signals in the parietal lobe

Dorsal area 5 is located on the exposed surface of the superior parietal lobule (SPL), and partly in the medial bank of the intraparietal sulcus. It is essentially a somatosensory and somato-motor centre, receiving its main cortical input from SI (mostly area 2, Jones *et al.*, 1978) and being endowed with a wide representation of the arm, with some crude somatotopy. Dorsal area 5 does not receive direct visual inputs, in contrast with the adjacent area of SPL lying within the medial bank of the intraparietal sulcus, area MIP (Johnson *et al.*, 1993; 1996). It has reciprocal cortico-cortical connections with M1 and M1/PMd border (Jones *et al.*, 1978; Strick & Kim, 1978; Johnson *et al.*, 1989; 1993). It is connected also with supplementary motor area (SMA), cingulate cortex, n. lateralis posterior and pulvinar of the thalamus (Jones *et al.*, 1978). The majority of neurones in dorsal area 5 have pure somesthetic receptive fields that are generally larger than those found in area 2 (Duffy & Burchfiel, 1971; Burbaud *et al.*, 1991). These fields are often multimodal (cutaneous and proprioceptive) and receive inputs from one or more limb segments (Duffy & Burchfiel, 1971; Sakata *et al.*, 1973; Mountcastle *et al.*, 1975; Burbaud *et al.*, 1991). Receptive fields encompassing the chest, shoulder, elbow and wrist have been reported (Burbaud

et al., 1991). Single joint neurones reflect sensitively steady joint positions (Mountcastle *et al.*, 1975). There is another population of neurones whose discharge is modulated weakly or not at all by passive mobilization of the limb, but is modulated strongly by active movements (Mountcastle *et al.*, 1975; Burbaud *et al.*, 1991), perhaps through a re-entrant mechanism of central origin. Motor-related cells can discharge well before the onset of the movement, as is the case for the motor areas of frontal cortex (Mountcastle *et al.*, 1975; Kalaska *et al.*, 1983; Chapman *et al.*, 1984; Burbaud *et al.*, 1991), and many such cells are also active during an instructed-delay period preceding directional movements (Seal *et al.*, 1983; Crammond & Kalaska, 1989; Ferraina & Bianchi, 1994). In sum, neural activity in area 5 cannot therefore be considered as a pure reflection of sensory re-afferences during movement. Many neurones in area 5 appear to encode primarily movement kinematics, and to a lesser extent dynamics (Kalaska *et al.*, 1990).

Coding of arm posture in area 5 may reside in the activity of populations of neurones which use sensory information to provide a high-order representation of movement. For instance, hand azimuth could be estimated by combining proprioceptive information about the horizontal rotation (yaw) of both shoulder and elbow joints, hand elevation and distance would be similarly derived from combinations of horizontal and vertical rotations of these two joints. As for the source of the vertical reference that is necessary for computing arm coordinates in geotropic space, area 5 could receive this information from area 2, which is in turn recipient of vestibular inputs. Alternatively, the reference could correspond to the trunk midsagittal axis. In this context, one may note that several neurones in area 5 have receptive fields encompassing both chest and shoulder.

Visuomotor transformations in parietal cortex

Recent neurophysiological studies (Ferraina *et al.*, 1997a, b; Galletti *et al.*, 1997; Johnson *et al.*, 1997) have illustrated some of the early mechanisms underlying coding of reaching in the parietal cortex of the medial wall of the hemisphere, area 7m and the rostral bank of the parieto-occipital sulcus. These superior parietal areas, thanks to the anatomical connections illustrated above, lie at the interface between vision and movement. These areas appear to sit at a relatively early stage in the process of sensor fusion leading from target and hand position sense to movement generation.

As for area PO, it has recently been parcellated into a dorsal part, area V6A, and a ventral part, area V6 or PO (Galletti *et al.*, 1996). Visual neurones in V6A have larger receptive fields and more complex properties, such as tuning to slow-motion stimuli, than those of V6. In addition, a significant proportion of neurones in V6A is not visually responsive. It has recently been shown that the activity of many neurones of both V6 (Johnson *et al.*, 1997) and V6A (Galletti *et al.*, 1997; Johnson *et al.*, 1997) relates to arm movements. Cell activity in these areas was studied while monkeys performed an instructed-delay reaching task which dissociates eye movement and position from hand movement and position (Johnson *et al.*, 1997); the task in addition separates in time the early events related to target localization from the latest ones concerning movement generation. Under these experimental conditions (Fig. 3), neural activity displays a directional modulation in most epochs of the task, i.e. during the saccadic eye movement and the preparation and execution of the hand movement. Interestingly, the activity of this neurone is modulated maximally during the reaction time, when the difference between the hand and target position is maximal. During target-holding time (THT), when the hand stays on the target, cell modulation decreases significantly. This suggests a potential processing mechanism of reaching-related

information in V6a, based on the specification of a motor error, signalling the difference between hand and target location. The spatial orientation of this cell's preferred direction did not change much across behavioural epochs, suggesting a spatial congruence between eye-and hand-related signals contributing to neural activity. This cell was not modulated by conventional visual stimuli during a visual fixation task.

Very similar results are obtained in area 7m (Ferraina *et al.*, 1997a, b). Here monkeys were trained to fixate and reach toward a peripheral target randomly selected from eight possible locations around a virtual circle. Three tasks were used to dissociate eye- from arm-related contributions. In the first task, the animal maintained fixation on a peripheral target. In the second task, it reached for the peripheral target while fixating the central target. In the third task, it looked and reached for the peripheral target. In general, the results show that the activity of some neurones is related to eye-position signals, some others to arm posture and movement, and for the majority of neurones to a combination of visuomanual and oculomotor information.

