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The posterior parietal area V6A: An attentionally-modulated visuomotor region involved in the control of reach-to-grasp action

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ABSTRACT

In the macaque, the posterior parietal area V6A is involved in the control of all phases of reach-to-grasp actions: the transport phase, given that reaching neurons are sensitive to the direction and amplitude of arm movement, and the grasping phase, since reaching neurons are also sensitive to wrist orientation and hand shaping. Reaching and grasping activity are corollary discharges which, together with the somatosensory and visual signals related to the same movement, allow V6A to act as a state estimator that signals discrepancies during the motor act in order to maintain consistency between the ongoing movement and the desired one. Area V6A is also able to encode the target of an action because of gaze-dependent visual neurons and real-position cells. Here, we advance the hypothesis that V6A also uses the spotlight of attention to guide goal-directed movements of the hand, and hosts a priority map that is specific for the guidance of reaching arm movement, combining bottom-up inputs such as visual responses with top-down signals such as reaching plans.

1. Introduction

In everyday life, people continuously interact with objects around them in their peri-personal space. These goal-directed voluntary movements are generally guided by vision, but can also be performed in total darkness, toward the location of previously seen objects, or even toward specific spatial locations without any visible target object. When performing goal-directed movements in the light a crucial point consists in the transformation of visual information regarding the target of action into the motor representation of this action. When reaching out for an object, for instance, the visual information concerning the location of the object is transformed into a motor vector that specifies arm direction and amplitude. When grasping, object features such as shape, size, orientation, etc., are transformed into motor vectors that specify the type of grip and wrist orientation that are appropriate for the object to be grasped. Specific brain mechanisms are needed to perform these visuomotor transformations. Anatomical and electrophysiological research carried out in non-human primates in the past decades has demonstrated the presence of specific circuits whose neurons encode reaching and/or grasping (Milner and Goodale, 1995; Jeannerod et al.,

1995; Wise et al., 1997; Galletti et al., 2003; Rizzolatti and Matelli, 2003; Janssen and Scherberger, 2015; Borra et al., 2017; Fattori et al., 2017). Among them, a dorsal circuit linking the superior parietal lobule to the dorsal premotor cortex is thought to be involved in coding target visual features and position, hand position, arm reaching direction and amplitude, wrist orientation, and the type of grip appropriate for the object to be grasped (Galletti et al., 2003, 2004; Fattori et al., 2017; Galletti and Fattori, 2018; Gamberini et al., 2020). A crucial node of this network is the medial posterior parietal area V6A, an area hidden within the depths of the parieto-occipital sulcus (Fig. 1), that hosts neurons encoding all these parameters, and that therefore seems to be involved in the control of all phases of reach-to-grasp action (Fattori et al., 2017). The present review summarizes the functional properties of reaching and grasping neurons of area V6A, with particular emphasis on the ability of V6A neurons to encode the spatial position of the target to be reached out to, or grasped. This information is provided by the visual system in retinotopic coordinates, but the motor system requires it in spatial coordinates in a body frame of reference. It is worth noting that even when the arm movement is performed in total darkness, toward the location of a previously seen object or toward a specific spatial location

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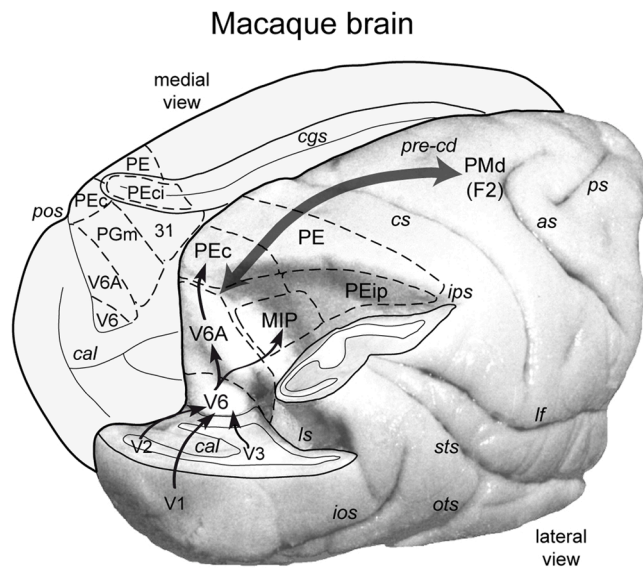


Fig. 1. Areal parcellation and main anatomical connections of the macaque superior parietal lobule (SPL). Posterolateral view of the macaque brain. The right hemisphere has been partially dissected at the level of the fundus of intraparietal, parietooccipital, and lunate sulci to show the hidden cortex of the SPL. The medial surface of the left hemisphere is also visible, with the cingulate sulcus open to show area PEci hidden inside. Dashed lines delimit different cortical areas of the SPL. Thin arrows connecting different areas in the posterior part of the brain indicate the flow of visual information from the occipital pole to the SPL, although all of these connections are actually reciprocal (Galletti et al., 2001); the thick arrow indicates the dorsomedial parieto-frontal stream related to the control of arm movement, that reciprocally connects the posterior parietal cortex of the SPL with the dorsal premotor cortex. Abbreviations: cal calcarine sulcus; ios inferior occipital sulcus; ots occipito-temporal sulcus; ps principal sulcus; pre-cd precentral dimple; as arcuate sulcus; cgs cingulate sulcus; cs central sulcus; If lateral fissure; ls lunate sulcus; sts superior temporal sulcus; ips intraparietal sulcus; pos parieto-occipital sulcus; V1, V2, V3, V6, V6A: visual areas V1, V2, V3, V6, V6A; MIP, PEip, PGm, 31, PEc, PE, PEci, PMd (F2): areas MIP, PEip, PGm, 31, PEc, PE, PEci, PMd (F2). Modified from (Galletti et al., 2003).

in the absence of any visible object, the motor centers which guide the arm/hand need to know the spatial position of the goal of movement in order to build up the motor representation of action, and the coordinates of this spatial position cannot, of course, be provided by the unavailable (in that case) visual information. We advance here the hypothesis that, at least in the dark, the goal of movement is indicated by the spotlight of attention, which is always present and is tied to the goal of an action whose location is dictated by spatial coordinates in a body frame of reference. The spotlight of attention also indicates the goal of an action when the action is performed in the light and when visual information about the action target is available, but of course it is much more important (we would say essential) when the action is performed in the dark and visual information is not available. Since it has been demonstrated that V6A neurons are able to encode the spatial location of objects (Galletti and Fattori, 2002) and are sensitive to the shifts of spotlight of attention (Galletti et al., 2010), they could play a role in this process. Experimental data in agreement with this view will be presented and discussed below in this review.

1.1. Encoding of eye/arm position/movement and of hand shaping during reaching-to-grasp actions

About 40% of V6A cells are somatosensory neurons that almost exclusively represent the upper limb, particularly the contralateral arm (Breveglieri et al., 2002; Gamberini et al., 2011, 2018). Most of these neurons are modulated by passive stimulation of the proximal joints

(shoulder, elbow) and some of them by the stimulation of the distal joints, mainly the wrist. Active arm movements are more effective at activating the neurons than passive ones. The examples reported in Fig. 2 summarize the neural modulations observed in V6A during arm actions. During goal-directed arm movements, about 70 % of V6A neurons are modulated by the direction (Fig. 2A; Fattori et al., 2005) and/or amplitude (Fig. 2B; Hadjimitsakis et al., 2014, 2017) of the arm movement; approximately 60 % by wrist orientation (Fig. 2C; Fattori et al., 2009) and grip formation (Fig. 2D; Fattori et al., 2010; Breveglieri et al., 2016, 2018). It is interesting to note that, in contrast with the traditional view that the medial parieto-frontal stream is only involved in reaching (proximal) arm movement (Kandel et al., 2000), more than half the V6A neurons are modulated by distal movements of the arm (for a full discussion of this matter see Fattori et al., 2017). The activity of many V6A cells is also modulated by the preparation of prehension acts (Fattori et al., 2009; Breveglieri et al., 2012; Santandrea et al., 2018). Fig. 2E shows an example of this phenomenon: the cell shows a rising activity before grasping a vertical handle (Fig. 2E, right), whereas such an activity is not present while preparing a reaching movement toward the same spatial location when grasping is not required (Fig. 2E, left). Most V6A cells are responsive to both reaching and grasping movements (Fattori et al., 2017), with some neurons more responsive to reaching and others to grasping, such as the cell shown in Fig. 2E.

Many V6A cells are sensitive to the direction of gaze (Galletti et al., 1995), as is the case for the reaching cell shown in Fig. 2B, the discharge rate of which during target fixation before the onset of arm movement changes according to the spatial location gazed at by the animal. The increase in activity before arm movement could be due to the preparation of movement, or to a particular visual stimulation present when the animal gazes at that spatial position, but we proved that gaze direction modulates neuronal activity even when an arm movement is not required and the animal is in complete darkness (Fig. 3; Galletti et al., 1995; Breveglieri et al., 2012). Gaze-dependent cells can be modulated by version (Fig. 3A) or vergence (Fig. 3B) of the eyes, or by both, and the hypothesis has been advanced that these neurons are able to encode gazed positions in three-dimensional space (Hadjimitsakis et al., 2011; Breveglieri et al., 2012).

Rarely were the cells in V6A modulated by only one parameter, such as eye position or arm movement direction. On the contrary, they typically showed a ‘mixed selectivity’, being sensitive to many factors related to both eye and arm position and movement, as in the example neuron shown in Fig. 4. In this cell, the discharge during fixation before the arm moves was remarkably higher for far positions than for the others (Fig. 4B). The neuron also preferred far positions during execution of hand reaching. For intermediate positions, the neural activity during fixation and arm movement execution was lower, and even lower for near positions. A comparative analysis of the discharge frequency in the different time epochs confirmed the ‘mixed’ selectivity of this cell, with at least six regressors (EYE POSITION, PREP, REMOV, MOV, HOLD, MOV2) among those we tested (Fig. 4C) significantly influencing cell discharge (Fig. 4D). Each V6A cell showed its own differential sensitivity to the regressors, so that we could define a typical “functional fingerprint” for each cell (Diomedi et al., 2020). Across the population, cells in V6A were not clustered in homogeneous groups according to their fingerprints, but were distributed in a functional continuum, leading to the impression that mixed selectivity is a crucial property that is necessary for V6A to perform its task.

1.2. Possible role of V6A in the neural control of reach-to-grasp

Overall, the functional properties of V6A cells suggest that this medial posterior parietal area is involved in the control of all phases of prehension during reach-to-grasp actions (Fattori et al., 2012, 2017). The short pathway of visual input along the dorsal visual stream (areas V1-V6-V6A, see Fig. 1; Galletti et al., 2001, 2004), the consequent short

