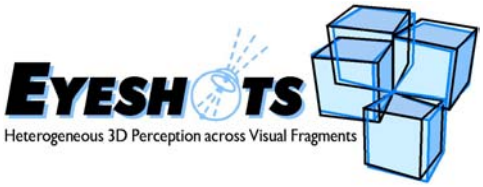

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Abstract:
The medial parieto-occipital cortex of the primate brain is a region where visual information and motor signals are integrated, to provide the dorsal visual stream with information suitable to perform the control of ocular movements and arm movements directed to targets of interest. Here, we provide preliminary results, which show that area V6A of the medial parieto-occipital cortex of the macaque elaborates information related to directing the eyes to a visual target in depth. We explored ocular movements performed to targets located near the body up to positions located far away from the body, well beyond the reachable space. We found strong neural modulations related to changes of the vergence angle, a result never reported so far for this cortical sector. Interestingly, neural discharges are stronger for oculomotor activity that brings fixation to targets located in the near space. These data suggest that V6A carries signals well suited to form a representation of the peripersonal/reachable space. This representation can be used to perform the sensori-to-motor transformations needed to perform successful reaching movements in depth.

Contents

1- Executive summary

This deliverable describes the research work performed by the Neurophysiology Lab of University of Bologna (UNIBO) and its partners with regard to Work Package 5 of the EYESHOTS project.

In particular, UNIBO activities have been focused on experimental set-up preparation, on monkey training, on electrophysiological recordings and data analysis. A new video-based eye tracking system was purchased and installed in the lab. The system, set in a binocular configuration, allows us to monitor the performance of the monkey in fixating the correct target during task execution. Using a custom-made algorithm, eye position signals are used to calculate on-line version and vergence angles and to monitor the performance of the monkey. Two devices to study the eye-movements in depth were designed and manufactured. The devices allow us to present the monkey with a set of fixation points placed at different distances, thus varying version/vergence eye signals, in order to assess the role of these oculomotor cues in the perception of the 3D space. The exact location of the targets in space was chosen in collaboration with the UG group taking into account some physical constraints.
Having solved the technical problems and completed the experimental set-up of the lab, the surgery necessary for electrophysiological experiments was performed, and the training of the monkey for fixation-in-depth task took place. After training, the monkey was able to execute the task performing a saccadic eye movement toward the correct position in space and keeping a steady fixation of the target for 2-2.5 s. At this point, we started the electrophysiological recording sessions.
After the end of recording sessions, the analysis of eye-movements and related neural discharges started. Concurrently, another part of the UNIBO team started to train a second monkey and the same experimental cycle was repeated for it. The recording from the second animal is presently going on.
A total of 297 neurons were recorded till now. Ninety-one have been fully analyzed. The remaining 206 are under analysis in the current time.

The deliverable summarizes the results obtained so far by UNIBO, in collaboration with UG: all these data, both behavioural and neuronal discharges, are already available for the entire consortium.

Focusing on the action-oriented dorsal stream of the brain, neuroscientific research, including findings from UNIBO, show that the sensorimotor transformations regarding arm reaching and vergence eye movements are likely coupled in the posterior parietal cortex of primates. An artificial agent endowed with an implicit coupling between its ocular and limb motor systems can more easily take advantage of both proprioceptive and exteroceptive signals in order to interact with its environment and construct an awareness of it. On these grounds, the research of UNIBO has casted biological data (already shared with UJI, UG and WWU), that will be summarized in the following sections. These data are the basis of joint papers already published in Conference Proceedings and Book Chapters, and others in preparation, to be published in international, peer-reviewed Journals.