In addition to the processing involving the superior parietal cortex, also areas of the inferior parietal cortex contribute to visual reaching (Hyvärinen & Poranen, 1974; Mountcastle *et al.*, 1975; MacKay, 1992; Sakata *et al.*, 1995; Snyder *et al.*, 1997). A large class of neurones in this cortex has been identified which is directly related to hand reaching to visual targets of interest. Moreover, recent work has indicated the processing of 3D spatial properties of visual targets in the inferior parietal cortex (Gnadt & Mays, 1995; Sakata, 1996). For instance, the neural activity of many cells in area 7a (Sakata *et al.*, 1980) and LIP (Gnadt & Mays, 1995) varies according to the depth of a visual target. The firing rate of these cells is modulated by both changes in stimulus blur and changes of vergence angle or absolute disparity. Thus, there is both psychophysical (McIntyre *et al.*, 1997; see the section on psychophysics above) and electrophysiological evidence (Gnadt & Mays, 1995) for the integration of vergence, disparity and accommodation signals within the CNS.

Moreover LIP neurones may encode both distance and direction information. Some cells signal actual or intended changes in eye position in the absence of retinal stimulation, to be used also in conjunction with memory-saccades (Gnadt & Andersen, 1988; Gnadt & Mays, 1995). The authors have argued that these neurones encode their activity in motor spatial parameters, with distinct directional and depth tuning (Gnadt & Mays, 1995). Thus, even at a very early stage of the information processing in the dorsal stream, different signals are combined in the compositions of motor commands for reaching.

Coding in an egocentric frame of reference in the superior parietal lobule

There is recent evidence that the dorsal area 5 of the superior parietal lobule might be a substrate for egocentric representations of reaching in the monkey (Lacquaniti *et al.*, 1995; Lacquaniti, 1997). In this study, monkeys were trained to make arm movements directed to visual targets placed in different parts of the 3D workspace in a reaction-time task. It was found that the mean activity of most neurones in area 5 during the movement is monotonically related to the position of either the target or the hand with respect to the head and body (Fig. 4). This is so irrespective of the starting position of the hand in the workspace and therefore of the direction of the movement. The activity of some neurones may reflect the current position of the limb, as derived from peripheral feedback or efferent copy of motor commands. However, the activity of many other neurones relates to the final point, although this has not yet been