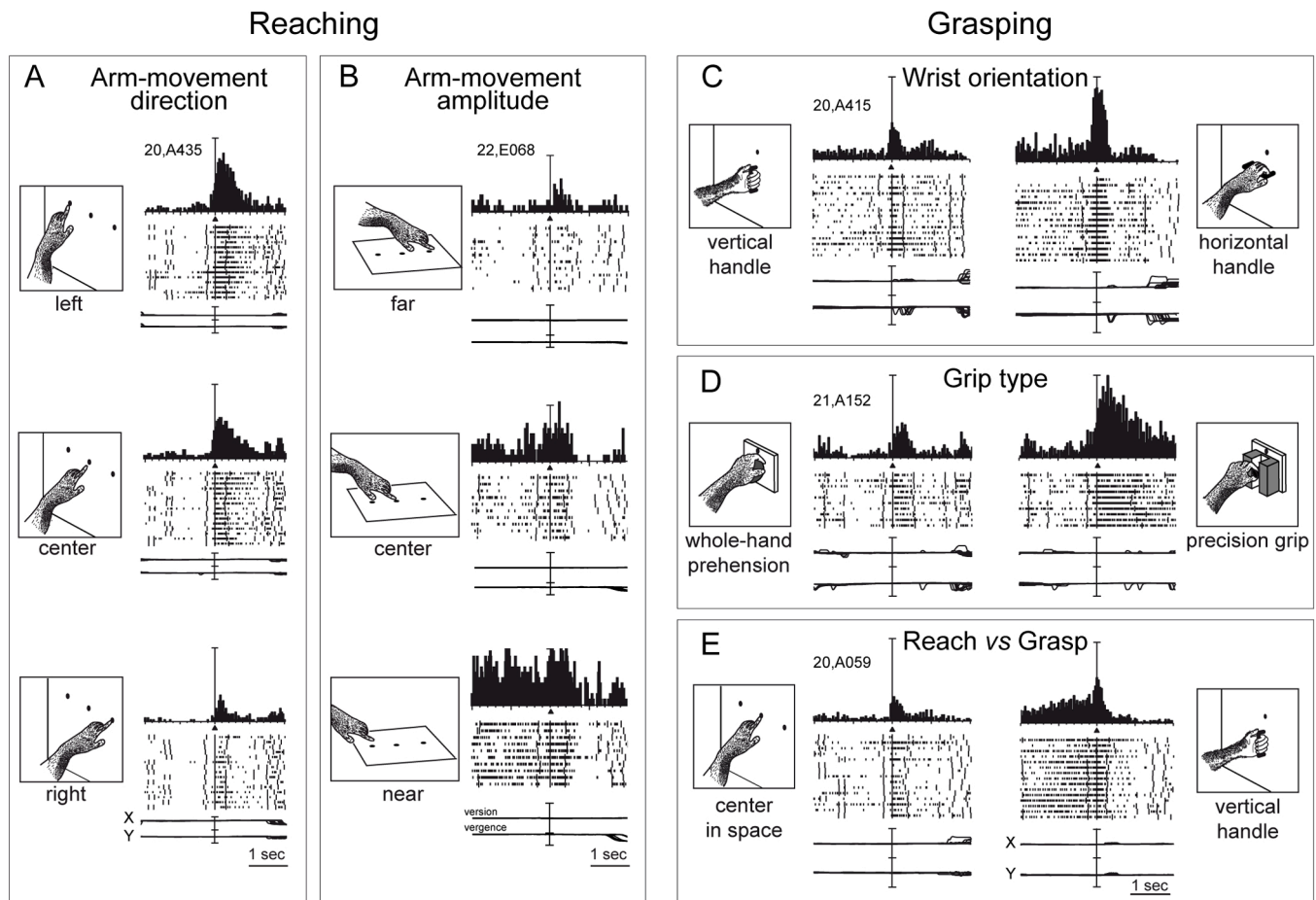


Fig. 2. Reaching and grasping properties of V6A neurons. A. Cell tuned by direction of arm reaching movement. B. Cell modulated by depth of arm reaching movement. C. Cell modulated by wrist orientation. D. Cell modulated by grip type. E. Cell modulated by both reaching and grasping activities. In each panel, cell responses are shown as peri-event time histograms and raster displays of impulse activity, aligned with the arm movement onset (black triangle). Long vertical ticks in raster displays are behavioral markers. Below cell responses, recordings of X and Y components of eye positions are reported in A, C, D, and E; recording of version and vergence are reported in B. Reaching and reach-to-grasp arm movements were performed in the dark during foveal reaching tasks. Sketches of hand actions performed by the monkey are shown to the left or right of cell responses. Scale in A, vertical bar on histograms = 65 spikes/s; eye traces = 60°/division. In B, vertical bar on histograms = 70 spikes/s; eye traces = version 60°/division; vergence 0° – 20°. In C, D, and E, vertical bar on histograms = 113 spikes/s; eye traces = 60°/division. Modified from (Marzocchi et al., 2008; Fattori et al., 2009, 2010, 2017; Hadjidimitrakis et al., 2014).

response latency to visual stimulation, and the direct anatomical connection with the frontal premotor cortex (see Fig. 1; Galletti et al., 2004; Gamberini et al., 2009) suggest that V6A is involved in the online control of prehension (Fattori et al., 2001, 2017; Galletti et al., 2003; Rizzolatti and Matelli, 2003), particularly when the action time is constrained (see Galletti and Fattori, 2018 for a discussion of this matter).

As shown in all the examples in Figs. 2 and 4, reaching and grasping neurons of area V6A discharge strongly during action execution. They typically start to discharge before the onset of movement, even before the earliest electromyographic activity (Galletti et al., 1997; Fattori et al., 2005). One might therefore be led to deduce that the activity of V6A reaching and grasping neurons is a command signal that is able to ‘guide’ the arm movement, like the premotor and motor neurons in the frontal cortex. However, we believe this is not the case, because area V6A is not directly connected with the spinal cord (Matelli et al., 1998) and, accordingly, low-level electrical stimulation of V6A does not evoke any arm movement (Galletti, personal observation). In addition, although reaching and grasping cells of V6A typically discharge during arm/hand movement, they are sometimes silent during the repetition of exactly the same arm movement (as is the case for some trials in the cells shown in Fig. 2), and this is unusual for a motor command, that must be systematically present to guide the action. Since V6A receives monosynaptic inputs from the ventro-rostral part of area F2 (Fig. 1; Gamberini

et al., 2009) that is from the part of the dorsal premotor cortex that represents the arm movement (Matelli et al., 1991; Luppino and Rizzolatti, 2000), and since the timing of neural discharges in V6A reaching neurons is very similar to that observed in F2 (see Raos et al., 2004), including the typical premotor activity starting before the earliest electromyographic activity (Fattori et al., 2005), we believe that what seem to be ‘motor’ discharges observed in V6A are actually corollary discharges of motor signals coming from the premotor area F2. We do not know the functional role of these discharges, nor the reason why they are absent in some trials where the animal repeats exactly the same arm movement. We can only advance speculations as to this phenomenon suggesting that it could be a possible modulating effect of attention upon cell activity (see below). In any case, since area V6A receives both the corollary discharge of motor commands related to arm/hand movement and the somatosensory signals related to these same movements (Gamberini et al., 2009, 2011, 2020), we suggest it compares these two inputs, thus acting as a state estimator of the arm/hand movement (Kawato, 1999; Desmurget and Grafton, 2000; Shadmehr and Krakauer, 2008; Grafton, 2010; Shadmehr et al., 2010; Fattori et al., 2017).

In an experiment designed to directly compare hand/arm position signals with target position as a function of time (Fig. 5), Hadjidimitrakis et al. (2014, 2017) found an interaction between proprioception and

Gaze modulation

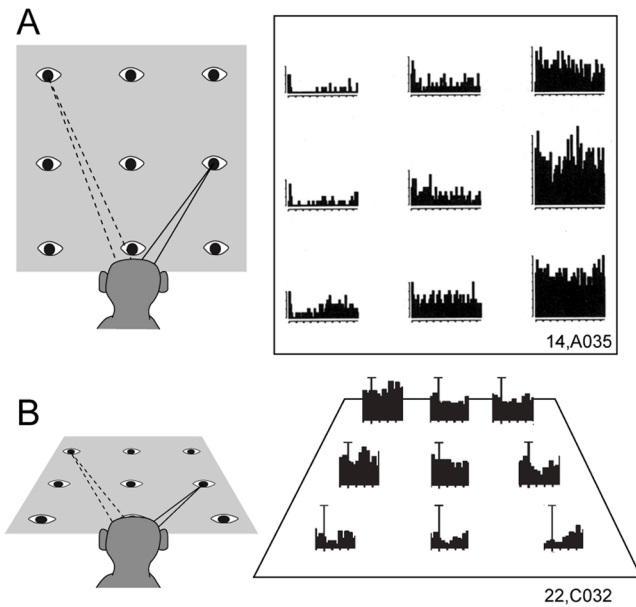


Fig. 3. Eye-position related activity of two V6A neurons. The animal sat in front of a vertical (A) or horizontal (B) screen while fixating different screen positions. Tests were performed in complete darkness. Nine directions of gaze (see positions of the eyes on the screen) were tested, with ten trials for each direction. The activity of two cells (A and B, respectively) is shown as peri-event time histograms within screen outlines. Cell activity (aligned at the start of fixation) is located on the screen in the positions gazed at by the animal during the test. Scale: (A) 2 spikes/vertical division; 300 ms/horizontal division. (B) vertical bar on histograms = 90 spikes/s; 100 ms/horizontal division. (a) Modified from (Galletti et al., 1995). (b) Modified from (Breveglieri et al., 2012).

motor commands in V6A. In this study, two conditions were compared: reaching activity during arm movement with two different trajectories, starting from two different initial positions, to reach a target (Fig. 5A top, red), and reaching with the same arm trajectory toward two spatially separated targets, again starting from the same two initial different positions as before (Fig. 5A bottom, black). From the comparison of the discharge pattern of the V6A neuronal population in these two situations (Fig. 5B), it is evident that most cells encoded the reaching activity in a body frame of reference (red), or in a mixed, body/hand frame of reference (green), while cells encoding activity in a hand frame of reference (black), which are present in the nearby areas PRR/MIP and PE (Lacquaniti et al., 1995; Chang and Snyder, 2010; McGuire and Sabes, 2011; Buneo and Andersen, 2012), were virtually absent. These data suggest a dynamic transformation of target coordinates in V6A from eye- to body- and to hand/body-centered coordinates (but, since the head and the body of the animal are fixed in relation to the world, these could also be world-centered coordinates), a transformation that is very useful in order to perform the monitoring of arm actions during their occurrence.

The output of V6A neurons could be used to adjust the motor plan in order to maintain consistency between the ongoing movement and the desired one (Fattori et al., 2001, 2005, 2017; Galletti et al., 2003; Bosco et al., 2010; Galletti and Fattori, 2018). As indicated in the diagram in Fig. 6, area V6A is thought to compare the desired position of the moving arm and the desired configuration of arm and hand (estimated through forward models of the movement that is to be executed) with the actual configuration of the limb monitored through somatosensory and visual inputs. Indeed, we found that V6A reaching cells received both visual input from a large part of the visual field, including the far periphery, and somatosensory input from the upper limbs (Bosco et al., 2010; Gamberini et al., 2011). Some cells discharged during arm reaching performed in the light but not in the dark (Fig. 7A), others discharged equally in the two conditions (Fig. 7B), and a third type of

Functional fingerprint

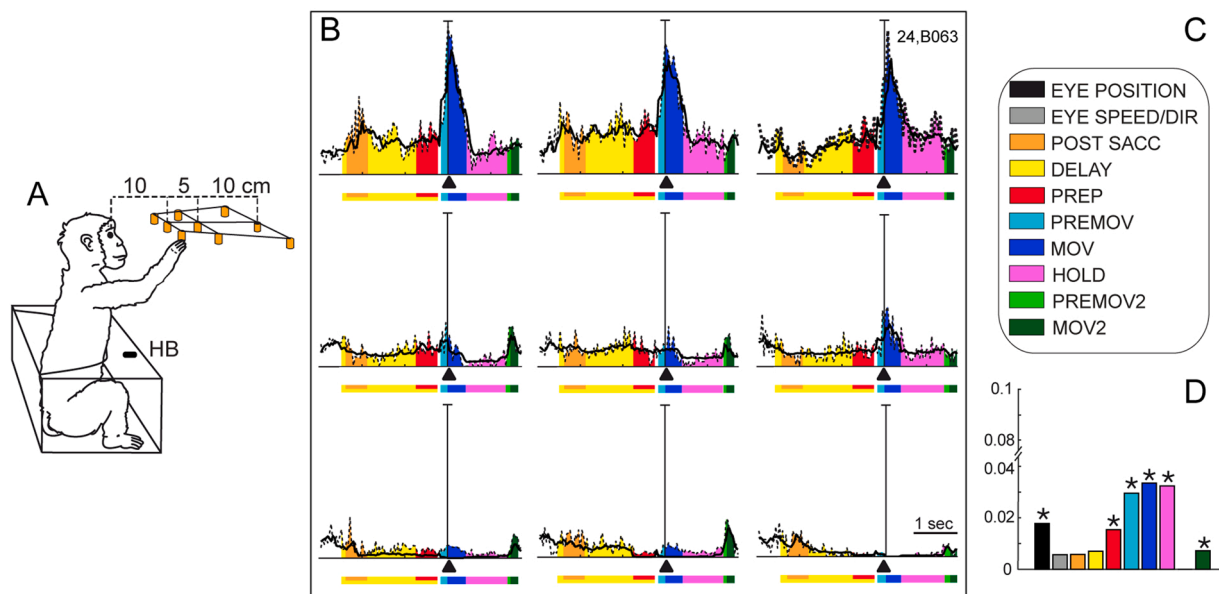


Fig. 4. Functional fingerprint of a single V6A neuron. A. Experimental setup. Reach movements were performed in darkness toward 1 of 9 LEDs (orange) arranged in different depths and directions on a panel mounted at eye level in front of the monkey. HB: Home Button. B. Plots of neural activity (peristimulus time histograms) arranged according to the spatial position of targets on the panel (rows for different depths; columns for different directions). Colors represent the epochs as reported in C. In each plot, data relative to the 10-fold validation sets are averaged across trials for each of the nine targets and aligned with movement onset (black triangle). Note that the cell activity is differently modulated in the different time epochs by the different positions gazed at by the animal. C. Parameters and time epochs considered in the analysis of neural activity, indicated by different colors: EYE POSITION = eye position; EYE SPEED/DIR = eye speed / eye direction of movement; POST SACC = post saccadic; DELAY = period of resting time before reaching; PREP = Preparation; PREMOV = premovement of forward arm movement; MOV = forward arm movement; HOLD = hand holding of the target; PREMOV2 = premovement of backward arm movement; MOV2 = backward arm movement. D. Column plot of the weights (w-values) of the 10 extrinsic blocks of regressors reported in C on the neural activity. Asterisks indicate significant w-values. Modified from (Diomedei et al., 2020).

