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Neurons with radial receptive fields in monkey area V4A: evidence of a subdivision of prelunate gyrus based on neuronal response properties

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Abstract In recordings from two awake, behaving macaque monkeys we found that neurons in the crown of the prelunate gyrus differed in their responsiveness to simple visual stimuli. Neurons in the posterior part of the gyrus (area V4) responded strongly to stationary or moving bars, while neurons in the anterior part (area V4A) responded only weakly to such stimuli. Most receptive fields in area V4A were elongated with long axes oriented radially towards the fovea. These neurons were sensitive to radial movements, especially to sudden shifts of real 3D objects. The border between areas V4 and V4A coincided with the representation of the horizontal meridian. Area V4A extended into the posterior bank of the superior temporal sulcus, where its border corresponded to the representation of the vertical meridian. The sequence of the representations of the horizontal and vertical meridians over the prelunate gyrus suggests the existence of another area between V4A and V4t.

Keywords Extrastriate areas · Area V4 · Area V4A · Macaque monkey

Introduction

In the first electrophysiological investigations of the prelunate gyrus, Zeki (1975, 1977, 1983) noticed a heterogeneity of neuronal properties in this cortical region.

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Neurons in the posterior part of the gyrus (area V4) responded strongly to stationary or moving bars, whereas neurons in the anterior part (area V4A) responded only weakly to such stimuli. The heterogeneity of response properties of neurons in the crown of the prelunate gyrus was also mentioned in subsequent studies (Tanaka et al. 1986; Schein et al. 1982; Maguire and Baizer 1984).

The retinotopic organization of the border between areas V4 and V4A was not investigated in detail at that time, and never was explicitly described. However, in a recent review by Bartels and Zeki (2000) it was mentioned that the earlier studies of Zeki noticed a coincidence of this border with the representation of the horizontal meridian. Later investigations of the retinotopic organization of the crown of the prelunate gyrus failed to find systematic representations of neither the vertical nor the horizontal meridians (Gattass et al. 1988). In subsequent studies, the entire surface of the prelunate gyrus, from the lunate sulcus to the border to area V4t in the superior temporal sulcus, was regarded as a single area, area “V4” (e.g., Felleman and Van Essen 1991).

We have investigated the activity of neurons in the prelunate gyrus in two macaque monkeys. During this work we noticed an obvious change of response properties around the middle of the crown of the gyrus. On the anterior side [approximately corresponding to Zeki’s (1983) area V4A] many neurons could not be driven by simple visual stimuli such as oriented, colored bars presented on a monitor which were either stationary or moving across the receptive field (RF). Those cells that did respond to these stimuli often had strongly elongated RFs; their long axes were oriented in radial directions. Neurons with such an RF organization have so far only been found in cats, in a region in the suprasylvian gyrus (Pigarev 1991; Pigarev and Rodionova 1998). In this article we describe the properties of these neurons and their location in the prelunate gyrus of monkeys. A report has been previously published in abstract form (Pigarev et al. 1996).

Materials and methods

The data presented in this study were collected in two male monkeys (*Macaca fascicularis*). The experimental procedures are described in detail elsewhere (Pigarev et al. 1997), and will only be summarized here.

Surgery and recordings

For neuronal recordings, the head of a monkey was painlessly fixed by posts installed through small skin incisions, and touching the surface of the skull from different directions. The posts were fixed to a rigid frame surrounding the head. The search coil technique was used to record eye position. Surgery was done with the animal under pentobarbital anesthesia (Nembutal, Sanofi, 5–8 mg/kg/h i.v.) under aseptic conditions, with postsurgical antibiotic (clindamycin, Sobelin Solubile 300, Upjohn, 20–40 mg/kg 3 times a day) and analgesic treatment (metamizol, Novalgin, Hoechst, 0.2 ml i.m.). All procedures were carried out under institutionally approved protocols and in accordance with the NIH guidelines for the care and use of animals.

Varnish-coated tungsten electrodes were moved into the brain through cone-shaped guide tubes and small holes in the skull that were drilled with the animal under ketamine hydrochloride anesthesia (Ketanest, Parke-Davis, 10–25 mg/kg/h). Electrodes were often left in the tube after recording, so that penetrations could be continued over several days. Penetrations were made perpendicular to the surface of the skull or tangential to the surface through a distant hole.