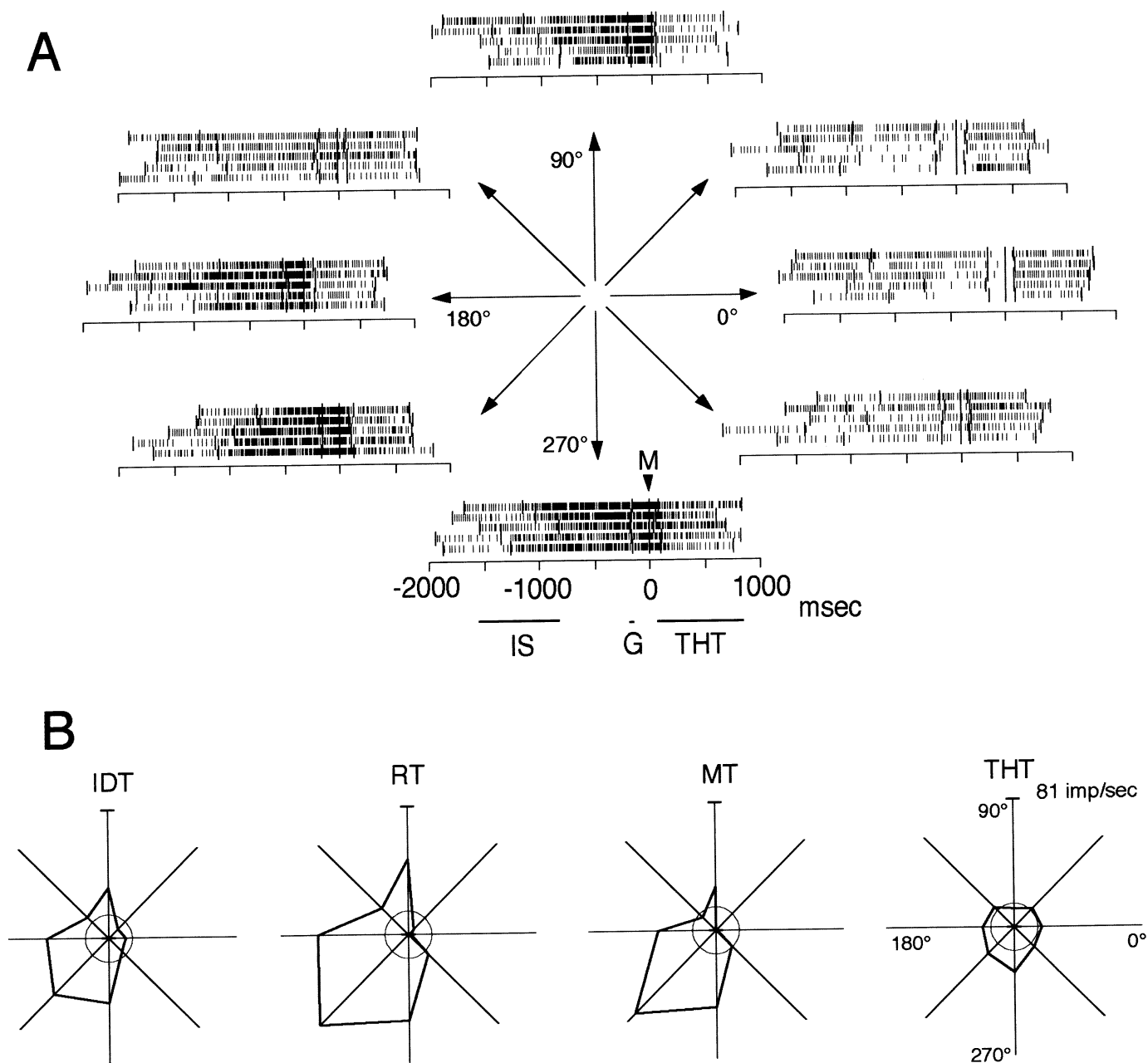


FIG. 3. Impulse activity of a neuron in area V6A, studied while a monkey made arm movements in eight different directions from a common central origin, in an instructed-delay reaching task. (A) The central target was lit red and the animals fixated and touched it with the hand for a variable centre holding time (CHT, 1–1.5 s), after which one of the eight peripheral targets was randomly lit green. Rasters of five replications for every movement directions were aligned to movement onset (M). Each vertical line indicates the occurrence of an action potential; longer vertical lines from left to right indicate the beginning of the trial (when the animal positioned the hand at the central position which served as origin of movement), the presentation of the instruction-signal (IS), telling the animals where to make the next arm movement upon presentation of the go-signal (G), the beginning of the arm movement (M), the end of arm movement, and the end of target holding time (THT), during which the hand was held immobile on the target. Horizontal bars above the acronyms indicate the temporal span of these events. The time elapsing between IS and G is the instructed-delay time (IDT), during which the animal withheld the arm movement until the go-signal was presented. The time between the presentation of the go-signal and the beginning of movement is the reaction-time (RT). (B) Polar plots of impulse activity during different epochs of the task. Circles indicate the mean frequency of discharge during CHT. (Modified from Johnson *et al.*, 1997.)

reached, i.e. during reaction time or movement time, reflecting a preplanned desired position or 'command function' (Mountcastle *et al.*, 1975), rather than current kinematics.

