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Role of the medial parieto-occipital cortex in the control of reaching and grasping movements

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Abstract The medial parieto-occipital cortex is a central node in the dorsomedial visual stream. Recent physiological studies in the macaque monkey have demonstrated that the medial parieto-occipital cortex contains two areas, the visual area V6 and the visuomotor area V6A. Area V6 is a retinotopically organized visual area that receives form and motion information directly from V1 and is heavily connected with the other areas of the dorsal visual stream, including V6A. Area V6A is a bimodal visual/somatosensory area that elaborates visual information such as form, motion and space suitable for the control of both reaching and grasping movements. Somatosensory and skeletomotor activities in V6A affect the upper limbs and involve both the transport phase of reaching and grasping movements. Finally, V6A is strongly and reciprocally connected with the dorsal premotor cortex controlling arm movements. The picture emerging from these data is that the medial parieto-occipital cortex is well equipped to control both proximal and distal movements in the online visuomotor guidance of prehension. In agreement with this view, selective V6A lesions in monkey produce misreaching and misgrasping with the arm contralateral to the lesion in visually guided movements. These deficits are similar to those observed in optic ataxia patients and suggest that human and monkey superior parietal lobules are homologous structures, and that optic ataxia syndrome is the result of the lesion of a 'human' area V6A.

Keywords Area V6 · Area V6A · Dorsal visual stream · Optic ataxia · Visuomotor transformation · Control of prehension

Introduction

Prehension under visual guidance entails two partially distinct motor processes: the 'transport' phase (reaching), in which the arm moves towards the object to be grasped, and the 'grasping' phase, in which shaping and orientation of the hand is adapted to the form and orientation in space of the object to be grasped. As the transport phase requires spatial information on object location and involves proximal muscles of the arm, whereas grasping involves distal muscles and needs information relative to the intrinsic attributes of the object, it was suggested that prehension movements under visual guidance are controlled by two parallel visuomotor channels, one for reaching, the other for grasping (Arbib 1981; Arbib et al. 1985; Jeannerod 1981; Jeannerod and Biguer 1982).

Functional and anatomical data suggested that reaching movements are controlled by a medial parietofrontal circuit that involves the superior parietal lobule (SPL) and the dorsal premotor cortex (PMd), while grasping movements are controlled by a lateral parietofrontal circuit involving the inferior parietal lobule (IPL) and the ventral premotor cortex (PMv, Jeannerod et al. 1995; Wise et al. 1997). In recent years, the theory of parallel visuomotor channels has been debated and criticized by several authors from both the experimental and theoretical points of view (see Desmurget et al. 1996; Mon-Williams and McIntosh 2000; Smeets and Brenner 1999). It has been demonstrated that the pathways linking posterior parietal cortex with PMd and PMv, though largely segregated, also partially overlap (Tanne-Gariepy et al. 2002). In addition, it is now clear that both PMd and PMv contain cells encoding the arm direction of movement (Caminiti et al. 1991; Kakei et al. 2001; Wise et al. 1986), as well as proximal and distal representations of the arm (Fogassi et al. 1999; Gentilucci et al. 1988; Rizzolatti et al. 1988). The conclusion is that the medial and lateral parietofrontal circuits can hardly be considered as two separate visuomotor channels for reaching and grasping. They seem more likely involved in both processes.

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Evidence from neurological studies strongly supports this view. Human patients suffering from optic ataxia syndrome after posterior parietal lesions are generally impaired in both reaching and grasping movements (Perenin and Vighetto 1988). It has been observed in both humans and monkeys that when the lesion involves the anterior lateral bank of the intraparietal sulcus, selective deficits in the coordination of finger movements during grasping can appear, whereas reaching is less disturbed (Binkofski et al. 1998; Gallese et al. 1997). However, the reverse dissociation, that is specific impairment of reach component alone, has never been described.

Further support for the view of a functional coupling between reaching and grasping channels comes from psychophysical data on human subjects: selective pertur-

bation of the size, orientation or location of the object to be grasped influences all the components of prehension movement (Paulignan et al. 1991; Stelmach et al. 1994). It has also been demonstrated that the arm transport and hand orientation required to reach and grasp objects with different orientations are neither planned nor controlled independently (Desmurget et al. 1996) and, in monkey, that object size and its location affect both reaching and grasping movements (Roy et al. 2002). All these data suggest a common pathway for reaching and grasping, or at least the existence of a strong functional coupling between different components of prehension movements that were originally thought to be controlled by parallel visuomotor channels.