Localization of recording sites in the brain

Because both monkeys were used in long-lasting chronic experiments, we could not verify recording sites histologically. Due to the small holes for recording, the prelunate gyrus could also not be identified visually. In order to localize the recording sites we therefore used a combination of magnetic resonance imaging (MRI) and stereotaxic technique. Sulci and gyri were exactly reconstructed in 3D stereotaxic coordinates, individually for each animal, from MRI scans that were obtained at the beginning of the study. Details of this procedure are reported elsewhere (Pigarev et al. 1997). In short, using the FLASH technique (Frahm et al. 1986), MR images of 1-mm sections of the head in frontal, sagittal and horizontal orientations were obtained, in which the stereotaxic planes had been marked by watermarks. The representation of the brain in parallel sections along all three orthogonal planes provided a continuous reconstruction of sulci and gyri that was far more precise than the 1-mm resolution of neighboring MRI scans. Given the width of the prelunate gyrus (about 5 mm), this precision was sufficient to identify neurons located within this gyrus. The reliability of our reconstruction was also confirmed using physiological criteria (see below).

Positions and tilts of the recording tubes were exactly measured and also defined in stereotaxic coordinates. Thus the place where the microelectrode entered the brain could be precisely evaluated. The data concerning the depth of the penetration and tilts of the electrode were loaded into a 3D computer model from which cell positions along the electrode path could be calculated and projected onto individual planes or sections of the brain in stereotaxic coordinates. Finally, cell locations in stereotaxic coordinates were superimposed on the MRI plans or the reconstructed brain maps.

Training procedure, visual stimulation and RF plotting

Monkeys were trained in a standard fixation task ($\pm 1^\circ$ control). During fixation, RFs could be investigated with bars of different size, orientation and color. Stimuli were presented on a 19-in. monitor at 57 cm distance, which covered about $30^\circ \times 40^\circ$ of the vi-

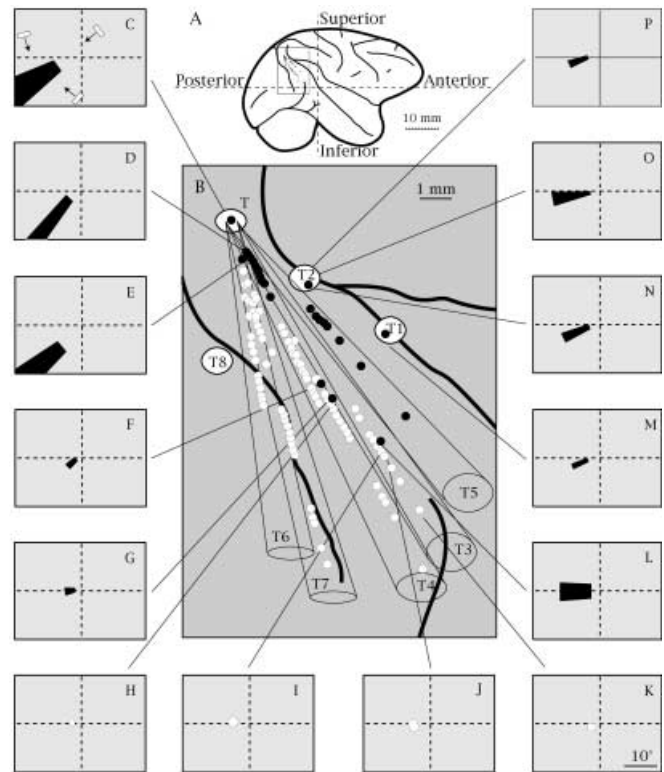


Fig. 1A–P Examples of RF plots and locations of different types of neurons in the prelunate gyrus (right hemisphere) of monkey M1. **A** MRI reconstruction of M1 cortical topography in stereotaxic coordinates. **B** Enlarged representation of the cortical region outlined in **A**. Recordings were made through four holes in the skull (*T*, *T1*, *T2* and *T8*), with differently oriented tubes (*T3–T7*) at *T*. Neurons with good responses to visual stimuli (*white*) and neurons with poor visual responses and/or with elongated radial RFs (*black*) are marked in a projection onto the lateral view of the brain. The cortical volumes potentially covered by these recording tubes are shown as cones. **C–P** RF plots of selected neurons of both types; RFs (*black areas*) are plotted onto a sketch of the monitor screen (*rectangular outline*) corresponding to a visual field of 40×30 deg. *Dashed lines* mark the vertical and horizontal meridians. In **C** small white rectangles show the relative size of stimuli which were used to plot the RF (*black*)

sual field. Their luminance differed between 1 and 47 cd/m² depending on the color; background luminance of the screen was 0.5 cd/m². The room was diffusely illuminated (luminance of the white walls was 5 cd/m²).