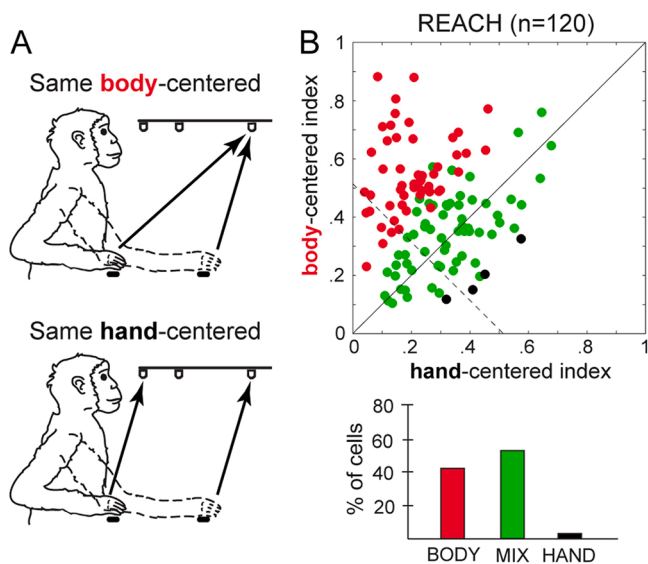


Fig. 5. Reach movements with different frames of reference. A. Side view of the reaching in depth setup task used to ascertain the integration of proprioceptive and movement-related signals for reaching in depth in V6A. Eye and hand movements were performed in darkness toward LEDs located at eye level at different depths and directions from one initial hand position located next to the body, and from another located 14 cm away. Top: pairs of movements for targets that had the same position in body coordinates. Bottom: Pairs of movements for targets with the same position in hand coordinates. B. Top: Population analysis of the reference frames of REACH activity. Each data point represents one neuron, showing its sensitivity (index), calculated as Euclidean distance, in a body-centered and in a hand-centered frame (Hadjidimitrakis et al., 2014). Red and black circles represent neurons with significantly (bootstrap estimated, $n = 500$, $P < 0.05$) different sensitivities for body (red) or hand (black) coordinates. Green circles represent neurons with equal sensitivities. The dashed line indicates the level below which differences could be due to noise. Bottom: incidence of the different categories of reference frames, as derived from Top. The V6A population has very few hand-centered neurons and a similar amount of body-centered and mixed hand/body-centered neurons. Modified from (Hadjidimitrakis et al., 2017).

cells discharged in the dark but not in the light (Fig. 7C). It is evident that cells similar to the one shown in Fig. 7A receive a visual but not a somatosensory input (lack of discharge in the dark); cells like that shown in Fig. 7B, conversely, receive a somatosensory/motor but not a visual input, the discharge in the light being unchanged from that in the dark,

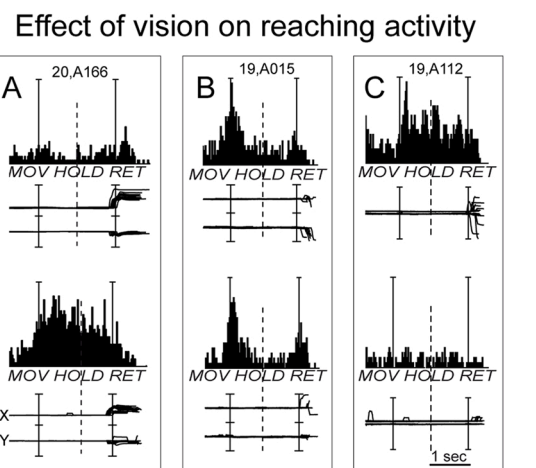
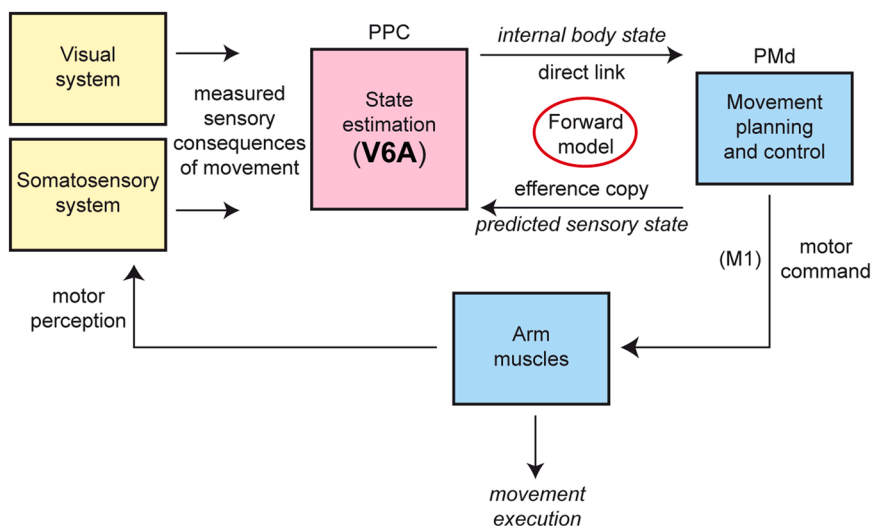


Fig. 7. Effects of vision on reaching activity of V6A neurons. Neural activity of three V6A cells recorded in foveal reaching tasks performed in the dark (above) and in the light (below); sketches of monkey hand actions are displayed to the left. Cell responses and eye traces are shown with conventions as in Fig. 2, and have been aligned twice (to the onset of outward reach movements and that of return movements, respectively). Trials were cut at the level of the dashed line to allow for the second alignment. A. Reaching neuron that is strongly responsive in the light, but not in the dark. Scale: vertical bar on histograms = 66 spikes/s; eye traces = 60° /division. B. Reaching neuron unaffected by the availability of visual information. Scale: vertical bar on histograms = 60 spikes/s; eye traces = 60° /division. C. Reaching neuron that is strongly responsive in the dark, but not in the light. Scale: vertical bar on histograms, 90 spikes/s; eye traces = 60° /division. Modified from (Bosco et al., 2010).

and cells like the one shown in Fig. 7C receive a somatosensory input (discharge in the dark) that is inhibited by the vision of the action (lack of discharge in the light). Overall, the visual input (the vision of reaching) could increase the discharge rate of V6A reaching cells (discharge in the light stronger than in the dark) or decrease it until the reaching response is even completely eliminated, as in the case shown in Fig. 7C. It is possible that the output of these reaching cells is an error signal indicating a mismatch between the actual and expected sensory feedback (Bosco et al., 2010). According to this view, patients with posterior parietal lesions that include the human homolog of V6A should fail to quickly adjust on-going actions in response to perturbations of the action target, as has actually been reported (Pisella et al., 2000; Gréa et al., 2002; Karnath and Perenin, 2005).

Fig. 6. Flow chart of a circuit involving area V6A in the neural control of arm movement. V6A receives sensory (visual and somatosensory) information from many cortical and subcortical sources, motor information (efferent copy related to arm movement) from the premotor frontal cortex (PMd), and sends signals related to the internal body state to the PMd, that guides the arm movement through the primary motor cortex (M1). Area V6A might be involved in the comparison of the anticipated motor plan with the current sensory feedback produced by the moving hand and visual background. The neuroanatomical data that give the experimental foundation to this circuitry come from (Gamberini et al., 2009; Passarelli et al., 2011). PPC: posterior parietal cortex; M1: primary motor cortex. Modified from (Fattori et al., 2017).

1.3. Encoding target position in goal-directed arm movements

The spatial position of a target to be reached out to, or grasped, is information that is expected to be provided by visual neurons. More than 60 % of neurons in V6A are visual, with a receptive field (RF) that is mainly located in the contralateral lower part of the visual field (Gamberini et al., 2011). More than half of V6A neurons discharge upon the presentation of real objects, and about half of them display object selectivity (Fattori et al., 2012). The V6A visual neurons could then provide the motor centers which guide the arm/hand in reach-to-grasp actions with the retinotopic coordinates of reachable and graspable objects which impinge upon their RF. However, since in everyday life the eyes are never still, the image of an object, even of a still object, does not stand within the limits of a RF for more than a fraction of a second; it will then impinge upon the RF of another neuron, and so on. Therefore, unless the eyes (and the head, and body) remain motionless before and during the entire duration of a goal-directed arm movement (a condition that rarely happens in everyday life), the retinotopic coordinates of a visual RF are not useful in guiding the hand toward the object. What the motor centers actually need is to receive the spatial coordinates of the object, and not the retinotopic coordinates of a visual RF stimulated for a while by that object.

It has been suggested that the spatial coordinates of objects in the visual field might be computed by a network of gaze-dependent visual neurons, that is, neurons which receive both the visual signal regarding the retinal image of the object and the signal related to the direction of gaze (Andersen et al., 1985, 1993; Galletti and Battaglini, 1989). In a gaze-dependent visual neuron, visual responsiveness is modulated by the eye position (see example in Fig. 8A), so that the neuron can encode different parts of the visual field with different frequencies of discharge (Fig. 8B). However, a single neuron encodes different parts of the visual space, even if distant from one another, with the same frequency of discharge (see points 'a' and 'b' in Fig. 8B). Many gaze-dependent visual neurons together, instead, could univocally encode the different parts of the visual field, as is schematically illustrated in Fig. 8C, where two neurons (continuous and dashed lines, respectively) together encode

three different spatial positions (a, b, c) with three different couples of discharge frequencies (position a = 50, 50; position b = 50, 0; position c = 0, 50). Area V6A hosts a high number of gaze-dependent visual neurons (Galletti et al., 1995), each one of them encoding the visual space differently, like the two neurons shown in the example of Fig. 8C. Working together in a distributed system, many gaze-dependent visual neurons could compute the spatial coordinates of any object present in the peri-personal space (Galletti et al., 1995; Galletti and Fattori, 2002). The same holds true for other parietal areas (Andersen et al., 1985, 1993), but area V6A also hosts a particular type of visual neuron whose RF remains constant in space regardless of eye movements (the so called 'real-position' cells; Galletti et al., 1993, 1995). These cells are able to directly encode the spatial coordinates of objects in the visual space (Galletti and Fattori, 2002), as shown in the example in Fig. 9. When the animal looked at different screen positions, the RF stimulation of this real-position cell evoked a response only when the animal looked at the bottom right-hand corner (Fig. 9A). On the contrary, the cell was always activated, and in a similar way, if the stimulated position was in the bottom right-hand part of the screen, no matter where the animal was looking (Fig. 9B). In other words, the cell received visual information only from the bottom right-hand corner of the screen, regardless of the position gazed at by the animal. Cells of this type encode specific spatial locations, different from cell to cell, so they can directly encode the position of objects in the visual space. The hypothesis has been advanced that these real-position cells directly provide the motor centers with the spatial coordinates necessary to guide the arm/hand toward the object to be reached out to/grasped (Galletti et al., 1995, 2003; Galletti and Fattori, 2002).