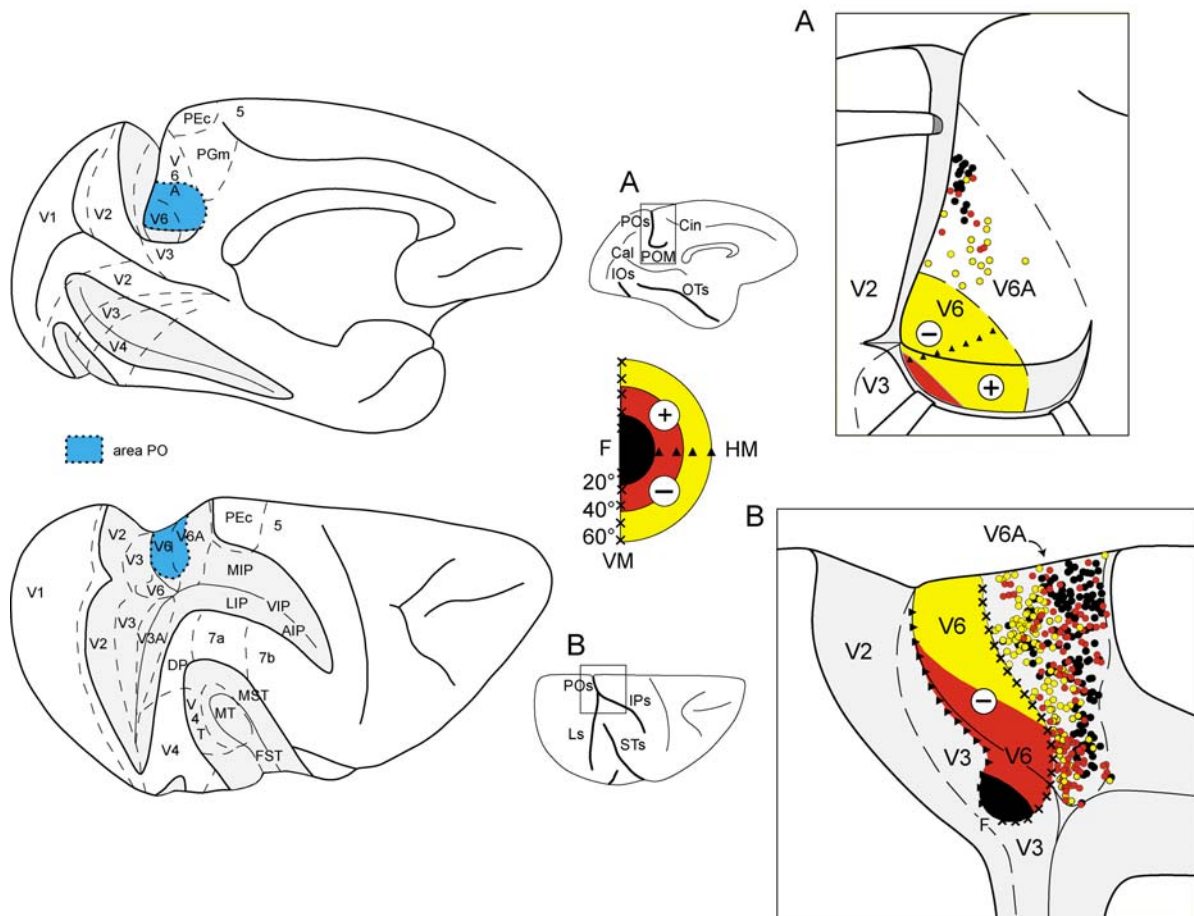


Fig. 1A, B Functional parcellation of the posterior part of the macaque brain. *Left* Medial and dorsal views of macaque brain. Parieto-occipital (POs), medial parieto-occipital (POM), inferior occipital (IOs), occipito-temporal (OTs), intraparietal (IPs), lunate (Ls) and superior temporal (STs) sulci are open in the depth of these sulci (modified from Colby et al. 1988). Sulci opened are shown in light grey, and as thickened lines on the brain silhouettes in the middle part of the figure. Dashed lines are the borders between different cortical areas, according to: Colby et al. 1988; Desimone and Ungerleider 1986; Galletti et al. 1999a, 1999b; Gattass et al. 1981, 1988; Gattass and Gross 1981; Pandya and Seltzer 1982. The location and extent of area PO (shown in blue) is according to Colby et al. (1988). *Right* Enlargements of medial (A) and dorsal (B)

views of the brain, respectively, in the region of POs. Sulci are opened as on left. In the inset in A, the peripheral lower and upper field representations of area V6 are visible on the mesial surface of the hemisphere and in the dorsal wall of POM, respectively. In the inset in B, the lower field representation of area V6 is visible in the parieto-occipital cleft. Black, red and yellow are used to indicate the eccentricities represented in different parts of V6 according to the colour coding shown in the middle. Triangles and crosses represent the horizontal (HM) and vertical (VM) meridians of area V6, respectively; F is the centre of gaze (modified from Galletti et al. 1999a). Coloured dots in the insets in A and B indicate location and eccentricity of single cells recorded from area V6A (modified from Galletti et al. 1999b)

Dorsomedial and dorsolateral visual streams

Many authors have searched for the anatomical substrate of reaching and grasping visuomotor channels, following the flow of visual information from the occipital pole to the frontal cortex. Visual information leaves the primary visual cortex following two main pathways: a dorsal one directed to the posterior parietal cortex, and a ventral one that reaches the cortex of the inferior temporal lobe (Ungerleider and Mishkin 1982). The functional characteristics of posterior parietal neurones, and the existence of direct connections between posterior parietal and premotor frontal cortices, suggested that the dorsal visual stream was involved in the visual guidance of prehension (see Milner and Goodale 1995 for review).

The dorsal visual stream includes at least two separate channels, a medial one passing mainly through the visual areas of the SPL, and a lateral one passing mainly through the visual areas of the IPL. In the dorsomedial visual stream, information about the periphery of the visual field flows from V1 to the medial parieto-occipital cortex, and from here to several visual areas of the posterior parietal cortex. In the dorsolateral visual stream, visual information relative to more central parts of the visual field flows from V1 to the lateral parieto-occipital cortex, and from here to several visual areas of the posterior parietal cortex (see Lewis and Van Essen 2000; Rossetti et al. 2000 for a review of these connections).

The dorsomedial visual stream has been supposed to carry out the visuomotor transformations necessary for guiding the reaching movements of the arm, while the dorsolateral visual stream the visuomotor transformations

necessary for grasping (Sakata and Taira 1994; Tanné et al. 1995). In contrast with this view, recent physiological and anatomical data suggest that the dorsomedial visual stream is involved in both reaching and grasping actions. This suggestion is based on new data on functional organization and anatomical connections of the medial sector of parieto-occipital cortex, the region of the brain visual information passes through on the way to reach the frontal cortex.

The term parieto-occipital cortex indicates a region of the cortical mantle located between occipital and parietal lobes. In the macaque, it refers to an extended cortical region hidden in the parieto-occipital (POs) and lunate (Ls) sulci. As shown in Fig. 1, this cortical region contains several extrastriate visual areas, namely V2, V3, V3A, PO, V6 and V6A. The *medial* parieto-occipital cortex is the cortex that occupies the anterior and posterior banks of POs as well as the caudalmost part of the precuneate cortex on the mesial surface of the hemisphere (see Fig. 1). The posterior bank of POs is almost completely occupied by areas V2 and V3, two retinotopically organized visual areas that represent the lower, contralateral part of the visual field (Gattass et al. 1981, 1988). A third visual area, called PO (Colby et al. 1988), occupies the ventral part of the anterior bank of POs and the caudal part of the mesial precuneate cortex. Area PO was reported to be non-retinotopically organized and to represent the periphery (above 20° of eccentricity) of both lower and upper quadrants of the contralateral visual field.

Recent recordings from behaving monkeys have suggested that PO is not a unitary area, at least from a functional point of view. As shown in Fig. 1, the cortical

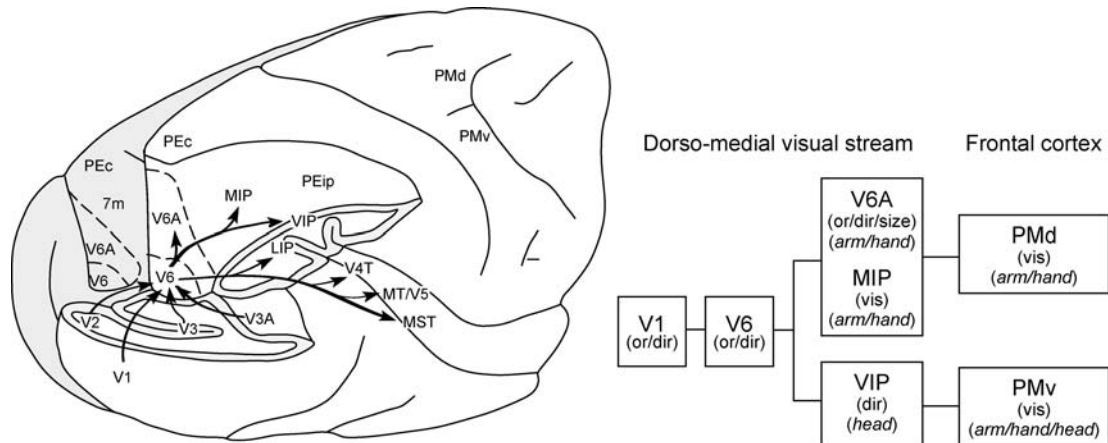


Fig. 2 Cortical connections of area V6. *Left* Posterolateral view of a partially dissected macaque brain (drawn from Galletti et al. 1996). The inferior parietal lobule of the right hemisphere has been cut away at the level of the fundus of the intraparietal sulcus to show the cortex of the medial bank of this sulcus. The occipital lobe of the same hemisphere has been cut away at the level of the fundus of the parieto-occipital and lunate sulci to show the cortex of the anterior bank of the parieto-occipital sulcus. The mesial surface of the left hemisphere and the grey matter of the cut-away regions are shown in grey. Arrows connecting different areas are used to indicate the flow of visual information from occipital to posterior parietal cortices, though all connections were originally reciprocal (Galletti et al. 2001). *Right* Most direct visual pathways to the frontal cortex.