An additional observation is that the tuning functions across the whole population of area 5 neurones are not uniformly distributed in 3D space. Instead, some neurones are tuned almost selectively along the coordinate axis of the azimuth (Fig. 4A,B), whereas

others are tuned for the elevation (Fig. 4C,D) and still others for the distance (Fig. 4E,F). Thus each spatial coordinate tends to be encoded in a different subpopulation of neurones. However, the separation is incomplete as there is significant cross-talk among the three channels.

There exist some important features which differentiate the behaviour of neurones in parietal area 5 (Lacquaniti *et al.*, 1995) and areas

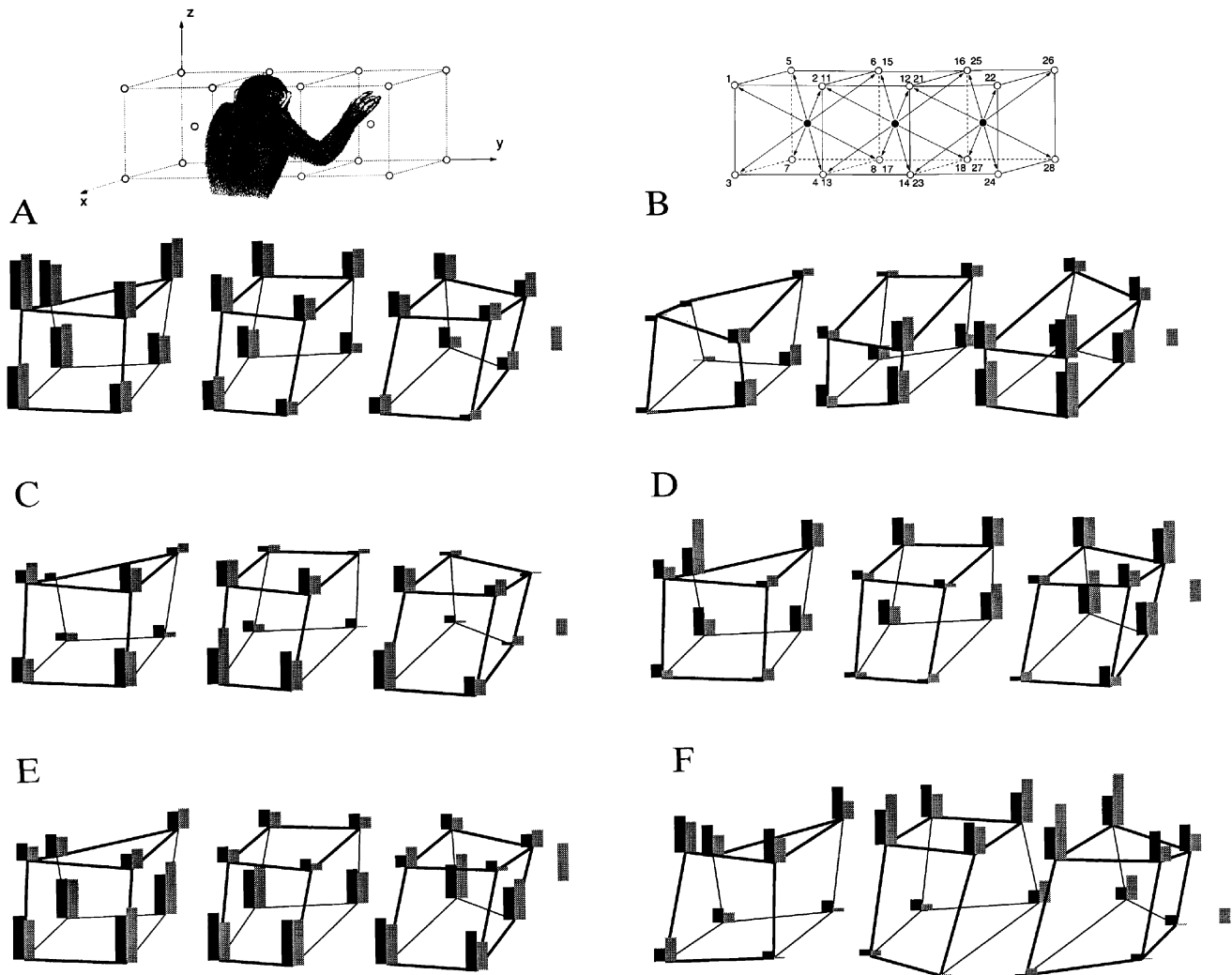


FIG. 4. Mean activity of six neurones of area 5 supports the notion that hand position is coded in egocentric coordinates. Each neurone is best tuned to the changes in one spatial coordinate of the hand: A and B, to azimuth (A, increasing from right to left; B, from left to right); C and D, to the distance of the hand from the body (the closer is the hand, the greater the activity in C and the smaller in D); and E and F, to elevation (increasing with downward movements in E, and with upward movements in F). The wire frames correspond to the three workspaces depicted in the insets (top), with the corners indicating the position of the wrist relative to the monkey at the end of the movement to the corresponding target. Grey bars, the activity averaged during movement time; black bars, the activity predicted by a linear model of final wrist position in spherical coordinates. Calibration bars: 20 spikes/s. (Modified from Lacquaniti *et al.*, 1995.)