As referenced above, goal-directed arm movements could also be performed toward the location of previously seen objects, or toward specific spatial locations in total darkness. In both cases, a retinal image of the object is not available, so neither gaze-dependent visual cells nor real-position cells are activated. There are posterior parietal neurons in area LIP of macaque monkey which remain active after target disappearance during the time period in which the monkey had to withhold the movement (specifically an eye movement) while remembering the

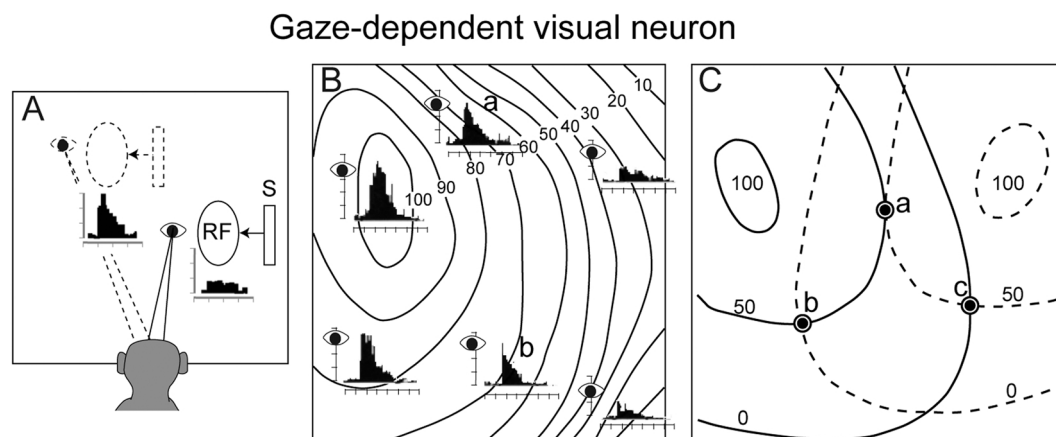


Fig. 8. Encoding of visual space by gaze dependent visual neurons. A. Visual responses of a gaze-dependent visual neuron. The square represents the screen in front of the animal, the eyes the fixation points; RF is the visual receptive field of the neuron; S, the visual stimulus used to activate the RF. Histograms below the RF are the cell responses (peristimulus time histograms) to RF stimulation. When the monkey directed its gaze to the top left part of the screen (dashed lines) the RF stimulation evoked a strong response, whereas when it gazed at the center of the screen (continuous lines) the RF stimulation evoked a weak cell response. B. Gaze modulation of the visual response in a V6A gaze-dependent visual cell. The responses were tested while the animal gazed at six different screen positions. The cell encoded the visual space in frequency of discharge: when the stimulus activated the RF on the left part of the screen it evoked a high discharge frequency (80–100%) from the cell; when the RF was activated on the right part of the screen it evoked a poor response (20–30%) from the cell. Curved lines are iso-excitability lines linking together spatial locations where the visual responses were the same. Note that visual stimulations delivered at points 'a' and 'b', though distant from one another, evoked the same visual response by the cell. C. Encoding of visual space by two gaze-dependent visual neurons, one represented by iso-excitability continuous lines, the other by iso-excitability dashed lines. Note that screen points 'a' and 'b' evoked the same visual response by the 'continuous line' cell, but different responses by the 'dashed line' cell. The reverse holds for points 'a' and 'c'. The two cells together encoded the three spatial positions differently. Modified from (Galletti et al., 1995; Battaglini et al., 1996).

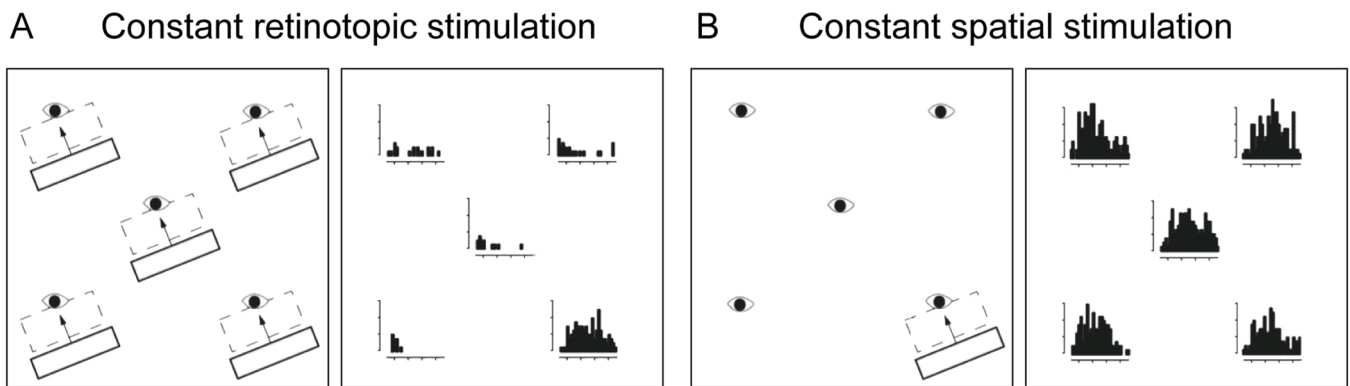


Fig. 9. Neural responses of a 'real-position' cell. Neural responses of a 'real-position' cell to the visual stimulation of (A) the same retinotopic location or (B) the same spatial location, while the animal gazed at five different screen positions. Each square represents the screen in front of the animal. In A and in B the experimental paradigm is shown to the left, where fixation-points are indicated by eye symbols and visual stimuli by full-line rectangles (moved across the RF - broken-line rectangles - at a speed of $18^\circ/s$), and the neural responses to visual stimulation are shown to the right. Responses are displayed in the screen position where fixation points were located. Scale: 4 spikes/vertical division, 300 ms/horizontal division. Note that the cell was almost equally activated by visual stimulations delivered in the bottom right part of the screen regardless of eye position (real-position cell; Galletti et al., 1993). Modified from (Galletti and Fattori, 2002).

desired target location of gaze (Gnadt and Andersen, 1988). It has been suggested that this activity represents a memory-related motor-planning signal encoding motor error, and the resulting motor vector may represent the intent to make eye movements of a specific direction and amplitude (Gnadt and Andersen, 1988; Snyder et al., 1997; Andersen and Buneo, 2002). Neurons in V6A (and perhaps in other parietal areas) could show similar motor vector activity representing the intention to make arm movements of a specific direction and amplitude, but the existence of such a type of cells has not been proven to date.

The reach target could also be provided by the direction of gaze, that could indicate the right spatial location toward which the hand should be directed even in total darkness. However, when we reach and grasp a previously seen object in complete darkness, or direct the hand toward a specific spatial location that we are fixating, we are able to successfully perform the action even if we have changed the direction of gaze and/or starting hand position. This means that we are able to successfully perform a correct reaching action even in conditions in which the original retinal coordinates of the goal of movement and the motor vector of movement itself are no longer useful to guide the movement. To sum up, visual and gaze signals can help in performing goal-directed arm/hand movements, but they cannot guide the arm/hand toward the right spatial location in all conditions of everyday life, particularly in darkness, without looking toward the region of space we want to reach out to.

1.4. Encoding target position by the spotlight of attention

To direct the arm/hand toward objects located anywhere in the space around us, regardless of eye direction and body position, in the light and in complete darkness, we suggest that motor centers use the coordinates of our spotlight of attention, which is directed at will anywhere in the visual space, regardless of eye and body position (Von Helmholtz, 1867). Attention is directed to the locations of planned movements (Rizzolatti et al., 1987; Kowler et al., 1995; Deubel and Schneider, 1996) but see (Sato and Schall, 2003; Messinger et al., 2021), so the coordinates of spotlight of attention could indicate the goal of movement to the motor centers in all the environmental conditions described above. The attentional spotlight is generally aligned with gaze (overt attention), but can also be dissociated from it (covert attention; Posner, 1980). Accordingly, we can perform foveal (by overt attention) as well as peripheral (by covert attention) reaching and grasping. The spotlight of attention is able to represent the goal of movement even when the arm/hand movements are not performed toward a given

object, but toward specific spatial locations around us in complete darkness, that is, without any visual or gaze signal that could guide the movement.

If the hypothesis that the attentional spotlight guides goal-directed movements is correct, then the *lack* of this mechanism could explain the deficits observed in optic ataxia patients. Optic ataxia syndrome is an impairment of visually guided reaching movements which is not attributable to primary visual, proprioceptive, or motor deficits (Perenin and Vighetto, 1988). Patients with optic ataxia show brain damage that likely includes the human homolog of area V6A (Battaglini et al., 2002; Karnath and Perenin, 2005). These patients can reach and grasp foveated targets accurately, but if requested to reach and grasp a non-gazed-at object they misreach the target. In some cases, patients show so-called 'magnetic misreaching', in that they reach toward the gazed point rather than toward the object presented in peripheral vision (Carey et al., 1997; Jackson et al., 2005). If in neurotypical conditions the spotlight of attention is locked onto the target of goal-directed movements, as we suggest, both peripheral mislocalisation and magnetic misreaching in optic ataxia patients may be explained by an impairment in decoupling the spotlight of attention from the direction of gaze (Rossetti and Pisella, 2018; Pisella et al., 2021). According to this view, when the impairment is partial the spotlight of attention is believed to be only partially decoupled from the direction of gaze, and the subjects thus misreach the target by directing the arm/hand toward an intermediate position between the actual position of the object and the position to which the gaze is directed. When the impairment is total, the spotlight of attention and the direction of gaze are not decoupled at all (they are aligned) and the subjects would show a magnetic misreaching by directing the arm/hand toward the gazed position instead of the object position.

1.4.1. Single cell evidence of spatial attentional modulation in V6A

The hypothesis that the target of goal-directed movements is encoded by the spotlight of attention has not been proved to date at a cellular level. Some decades ago, it was reported that many V6A reaching neurons were strongly modulated by the direction of gaze (Fig. 3; Galletti et al., 1995; Fattori et al., 2005). Since in those experiments gaze and spotlight of attention were aligned (overt attention), it is possible that the modulation was due to the attentional spotlight instead of to eye position. Fig. 10 suggests that at least for some cells this was actually the case. The cell shown in Fig. 10 was recorded while a macaque monkey was fixating a target on a panel in front of it and was planning a reaching movement while its hand was motionless near its chest (Fattori et al.,

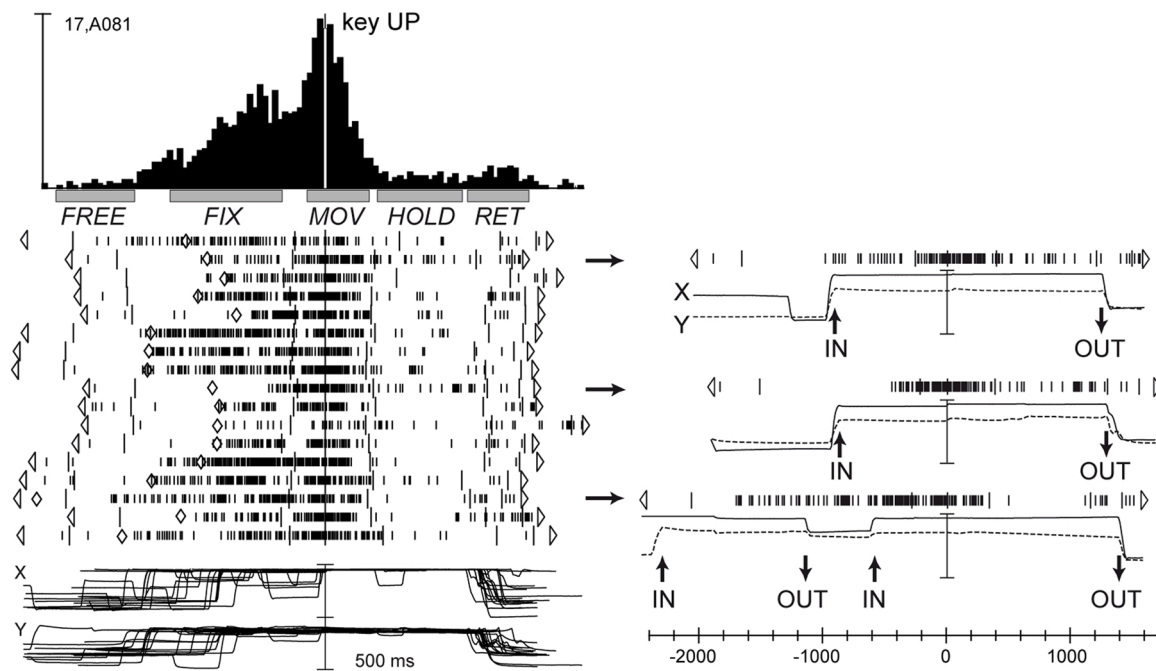


Fig. 10. Arm-reaching neuron of area V6A strongly modulated before and during movement execution. Cell activity and eye traces were recorded during a foveal reaching task performed in the darkness and are shown, on the left, with conventions as in Fig. 2. Data are aligned with the onset of forward arm movement. Diamonds in spike rasters indicate the onset time of the saccadic eye movement that brings the eye focus onto the reach target (start of fixation). Arrows indicate the three trials, whose neural activity and eye traces of which are shown separately to the right, aligned with the onset of forward arm movement as in the left part of the figure. Arrows below eye traces in the right part of the figure indicate saccades that during the task bring the gaze onto the fixation target (IN) or move it away from the fixation target (OUT). Scale: vertical bar on histograms = 140 spikes/s; eye traces = 60° / division. Modified from (Fattori et al., 2001).