The main functional characteristics of each area are indicated in normal type (the visual features), and in italics (the somatic features), according to the following symbols: 'or' cells sensitive to orientation of visual stimuli, 'dir' cells sensitive to direction of visual stimuli, 'size' cells sensitive to size of visual stimuli; 'arm' representation of the arm, 'hand' representation of the hand, 'head' representation of the head. Pathways are assembled from the work of the following authors: Galletti et al. 2001; Luppino et al. 1999; Matelli et al. 1998; Shipp et al. 1998. Functional properties are from: Colby and Duhamel 1991; Duhamel et al. 1998; Fattori et al. 2001; Fogassi et al. 1999; Galletti et al. 1996, 1997a, 1999a, 1999b; Gentilucci et al. 1988; Hubel and Wiesel 1977; Rizzolatti et al. 1988, 1997; Wise et al. 1997

region indicated as PO contains a retinotopically organized visual area, called V6 (Galletti et al. 1999a), as well as the ventral part of a visual area that is non-retinotopically organized, called V6A (Galletti et al. 1999b), located dorsally to V6. Area V6 represents the entire contralateral hemifield, with the lower field representation located in the POs and the upper field on the mesial surface of the hemisphere and on the dorsal bank of POM (Fig. 1, right). The central 20° of the visual field is represented in the lateralmost part of the *posterior* bank of POs. This central representation is not emphasized as in the other extrastriate areas. Eccentricities higher than 20° are represented in the fundus of POs, in the ventral part of the anterior bank of POs, on the mesial surface of the hemisphere and in the dorsal bank of the medial aspect of POs (Fig. 1, right).

Area V6, like V2 and V3, receives a direct input from the primary visual area V1 but, in contrast to the other two, does not project to the parietal areas of the ventral visual stream: *V6 is connected only to the dorsal visual stream* (see Fig. 2; Galletti et al. 2001). Area V6 is strongly interconnected with the parieto-occipital areas V2, V3 and V3A, as well as with several areas of the posterior parietal cortex (Fig. 2, left). The visual information leaving V6 directed towards the higher order visual areas of the parietal lobe follows two main pathways: a lateral one that reaches the visual areas of the dorsal stream (LIP, V4T, V5/MT, MST) and a medial one that reaches the bimodal (visual/somatosensory) areas of the dorsal stream (V6A, MIP, VIP). As several posterior parietal areas are directly connected with the premotor cortex, visual information can reach the frontal cortex through several pathways along both the lateral and medial channels of the dorsal stream, though the medial channel represents the straightest path to reach the frontal cortex (Fig. 2, right; Galletti et al. 2003; see also Tanné et al. 1995). In the following, we will analyze the type of visual information processed by the medial parieto-occipital cortex, which represents the gate through which visual information enters the medial channel of the dorsal stream. The aim is to check whether this information is useful for guiding reaching movements of the arm, or for controlling grasping movements of the hand, or whether it can be used for both processes.

Visual information processed by the medial parieto-occipital cortex

Cells of area V6 are very sensitive to the orientation and direction of movement of uncoloured visual stimuli (Galletti et al. 1999a). This behaviour reflects the functional characteristics of the input they receive from the primary visual area. In fact, the V1 input to V6 comes from cells of layer IVB (Galletti et al. 2001), which in turn receive from the magnocellular layers of the lateral geniculate nucleus. Cells of layer IVB of V1 are sensitive to orientation and direction of uncoloured visual stimuli with low spatial frequency, the same features that strongly modulate the cell's activity in area V6.

The parietal areas of the dorsomedial visual stream that receive from V6 are V6A, MIP and VIP (see Fig. 2). All three areas receive visual information from both central and peripheral field representations of V6 (Galletti et al. 2001, see also the right part of Fig. 1 for the visual field representation in V6A). Visual cells in V6A are sensitive to size (Galletti, unpublished observation), orientation and direction of movement of visual stimuli (Galletti et al. 1996, 1999b). Area VIP is rich in cells sensitive to the direction of movement of visual stimuli, in particular when visual stimulations are delivered near the head (Colby et al. 1993). In area MIP, visual cells are more concentrated in the ventral part of the area, in the depth of the medial wall of IPs (Colby and Duhamel 1991). MIP visual cells were reported to be insensitive to the direction of movement of the stimuli, while nothing was reported about their sensitivity to the size and orientation of stimuli. These data indicate that V6 distributes visual information on form and motion to different parietal areas of the dorsal stream, likely along fast-conducting magnocellular channels.

Among the three medial parietal areas that receive a direct input from V6, the parieto-occipital area V6A is the only one that contains cells able to encode object attributes relevant for grasping, like orientation in space and size. In addition, V6A largely represents the central part of the visual field (see the right part of Fig. 1), i.e. the part of the visual field that is critical to collecting visual information on the interaction between hand and object during grasping.

Area V6A is directly connected with the premotor cortex (Matelli et al. 1998; Shipp et al. 1998). It is worth noting, in this regard, that the rostroventral part of the premotor area F2 (Matelli et al. 1991), which receives from area V6A, contains visual cells activated by the presentation of the object to be grasped, as well as cells activated by distal movements, like wrist orientation and finger movements (Fogassi et al. 1999). We suggest that this region of premotor cortex uses the visual information on object attributes coming from V6A to control grip aperture and wrist orientation according to object size and orientation in space.

Area V6A contains also cells able to encode the spatial location of objects in the visual scene (Galletti et al. 1993, 1995). Some cells, called real-position cells, are able to code directly the spatial location of objects in at least head-centred coordinates, as their visual receptive fields remain anchored to the same spatial location regardless of eye movements (Galletti et al. 1993). These cells could transmit object spatial coordinates to the premotor areas in the frontal cortex. The premotor cortex, in turn, could use this visual information to direct the arm towards the object to be grasped, during the transport phase of the arm-reaching movement.

The spatial coordinates of the object to be grasped could also be transmitted to structures (such as area LIP, regions of frontal/prefrontal cortex) that could direct the selective attention towards that object just before the beginning of reaching movement. Focusing our attention on the object

to be grasped is certainly useful to improve the visual guidance of prehension. In line with this view, a clear effect of the attentional level on neuronal activity has been reported in V6A itself (Galletti et al. 1996).

Finally, the visual guidance of the transport phase of arm reaching could be improved by the acquisition of data on the direction of movement of the object to be grasped, as well as on the direction of movement of the arm while the hand approaches the object, all visual information that could be supplied to the premotor cortex by cells of area V6A as many cells in this area are very sensitive to the direction of movement of visual stimuli (Galletti et al. 1996, 1999b).

In summary, all these data suggest that visual activity in V6A is involved in the control of both reaching and grasping movements.

Somatosensory information processed by the medial parieto-occipital cortex

Among the areas of the medial parieto-occipital cortex, V2, V3 and V6 are purely visual whereas V6A contains also cells sensitive to somatosensory stimulations (Breveglieri et al. 2002; Galletti et al. 1997a). The somatic representation in V6A is restricted to the upper limbs, as in the nearby area MIP (Colby and Duhamel 1991). Many somatosensory cells in V6A are sensitive to the passive

rotation of the joints of the upper contralateral limb. Figure 3A shows the behaviour of a joint cell modulated by passive rotation of the shoulder. The cell had a sustained discharge when the arm was near the chest, outside the field of view of the monkey. When the arm was behind, the cell became silent, while it discharged again when the arm returned to its initial position. Most joint cells were modulated by passive rotation of the shoulder, many by rotation of the elbow and some of the wrist (Fig. 3B).

Figure 3C shows the distribution of somatosensory receptive fields of the V6A cells modulated by tactile stimulations. They are located on the upper limbs, mostly on the contralateral limb, as well as in regions of the body close to the arm. Tactile receptive fields are quite small in size, covering only restricted parts of the limb or body. They are present on both proximal and distal parts of the arm, though they are more frequent on the former.