3, 1 and 2 of the primary somatosensory cortex (Helms Tillery *et al.*, 1996) from the behaviour of neurones in motor and premotor cortex (cf. Caminiti & Johnson, 1992; Georgopoulos, 1995). First, in all these parietal areas there is a positional code of hand location rather than the kind of vector code of movement direction that is normally found in the frontal areas. Second, the sensitivity of neurones to changes in hand location is non-uniform for all directions in space in the parietal areas, but it tends to be more or less uniform in the frontal areas unless arm posture is changed (Scott & Kalaska, 1997).

As for the functional significance of non-uniform representations of space in neuronal ensembles, the following considerations are in order. Neural parcellation could be a correlate of the psychophysical observation that these spatial parameters are processed in parallel and largely independent of each other (Flanders *et al.*, 1992). Projecting the spatial information on to separate axes of neural coding could be important for sensorimotor coordination, because information related to motor commands could be matched more easily with incoming sensory feedbacks. Spatial axes which result from a hybrid combina-

tion of sensory and motor axes would be best suited to accomplish this matching process (Carrozzo & Lacquaniti, 1994). Although spatial information is parcellated at the level of single neurones, the complete information about limb position can be reconstructed by simple summation of the individual contributions over a population of neurones, because positive and negative spatial coefficients tend to be evenly distributed (Lacquaniti *et al.*, 1995). This can be demonstrated by using a neural network model. A layered neural network whose intermediate layer contains positionally tuned neurones can be trained to generate the position of the hand in body-centred coordinates. It is not known whether global reconstruction of limb position takes place at a cortical level or at a subcortical level (Mountcastle, 1995).

Functional anatomy of the human parietal networks during visuomanual coordination

In general, the organization of the cortical networks for visuomotor coordination demonstrated in man by neuroimaging (with positron

emission tomography, PET, or magnetic resonance, MR) is coherent with that described in non-human primates (cf. Ungerleider, 1995). In humans, tracking a moving target with the finger (Grafton *et al.*, 1992), preparation for reaching (Decety *et al.*, 1992), actual reaching (Kawashima *et al.*, 1995; Grafton *et al.*, 1996; Lacquaniti *et al.*, 1997), and imaginary arm movements (Decety *et al.*, 1994; Stephan *et al.*, 1995), all involve prestriate areas along the dorsal stream of the visual cortico-cortical pathways, posterior parietal areas, and motor and premotor areas in the frontal lobe.

Visual inputs

Striate (V1) and prestriate (V2, V3a) areas can be coactivated with a region in the middle occipital gyrus (Brodmann area, BA 19/37), at the junction with the temporal lobe. This region corresponds closely with the visual motion area described in several studies (Corbetta *et al.*, 1991; Dupont *et al.*, 1994; Decety *et al.*, 1994; Tootell *et al.*, 1995; Watson *et al.*, 1993), corresponding to the MT/MST complex (V5) in the monkey. The visual monitoring of hand movements is responsible for the involvement of this area. In addition to the MT/MST complex, also the dorsolateral occipital area described by Haxby *et al.* (1994) for visuospatial vision can be involved in visuomanual coordination. This lateral occipital region could be the human homologue of the dorsal part of area PO (V6A) in the monkey (De Jong *et al.*, 1994; Dupont *et al.*, 1994).

Posterior parietal cortex

The supramarginal gyrus (BA 40) contralateral to the moving arm can be activated in visuomotor tasks. This activation has been reported in pointing to visual targets (Lacquaniti *et al.*, 1997), as well as in other tasks involving directional movements of the arm (Colebatch *et al.*, 1991; Decety *et al.*, 1992). Eidelberg & Galaburda (1984) have proposed a homology between human BA 40 and area 7b in the monkey. The latter is located in the anterior part of the inferior parietal lobule and is extensively interconnected with the ventral premotor cortex (Jeannerod *et al.*, 1995) where neurones are endowed with spatially aligned visual and somatosensory receptive fields (Gentilucci *et al.*, 1988; Graziano *et al.*, 1994), as is also observed in area 7b (Hyvärinen, 1981).

Pointing under visual guidance involves another region in the inferior parietal lobule (BA 40) of the hemisphere contralateral to the moving arm, located more dorsally relative to the supramarginal gyrus, in the proximity of the interparietal sulcus (Grafton *et al.*, 1992; Seitz *et al.*, 1994; Lacquaniti *et al.*, 1997). A similar involvement has been reported in tasks involving executed or imagined arm movements (Decety *et al.*, 1994; Stephan *et al.*, 1995), and visuospatial detection tasks (Haxby *et al.*, 1994).

Neurological studies of patients affected by optic ataxia, a disturbance of visuomotor coordination in the absence of visual or motor deficits capable of explaining the symptoms, are especially pertinent in this context (Rondot *et al.*, 1977). These patients exhibit a specific deficit in localizing a visual target with respect to their body (egocentric localization), whereas they do not have problems in localizing the object relative to other external objects and the environment (allocentric localization). The most common site of the lesion is centred around the interparietal sulcus and the superior parietal lobule contralateral to the affected arm (Ratcliff & Davies-Jones, 1972; Levine *et al.*, 1978; Auerbach & Alexander, 1981; Perenin & Vighetto, 1988).