2- Introduction

The posterior parietal cortex (PPC) of the primate brain is a crucial node in the organization of actions in peripersonal space. This fundamental role of PPC in interaction with three-dimensional (3D) space has been obvious since the beginning of the '900, when Holmes described spatial deficits after lesions of PPC in humans (Holmes, 1919; Holmes and Horrax, 1919). Since then, many neuropsychological studies reported impairments in the performance of actions in depth following lesions of medial sectors of PPC. Patients suffering from optic-ataxia, for instance, are able to perceive objects in space, but not to interact correctly with them (Perenin and Vighetto, 1988), especially in depth (Brain, 1941).
Despite these demonstrations of the essential role of human PPC for the correct performance of everyday actions in 3D space, very few neurophysiological work has been done so far to investigate the neuronal coding of action performance in depth. The fact that this matter has been so far neglected is partially due to the intrinsic difficulty of exploring the challenging topic of hand (and eye) actions in depth.
The study of the neuronal coding of eye movements in depth has been performed so far only in a few studies. In his pioneering studies in the 80's, Sakata (Sakata et al., 1980) explored the influence of eye-position signals on neuronal discharges by varying the position of the fixation target, not only in the frontal plane, but also in depth. Changing fixation point in a frontal plane requires the change in the version of the eyes; changing fixation point in depth requires a change in eye vergence. The data collected by Sakata first demonstrated that neural activity in PPC could be modulated by both version and vergence angle of the eyes (Sakata et al., 1980). They found that many neurons in area 7a have a specific selectivity for the depth of fixation. Later on, another area of inferior parietal lobule, area LIP, has been shown to carry on signals related to horizontal retinal disparity (hence to depth) and to fixation distance (Gnadt and Mays, 1995; Genovesio and Ferraina, 2004). No functional study has been so far performed to study the coding of eye movements in depth in medial parieto-occipital cortex, that is reported to be sensitive to eye movements in 2D (Kutz et al., 2003) and that is strongly and directly connected with the only 2 areas so far known to be involved eye-movement signals in depth, area 7a and LIP (Gamberini et al., 2009).

2.1 The medial parieto-occipital cortex

The medial parieto-occipital cortex is located in the caudal part of the superior parietal lobule. There, in the depth of the parieto-occipital sulcus, the occipital visual cortical areas adjoint parietal

visuomotor areas. Accordingly, in the deepest part of the anterior bank of the parieto-occipital sulcus, there is an extrastriate visual area named V6, that borders dorsally a visuomotor area called V6A (see Fig. 1). This brain region is at the boundary between cortical areas which analyze passive sensory modalities and areas involved in active eye- and arm-movements (Galletti et al., 2003).
In areas V6 and V6A, the effect of the direction of gaze in a 2D domain has been extensively studied both on spontaneous activity (gaze fixation in darkness) and on visual responses (visual stimulation of the receptive field) (Galletti et al., 1995). About 50% of visual and 30% of non-visual neurons showed eye-position related activity in total darkness (i.e. the activity modulation was truly due to the oculomotor activity, rather than to a different visual stimulation evoked by the change in the direction of gaze). In about 60% of visual neurons the visual response was modulated by the direction of gaze. Another study (Kutz et al., 2003) investigated the saccade-related activity in area V6A, showing that about 10% of tested neurons presented responses correlated with saccades (with fixation targets projected on a tangent screen). Both fixational signals and saccadic related signals in 2D are well represented in the medial parieto-occipital cortex.

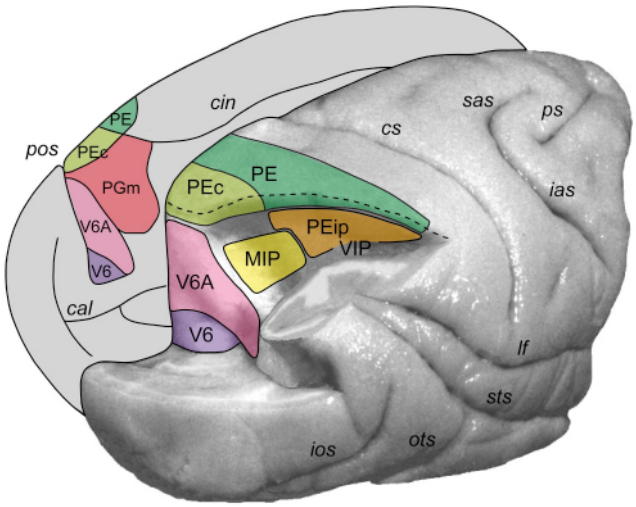

Fig. 1: Cortical areas of the macaque superior parietal lobule.
Postero-lateral view of a partially dissected right hemisphere with a part of the inferior parietal lobule of the occipital lobe cut away in order to show the medial parieto-occipital cortex hidden in the parieto-occipital sulcus, the medial view of a part of the left hemisphere is also visible.
Labels on different brain regions indicate cortical areas according to anatomical (architectural and/or connectional) and functional criteria.