These data suggest that V6A is involved in the control of arm movement. Somatosensory cells could provide information about position of the hand/arm in space, and with respect to the trunk. This could be useful to construct the shoulder/arm/hand frames of references used in planning and performing reaching movements to targets in the peripersonal space (Flanders et al. 1992; Soechting et al. 1990). Tactile receptive fields on the arm could be useful in recognizing the interaction between moving arm and environment, hence in confirming the actual location

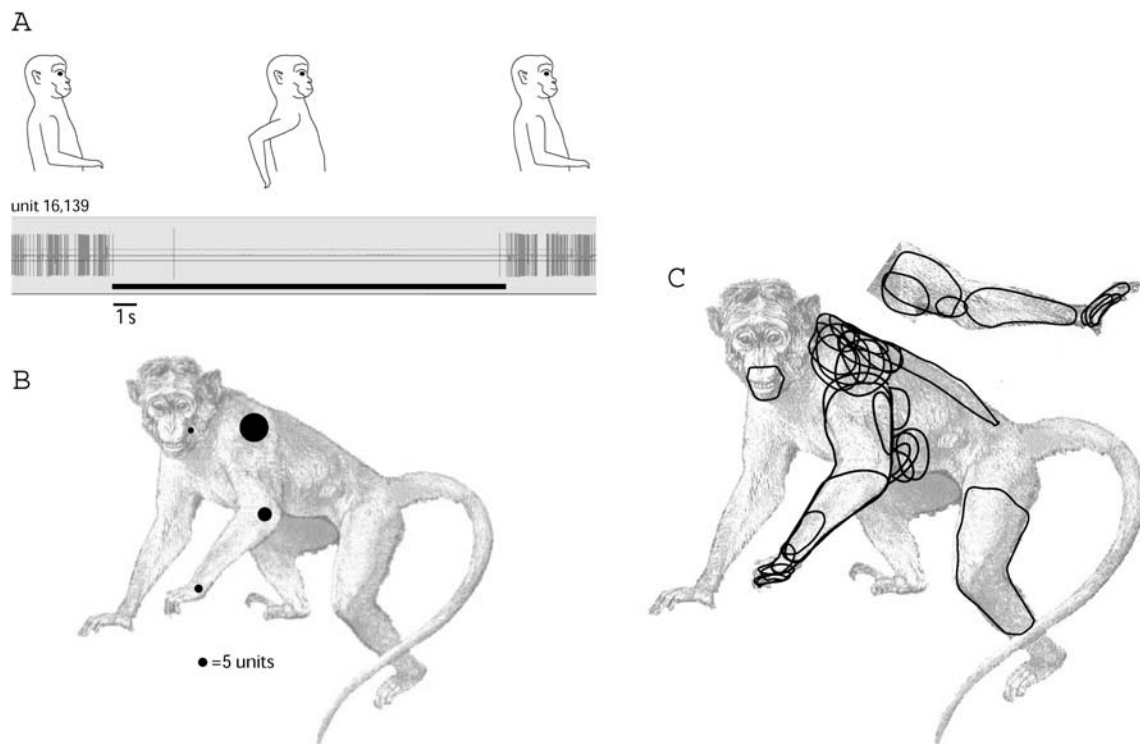


Fig. 3A–C Passive somatosensory modulations in V6A (modified from Breveglieri et al. 2002). **A** Neural activity of a cell sensitive to passive rotation of the contralateral shoulder. The audio band of the videoclip below the animals' silhouettes indicates the activity of the recorded cell (vertical bars are action potentials). Horizontal thick

bar below the audio band indicates the period during which the arm was behind. **B** Joints (black dots) modulating V6A cells. The size of each dot is proportional to the number of modulated units. **C** Body locations of V6A tactile receptive fields. Note that receptive fields are all reported on the left part of the body

and status of the arm. Tactile receptive fields on the hand could inform about the interaction between the hand and grasped object during grasping.

Again, experimental data suggest that V6A is involved in the control of both reaching and grasping processes.

Arm movement-related activity in the medial parieto-occipital cortex

Cells in areas V2, V3 and V6 are not modulated by movement of the arms in darkness. In contrast, many cells in area V6A are modulated during arm movements aimed at reaching objects in the peripersonal space (Fattori et al. 2001; Galletti et al. 1997a). Movements with similar kinematic characteristics but not aimed at reaching objects are unable to activate the cells.

When reaching movements are carried out in light, the great majority of V6A cells are modulated, presumably activated by the sight of graspable objects and/or the sight of monkey arm. When the same purposeful movements are carried out in darkness, about 50% of V6A cells continue to be modulated (Fattori et al. 2001). The persistence of

activity modulation in darkness suggests that these cells do not receive only visual information.

Reaching activity in darkness could be the result of somatosensory inputs coming from the moving arm. The somatosensory responses we have recently found in V6A (Breveglieri et al. 2002) actually support this view. However, the observation that V6A reaching cells are generally more active during arm movements aimed at reaching objects than during passive arm movements (Galletti et al. 1997a) indicates that the skeletomotor activity could be at least partially responsible for the movement-related activity in darkness.

This is the case for the cell in Fig. 4, as the movement-related activity cannot be fully accounted for by either visual or somatosensory input. The animal was performing a fixation task in darkness, with the hands outside its field of view. It was required to pull a lever when a green spot of light appeared on the screen it faced, and to push the lever when the green spot became red (go signal for the arm movement). Each time the animal pushed the lever during the task, the cell showed a clear transient increase in discharge rate. Arm movement-related activity started about 200 ms before the onset of arm movement, that is

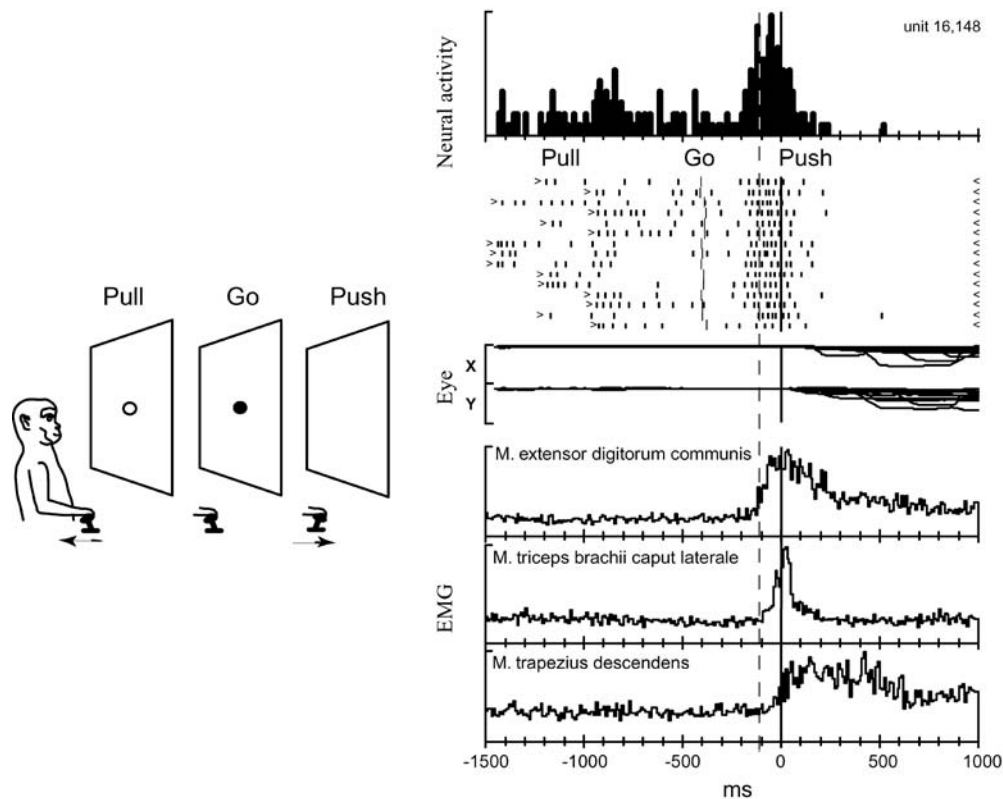


Fig. 4 V6A arm movement-related neurone (modified from Galletti et al. 1997a). *Left* Sketch illustrating the fixation task carried out by the animal. *Right, from top to bottom* Peristimulus time histogram and raster displays of impulse activity; recordings of X and Y components of eye position; electromyographic activities from muscles of the forearm (*m. extensor digitorum communis*), proximal part of the arm (*m. triceps brachii caput laterale*) and shoulder/neck/trunk (*m. trapezius descendens*). *Open and closed circles in the top sketch* indicate green and red colours, respectively, of the fixation