Functional neuroimaging studies indicate that the SPL (BA 5/7) is involved in reaching under visual guidance (Lacquaniti *et al.*, 1997), during automatic and voluntary shifting of visuospatial attention

(Corbetta *et al.*, 1993, 1995), spatial vision (Haxby *et al.*, 1994) and visual imagery (Kosslyn *et al.*, 1993). As described above, neurones in the SPL of the monkey take part in the process of coordinate transformations by encoding reaching movements in an egocentric frame of reference (Lacquaniti *et al.*, 1995). Finally, reaching under visual guidance involves also cuneate and precuneate regions on the mesial side of the hemisphere contralateral to the moving arm (Kawashima *et al.*, 1994; Grafton *et al.*, 1996). These regions could be the human homologue of area 7m in the monkey.

Recent work has provided evidence that regions in the superior parietal lobule related to finger movements have gaze-dependent activation (Sanes *et al.*, 1996). In this functional MR study, regions located largely posterior to the postcentral sulcus and extending into anterior portions of the interparietal sulcus that are activated by repetitive and sequential finger tapping also exhibited increased areal activation when gaze was directed toward the sector of space occupied by the moving digits. In addition, a specific role of posterior parietal cortex in the recalibration of visually guided reaching has been demonstrated in a PET study in which subjects wore displacing prisms while reaching to visual targets (Clower *et al.*, 1996). On the whole, these data indicate that neural substrates also exist in the human cerebral cortex for co-ordinating interactions between eye (or gaze) position and hand movements.

In sum, the gist of this review has been that the end-point positions of reaching with visual feedback of the hand are specified by combining visuo-spatial, gaze and arm information in an egocentric, viewer-based frame of reference, and that posterior parietal cortex represents a key node in the distributed cortical network involved in the process of multisensory fusion.

Abbreviations

BA	Brodmann area
LIP	lateral intraparietal area
MIP	medial intraparietal area
MR	magnetic resonance
MST	medial superior temporal area
MT	middle temporal area
PET	positron emission tomography
PMd	dorsal premotor cortex area
PMdr	rostral part of dorsal premotor cortex
PMv	ventral premotor area
PO	parieto-occipital area
SMA	supplementary motor area
SPL	superior parietal lobule
THT	target-holding time
VIP	ventral intraparietal area

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References

- Andersen, R.A. (1995) Encoding of intention and spatial location in the posterior parietal cortex. *Cereb. Cortex*, **5**, 457–469.
- Andersen, R.A., Asanuma, C., Essick, G.K. & Siegel, R.M. (1990a) Corticocortical connections of anatomically and physiologically defined subdivisions within inferior parietal lobule. *J. Comp. Neurol.*, **296**, 65–13.
- Andersen, R.A., Bracewell, R.M., Barash, S., Gnadt, J.W. & Fogassi, L. (1990b) Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.*, **10**, 1176–1196.
- Anderson, R.A. & Mountcastle, V.B. (1983) The influence of the angle upon the excitability of the light-sensitive neurones of the posterior parietal cortex. *J. Neurosci.*, **3**, 532–548.