The target of the research performed in the EYESHOTS project is area V6A (visible in Fig. 1), a cortical visuomotor area (see Galletti et al., 1999; Galletti et al., 2003) of the medial parieto-occipital cortex. Area V6A contains neurons responsive to visual stimuli (Galletti et al., 1996; Galletti et al., 1999), as well as cells modulated by somatosensory inputs, mainly from the upper limbs (Breveglieri et al., 2002), and arm movement-related neurons (Galletti et al., 1997; Fattori et al., 2001). It has been reported that V6A reach-related neurons are able to code the direction of arm movement (Fattori et al., 2005). More recently, a direct demonstration of separate effects of the direction of gaze and the direction of arm movement on the activity of V6A neurons has been reported (Marzocchi et al., 2008).

2.2 Aim of the present study

In all the previous studies on area V6A, the animals performed arm movements and eye movements to targets located always on the same plane, the fronto-parallel one. In the EYESHOTS project, we extended these studies to the 3D space, using fixation points placed in different locations in the monkey 3D space. Specifically, we started to test the involvement of the monkey medial parieto-occipital area V6A in coding depth information of gazed objects.
The scientific questions we wanted to answer was:
- is area V6A involved in coding fixation in depth?
- is vergence angle an information that reaches area V6A?
- is there a privileged part of space represented in V6A?

3- Material and methods

Two *Macaca fascicularis* monkeys were studied using the general procedures described recently (Fattori et al., 2009; Fattori et al., 2010). Experiments were approved by the Bioethical Committee of the University of Bologna and were performed in accordance with National laws on care and use of laboratory animals and with the European Communities Council Directive of 24th November 1986(86/609/EEC), recently revised by the Council of Europe guidelines (Appendix A of Convention ETS 123: http://conventions.coe.int/Treaty/EN/ Treaties/PDF/123-Arev.pdf).
In each monkey, after general anesthesia, a head restraint system and a recording cylinder were surgically implanted. Single neurons were extracellularly recorded from the anterior bank of the parieto-occipital sulcus with the use of a multielectrode system (Thomas Recordings). Signals from both eyes were recorded simultaneously with an infrared oculometer (ISCAN, Inc).
Each monkey sat in a primate chair with its head restrained and faced a horizontal panel located 10 cm below its eyes that contained ten light emitting diodes (LEDs) at different distances from the eyes (Fig 2). The target LEDs were grouped in two rows, one along the midsagittal plane and one contralateral to the recording hemisphere. In each row, LEDs were spaced 15cm apart, the nearest LED being at 15 cm from monkey eyes, the farthest at 75 cm.. The required mean angle of vergence for fixating the LEDs located in the central row from the nearest to the farthest one was 12^0, 8^0, 6^0, 5^0, 4^0, respectively. The corresponding average vergence values for the LEDs of the lateral row were 10^0, 6^0, 4^0, 3^0 and 2^0.