point. Signs > and < in raster displays indicate the beginning and end of neural acquisition, respectively, in each trial. *Long vertical thick lines* in raster displays are behavioural markers relative to change in colour of fixation point (*Go*) and to lever pushing. The neural activity has been aligned with the onset of pushing movement. *Scales: vertical bar* on histogram: 50 spikes/s; *eye traces* 60 degrees/division; *electromyographic activity* arbitrary units

well before the earliest EMG activity (that began about 100 ms before the onset of movement). Therefore, though a somatic input to the cell cannot be excluded, proprioceptive signals and tactile stimulations cannot fully explain the cell's activation: at least the earliest 100–150 ms of the neural discharge must be due to something else.

The early premotor activity could be a 'preparatory' motor signal, as suggested for about 30% of V6A reaching cells (Fattori et al. 2001) as well as for many cells of the neighbouring PRR region (Snyder et al. 1997). However, this is certainly not the case for the cell shown in Fig. 4, neither for other cells with a similar behaviour we recorded in V6A. In our experimental conditions, a preparatory motor activity would appear well before the go signal, as the animal repeated the same arm movement 15 times, so it knew in advance, at the beginning of each trial after the first one, the type of movement it would be required to perform. The premotor activity in Fig. 4, in contrast, always starts *after* the go signal. We suggest that it is due to an efference copy of the motor signal, delivered by the dorsal premotor areas F2 and F7 (Matelli et al. 1991), which are known to be reciprocally connected with V6A (Matelli et al. 1998; Shipp et al. 1998).

Figure 5 shows two V6A arm-reaching cells studied in darkness. One was activated for movements of the arm directed towards a visual target (M1), the other for arm movements directed towards a target that was outside the field view of the animal (M2). In both cases, the movement-related activity started before the onset of movement and lasted for its whole duration. A trial by trial analysis of neural and oculomotor activities excluded that the movement-related discharge was due to the concurrent eye movements, a reliable possibility in V6A as several cells are strongly modulated by the movement of the eyes (Galletti et al. 1991, 1995, 1996).

The activity of arm-reaching cells changes according to the direction of movement of the arm. The two cells in Fig. 5, for instance, showed completely different frequencies of discharge for opposite directions of movement (compare the activity in M1 with that in M2 in each cell). The unit of Fig. 6 showed a direction-sensitive modulation for small changes in movement directions. This cell had the highest movement-related activity when the monkey moved the arm in the right bottom space, and the weakest one when movements were in the left upper space. For directions in between these two, the neural activity changed smoothly accordingly to changes in the direction of movement.

The cell of Fig. 6 was also strongly activated when the animal held the hand still on the left bottom part of the panel, but not when it held the hand in the other positions of the panel. Other V6A reaching cells preferred different directions of movement or positions in space of the arm (Fattori et al. 1999).

In natural conditions, when the animal is reaching out for objects in a lightened environment, many reaching cells in V6A are activated during the movement of the hand towards the object to be grasped. We often observed

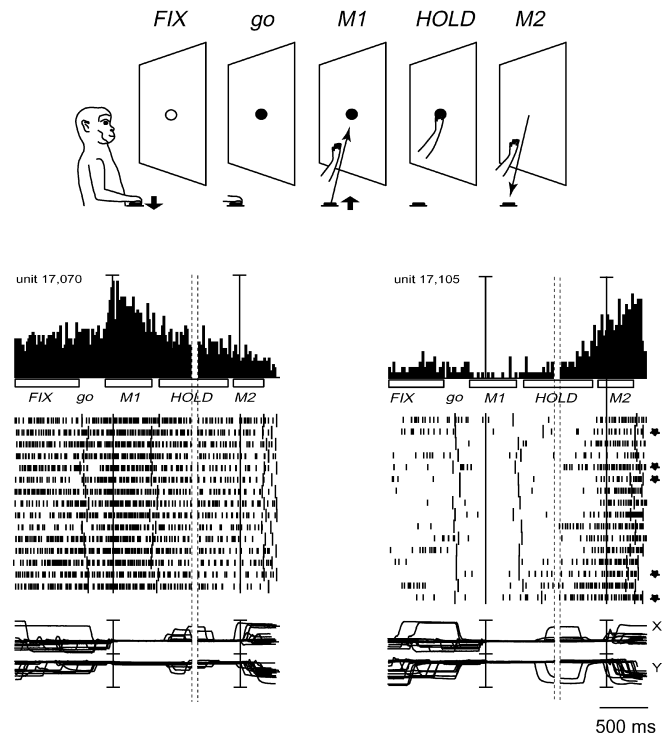
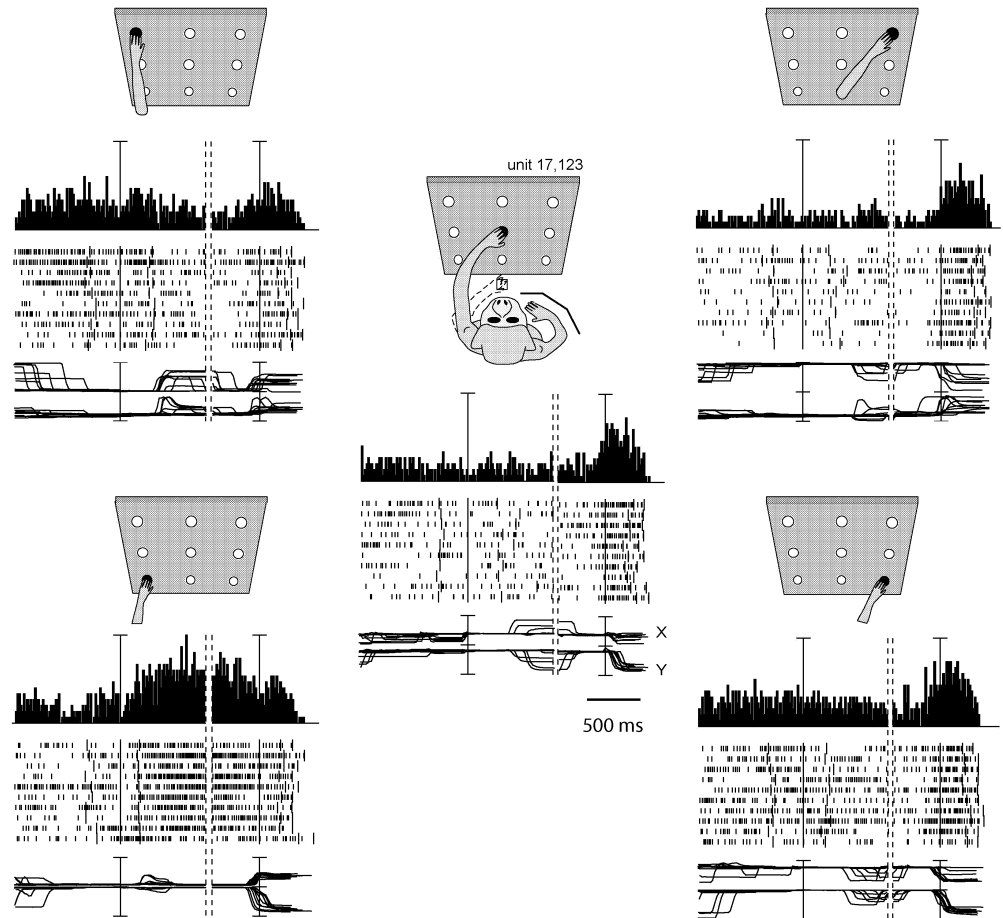