- Andersen, R.A., Essick, G.K. & Siegel, R.M. (1985) Encoding of spatial location by posterior parietal neurons. *Science*, **230**, 456–458.
- Auerbach, S.H. & Alexander, M.P. (1981) Pure agraphia and unilateral optic ataxia associated with a left superior parietal lobule lesion. *J. Neurol. Neurosurg. Psychiatry*, **44**, 430–432.
- Boussaoud, D. (1995) Primate premotor cortex: modulation of preparatory neuronal activity by the gaze angle. *J. Neurophysiol.*, **73**, 886–890.
- Boussaoud, D., Barth, T.M. & Wise, S.P. (1993) Effects of gaze on apparent visual responses of frontal cortex neurons. *Exp. Brain Res.*, **93**, 423–434.
- Boussaoud, D., Ungerleider, L.G. & Desimone, R. (1990) Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *J. Comp. Neurol.*, **296**, 462–495.
- Bremmer, F., Distler, C. & Hoffmann, K.-P. (1997b) Eye-position effects in monkey cortex. II. Pursuit-and fixation-related activity in posterior parietal areas LIP and 7a. *J. Neurophysiol.*, **77**, 962–977.
- Bremmer, F., Ilg, U.J., Thiele, A., Distler, C. & Hoffmann, K.-P. (1997a) Eye-position effects in monkey cortex. I. Visual and pursuit-related activity in extrastriate areas MT and MST. *J. Neurophysiol.*, **77**, 944–961.
- Burbaud, P., Doegle, C., Gross, C. & Bioulac, B. (1991) A quantitative study of neuronal discharge in area 5, 2, and 4 of the monkey during fast arm movements. *J. Neurophysiol.*, **66**, 429–443.
- Caminiti, R. & Johnson, P.B. (1992) Internal representations of movement in the cerebral cortex as revealed by the analysis of reaching. *Cereb. Cortex*, **2**, 269–276.
- Caminiti, R., Ferraina, S. & Johnson, P.B. (1996a) The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb. Cortex*, **6**, 319–328.
- Caminiti, R., Hoffmann, K.-P., Lacquaniti, F. & Altman, J. (1996b) (eds) *Vision and Movement Mechanisms in the Cerebral Cortex*. Human Frontier Science Program, Strasbourg.
- Carrozzo, M. & Lacquaniti, F. (1994) A hybrid frame of reference for visuomotor coordination. *NeuroReport*, **5**, 453–456.
- Cavada, C. & Goldman-Rakic, P.S. (1989) Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory cortico-cortical connections. *J. Comp. Neurol.*, **287**, 393–421.
- Chapman, C.E., Spidalieri, C. & Lamarre, Y. (1984) Discharge properties of area 5 neurones during arm movements triggered by sensory stimuli in the monkey. *Brain Res.*, **309**, 63–77.
- Clover, D.M., Hoffman, J.M., Votaw, J.R., Faber, T.L., Woods, R.P. & Alexander, G.E. (1996) Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature*, **383**, 618–621.
- Colby, C.L., Gattass, R., Olson, C.R. & Gross, C.G. (1988) Topographic organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *J. Comp. Neurol.*, **269**, 392–413.
- Colebatch, J.G., Deiber, M.-P., Passingham, R.E., Friston, K.J. & Frackowiak, R.S.J. (1991) Regional cerebral blood flow during voluntary arm and hand movements in human subjects. *J. Neurophysiol.*, **65**, 1392–1401.
- Collewijn, H. & Erkelens, C.J. (1990) Binocular eye movements and the perception of depth. In Kowler E. (ed.) *Eye Movements and Their Role in Visual and Cognitive Processes*. Amsterdam: Elsevier, pp. 213–260.
- Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L. & Petersen, S.E. (1991) Selective and divided attention during visual discriminations of shape, color, and speed – Functional anatomy by positron emission tomography. *J. Neurosci.*, **11**, 2383–2402.
- Corbetta, M., Miezin, F.M., Shulman, G.L. & Petersen, S.E. (1993) A PET study of visuospatial attention. *J. Neurosci.*, **13**, 1202–1226.
- Corbetta, M., Shulman, G.L., Miezin, F.M. & Petersen, S.E. (1995) Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, **270**, 802–805.
- Covey, E.R., Gattass, R. & Gross, C.G. (1982) A new visual area in the parieto-occipital sulcus of the macaque. *Soc. Neurosci. Abstr.*, **8**, 681.
- Crammond, D.J. & Kalaska, J.F. (1989) Neuronal activity in primate parietal area 5 varies with intended movement direction during an instructed-delay period. *Exp. Brain Res.*, **76**, 458–469.
- Decety, J., Kawashima, R., Gulyas, B. & Roland, P.E. (1992) Preparation for reaching: a PET study of the participating structures in human brain. *NeuroReport*, **3**, 761–764.
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J.C. & Fazio, F. (1994) Mapping motor representations with positron emission tomography. *Nature*, **371**, 600–602.
- Duffy, F.H. & Burchfiel, J.L. (1971) Somatosensory system: organizational hierarchy from single units in monkey area 5. *Science*, **172**, 273–275.
- Duffy, C.J. & Wurtz, R.H. (1991) Sensitivity of MST neurones to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *J. Neurophysiol.*, **65**, 1329–1345.
- Dupont, P., Orban, G.A., De Bruyn, B., Verbruggen, A. & Mortelmans, L. (1994) Many areas in the human brain respond to visual motion. *J. Neurophysiol.*, **72**, 1420–1424.
- Eidelberg, D. & Galaburda, A.M. (1984) Inferior parietal lobule. Divergent architectonic asymmetries in the human brain. *Arch. Neurol.*, **41**, 843–852.
- Felleman, D.J. & Van Essen, D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex*, **1**, 1–47.
- Ferraina, S. & Bianchi, L. (1994) Posterior parietal cortex: functional properties of neurones in area 5 during an instructed-delay reaching task within different parts of space. *Exp. Brain Res.*, **99**, 175–178.
- Ferraina, S., Garasto, M.R., Battaglia-Mayer, A., Ferraresi, P., Johnson, P.B., Lacquaniti, F. & Caminiti, R. (1997a) Visual control of hand reaching movement: Activity in parietal area 7m. *Eur. J. Neurosci.*, **9**, 1090–1095.
- Ferraina, S., Johnson, P.B., Garasto, M.R., Battaglia-Mayer, A., Ercolani, L., Bianchi, L., Lacquaniti, F. & Caminiti, R. (1997b) Neural correlates of eye-hand coordination during reaching: Activity in area 7m in the monkey. *J. Neurophysiol.*, **77**, 1034–1038.
- Flanders, M., Helms Tillery, S.I. & Soechting, J.F. (1992) Early Stages in a Sensorimotor Transformation. *Behav. Brain Sci.*, **15**, 309–362.
- Galletti, C. & Battaglini, P.P. (1989) Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *J. Neurosci.*, **9**, 1112–1125.
- Galletti, C., Battaglini, P.P. & Fattori, P. (1993) Parietal neurones encoding spatial locations in craniotopic coordinates. *Exp. Brain Res.*, **96**, 221–229.
- Galletti, C., Fattori, P., Battaglini, P.P., Shipp, S. & Zeki, S. (1996) Functional demarcation of a border between areas V6 and V6A in the superior parietal gyrus of the macaque monkey. *Eur. J. Neurosci.*, **8**, 30–52.
- Galletti, C., Fattori, P., Kutz, D.F. & Battaglini, P.P. (1997) Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. *Eur. J. Neurosci.*, **9**, 410–413.
- Gattass, R., Sousa, A.P.B. & Covey, E. (1985) Cortical visual areas of the macaque: possible substrates for pattern recognition mechanisms. *Pont. Acad. Sci. Scripta Varia*, **54**, 1–20.
- Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R.M. & Rizzolatti, G. (1988) Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp. Brain Res.*, **71**, 475–490.
- Georgopoulos, A.P. (1991) Higher Order Motor Control. *Annu. Rev. Neurosci.*, **14**, 361–377.
- Georgopoulos, A.P. (1995) Current issues in directional motor control. *Trends Neurosci.*, **18**, 506–510.
- Gnadt, J.W. & Andersen, R.A. (1988) Memory related motor planning activity in posterior parietal cortex of macaque. *Exp Brain Res.*, **70**, 216–220.
- Gnadt, J.W. & Mays, L.E. (1995) Neurones in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *J. Neurophysiol.*, **73**, 280–297.
- Goodale, M.A. & Milner, A.D. (1992) Separate visual pathways for perception and action. *Trends Neurosci.*, **15**, 20–25.
- Gordon, J., Ghilardi, M.F. & Ghez, C. (1994) Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Exp. Brain Res.*, **99**, 97–111.
- Grafton, S.T., Fagg, A.H., Woods, R.P. & Arbib, M.A. (1996) Functional anatomy of pointing and grasping in humans. *Cereb. Cortex*, **6**, 226–237.
- Grafton, S.T., Mazziotta, J.C., Woods, R.P. & Phelps, M.E. (1992) Human functional anatomy of visually guided movements. *Brain*, **115**, 565–587.
- Graziano, M.S., Yap, G.S. & Gross, C.G. (1994) Coding of visual space by premotor neurones. *Science*, **266**, 1054–1057.
- Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P. & Grady, C.L. (1994) The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J. Neurosci.*, **14**, 6336–6353.
- Helms Tillery, S.I., Soechting, J.F. & Ebner, T.J. (1996) Somatosensory cortical activity in relation to arm posture: nonuniform spatial tuning. *J. Neurophysiol.*, **76**, 2423–2438.
- Hyvärinen, J. (1981) Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res.*, **206**, 287–303.
- Hyvärinen, J. & Poranen, A. (1974) Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain*, **97**, 673–692.
- Jeannerod, M. (1988) *The Neural and Behavioural Organization of Goal-directed Movements*. Clarendon Press, Oxford.
- Jeannerod, M. (1991) A neurophysiological model for the directional coding of reaching movements. In Paillard J. (ed.), *Brain and Space*. Oxford University Press, Oxford, UK, pp. 49–69.
- Jeannerod, M. (1996) The neural control of object-oriented actions. In Lacquaniti, F. and Viviani P. (eds), *Neural Bases of Motor Behaviour*. Kluwer, Dordrecht, pp. 41–76.