2001). The cell discharged unevenly during the delay between target presentation and go-signal, and strongly during the arm movement. Close inspection of single trial data showed that in most of the trials there was a sudden increase in discharge rate contemporary with the change in gaze direction occurring when the animal decided to look at the reach target during the delay period (indicated by a diamond in the raster plot). The second trial, replicated alone with its eye traces on the right part of Fig. 10 (top arrow), shows an example. The cell started to discharge tonically when the animal gazed at the reach target (IN) and continued to discharge up to when the gaze was averted at the end of the trial (OUT). In some cases, however, as in the other two trials indicated by arrows and replicated to the right, this was not the case. In the first case (middle arrow), cell discharge was delayed about 400 ms after the saccade onset (IN). In the other case (bottom arrow), the target was firmly gazed at by the animal from the beginning of the trial (IN), but, irrespective of this, the cell only started to discharge about 650 ms after target fixation. It should also be noted that in this trial the neuron continued to discharge despite the occurrence of a saccade that shifted the gaze away from the previous fixation point for a while (OUT-IN), and stopped discharging after the hand reached the target (first marker after alignment in raster plot) even though eye and arm position did not change at that moment; this latter phenomenon was observed in most trials (see the left part of Fig. 10). In summary, although at first glance the neural discharge seems to be related to the direction of gaze, close inspection of data reveals that this is not always the case, and cell discharge is not monotonically related to the fixation point, nor temporally coupled with the changes in gaze direction. Evidently it is another factor that governs the neural activity of this neuron.

We are aware that the preparation of arm movement could be a factor that influences cell activity during the delay before movement execution. However, if this were the reason of the discharge appearance during the delay period, the onset of discharge in Fig. 10 would start more or less at the same time in all trials, because trials were aligned

with the onset of arm movement and the animal performed exactly the same action in each trial. This was simply not the case.

To sum up, the premovement modulation of the cell shown in Fig. 10 (and of most of the other V6A reaching cells we studied) was not due to the change in gaze direction, nor to the preparation of arm movement. We suggest it was due to the covert shift of spotlight of attention toward the target of reaching, a shift that occurred each time the animal decided to pay attention to the target in order to prepare an action. In most cases, this was coincident with the saccade executed to catch the target in foveal vision, but sometimes the two events - foveal catch and shift in the spotlight of attention - did not temporally overlap.

In foveal reaching, as is the case shown in Fig. 10, gaze and spotlight of attention are aligned (overt attention) and should move together, and at the same time, when the animal changes its direction of gaze. But the animal knows very well what is going to happen and could decide, at will, to briefly pay attention to other objects in its surroundings while waiting for the go signal, without risking the loss of signals that are critical for its behavior. In particular, it could decide to delay paying attention to the target after its appearance, or to anticipate paying attention to the likely location of target before its appearance. This could explain the temporal misalignment between the onset of discharge and of fixation observed in the second and third arrowed trials in Fig. 10. If our hypothesis is correct, the discharges during the delay period signal the shift of spotlight of attention instead of the shift of the direction of gaze. Interestingly, the same phenomenon could explain why, in other areas of the macaque dorsal visual cortex, including LIP, VIP, MT, and MST, neurons with tonic eye-position-related activity during fixation showed a variety of transient changes in activity around the time of saccades ranging from 100 ms before to 200 ms after the saccade itself (Morris et al., 2012). The hypothesis that neural modulation depends on shifts of attentional spotlight could also explain why, in most trials of Fig. 10, the cell became silent, or strongly reduced its activity, after the target was reached; it is plausible that after reaching the target the

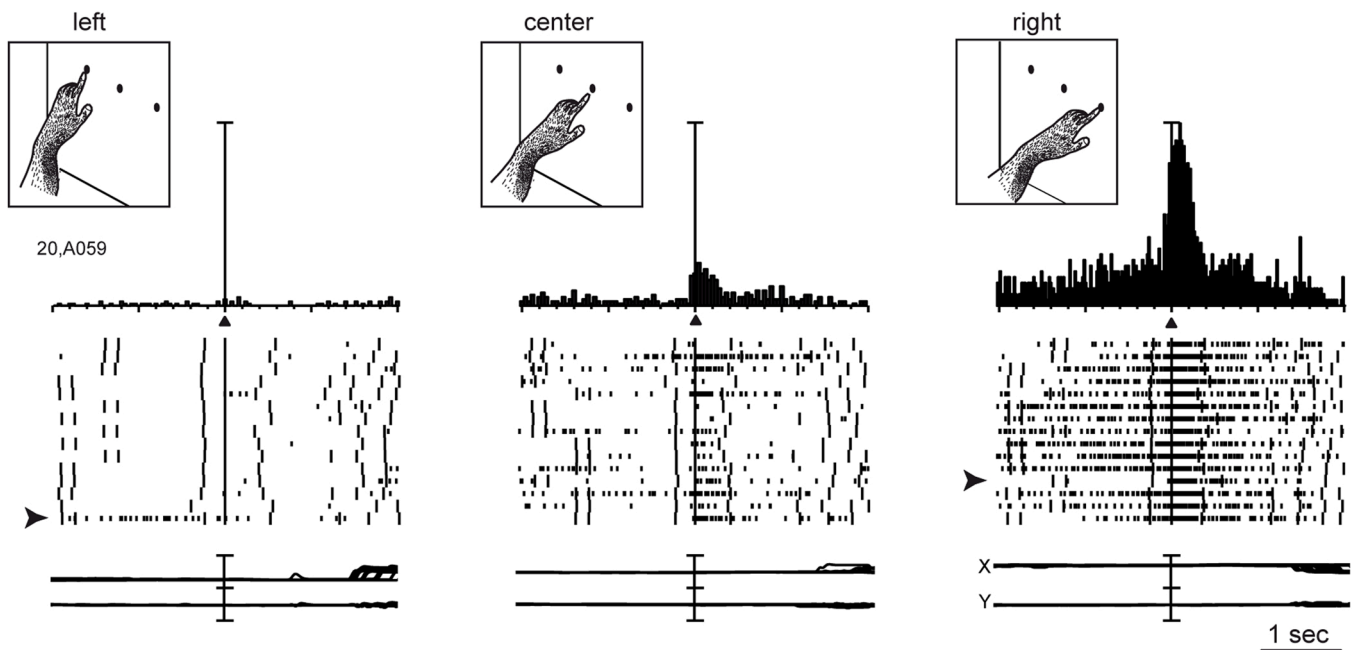


Fig. 11. V6A reaching neuron tuned by direction of gaze and arm movement. Cell responses and eye positions were recorded from V6A during a foveal delayed reaching task performed in the dark. The monkey was required to reach and touch three targets located in different spatial positions, in a random order. The activity is aligned with the arm movement onset (black triangle) and is shown with conventions as in Fig. 2. Sketches of monkey hand actions are shown at the top. Arrowheads indicate two trials with very different activity compared to the others. We suggest that in these trials the animal was attending toward the opposite side of space from the target (see text). Scale: vertical bar on histograms = 113 spikes/s; eye traces = 60° /vertical division. Modified from (Fattori et al., 2017).

spotlight of attention shifted away from the target while the gaze remained fixed on it due to the task requirement.

Fig. 11 shows another clear example of occasional disalignment between neural discharge and gaze direction, and supports the view that the origin of this phenomenon is tied to the spotlight of attention. The animal carried out a foveal reaching task. It was required to fixate and reach three targets located in three different spatial positions (left, center, or right) in successive trials presented in random order. It is evident from Fig. 11 that the cell was strongly modulated by both the direction of gaze and the direction of arm movement, like most cells in area V6A (Galletti et al., 1995; Fattori et al., 2005; Breveglieri et al., 2012). When the animal looked to the left the cell was silent and when it looked to the right the cell strongly discharged. However, in some trials, the cell discharged strongly even when the animal looked leftward (last trial in the left part of Fig. 11; see arrowhead) and in others it was silent even when it looked rightward (arrowed trial to the right). Since in all trials of each block in Fig. 11 the direction of gaze remained stable (see eye traces) and the animal was always required to prepare the same arm movement, that was then correctly performed, we can exclude gaze direction or arm movement preparation being responsible for the change in activity. We suggest that the direction of spotlight of attention could be responsible for the phenomenon, because when the animal was required to attend to the left (reaching to the left), it could occasionally pay attention to the right, and viceversa, and this could explain the dramatic difference in the discharge rate observed in arrowed trials. When the animal looked at the central position the cell activity was quite variable: in some trials it was silent, while in others it discharged. It could be because the animal was sometimes tempted to attend either to the right or to the left, a phenomenon that was likely promoted by the random presentation of the target in different locations.

We are aware that the possible effect of attentional spotlight on neural discharge is a speculation without direct proof of validity; however, we have observed this phenomenon in many V6A cells, and in all cases the hypothesis of spotlight of attention explained the data, whereas an effect of gaze shift or arm movement preparation did not. We

are also aware that to demonstrate that cell activity modulation is the consequence of the shift of spotlight of attention and not of the change in gaze direction, or the preparation of arm movement, one must disengage the direction of gaze from the direction of attention (covert shift of spatial attention) in a task in which the animal works in complete darkness and is not preparing any arm or eye movement. In such an experimental condition, the animal can be required to change the direction of spatial attention without changing the direction of gaze, and one can check whether cell activity changes accordingly. We performed such an experiment about a decade ago and demonstrated that there were neurons in V6A whose activity was actually modulated by the covert shift of spatial attention (Galletti et al., 2010). Fig. 12 shows an example of such a neuron. The animal maintained its gaze fixed on a small, motionless target at the center of the screen in front of it. When the animal's attention (but not the gaze, see eye traces below neural responses in Fig. 12) shifted toward the bottom of the visual space, the cell discharged more strongly than when the animal's attention was shifted upward. Other V6A cells preferred different parts of space, and we speculated that, together, these cells could encode the whole visual space around the fixation point (Galletti et al., 2010).

1.4.2. A priority map for reaching in area V6A

The modulation of cell activity by the direction of spotlight of attention could also explain why real-position cells (Galletti et al., 1993) respond equally well to the visual stimulation of the same spatial location regardless of gaze direction (see Fig. 9). Indeed, the cell in Fig. 9 could be modulated by the attentional spotlight with a selective preference for the bottom right part of the field of view. If this is the case, the cell discharges only when visual stimulation is delivered in the bottom right part of the screen because the visual stimulus attracts the animal's spotlight of attention there. In other words, it could be that real-position cells encode visual space in spatiotopic coordinates because they are actually activated by the spotlight of attention instead of, or in addition to, the visual stimulus *per se*. Area V6A could host a priority map that is specific for the guidance of reaching arm movement, similar to the