Fig. 5 V6A arm-reaching neurones (modified from Fattori et al. 2001). *Top* Reaching task. Reaching movements were performed in darkness between a push button located near the monkey chest and an LED placed on a panel in front of the animal, 14 cm in the straight-ahead direction. Animal pushed the button and fixated the LED lit green (*open circle*) until the LED changed in colour from green to red (*closed circle*). This was the 'go' signal for the movement of the arm. After the forward arm movement (*M1*), the animal was required to hold the hand on the LED until it disappeared (*HOLD*), then it had to perform a backward arm movement (*M2*) to press again the button in order to receive the reward and to start another trial. *Bottom* Peri-event time histograms, time epochs, raster displays of impulse activity, and recordings of X and Y components of eye positions in two V6A cells. *Long vertical thick lines* in raster displays are behavioural markers relative to the target change in colour, button release, LED touch, LED release, button press. Activity has been aligned twice for each cell, with the onset of forward and backward arm movements respectively. *Stars on the right* indicate trials without changes in gaze direction during M2. Note that the cell discharged during M2 period regardless of eye movements. *Scales: vertical bar on histogram 140 (unit on the left) and 75 (unit on the right) spikes/s; eye traces 60 degrees/division*

that the discharge suddenly stopped, or was strongly reduced, when the animal touched the target of reaching. As noted in the reaching tests, also in natural conditions the movement-related activity changed according to the working space. As the monkey head was restrained, the working space was in some cases below the animal's line of sight. In these cases, the animal could not see the object to be grasped, and both searching and grasping movements were carried out under somatosensory control alone. Some V6A cells that were not active during reaching in the working space under visual control became active when the animal's hand searched for pieces of food in the working space outside the field of view of the animal. Even in these cases, as in those under visual control, we

Fig. 6 Directional tuning of arm-reaching activity. The reaching task was as described in Fig. 5. The animal reached out to five different positions on the panel it faced, a central one in the straight-ahead direction, and four peripheral positions, each 40° distant from the central one. *From top to bottom (in each inset):* sketch indicating the arm position on the panel reached out to by the animal (the starting position of the arm is shown—as a dashed line—in the central inset); perievent time histograms; raster displays of impulse activity; recordings of X and Y components of eye positions. *Long vertical thick lines* in raster displays are behavioural markers as in Fig. 5. Activity has been aligned twice for each inset, with the onset of forward and backward arm movements respectively. *Scales:* vertical bar on histogram: 100 spikes/s; eye traces: 60 degrees/division



often observed that cells became silent, or strongly reduced their activity, as soon as the hand touched the food.

Some V6A cells were not active during the transport phase of reaching but discharged during grasping. Figure 7 shows the behaviour of one of these cells during three successive episodes of grasping. The cell was silent while the animal fed or reached out for food (thin and dotted lines, respectively, under neural trace in Fig. 7), but discharged during grasping (thick line under neural trace). The TV frames in Fig. 7 illustrate the sequence of events during one episode of grasping, and their correlation with neural activity (comparison of video images and neural activity was done by the technique developed by Gardner and co-workers; Gardner et al. 1999; Ro et al. 1998). It is evident that the cell began to discharge when the fingers touched the piece of food (frame C), continued to discharge during grasping (frames D, E), and suddenly stopped firing as soon as the hand with the grasped food returned back to the mouth (frame F). This type of neurone likely encodes the grasping phase of prehension.

In summary, arm-reaching neurones in V6A are modulated during reaching towards visual targets as well as towards targets located outside the field of view. They are able to encode the direction of arm movement, and therefore to guide the arm during the transport phase of reaching movement, no matter whether the action is

visually guided or not. Some reaching cells show different frequencies of discharge according to the position in space of the arm; some others do not discharge during the transport phase of reaching, but only during grasping of objects.

These data further support the view that V6A is involved in the control of both the transport phase of reaching, and the grasping.

Role of the medial parieto-occipital area V6A in the control of reaching and grasping movements

In the past, we repeatedly suggested an involvement of monkey area V6A in the visuomotor transformation that converts retinal information into appropriate spatiomotor coordinates to direct the movement of the arm in visually guided actions (Galletti et al. 1993, 1995, 1996, 1997b, 1999b; Galletti and Fattori 2002). According to this view, at the beginning of the transport phase the real-position cells of V6A would send the spatial coordinates of a graspable object to the ipsilateral premotor cortex, to direct the contralateral hand towards the target to be grasped. In agreement with this hypothesis, brain lesions restricted to area V6A in monkey produce misreaching with the arm contralateral to the lesion in visually guided movements (Fig. 8A–C; Battaglini et al. 2002).