- Jeannerod, M., Arbib, M.A., Rizzolatti, G. & Sakata, H. (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.*, **18**, 314–320.
- Johnson, P.B., Angelucci, A., Ziparo, R.M., Minciocchi, D., Bentivoglio, M. & Caminiti, R. (1989) Segregation and overlap of callosal and association neurones in frontal and parietal cortices of primates. A spectral and coherency analysis. *J. Neurosci.*, **9**, 2313–2326.
- Johnson, P.B., Ferraina, S., Bianchi, L. & Caminiti, R. (1996) Cortical networks for visual reaching. Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cereb. Cortex*, **6**, 102–119.
- Johnson, P.B., Ferraina, S. & Caminiti, R. (1993) Cortical networks for visual reaching. *Exp. Brain Res.*, **97**, 361–365.
- Johnson, P.B., Ferraina, S., Garasto, M.R., Battaglia-Mayer, A., Ercolani, L., Burnod, Y. & Caminiti, R. (1997) From vision to movement: cortico-cortical connections and combinatorial properties of reaching-related neurones in parietal areas V6 and V6A. In Theier, P. and Karnath, O. (eds), *Parietal Lobe Contributions to Orientation in 3D Space*. Springer-Verlag, Heidelberg, pp. 221–236.
- Jones, E.G., Coulter, J.D. & Hendry, S.H.C. (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. *J. Comp. Neurol.*, **181**, 291–348.
- de Jong, B.M., Shipp, S., Skidmore, B., Frackowiak, R.S.J. & Zeki, S. (1994) The cerebral activity related to the visual perception of forward motion in depth. *Brain*, **117**, 1039–1054.
- Kalaska, J.F., Caminiti, R. & Georgopoulos, A.P. (1983) Cortical mechanisms related to the direction of two-dimensional arm movements: Relations in parietal area 5 and comparison with motor cortex. *Exp. Brain Res.*, **51**, 247–260.
- Kalaska, J.F., Cohen, D.A.D., Prud'homme, M. & Hyde, M.L. (1990) Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. *Exp. Brain Res.*, **80**, 351–364.
- Kalaska, J.F. & Crammond, D.J. (1992) Cerebral cortical mechanisms of reaching movements. *Science*, **255**, 1517–1523.
- Kawashima, R., Roland, P.E. & O'Sullivan, B.T. (1994) Fields in human motor areas involved in preparation for reaching, actual reaching, and visuomotor learning: a positron emission tomography study. *J. Neurosci.*, **14**, 3462–3474.
- Knudsen, E.I. & Brainard, M.S. (1995) Creating a unified representation of visual and auditory space in the brain. *Annu. Rev. Neurosci.*, **18**, 19–43.
- Kosslyn, S.M., Alpert, N.M., Thompson, W.L., Maljkovic, V., Weise, S.B., Chabris, C.F., Hamilton, S.E., Rauch, S.L. & Buonanno, F.S. (1993) Visual mental imagery activates topographically organized visual cortex – PET investigations. *J. Cogn. Neurosci.*, **5**, 263–287.
- Lacquaniti, F. (1997) Frames of reference in sensorimotor coordination. In Boller, F. and Grafman, J. (eds), *Handbook of Neuropsychology*, Vol. 11. Elsevier, Amsterdam, pp. 27–64.
- Lacquaniti, F., Guigon, E., Bianchi, L., Ferraina, S. & Caminiti, R. (1995) Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb. Cortex*, **5**, 391–409.
- Lacquaniti, F., Perani, D., Guigon, E., Bettinardi, V., Carrozzo, M., Grassi, F., Rossetti, Y. & Fazio, F. (1997) Visuomotor transformations for reaching to memorized targets: A PET study. *NeuroImage*, **5**, 129–146.
- Levine, D.N., Kaufman, K.J. & Mohr, J.P. (1978) Inaccurate reaching associated with a posterior parietal lobe tumor. *Neurology*, **28**, 556–561.
- MacKay, W.A. (1992) Properties of reach-related neuronal activity in cortical area 7a. *J. Neurophysiol.*, **67**, 1335–1345.
- Matelli, M., Camarda, R., Glickstein, M. & Rizzolatti, G. (1986) Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J. Comp. Neurol.*, **251**, 281–298.
- McIntyre, J., Stratta, F. & Lacquaniti, F. (1997) Viewer-centered frame of reference for reaching to memorized targets in three-dimensional space. *J. Neurophysiol.*, **78**, 1601–1618.
- Mountcastle, V.B. (1995) The parietal system and some higher brain functions. *Cereb. Cortex*, **5**, 377–390.
- Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H. & Acuna, C. (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J. Neurophysiol.*, **38**, 871–908.
- Paillard, J. (1991) Motor and representational framing of space. In Paillard, J. (ed), *Brain and Space*. Oxford University Press, New York, pp. 163–182.
- Perenin, M.T. & Vighetto, A. (1988) Optic ataxia: a specific disruption in visuomotor mechanisms. *Brain*, **111**, 643–674.
- Ratcliff, G. & Davies-Jones, G.A.B. (1972) Defective visual localization in focal brain wounds. *Brain*, **95**, 49–60.
- Rondot, P., Recondo, J.D. & Ribadeau Dumas, J.L. (1977) Visuomotor ataxia. *Brain*, **100**, 355–376.
- Sakata, H. (1996) Coding of 3D features of objects used in manipulation by parietal neurones. In Caminiti, R., Hoffmann, K-P., Lacquaniti, F., Altman, J. (eds), *Vision and Movement Mechanisms in the Cerebral Cortex*. Human Frontier Science Programme, Strasbourg, pp. 55–63.
- Sakata, H., Shibutani, H. & Kawano, K. (1980) Spatial properties of visual fixation neurones in posterior parietal association cortex of the monkey. *J. Neurophysiol.*, **43**, 1654–1672.
- Sakata, H., Shibutani, H., Kawano, K. & Harrington, T.L. (1985) Neural mechanisms of space vision in the parietal association cortex of the monkey. *Vision Res.*, **25**, 453–464.
- Sakata, H., Taira, M., Murata, A. & Mine, S. (1995) Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb. Cortex*, **5**, 429–438.
- Sakata, H., Takaoka, Y., Kawarasaki, A. & Shibutani, H. (1973) Somatosensory properties of neurones in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Res.*, **64**, 85–102.
- Sanes, J.N., Donoghue, J.P., Siewert, B., Edelman, R.R. & Warach, S. (1996) Gaze direction modifies human motor cortical hand representations. *Soc. Neurosci. Abstr.*, **22**, 1450.
- Scott, S.H. & Kalaska, J.F. (1997) Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *J. Neurophysiol.*, **77**, 826–852.
- Seal, J., Gross, C. & Bioulac, B. (1983) Different neuronal populations within area 5 of the monkey. *Exp. Brain Res. (Suppl.)*, **7**, 156–163.
- Seitz, R.J., Canavan, A.G.M., Yaguez, L., Herzog, H., Tellman, L., Knorr, U., Huang, Y. & Homberg, V. (1994) Successive roles of the cerebellum and premotor cortices in trajectory learning. *NeuroReport*, **5**, 2541–2544.
- Simpson, J.I. & Graf, W. (1985) The selection of reference frames by nature and its investigation. *Rev. Oculomot. Res.*, **1**, 3–20.
- Snowden, R.J., Treue, S. & Andersen, R.A. (1992) The response of neurones in areas V1 and MT of the alert rhesus monkey to moving random dot patterns. *Exp. Brain Res.*, **88**, 389–400.
- Snyder, L.H., Batista, A.P. & Andersen, R.A. (1997) Coding of intention in the posterior parietal cortex. *Nature*, **386**, 167–170.
- Soechting, J.F. & Flanders, M. (1989) Sensorimotor representations for pointing to targets in three-dimensional space. *J. Neurophysiol.*, **62**, 582–594.
- Soechting, J.F. & Flanders, M. (1992) Moving in three-dimensional space: frames of reference, vectors, and coordinate systems. *Annu. Rev. Neurosci.*, **15**, 167–191.
- Squatrito, S. & Maioli, M.G. (1996) Gaze field properties of eye position neurones in areas MST and 7a of the macaque monkey. *Visual Neurosci.*, **13**, 385–398.
- Stein, J.F. (1992) The representation of egocentric space in the posterior parietal cortex. *Behav. Brain Sci.*, **15**, 691–700.
- Stephan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos-Baumann, A.O., Frith, C.D. & Frackowiack, R.S.J. (1995) Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.*, **73**, 373–386.
- Strick, P.L. & Kim, R. (1978) Input to primate motor cortex from posterior parietal cortex (area 5). I. Demonstration by retrograde transport. *Brain Res.*, **157**, 325–330.
- Tanné, J., Boussaoud, D., Boyer-Zeller, N. & Rouillier, E. (1995) Direct visual pathways for reaching movements in the macaque monkey. *NeuroReport*, **7**, 267–272.
- Thier, P. & Erickson, R.G. (1992) Responses of visual-tracking neurones from cortical area MST-1 to visual, eye and head motion. *Eur. J. Neurosci.*, **4**, 539–553.
- Tootell, R.B.H., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R. & Belliveau, J.W. (1995) Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.*, **15**, 3215–3230.
- Trotter, U., Celebrini, S., Sticenne, B., Thorpe, S. & Imbert, M. (1992) Modulation of neural stereoscopic processing in primate area V1 by the viewing distance. *Science*, **257**, 1279–1289.
- Ungerleider, L.G. (1995) Functional brain imaging studies of cortical mechanisms for memory. *Science*, **270**, 769–775.
- Ungerleider, L.G. & Mishkin, M. (1982) Two cortical visual systems. In Ingle, D.J., Goodale, M.A. and Mansfield, R.J.W. (eds), *Analysis of Visual Behavior*. MIT Press, Cambridge, pp. 549–586.
- Watson, J.D.G., Myers, R., Frackowiak, R.S.J., Hajual, J.V., Woods, R.P., Mattiona, J.G., Skipp, S. & Zeki, S. (1993) Area V5 of the human brain: evidence from a combined study using PET and MR imaging. *Cereb. Cortex*, **3**, 79–94.
- Wise, S.P., Boussaoud, D., Johnson, P.B. & Caminiti, R. (1997) Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Ann. Rev. Neurosci.*, **20**, 25–42.