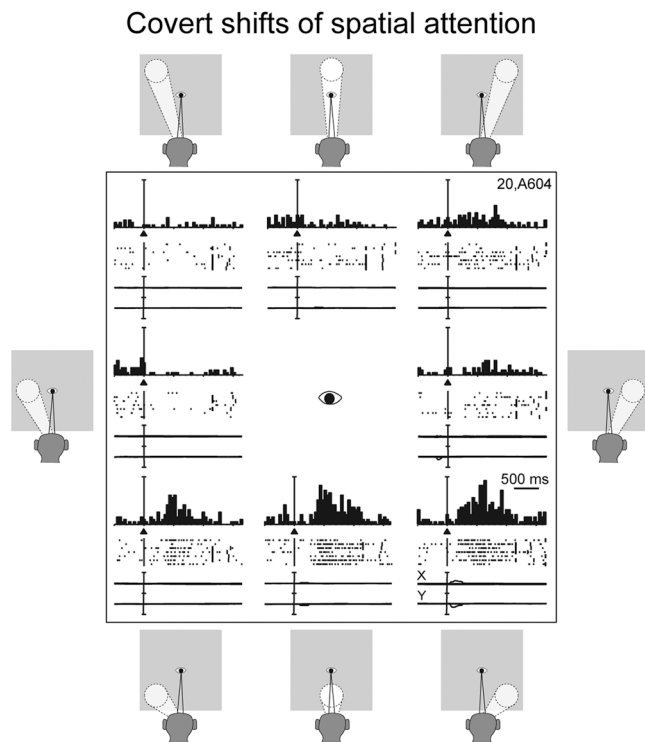


Fig. 12. V6A cell modulated by the covert shift of spatial attention. Experimental conditions: the animal sat in front of a screen in the dark, gazed a small stationary target presented at the center of the screen (eye symbol), and was required to covertly attend to one of 8 peripheral regions in a random sequence. While fixating, the monkeys had to detect a target (5 ms red flash) in one out of several peripheral positions and respond to it by releasing the button without moving the eyes. The target position was cued by a yellow flash (30–150 ms) preceding the target onset by 1–1.5 s. The cue signal prompted the monkeys to covertly displace attention toward the periphery. After target detection, the monkeys shifted attention back toward the straight-ahead position to detect the change in color of the fixation LED. This change in color had to be reported by pressing the button again. The monkeys were trained to maintain their gaze in the straight-ahead position throughout the trial. To check whether our experimental conditions induced covert attention shifts, we measured reaction times between target onset and button release. These measurements were collected in separate behavioral testing sessions before the onset of single unit recording. These sessions contained valid trials as described above, and invalid trials in which the cue was misleading because the target appeared on the opposite side. The reaction times of valid trials resulted significantly shorter than those of invalid trials and this proved that the location in which the target appeared benefitted from attentional enhancement evoked by cue appearance; in other words, this proved that the spotlight of attention was directed toward the location in which the target appeared. Cell activity and eye traces collected during recording sessions are shown inside the large square (conventions are as in Fig. 2). Trials were aligned with the shift of spotlight of attention (black triangle), in the locations to which the spotlight of attention was directed in that block of trials, as indicated in the small drawings displaced all around the screen (the circle in each drawing represents the spotlight of attention). Scale: vertical bar on histograms, = 70 spikes/s; eye traces = 60°/vertical division. Modified from (Galletti et al., 2010).

priority map described by Bisley and Goldberg (2010) in area LIP for the guidance of saccadic eye movements. The V6A priority map could combine bottom-up inputs such as visual responses with top-down signals like reaching plans. In this map, the real-position cells would represent the spatial locations in the peripersonal environment and constitute a sort of earth-based, three-dimensional map of objects around us that is maintained when we move around. In summary, V6A would encode the reach target as a result of the visual information about the target, the direction of gaze, and the direction of the spotlight of attention. In a lighted environment, all these three factors are likely to

be involved in the encoding process. In the dark, visual information is not available, so motor centers most likely use the coordinates of the direction of gaze and those of the spotlight of attention to direct the hand toward the object to be reached out to. But if the subject in the dark shifts its gaze and/or the body before or during arm movement, the only spatial coordinates that motor centers can use to direct the hand are those of the spotlight of attention, that is, the output of real-position cells. The V6A priority map, in this case, would thus allow the somatomotor system to guide the arm/hand toward objects in any condition of the everyday life.

It is well known that the allocation of spatial attention is under the control of an attentional network which involves many brain regions (Posner and Petersen, 1990; Corbetta et al., 1993, 1998, 2008; Kastner et al., 1999; Kastner and Ungerleider, 2000; Nobre et al., 2000; Corbetta and Shulman, 2002; Bisley and Goldberg, 2003, 2010; Petersen and Posner, 2012; Fiebelkorn and Kastner, 2020) including, among others, the frontal eye fields (FEF) and area 46 in the prefrontal cortex (Squire et al., 2013; Messinger et al., 2021), and the medial and lateral pulvinar nuclei in the thalamus (Petersen et al., 1987; Saalmann and Kastner, 2011). Monkey electrophysiology studies have shown that: (a) FEF neurons are engaged during covert shifts of spatial attention (Wardak et al., 2006; Buschman and Miller, 2007), (b) clusters of neurons in area 46 show activity which changes contextually with shifts of spotlight of attention (Kaping et al., 2011), and (c) spatial attention modulates the response magnitude of neurons in dorsal, lateral, and inferior parts of the pulvinar (Petersen et al., 1985; Bender and Youakim, 2001). It has also been reported that dorsal pulvinar lesions provoke deficits in coding spatial information in the contralesional visual field and affect visually guided behavior such as reaching and grasping contralesional targets (Wilke et al., 2010). Because area V6A receives a strong direct input from the caudal part of prefrontal area 46 and a much weaker, if any, input from FEF (see Fig. 13A; Gamberini et al., 2009, 2020; Passarelli et al., 2011) together with a strong input from the thalamic lateral posterior nucleus and medial pulvinar (Fig. 13D, E; Gamberini et al., 2016, 2021), it is likely that area 46, the lateral posterior nucleus, and the medial pulvinar convey information regarding the direction of spotlight of attention to area V6A, and that this input is responsible for the neural discharges and the high variability in neural activity observed in the examples shown in Figs. 10–11.

According to this view, in recent neuroimaging studies in macaques Vanduffel and coworkers (Caspari et al., 2015) have shown that areas 46 and V6A, but not FEF, are strongly activated during covert shifts of spatial attention (see Fig. 14). Similar results have been obtained in humans, where the caudal part of area 46, but not FEF, and a portion of the medial superior parietal lobule, which likely includes the homolog of macaque area V6A, are consistently activated during covert spatial attention shifts (Yantis et al., 2002; Molenberghs et al., 2007; Kelley et al., 2008; Caspari et al., 2018). Fig. 15 shows that the region of the human superior parietal lobule activated by covert shifts of spatial attention (Fig. 15A; Vandenberghe et al., 2001) is the same region (located in the caudal part of the superior parietal lobule, anterior to the parieto-occipital sulcus) described by Pitzalis and coworkers as human area V6Ad (Fig. 15B; Pitzalis et al., 2013, 2015; Tosoni et al., 2015). Interestingly, this is also the same region that, if damaged (Fig. 15D), produces strong contralateral attentional deficits when shifts of spotlight of attention are required (Fig. 15C; Gillebert et al., 2011). In the study by Gillebert et al. (2011), subjects had to orient attention based on a prior spatial cue and discriminate the orientation of a grating. As shown in Fig. 15C, patient H.H. was impaired for contralesional targets in trials with an invalid spatial cue, and was even more impaired in trials with the presence of a competing distractor in the visual field contralateral to the target. In other words, patient H.H. was impaired when the shifting of spotlight of attention was required (invalid spatial cue), and the impairment was more severe when the shift was repeated several times due to the presence of a distractor (double valid). It is interesting to note that the unusual small lesion of patient H.H. (volume = 1.8 cm³)

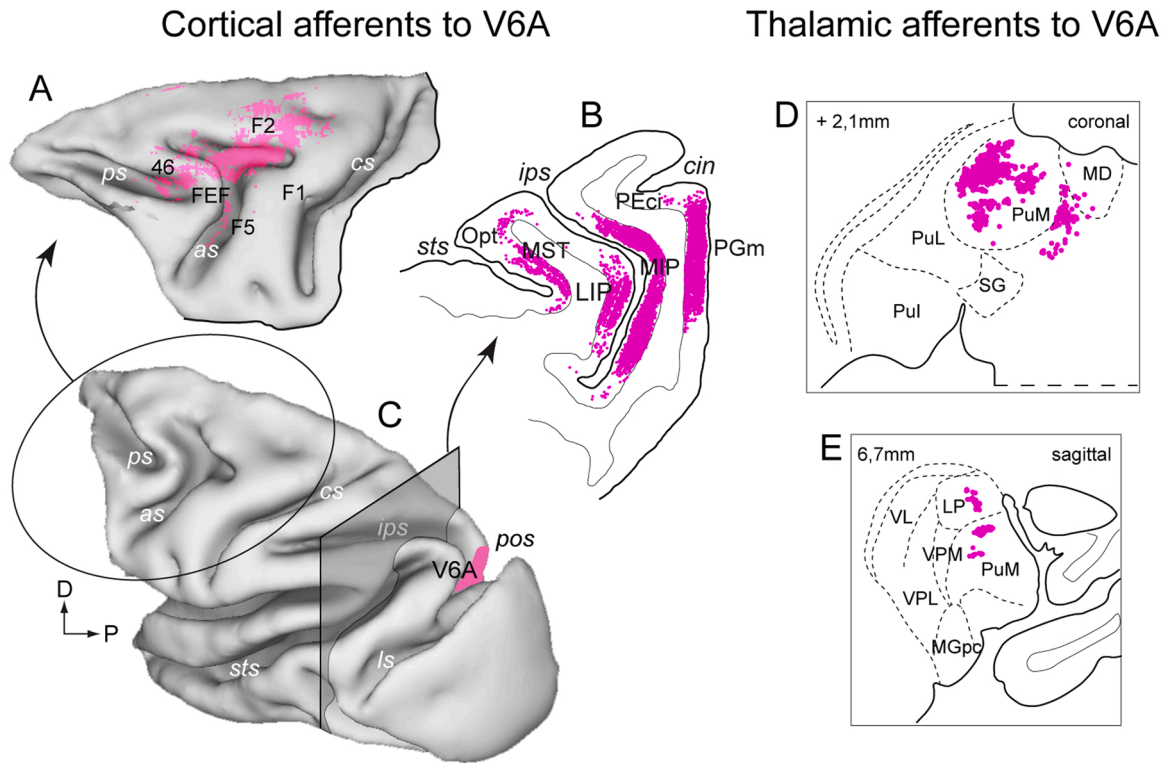


Fig. 13. Cortical and thalamic afferents to area V6A. A, C. Lateral view of the left hemisphere of the macaque brain partially inflated to show the cortex hidden within the sulci, in particular the arcuate and principal sulci where areas F2, F5, and 46 are located (A), and the parieto-occipital sulcus where area V6A is located (C). B. Coronal section of the brain showing the locations of cortical neurons projecting to area V6A, labeled after retrograde tracer injection in V6A. Note in particular area LIP located in the depths of the intraparietal sulcus. D, E. Coronal (D) and sagittal (E) sections of the thalamus showing the locations of neurons projecting to area V6A. Abbreviations. Cortical areas: F1, F2, F5, 46, FEF, MST, MIP, PGm, Peci, LIP, Opt: areas F1, F2, F5, 46, FEF, MST, MIP, PGm, Peci, LIP, Opt. Other abbreviations as in Fig. 1. Thalamic nuclei (according to Olszewski, 1952; Ilinsky and Kultas-Ilinsky, 1987): LP Lateral posterior; MD Mediodorsal; MGpc Medial geniculate, pars parvocellularis; PuI Pulvinar, inferior subdivision; PuL Pulvinar, lateral subdivision; PuM Pulvinar, medial subdivision; SG Suprageniculatus; VL Ventral lateral; VPM Ventral posterior medial; VPL Ventral posterior lateral. Modified from (Cortical afferents) (Gamberini et al., 2009) and (Thalamic afferents) (Gamberini et al., 2016).

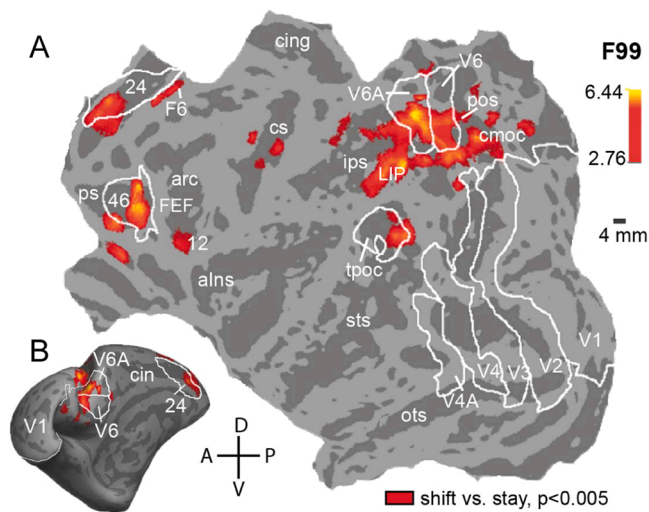


Fig. 14. Activation areas in the macaque brain for shifting of the spotlight of attention. A. Two-dimensional map of the macaque left hemisphere, with activation areas obtained by contrasting attentional shift with stay. Shift activations are displayed on the inflated and flattened F99 template of the macaque brain, with corresponding ROI labels. Origins of ROI-labels are listed in Supplementary Table 6 of Caspari et al. (2018). Notice that locations of areas FEF and LIP, not reported in the original figure, are indicated here. B. posterior-medial view of the inflated brain, exposing the medial parietal cortex and areas within the parieto-occipital sulcus (V6 and V6A). Sulci: cing, cingulate; ains, anterior insular; sts, superior temporal; cs, central; ips, intraparietal; pos, parieto-occipital; ots, occipito-temporal; ps, principal; arc, arcuate sulcus. Modified from (Caspari et al., 2018).

occupies a cortical region located in the caudal part of the superior parietal lobule, anterior to the parieto-occipital sulcus, which is very similar in location and extent to the area V6Ad described by Pitzalis and coworkers, as can be easily checked by comparing the right part of Fig. 15B with Fig. 15D. Altogether, these data suggest that the human V6Ad is involved in the control of covert shifts of spatial attention in a similar way to the macaque area V6A.