In some cells, RFs were so large that only their central borders could be determined due to the limited size of the monitor. To investigate larger areas of the visual field we sometimes installed an additional screen which covered about 50° of the visual field in each direction. Visual stimuli on this screen (bars of different orientation and size) were projected and moved with a handheld slide projector. In some experiments we also used real objects from the laboratory environment as stimuli.

Neuronal firing was presented on a loudspeaker and eye movements were displayed on an X-Y monitor, which allowed direct comparison of the neuronal firing with eye movements during the intervals between fixations. Receptive fields were plotted while animals were fixating. Losses of fixation were indicated by a special sound and immediately interrupted the RF plotting procedure. Visual stimuli could be presented stationarily and switched on and off, or could be moved by means of a computer mouse under visual control. Thus, RF plotting was a highly interactive process, and

was visualized on a second (control) monitor in front of the investigator. For each new cell, first size, orientation and color of the stimulus bar were adjusted to evoke a good response from the cell; this stimulus was then used to determine the borders of the RF. Even neurons with large, radial RFs were driven best by stimuli that were relatively small and, in fact, much smaller than the size of the RF (cf. Fig. 1C). To such small bars, the cells showed only little orientation selectivity, so that their RF borders could be estimated by moving the bar in various directions across the screen while indicating the onset and offset of responses from the cell. Plotting the shape of a single RF usually required 20–30 subsequent trials each with a new presentation of the fixation point, the behavioral task (detection of its disappearance) and the reward, and could last up to 15 min.

Results

Verification of cortical topography

Topography of the prelunate gyrus in stereotaxic coordinates was reconstructed from MR images at different sections of the brain (Pigarev et al. 1997). To confirm this reconstruction, the anterior and posterior borders of the prelunate gyrus were also determined using physiological criteria. The anterior border (superior temporal sulcus) is characterized by representations of different sensory modalities on the anterior and the posterior banks. Neurons of the posterior bank respond to visual stimuli, and neurons in the anterior bank to auditory stimuli. Perpendicular penetrations close to the anterior border of the prelunate gyrus usually cross both these banks (Tanaka et al. 1986).

The posterior border of the prelunate gyrus (the lunate sulcus) separates V4 located on the anterior bank of the sulcus from area V2 on the opposite bank. Neurons located in this region of V2, which is near the V1/V2 border, can be easily recognized by their strong orientation selectivity and their small RFs located along the vertical meridian. Both these anterior and posterior boundaries of the prelunate gyrus were determined in our recordings. We placed one recording tube (T1 in Fig. 1) over the reconstructed location of the superior temporal sulcus. In penetrations through this tube, perpendicular to the surface of the skull, we found neurons with either visual or auditory responses. Another tube (T8 in Fig. 1) was located 1 mm behind the presumed location of the lunate sulcus, over the expected border between areas V1 and V2. In penetrations through this tube, we exclusively found orientation selective neurons with very small RFs located along the vertical meridian. These results confirmed the reliability of the reconstruction of the cortical topography from MRI scans.

General characteristic of visual responses in the crown of the prelunate gyrus

The first penetrations in each animal (M1, M2) were made on the anterior border of the prelunate gyrus, close to the superior temporal sulcus (T, T1, T2 in Fig. 1 for

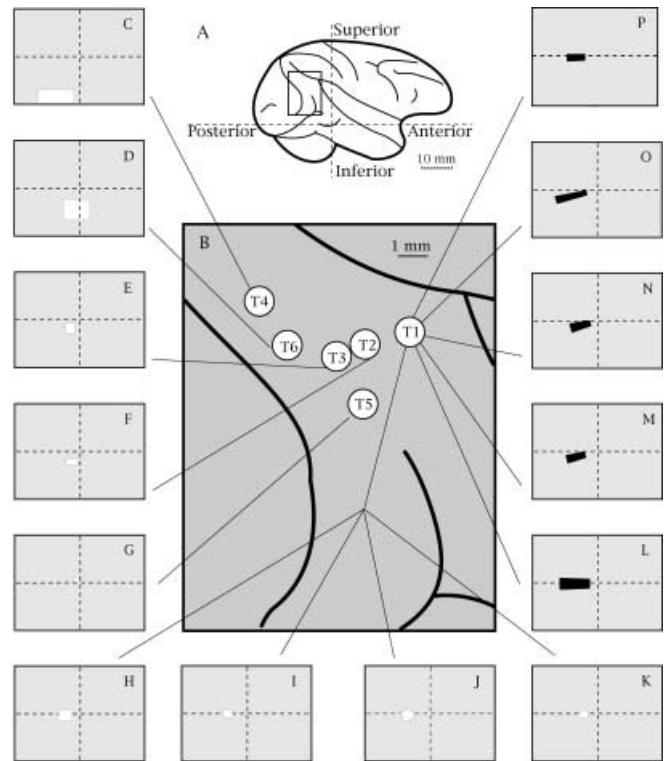


Fig. 2A–P Examples of RF plots and locations of different types of neurons in the monkey M2. Recordings were made through six holes in the skull (T1–T6). Other indications as in Fig. 1