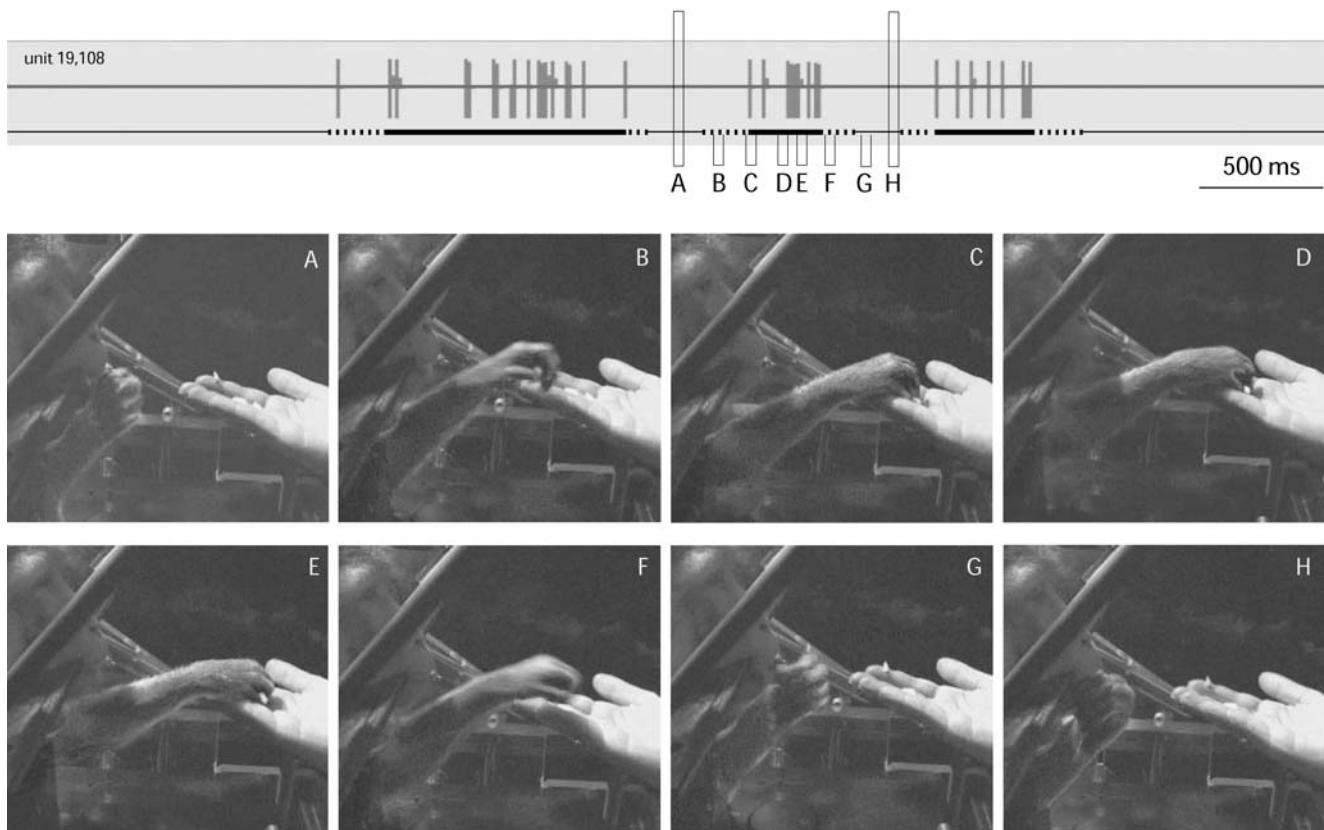


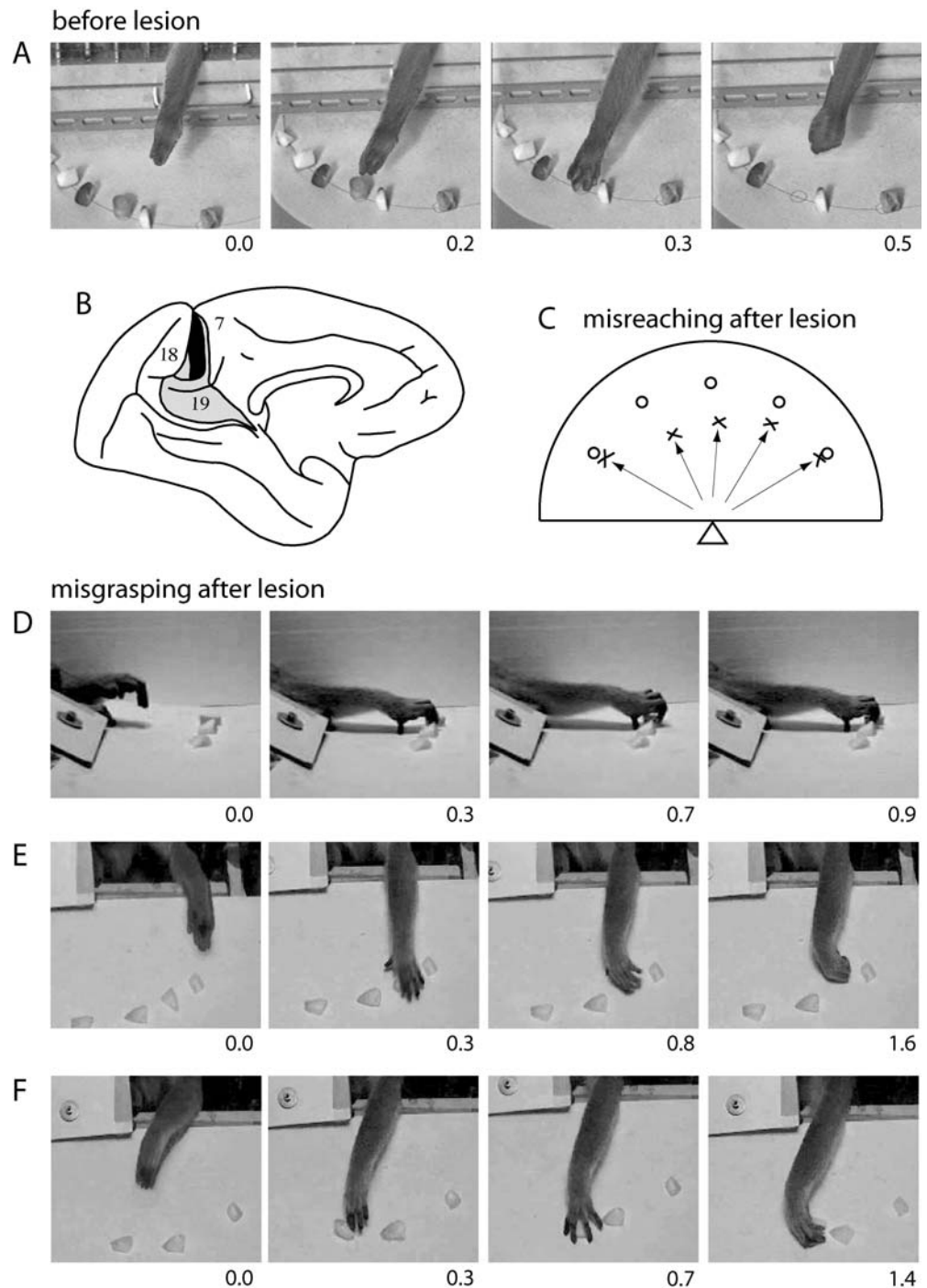
Fig. 7A–H V6A grasping neuron. *Top* Neural activity of a V6A cell during three successive episodes of grasping (*vertical bars* are action potentials recorded in the audio band of a videoclip). Different types of lines under the neural trace indicate different behavioural periods. *Thin lines* mark periods of feeding, *dotted lines* the movement time, and *thick lines* the occurrence and duration of grasping movements, from food touching to the onset of backward arm movement. *Letters A–H* below the neural trace indicate the

times of occurrence of the digital frames reported in the bottom part of the figure. The *width of rectangles* respects the duration (40 ms) of each frame. *Bottom* Frames from a digital TV camera (recorded at 25 Hz) illustrating an episode of grasping food from the experimenter's hand. The sequence of frames shows feeding (**A**), arm movement towards the pieces of food (**B**), food grasping (**C**, **D**), arm movement backward to the mouth (**E**) and feeding again (**G**, **H**)

In the human brain, lesions of the superior parieto-occipital junction, a region not dissimilar from that containing area V6A in monkey, lead to misreaching in visually guided movements (optic ataxia; Balint 1909; Perenin and Vighetto 1988; Ratcliff and Davies-Jones 1972). Optic ataxia patients are impaired in directing actions to objects presented in their visual field, though they have no difficulties in the recognition of these objects. In many cases, patients with optic ataxia misreach only when targets are presented in non-foveal vision, and not when they are viewed directly. This behaviour suggested to Buxbaum and Coslett (1997) that optic ataxia is not the result of disconnection of visual information from the motor system, as traditionally thought, but reflects a failure to transform retinal information into appropriate spatiomotor coordinates for action (e.g. shoulder-, arm- and hand-centred coordinates). According to Buxbaum and Coslett (1997), these visuomotor transformations would allow normal subjects to direct the hand towards the object to be grasped regardless of their posture and of where they are looking at.