It is interesting to note that the lateral intraparietal area (LIP), which in the macaque hosts a priority map (Gottlieb et al., 1998; Bisley and Goldberg, 2003, 2010) and sends a strong monosynaptic input to V6A (Fig. 13B; Gamberini et al., 2009), is also activated during covert shifts of spatial attention in both non-human (Fig. 14) and human primates (Caspari et al., 2018). In addition, it has been reported that the caudal part of area 46 is involved in controlling spatial shifts of attention during motor behavior rather than cognitive processes (Gerbella et al., 2013; Borra et al., 2017). The overall emerging picture provides strong support to the view we advance here that in both non-human and human primates V6A receives information relative to the direction of spotlight of attention (from cortical areas 46 and LIP and, possibly, from thalamic lateral posterior nucleus and medial pulvinar), to be used in encoding the spatial locations of reach targets.

1.5. Functional role(s) of V6A

In previous papers, and above in this review, we have suggested that damage to area V6A could be responsible for the misreaching observed in optic ataxia patients because of their impairment in decoupling the spotlight of attention from the direction of gaze. Twenty years ago it was demonstrated that a lesion of V6A in the macaque monkey produced

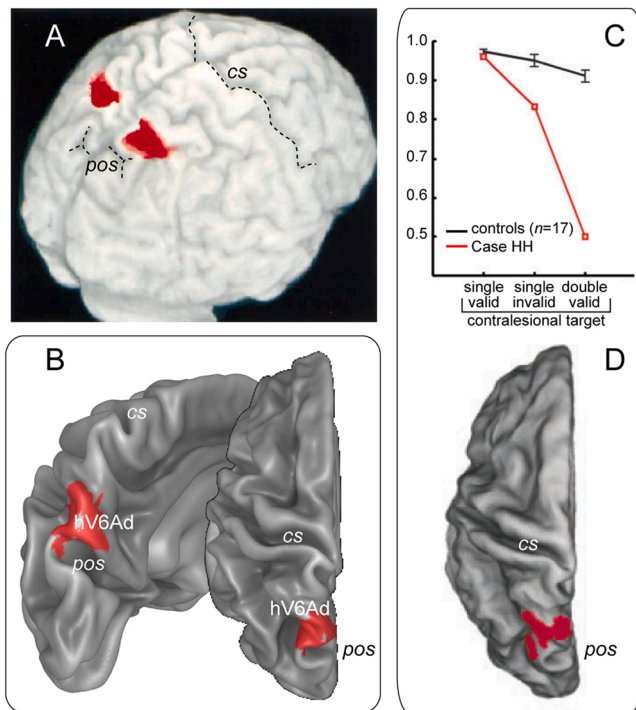


Fig. 15. Activation areas for attentional shifts in the human brain versus location of area V6A. A. Regions of human brain (in red) activated during shifting of spatial attention. Dashed lines indicate the parieto-occipital sulcus (pos) and the central sulcus (cs). B. Dorsomedial (left) and dorsal (right) views of the left hemisphere of the human brain showing the location and extent of area hV6Ad in red. Data were obtained by overlapping individual ROIs derived from independent samples of 25 participants onto an inflated Conte69 brain atlas. cs = central sulcus; pos = parieto-occipital sulcus. C. Performance of Case H.H. (in red) versus age-matched controls (in black) in a behavioral experiment involving shifting of spatial attention. Subjects were required to reorient their spatial focus of attention (invalid spatial cue) or to select between competing stimuli in validly cued trials with distracter (double valid). Taken from (Gillebert et al., 2011). D. Brain lesion (colored in red) in Case H.H. The lesion is very small and restricted to the caudal part of the superior parietal lobule. Notice the similarity in location and extent of the lesion with area hV6Ad, shown in panel B. Details on sulci as in B.

(a) Modified from (Vandenberghe et al., 2001). (b) Modified from (Pitzalis et al., 2013, 2015). (c) Modified from (Gillebert et al., 2011).

misreaching and misgrasping similar to that observed in optic ataxia patients (Battaglini et al., 2002), thus confirming the causal role of V6A in the control of reaching and grasping and its likely involvement in optic ataxia syndrome (Galletti et al., 2003; Karnath and Perenin, 2005). However, Battaglini et al. (2002) observed that the animal impairment, in particular the misreaching, was a transient phenomenon. Looking at the animal behavior in recordings from TV closed circuit (personal observations), it was clear that at the beginning of testing, during reaching, the animal did not gaze at the raisin it wanted to grasp, and misreached it. Then, after several erroneous attempts to grasp the raisin, it began to look at it more attentively, and reaching became more and more correct. Our personal conclusion is that, as in optic ataxia patients, the animal misreached non-gazed-at targets, while it reached and grasped the directly fixated targets in a more accurate manner. In other words, in both human and nonhuman primates, V6A is thought to be essential for a correct reaching when the direction of gaze and the location of object are not aligned, that is, when the direction of gaze and spotlight of attention are decoupled (Rossetti and Pisella, 2018; Pisella et al., 2021).

Overall, the data summarized in this review show that, in both the macaque and human brain, area V6A is involved in attentional reorienting and in motor planning updates. The experiments carried out by Ciavarro et al. (2013) on healthy human subjects clearly support this

view. These authors used online rTMS over the putative human V6A (Fig. 16 A1) during an attention task requiring covert shift of attention, and during a reaching task requiring planning of reaching movements toward peripheral cued targets in space (Fig. 16 A2). They found that rTMS increased the reaction times to invalidly cued, but not to validly cued, targets during both the attention (Fig. 16 B1) and reaching (Fig. 16 B2) task. These results suggest that V6A plays a causal role in attentional reorienting, but not in attentional orienting. They are in agreement with neuroimaging results in humans showing that signals for shifting attention between peripheral locations (reorienting) are specifically encoded in the medial aspect of the superior parietal cortex (Wojciulik and Kanwisher, 1999; Yantis et al., 2002; Serences and Yantis, 2006; Molenberghs et al., 2007; Kelley et al., 2008; Vossel et al., 2009; Tosoni et al., 2013), whereas signals for maintaining attention at a spatial location (orienting) are encoded in more lateral parietal regions (Corbetta and Shulman, 2002; Serences and Yantis, 2007). According to Ciavarro et al. (2013), area V6A seems to be specifically implicated in the disengagement phase of reorienting rather than in the subsequent shift of the attentional spotlight (Posner et al., 1984). Ciavarro and co-workers suggested that reorienting signals are used by V6A to rapidly update the current motor plan or the ongoing action when a behaviorally relevant object unexpectedly occurs in an unattended location. The rTMS over V6A also induced a deviation of reaching endpoints toward visual fixation (Fig. 16 B3) that resembles the “magnetic misreaching” found in optic ataxia patients (Carey et al., 1997). This further supports the view that V6A is involved in decoupling the spotlight of attention from the direction of gaze, and that in V6A the attentional spotlight signals the location of the reach target.

1.6. Two grasping areas in the macaque brain

Many of the features of neural activity in V6A are also found in the anterior intraparietal area AIP, and both these areas are suggested to be involved in the control of grasping (Galletti and Fattori, 2018). Areas AIP and V6A are reciprocally connected (Fig. 17A, B), so a direct transfer of grasping information can occur between the two areas (Borra et al., 2008; Gamberini et al., 2009; Passarelli et al., 2011). However, the two areas show anatomical and functional differences that suggest possible different functional roles. As shown in Fig. 17C, AIP is more strongly connected with the inferior parietal lobule than V6A (70 % versus 15 % of the total input). Conversely, V6A receives nearly 40 % of inputs from extrastriate visual cortices and 30 % from other areas of the superior parietal lobule, whereas AIP is practically devoid of inputs from these two cortical sectors. Area AIP has preferential connections with the ventral premotor cortex, whereas V6A links to the dorsal premotor cortex. The inferior temporal cortex is connected with AIP but not with V6A and, conversely, the mesial cortex is connected with V6A but not with AIP. In summary, while AIP receives visual input from the ventral and dorsolateral visual streams (Borra et al., 2008), V6A receives information from the dorsomedial and dorsolateral visual streams and the mesial cortex, but does not receive a direct input from the ventral visual stream (Gamberini et al., 2009; Passarelli et al., 2011). It is likely that the inferior temporal input to AIP is useful in providing object information in order to generate object-oriented actions (Rizzolatti and Matelli, 2003; Borra et al., 2008), while the dorsomedial visual stream and the mesial cortex input to V6A is probably useful to coordinate arm movement and grasping during navigation (Kravitz et al., 2011; Hutchison et al., 2015; Gamberini et al., 2020, 2021).

Functional data suggest that the use of visual information by AIP during grasping is different compared to that of V6A, confirming that the two areas play a different functional role. In AIP, grasping in light activates the cells to a greater extent than grasping in darkness (Murata et al., 2000), whereas in V6A about half of the neurons are inhibited by the vision of grasping (Bosco et al., 2010; Breveglieri et al., 2016). While cell activation by vision of grasping suggests a use of the visual feedback as supplemental information to control grasping movements, the cell's

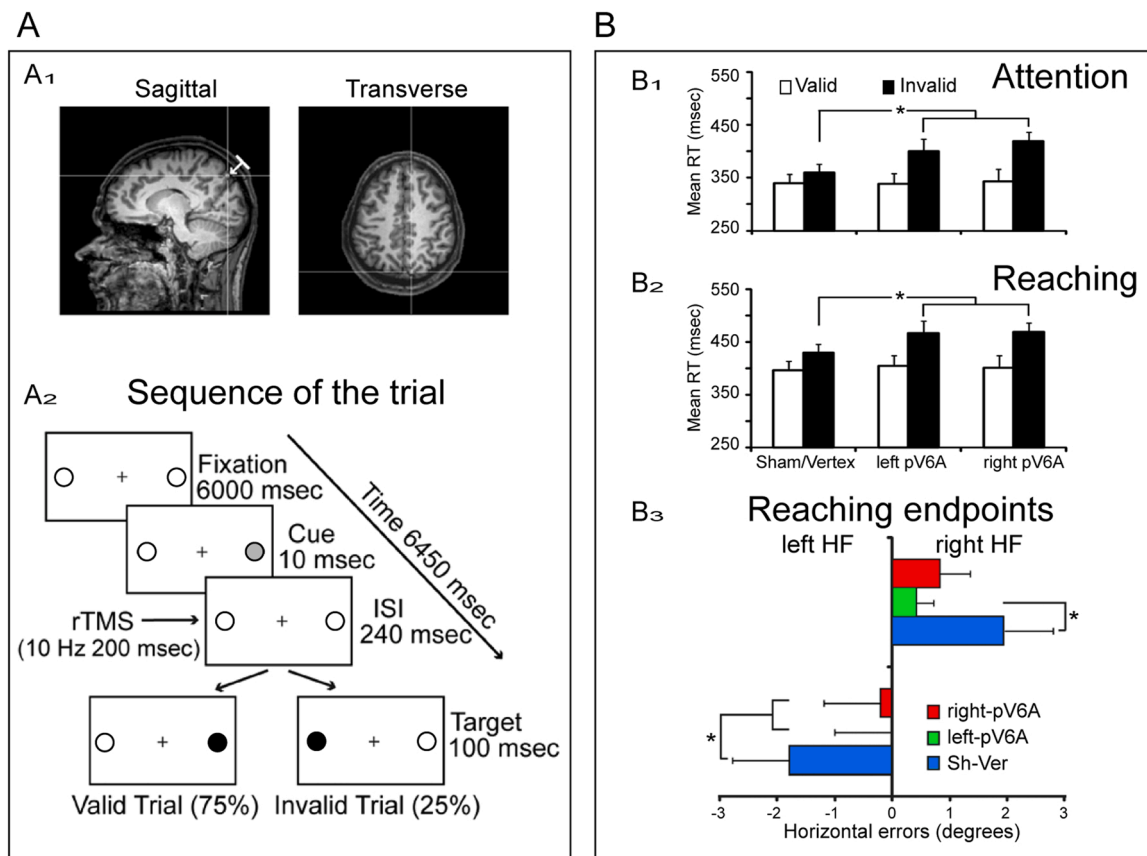


Fig. 16. Effect of the rTMS over the putative human V6A. **A.** Stimulation site and trial structure. **A1:** The neuroanatomical region stimulated with rTMS (white arrow) is indicated by intersection lines in a sagittal (left) and a transverse (right) section of the T1-weighted MRI. Average (\pm SD) Talairach (Talairach and Tournoux, 1988) coordinates of the stimulated region are the following: left hemisphere, $x = -10.4 \pm 3.5$, $y = -78.2 \pm 3.5$, $z = 40.2 \pm 2.7$; right hemisphere, $x = -10.7 \pm 1.7$, $y = -77.6 \pm 5.0$, $z = 40.4 \pm 3.2$. **A2:** Display sequence for a valid and an invalid trial. **B.** rTMS effects on attentional orienting and reorienting during the attention (**B1**) and the reaching (**B2**) task. Mean RTs (\pm SEM) to valid and invalid trials as a function of stimulation condition show that a similar effect of validity was observed in both the attention and the reaching task. **B3:** rTMS effect on reaching endpoints. Mean horizontal errors (\pm SEM) in degrees as a function of stimulation site and visual hemifield (HF). * indicates significant post hoc comparisons ($p < 0.05$). Modified from (Ciavarrò et al., 2013).