M1; and T1 in Fig. 2 for M2). Neurons were poorly responsive here, but changes in neuronal firing were often noticed in combination with eye movements in the intervals between fixation (not recorded). Thus, it was obvious that activity was connected with visual stimulation. Although it was sometimes possible to plot receptive fields, many neurons gave only weak responses or did not respond at all to our stimuli. That was not in agreement with most descriptions of neuronal properties in area V4 (e.g., Zeki 1973; Schein et al. 1982; Desimone et al. 1985). On the other hand, neurons with such properties have been described in area V4A (Zeki 1975). Later penetrations were done more posterior (T3–T8 for M1; T2–T6 for M2) close to the lunate sulcus, and recording sites even spread into the anterior bank of this sulcus (T8, M1). There we found neurons with easily driven visual RFs and properties as reported for area V4.

RF properties of neurons in the anterior part of the prelunate gyrus: radial receptive fields

Because of the poor responses to simple visual stimuli, the anterior region of the prelunate gyrus was difficult to investigate. For 29 (out of 50) neurons in one animal (M1), the RFs could not be plotted in spite of a frequent impression of an increased firing with eye movements. However, the other neurons did respond to our stimuli,

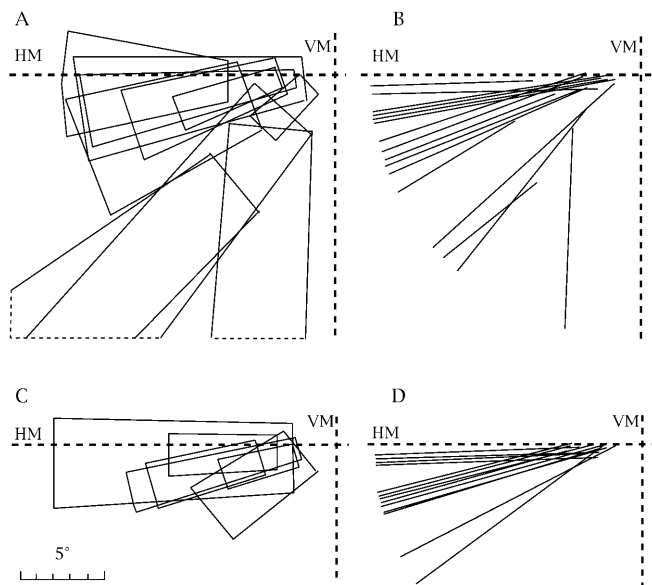


Fig. 3 Examples of elongated and radially oriented RFs in M1 (A) and M2 (C) and the long axes of all elongated RFs in these animals superimposed (B, D) [dashed lines vertical (VM) and horizontal (HM) meridians]

and their RFs could be investigated. Most of them (19 of 21) had a rather unusual elongated shape (Fig. 1C–G and L–P). In the second monkey, ten neurons with similarly elongated RFs were found at a corresponding location (Fig. 2L–P). Examples of these RFs are presented in Fig. 3A, C. The RFs tended to be oriented radially with their long axes. That is seen in Fig. 3B, D, where the long axes of all those RFs are superimposed.

The shapes of these elongated RFs often resembled comets. Their “heads,” oriented towards the center of the visual field, were more sensitive to stimulation, and had very sharp borders. Their tails were radially oriented. The width of the tails usually enlarged towards the periphery of the visual field, and RF borders became more diffuse. We never saw elongated radial RFs which included the fovea.

We investigated response properties in a qualitative manner using a variety of bar-shaped stimuli on the monitor. Neurons with radially elongated RFs preferred visual stimuli moving in a radial direction, along the long axis of the RF. Nine out of 19 neurons with radial RFs in animal M1 demonstrated directional selectivity; five neurons preferred movement towards the fovea, and four the opposite direction of movement. The remaining ten neurons in M1 and all neurons in M2 did not have a clear direction preference. Usually the responses of cells with radial RF were best for small stimuli, with sizes below the width of the RF’s “heads,” so that the shape of the RF could be plotted rather precisely. An example is given in Fig. 1C. However, neurons also responded to bars extending the width of the RF. Responses to large bars were orientation selective; the preferred orientations were parallel or perpendicular to the long axis of the RF.