We suggest that optic ataxia patients cannot perform the above-described visuomotor transformations because their brain damage involves a 'human' area V6A, in which the real-position behaviour is built up (see Galletti et al. 1995; Galletti and Fattori 2002). This view suggests a strict homology between human and monkey brains (see Galletti et al. 1997b), which is in contrast with the common view that human and monkey SPL are not homologous structures. In fact, though large posterior parietal lesions in monkeys produced misreaching like in humans (Faugier-Grimaud et al. 1978; Haaxma and Kuypers 1975; see also Milner and Dijkerman 1998 for a recent review of this argument), it was reported that only posterior parietal lesions restricted to the IPL in monkey produced visuomotor impairments similar to those observed in optic ataxia patients (Rushworth et al. 1997; Stein 1978). In other words, SPL lesions in humans produced deficits similar to those observed after IPL lesions in monkeys, thus it was postulated that monkey IPL (namely area 7a) was the counterpart of the underlying lesion in optic ataxia patients. It is worth noting that in all the above-referred experiments in monkey, the lesions spared the caudalmost part of SPL. In particular, they

Fig. 8A–F Misreaching and misgrasping after lesion of monkey area V6A. **A** Frames from a digital TV camera illustrating the behaviour of a normal animal in reaching and grasping food. Time below frames is in seconds. **B** Reconstruction of location and extent of the brain damage in case V6M2 of Battaglini et al. (2002). The lesion is indicated on the silhouette of monkey brain reported by Brodmann (1909), adapted in size to match the brain of the monkey reported by Battaglini et al. (2002). The lesion was bilateral, but here is reported (in *black*) only the lesion in the left hemisphere; that in the right hemisphere was very similar in location and extent (see Battaglini et al. 2002). Dorsal area 19 is shown in *grey*; its location and extent, as well as locations of areas 18 and 7, are according to Brodmann (1909). **C** Misreaching after bilateral V6A lesion. Food (raisins) was distributed on a semicircular plate placed horizontally in front of the animal, as shown in the frames at the *top of the figure*. The plate is seen here from above, and the position of the monkey is indicated by the *triangle*. *Open circles* indicate food locations. *Crosses* indicate the locations where the hand landed in the first attempt to reach the food. **D–F** Frames from a video camera illustrating the excessive widening of grip aperture, the delayed grip of the object (see times below frames), and the anomalous rotation of the wrist that led the fingers to close laterally rather than downward. Time below frames is in *seconds*



spared the cortex of the anterior bank of parieto-occipital sulcus (that containing area V6A), which is instead generally affected in optic ataxia patients. Given the similarities of impairments observed in monkey after selective V6A lesions (Battaglini et al. 2002) and in optic ataxia patients (Perenin and Vighetto 1988), we believe that human and monkey SPL are homologous structures, and suggest that most of the deficits observed in optic ataxia patients are the result of the lesion of a 'human' area V6A.

Lesions of V6A in monkey also produce deficits in wrist orientation and grasping movements (Battaglini et al. 2002). The animal is unable to appropriately rotate the wrist during grasping in order to adapt the hand orientation to the orientation of the slit containing the food. As shown in frames D–F in Fig. 8, when grasping a piece of food on a plate, the monkey with V6A lesion widened the grip aperture too much, delayed the grip of the object and rotated the hand abnormally, so that the fingers closed laterally rather than downwards.

These results again suggest a homology between monkey V6A and the region damaged in optic ataxia patients, as these patients, besides misreaching, also exhibit deficits in adjusting hand orienting (Perenin and Vighetto 1988) and shaping (Jakobson et al. 1991; Jeannerod 1986) during prehension of objects under visual guidance. The misgrasping observed after V6A lesion is also congruent with the functional characteristics of single V6A cells. As reported in this chapter, area V6A contains cells modulated by wrist rotation, cells active only during grasping movements when the animal picks up pieces of food, and cells with a somatosensory receptive field located on the distal part of the arm, particularly on the hand. It is interesting to note that during grasping movements the object could be partially hidden by the hand, and therefore not under direct view. In this situation, the activity of pick-up cells and the distal stimulation provided by somatosensory fields located on the hand could help grasping to be completed.

The picture emerging from data reviewed in this work is that V6A is a cortical region involved in the control of many components of the act of prehension: in transporting the hand to the target object, in orienting the hand according to the object tilt, and in adapting the grip aperture to the object size. This view could explain why in a PET study conducted on normal subjects performing pointing and grasping tasks, an activation of the medial parieto-occipital cortex was found in both tasks (Grafton et al. 1996). We suggest that the dorsal parieto-occipital region that is active in both reaching and grasping tasks contains a human homologous structure of area V6A, which would be activated during both the transport phase (pointing) and the hand orienting and shaping (grasping) of reaching. The lack of activation in the same PET study (Grafton et al. 1996) of intraparietal and ventral premotor cortices suggests that these two cortical regions are involved in other tasks, like extraction of intrinsic object properties further than size and orientation, and their use in the choice of grip type and the control of finger movements during prehension and manipulation, as suggested by overwhelming experimental data in both humans and monkeys (see Binkofski et al. 1999; Jeannerod et al. 1995; Rizzolatti et al. 1997).

In normal subjects, the visually guided actions are under the control of two psychophysically separable visual systems, a 'slow' one responsible for cognitive responses, and a 'fast' one responsible for sensorimotor behaviour (Bridgeman et al. 1979). While the slow, cognitive system decides the onset of voluntary movements, the fast sensorimotor system performs unconscious online corrections of the direction of hand movement in the case of unexpected target jumps after movement onset (Goodale et al. 1986; Pelisson et al. 1986). Similar unconscious online corrections of *distal* movements occur after perturbation of target orientation (Desmurget et al. 1995; Desmurget and Prablanc 1997).

It has been recently reported that the fast sensorimotor system is located in the posterior parietal cortex, as both posterior parietal lesion and transcranial magnetic stimu-

lation applied to the posterior parietal cortex disrupt the online correction of movements (Desmurget et al. 1999; Gréa et al. 2002; Pisella et al. 2000). We suggest that area V6A is part of this system. V6A contains visual cells that respond quickly to changes in location, orientation, size and direction of movement of the graspable objects. These visual signals are transferred directly from V6A to the premotor cortex, that could in turn activate the motor centres in order to correct the ongoing arm movement. The short latency of visual responses in V6A (on average about 60 ms, Fattori et al. 2001) and the direct connection between V6A and premotor cortex (Matelli et al. 1998; Shipp et al. 1998) are compatible with the very fast motor response of the automatic system, which operates as soon as 110 ms after object displacement (Paulignan et al. 1991; Prablanc and Martin 1992). During the transport phase of reaching, area V6A could also evaluate whether a match exists between the programmed movement (signalled by intrinsic activity or efference copies of the motor command from premotor cortex) and the movement on the way to be executed (signaled by somatosensory inputs). Thus, V6A could interact continuously with the premotor cortex in order to further correct, if the case, the ongoing arm movement.

Summary and conclusions

The medial parieto-occipital cortex in macaque monkey contains (1) a retinotopically organized visual area (V6) that receives visual information on form and motion directly from V1 and distributes this information to the parietal areas of the dorsal visual stream and (2) a bimodal visual/somatosensory area (V6A) that elaborates form and motion visual information as well as somatosensory and skeletomotor information relative to the upper limbs. V6A also contains cells that encode the spatial location of objects in the field of view in at least a head frame of reference.

Area V6A seems to be well equipped to play a role in controlling the arm movements that are aimed at reaching and grasping objects in the peripersonal space, namely in directing the hand towards the object to be grasped, in orienting the wrist so that the hand grip matches the orientation in space of the object, in adapting the grip aperture to the size of the object, and in controlling the fast automatic process of online visuomotor guidance of prehension. These considerations, together with the fact that selective V6A lesions in monkey produce deficits similar to those observed in optic ataxia patients, suggest that optic ataxia syndrome is the result of the lesion of a 'human' area V6A.

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