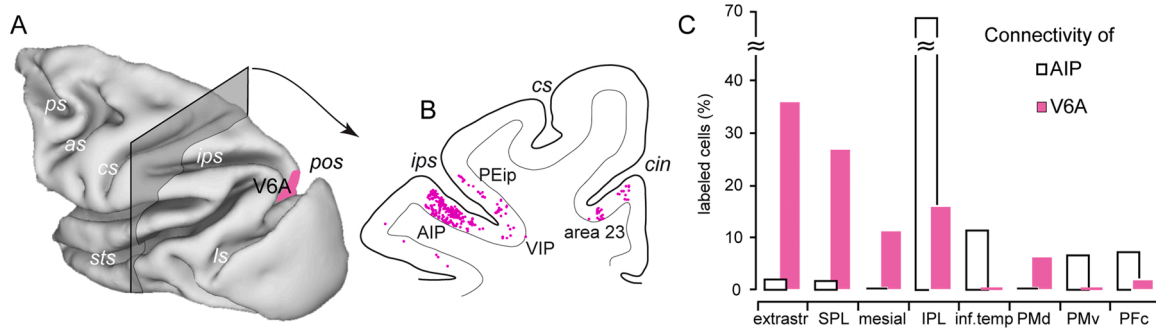


Fig. 17. Cortico-cortical connections of the macaque parietal areas V6A and AIP. **A.** Three-dimensional reconstruction of the injection site in Case 11 L (area V6Ad). **B.** cortical distribution of retrogradely labeled cells in a coronal section taken at the level of area AIP. Each pink dot represents a labeled cell after WGA-HRP injection in area V6Ad. Cin, cingulate sulcus; Cs, central sulcus; Ips, intraparietal sulcus; Lat, lateral sulcus; STs, superior temporal sulcus. Locations of areas 23, PEip, VIP, AIP are also indicated. **C.** Cortico-cortical connections of the macaque parietal areas V6A and AIP. Columns show the incidence of V6A (pink) and AIP (white) connections with different regions of the cortical mantle. Extrastr, extrastriate cortex (areas V2, V3, V4, MST, V6); SPL, superior parietal lobule; Mesial, areas of the mesial surface of parietal lobe; IPL, inferior parietal lobule; Inf.temp, interior temporal cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex. PFC, prefrontal cortex. Data derived from (Borra et al., 2008) and personal communication; (Gamberini et al., 2009; Passarelli et al., 2011). (a and b) Modified from (Gamberini et al., 2009). (c) Modified from (Galletti and Fattori, 2018).

inhibition is difficult to interpret. It could represent an aspect of the modulation of reaching activity by vision, that could enhance or reduce cellular activity (Bosco et al., 2010), but specific experiments are required to check the validity of this hypothesis, or to advance other

possible interpretations.

A second functional difference between AIP and V6A concerns the sensitivity to visual stimulations performed outside the grasping context. While the overwhelming majority of neurons in AIP (90 %) are

sensitive to simple visual stimuli presented to the animal without any request for interaction with them (Romero et al., 2014), only a minority of V6A neurons respond to simple visual stimuli passively presented to the animal (Galletti et al., 1999; Gamberini et al., 2011). However, real object presentation in tasks where the object is the target of delayed grasping activates the majority of V6A neurons (Fattori et al., 2012), and it has been reported that several V6A neurons are activated by the affordance evoked by the object presented to the animal, irrespective of its visual features (Breviglieri et al., 2015). Taken together, these data seem to reflect that V6A is more deeply involved in encoding vision for action (Fattori et al., 2012), and, conversely, AIP is more deeply involved than V6A in object recognition (Fattori et al., 2017).

To speculate, we could hypothesize that when we want to grasp an object, areas AIP and V6A are both, albeit differently, activated according to the type of object and the context in which grasping has to be performed. AIP seems to be particularly involved in the precise manipulation of the objects, and/or in grasping delicate and fragile objects, whereas V6A is concerned with directing the hand toward moving objects and/or in grasping them rapidly, with the correct hand orientation and grip aperture (Galletti and Fattori, 2018).

1.7. The human homolog of monkey area V6A

In the macaque monkey, the visuomotor area V6A is located in the depth of the parieto-occipital sulcus (POs), anterior to the visual area V6 (see Fig. 1). Since in the human area V6 (hV6) is located in the posterior wall of the dorsalmost part of the POs (Pitzalis et al., 2006), the human V6A (hV6A) was expected to be located anterior to it, in the fundus and anterior wall of the dorsalmost part of the POs. Moreover, similar to that of the macaque, the hV6A was expected to be a visuomotor area that is sensitive to arm reaching and grasping. In line with these predictions, in the past decades many studies have observed broad activations in response to arm pointing (Astafiev et al., 2003; Connolly et al., 2003), as well as to reaching and grasping movements (Beurze et al., 2009; Gallivan et al., 2009; Filimon et al., 2009; Vesia et al., 2010, 2017; Cavina-Pratesi et al., 2010; Galati et al., 2011), in a cortical region that likely included hV6A. Connolly and colleagues (2003), for instance, observed a large swath of activation for goal-directed, arm-related movements in the medial aspect of the posterior parietal cortex, anterior to the POs (Fig. 18A). Other studies reported distinct foci of activation for pointing, reaching, and grasping movements anterior, and sometimes posterior, to the POs (Fig. 18B; Tosoni et al., 2008; Beurze et al., 2009; Gallivan et al., 2009, 2011; Filimon et al., 2009; Cavina-Pratesi et al., 2010; Galati et al., 2011; Cappadocia et al., 2017). The cortical region where these foci of activation were distributed was called ‘the superior parieto-occipital cortex’ (SPOC) by Culham’s group (Gallivan et al., 2009, 2011; Cavina-Pratesi et al., 2010). Similar to macaque V6A,

the activity of the SPOC was modulated by the direction of goal-directed arm movements (Cavina-Pratesi et al., 2010; Gallivan et al., 2011; Monaco et al., 2011) as well as by wrist orientation (Monaco et al., 2010) and grip size (Monaco et al., 2014).

In the macaque, area V6A has been subdivided into a ventral and a dorsal part (V6Av, V6Ad) on the basis of cyto- and myelo-architecture, as well as anatomical connections and functional properties (Luppino et al., 2005; Gamberini et al., 2011). In humans, we have recently described the homologs of monkey areas V6Av (Pitzalis et al., 2013) and V6Ad (Tosoni et al., 2015) using a combination of fMRI brain mapping methods, cortical surface-based analysis, wide-field video retinotopy, task-evoked activity, and functional connectivity. As shown in Fig. 18C, the human homologs of monkey areas V6Av and V6Ad have been identified in the fundus and the anterior bank of the dorsalmost portion of the POs, respectively (Pitzalis et al., 2013; Tosoni et al., 2015). The hV6Av is a visuomotor area representing the arm, but is mainly involved in the visual analysis of motion (Pitzalis et al., 2013). Area hV6Ad, on the other hand, is more specifically involved in the visuomotor control of arm movements (Tosoni et al., 2015). Notably, the anatomical position, neighbor relations, and functional properties of hV6Av (Pitzalis et al., 2013) and hV6Ad (Tosoni et al., 2015) closely resemble those of macaque areas V6Av and V6Ad, respectively (Gamberini et al., 2011), strongly supporting the view that macaque and human V6A are homologous structures.

2. Conclusions

The medial posterior parietal area V6A in the macaque hosts neurons that are able to encode different parameters that are crucial for correctly orchestrating goal-directed arm movements such as reaching and grasping. Since we are able to reach and grasp an object in complete darkness even if the object is no longer visible, and even if we have changed initial eye and hand position before the onset of movement (hence we have no visual, nor memory motor signals related to the arm movement), we suggest that the motor centers that guide the arm use the spatial coordinates of the spotlight of attention to guide goal-directed movements. Because the direction of spotlight of attention modulates the activity of V6A reaching and grasping neurons (Galletti et al., 2010), area V6A could be part of the neural network that guides goal-directed movements.

Area V6A hosts a priority map that combines bottom-up inputs such as visual responses with top-down signals such as reaching plans and is specific for the guidance of reaching arm movement. We suggest that a population of a particular type of cells in V6A, the real-position cells, represents an earth-based, three-dimensional map of objects present in the space around us, that stays in place when we move around and that can guide the goal-directed movements of the arm. Such a map may be

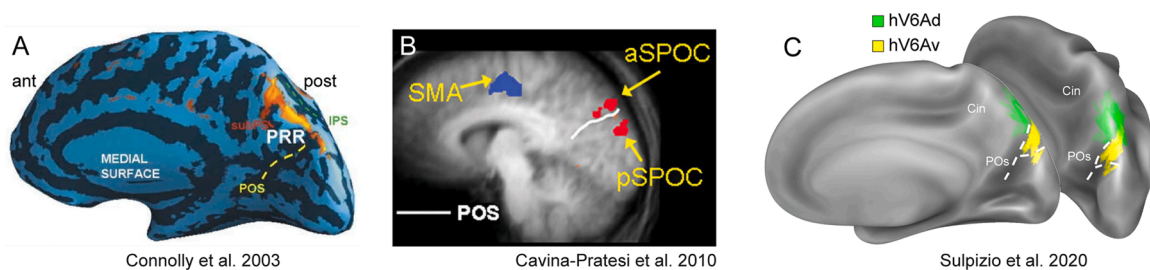


Fig. 18. Cortical regions of the human brain activated for pointing, reaching and/or grasping. A. Medial view of the right hemisphere, inflated to show unfolded sulci and gyri and the position of a region located along the medial surface of the superior aspect of the posterior parietal cortex that responds preferentially when the subject plans to point rather than to make a saccade to a remembered location. According to the authors (Connolly et al., 2003), this region may be homologous to the monkey “parietal reach region” (PRR; Snyder et al., 1997). B. Medial view of the right hemisphere showing the activation of area SPOC during the transport of the arm to the spatial position of the target (image taken from Cavina-Pratesi et al., 2010). Cgs: cingulate sulcus; IPs: intraparietal sulcus; POs: parieto-occipital sulcus; SPs: sub-parietal sulcus; STPs: secondary transverse parietal sulcus. C. Brain location of areas hV6Av and hV6Ad shown in dorsomedial and medial views on the right hemisphere of an inflated Conte69 brain atlas (modified from Sulpizio et al., 2020).

present not only in area V6A, but in all areas hosting real-position cells, and could be used to guide the goal-directed movements of different effectors, including the arm.

In this review, after recalling the functional properties of V6A reaching and grasping neurons, we have highlighted different pieces of evidence showing how information on the direction and re-direction of the spotlight of attention reach V6A from cortical and subcortical nodes. In addition, we have referred to the point that shifts of spotlight of attention activate area V6A in monkeys and humans (Caspari et al., 2018), and that the absence of such activation could explain the reaching deficits shown in monkeys (Battaglini et al., 2002) and humans after permanent (Pisella et al., 2000; Gréa et al., 2002) and temporary (Ciavarrò et al., 2013) lesions of V6A. In summary, we believe that V6A, which in both human and non-human primates occupies the posterior part of Brodman's area 7 (Gamberini et al., 2020), has all the functional requisites needed to guide and control goal-directed arm/hand movements in the different conditions encountered in everyday life.

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