We recorded only four neurons with non-elongated RFs which likely belonged to area V4A. These neurons were found in the first recordings from tube position T4 (M1) and were located among both neurons with radially elongated RFs and non-responding neurons.

In six neurons with elongated RFs we observed an enhancement of responses when the animal subsequently moved its eyes towards the RF. If we presented the stimulus in the RF shortly before or at the time when the fixation point was switched off, the monkey often made a first saccade towards this new stimulus. In these cases the responses to the visual stimulus in the RF were strongly enhanced. This effect was described earlier in this part of the cortex (Fischer and Boch 1981, 1982; Spitzer et al. 1988).

For many neurons in area V4A we were not able to plot the RFs on the monitor, although cell activity was obviously related to eye movements and probably visual stimulation. To exclude the possibility that RFs of these neurons were located outside the monitor, we performed three experiments with an enlarged screen that covered $100^\circ \times 100^\circ$ of the visual field. However, this did not help us to find the RFs, and we considered that this failure was not related to an improper location of the monitor but was instead due to suboptimal stimuli. This was confirmed by strong responses to occasionally tested real objects, e.g., a sponge. When these were moved fast or thrown in a radial direction across the expected location of the RF, previously unresponsive neurons often vigorously responded to this stimulation. Responses were especially strong when the visual stimuli were shown at larger distances. These observations suggest that the mode of stimulus presentation, eye movements, and the distance from the eyes are all important parameters for neuronal responses in area V4A.

Localization of area V4A in the prelunate gyrus and representations of the main meridians

Figure 1 shows the cortical locations of all neurons that were recorded in the crown of the prelunate gyrus and in the anterior bank of the lunate sulcus of M1, projected on a lateral view of the brain. Unresponsive neurons and neurons with radial RFs (black dots) occupy the anterior part of the crown. In contrast, neurons responsive to conventional stimuli such as bars (white dots) were found at more posterior locations and spread into the lunate sulcus. The different locations of these neurons are also seen in Fig. 4P–R, where the locations of cells are superimposed on horizontal MRI sections of the brain.

In M2, neurons with radial RFs were only seen in penetrations through T1 (Fig. 2), which was the most anterior hole, drilled close to the superior temporal sulcus. In the other holes (T2–T5) all neurons responded well to our stimuli and did not have elongated RFs.

If the different locations of these two types of neurons do indicate the existence of two distinct areas, one should expect to find a representation of one of the main

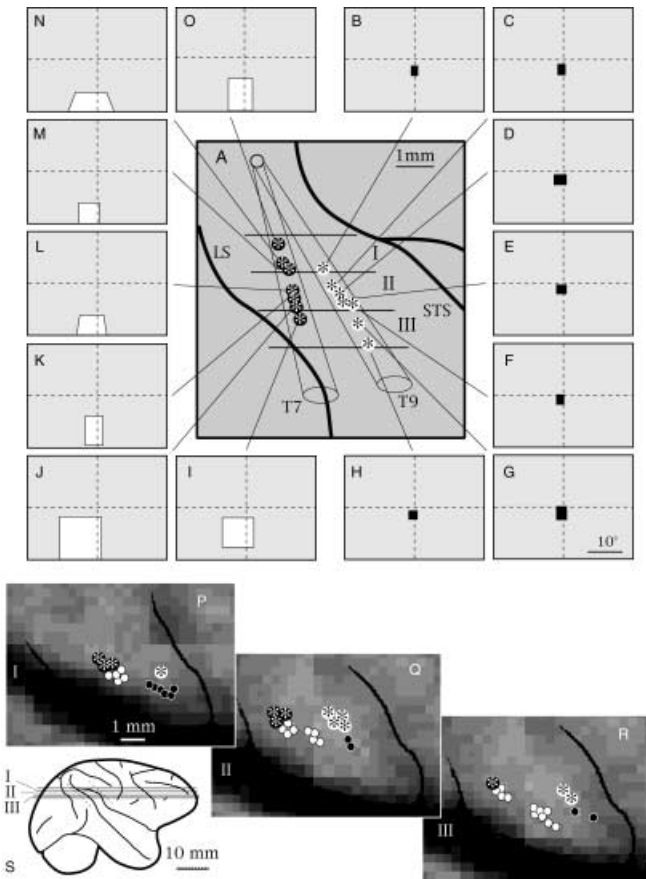


Fig. 4A–S Representations of the vertical meridian in the prelunate gyrus. **A** Locations of neurons with RFs along the vertical meridian in the lunate sulcus (*T7*, white asterisks) and in the superior temporal sulcus (*T9*, black asterisks) projected onto the lateral view of the brain. *Sections I, II and III* correspond to the MRI scans **P, Q**, and **R**. **B–O** RF plots of individual neurons, as in Fig. 1. **P–R** MRI plots of *sections I, II, and III* in **A** and **S** with marked locations of the neurons recorded in these levels. Neurons with easily driven visual responses are marked by *white dots*, neurons with poor visual responses or elongated radial RFs by *black dots*. Asterisks mark neurons with RFs along the vertical meridian as indicated in **A–O**. **S** The locations of levels *I, II and III* in the brain

meridians along their borders. Indeed, in recordings from *T3* and *T4* in monkey *M1*, the RFs of well-responsive neurons were located along the horizontal meridian (Fig. 1*H, I, J, K*). In the same penetrations we recorded three neurons with elongated and radially oriented RFs which were also oriented along the horizontal meridian (Fig. 1*F, G, L*).

Apparently, the tube *T1* in *M2* happened to be located exactly overlying the border between areas *V4* and *V4A*. In penetrations through this tube easily driven neurons with small, non-elongated RFs and neurons with elongated and radially oriented RFs were recorded either simultaneously or in subsequent experiments. Examples of these RFs are shown in Figs. 2*I, J, L, P* and 5*C, D*. Most RFs in this tube were located close to the horizontal meridian. In all cases in which well-responsive neurons with small RFs and neurons with elongated and radially

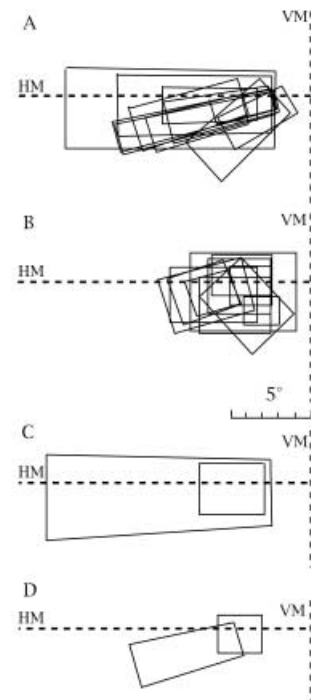


Fig. 5 RF plots of all elongated (**A**) and non-elongated (**B**) RFs recorded through *T1* in monkey *M2* (Fig. 2). **C, D** Examples of elongated and non-elongated RFs recorded simultaneously by one electrode in *M2*

oriented RFs were recorded simultaneously, both RFs touched the horizontal meridian and the long axes of the elongated RFs were oriented horizontally or nearly horizontally (Figs. 2, 5). Since the recording tubes in this animal were oriented normal to the surface, neurons recorded through the same tube should naturally represent close positions in the retina. The comparison of RF positions of all elongated and non-elongated RFs recorded in *T1* (Fig. 5*A, B*) led us to conclude that the retinotopic arrangement of elongated RFs does not correspond to the geometrical center of the RFs, but rather to their “heads” directed towards the fovea. This is also seen in the RFs of simultaneously recorded pairs of neurons (Fig. 5*C, D*).

If the border between area *V4A* and area *V4* is associated with the representation of the horizontal meridian, one may expect that the representation of the vertical meridian would form the border of this area on the opposite side, in the posterior bank of the superior temporal sulcus. We have not systematically investigated neurons in the superior temporal sulcus. Only with one tube orientation in *M1* (*T9* in Fig. 4) did we make some oblique penetrations which, at the beginning, went along the posterior bank of the superior temporal sulcus and later, in the region of the foveal representation, came back to the surface of the crown. Along these penetrations, in the wall of the superior temporal sulcus, we found cells with good visual responses and with small and non-elongated RFs, and these RFs were located along the vertical meridian (black asterisks, *T9* in Fig. 4*B–H*). Another representation of the vertical meridian was found in the lunate

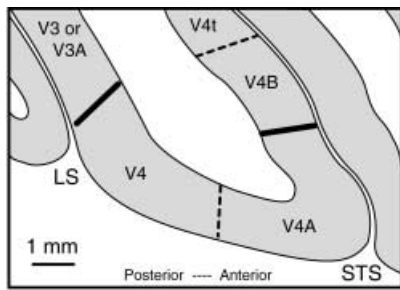


Fig. 6 Location of visual areas V3/V3A, V4, V4A, V4B, and V4t in the crown of the prelunate gyrus in monkey 1. The drawing is reconstructed from the horizontal MRI section corresponding to level III in Fig. 4. Representations of the vertical meridian are shown as *solid black lines*, and representations of the horizontal meridian as *dashed lines* (LS lunate sulcus, STS superior temporal sulcus)

sulcus, probably corresponding to the border between areas V3 (or V3A) and V4 (white asterisks, T7 in Fig. 4I–O). In the lower part of Fig. 4, locations of these neurons are shown on MR images of the corresponding parts of the brain.

Discussion

The observations reported here demonstrate that neurons in the crown of the prelunate gyrus can be subdivided into two groups according to their responsiveness to simple visual stimuli. Neurons with robust responses to the stimuli used in this study were found on the posterior side of the gyrus immediately anterior to the representation of the vertical meridian in the lunate sulcus. Their locations extended anteriorly to its crown on approximately two-thirds of its width (Fig. 6). Mainly these neurons were studied in most of the investigations of area V4 (Zeki 1973; Schein et al. 1982; Desimone et al. 1985; Tanaka et al. 1986). However, the extent of V4 defined by this criterion appears smaller than that proposed by Gattass et al. (1988).

Neurons with poor responses to simple visual stimuli adjoin area V4 anteriorly. This representation was named “area V4A” by Zeki (1975). Later, area V4A was also associated with a higher concentration of color-selective cells (Zeki 1977) and with a particular pattern of neural connections (Shipp and Zeki 1995). However, it was always stressed that “colour is not the only feature analysed in this area” (Zeki 1977, 1996). In our study it was found that area V4A also included neurons with strongly elongated and radially oriented RFs, which were especially sensitive to movement in radial directions. Their responses appeared to be enhanced when the gaze was subsequently moved towards the RF.

Examples of elongated RFs can also be found in earlier reports of RF properties in the prelunate gyrus, e.g., Figs. 12 and 13 of Zeki (1973) or Fig. 13 of Zeki (1977). However, the radial organization of these RFs has never been mentioned previously, although the enhancement of

responses prior to eye movements towards the RF has been reported and investigated previously (Fischer and Boch 1981, 1982; Spitzer et al. 1988), as has been the particular sensitivity of neurons in the posterior bank of the superior temporal sulcus to sudden shifts of visual objects (Maguire and Baizer 1984).

In our study, the border between neuronal populations of areas V4 and V4A coincided with the representation of the horizontal meridian. This provided additional support for the idea that these two neuronal populations represent two distinct areas. The anterior border of the large area V4 proposed by Gattass et al. (1988) was also associated with a representation of the horizontal meridian along the border with area V4t. Area V4t was described as a thin band along area MT, deep in the superior temporal sulcus. The representation of the horizontal meridian found in our work, and proposed as a border between areas V4 and V4A, was located far from this place, in the crown of the prelunate gyrus (Fig. 6). The representation of the horizontal meridian in the crown of the prelunate gyrus can also be found in other works, e.g., Fig. 6A, B in Boussaoud et al. (1991), Fig. 1B in Tanaka et al. (1986), Figs. 3–5 in Maguire and Baizer (1984), and even Figs. 10 and 16 in the work of Gattass et al. (1988).

It is not exactly known how far area V4A extends into the superior temporal sulcus. If its border with area V4 coincides with the representation of the horizontal meridian, the vertical meridian is likely to lie on the opposite side. In the early work of Zeki (1975) it was shown that callosal terminals (often indicating the representation of the vertical meridian) were located at the expected border of area V4A in the superior temporal sulcus. There were several physiological indications that the vertical meridian (different from the border of area MT) is indeed represented in the middle of the posterior bank of the superior temporal sulcus, e.g., Fig. 13 in Zeki (1973), Fig. 6A in Maguire and Baizer (1984), Fig. 6A, C in Boussaoud et al. (1991), and finally Fig. 4 in this paper. Deeper in the superior temporal sulcus, area V4t was located. This area has the representation of the horizontal meridian on its border towards the crown of the gyrus, and thus is unlikely to touch area V4A directly. The thin strip of cortex which is left between the representation of the horizontal meridian along the border of area V4t and the representation of the vertical meridian along the border of area V4A may correspond to another area which has not yet been identified (hypothetical area V4B) (Fig. 6). It is important to stress that the representations of meridians and consequently of borders between areas in Fig. 6 reflect the individual topography of the particular monkey. Borders tend to move in the anterior direction, in the superior levels, and posterior in the inferior sections. In different animals one would expect substantial variations in the location of these borders relative to anatomical landmarks. However, their relative sequence should stay constant. Our recordings were limited to the representation of the lower visual field in the dorsal wings of areas V4 and V4A. The topography

of upper visual field representation in the ventral wing of area V4 and adjacent area TEO was studied by Boussaoud et al. (1991). In their work, in one animal, two parallel penetrations happened to pass in front of the anterior border of the ventral wing of area V3, 2.5 mm from one another. These penetrations revealed long parallel representations of the horizontal and the vertical meridians in the middle of the "V4 complex," which may also be interpreted as the borders between areas V4 and V4A (horizontal meridian), and area V4A and the proposed area V4B (vertical meridian). This suggests that analogs of area V4A and the proposed area V4B may also exist in the representation of the upper visual field. Possible equivalence of the posterior part of area TEO to anterior subdivisions of the "V4 complex" and particularly to area V4A was discussed by Zeki (1996).

Thus, the crescent-like structure of the extrastriate areas, which was well established for areas V2 and V3, is most likely preserved also in the prelunate gyrus of macaques, in extrastriate areas V4, V4A, in the proposed area V4B, and in V4t.

One may ask how the distinction of areas V4 and V4A, which was first noticed in the early studies (Zeki 1975), could be missed in later works? Perhaps this was due to a different strategy of investigation: while the earlier studies paid attention mainly to neuronal response properties, the later studies of Maguire and Baizer (1984) and Gattass et al. (1988), which were directly devoted to the investigation of topography within the prelunate gyrus, investigated the mean retinotopic positions of multiunit recordings. In these studies, the prelunate gyrus was "scanned" in vertical penetrations located at least 1 mm apart, often more. This resolution, although quite good for large visual areas such as area V1, would hardly be sufficient for the likely multicrescent organization of the prelunate gyrus. Identical retinotopic positions found with this resolution may, in fact, belong to different functional areas. For the same reason, representations of the vertical or horizontal meridians, which actually corresponded to the borders between different areas but were located not far from another, could be regarded as parts of a single representation. In fact, pictures of the retinotopic organization of this cortical area are controversial between these two studies and also for different animals from the same study (Maguire and Baizer 1984). However, there were no substantial conflicts between the published data from these studies and our model.

Most recording sites in both studies were located in the posterior or anterior banks of the prelunate gyrus, where long tangential penetrations were performed. In both studies, one representation of the vertical meridian was found in the posterior bank of the gyrus, in the lunete sulcus. We also found this representation, which was proposed to be the border between area V3 (and/or V3A) and V4 in the lunete sulcus – a view taken from Gattass et al. (1988).

In the anterior bank of the prelunate gyrus, in the superior temporal sulcus, Maguire and Baizer (1984) also

reported a representation of the vertical meridian near the crown of the gyrus, which is far from the expected border of area MT. This bank of the gyrus was not studied extensively by Gattass and colleagues (1988); however, in several penetrations along the sulcus RFs were found within 3°–5° from the vertical meridian. Thus, one can assume that the meridian was localized within a few hundred microns from those penetrations. The vertical meridian in this part of the posterior bank of the superior temporal sulcus may be associated with the border between area V4A and the proposed area V4B.

The border between V4 and V4A along the crown of the prelunate gyrus (in our view associated with the horizontal meridian) may be regarded as a conflicting point between our and previous studies. However, the representation of this meridian was already reported in earlier studies (Boussaoud et al. 1991; Tanaka et al. 1986). In Maguire and Baizer (1984), this representation was also shown, for all three monkeys. In Gattass et al. (1988), the location of the horizontal meridian in the crown of the prelunate gyrus can be directly seen from the data of two monkeys (from four presented in their figures); for the two other animals the location of this meridian can be deduced from RF positions in surrounding recording sites. However, the horizontal meridian was always regarded as the border between V4 and V4t in this study. As a result, this border was located deeply in the superior temporal sulcus for some cases, or in the crown of the gyrus for others. One way to investigate whether the topographic maps in those studies were really associated with particular cortical areas would be to compare neuronal properties across the borders of the areas. However, this has not been done.

In our study cortical topography was not studied over a large cortical distance. However, the very special neurons with elongated and radially oriented RFs found along the anterior border of the prelunate gyrus helped us to link the representation of the horizontal meridian with the border between the thin strip of cortex in which these neurons were found, and other regions with "classical" type neurons of area V4. The unique response properties of these neurons together with their topographic location and the meridional sequence indicated that neurons with radially organized RFs are located in the area previously described as area V4A.

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