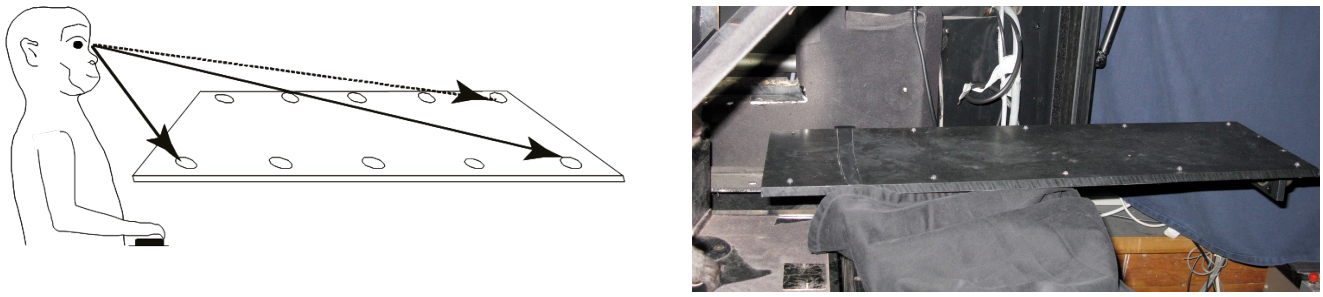

Fig. 2: Schematic representation (left) and photo (right) of the horizontal panel that was used for the fixation-in-depth task.
Target LEDs are placed in 2 rows, one in the midsagittal plane, and the other contralateral to the recording side. Each LED is 15 cm apart one from another in each row and 20 cm apart one form another in the 2 rows.

3.1 Behavioural task

The time sequence of the task is shown in Fig. 3. A trial began when the monkey pressed a button near its chest (button press) while being free to look at any point of the scene in its field of view. After 1000 ms, one of the LEDs turned on (LED). The animal was required to make an eye movement to fixate the LED within 600 ms. After either 1.5 or 2 sec from the time when the LED had switched on, it changed colour from green to red and this signalled the end of the task (Task). The monkey then released the button in order to receive its reward (Fig. 3, button release). As shown in Fig. 3, eye movements were frequently a combination of conjugate (version) and disjunctive (vergence) movements. Pure conjugate and combined conjugate/disjunctive eye-movements could be evoked, depending on the LED that turned on according to a randomly ordered sequence, chosen by the computer. Trials with conjugate and combined conjugate/disconjugate eye movements were intermingled. The initial eye position varied from trial to trial, as the monkey was free to look anywhere at the beginning of the task. During fixation, eye position was controlled by an electronic window (4°x4°) centered on each LED.

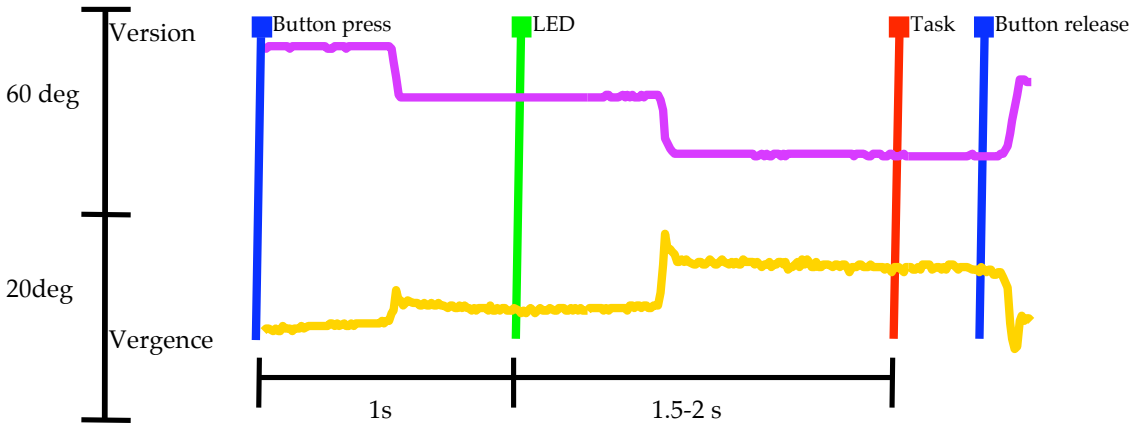

Fig.3: Time course of the fixation-in-depth task with the behavioural markers shown as coloured vertical lines. The horizontal version (magenta) and the vergence (gold) eye position traces are shown as a function of time. Upward deflections correspond to rightward and convergence movements in the 2 traces, respectively. Calibration bars are to the left.

Calibration of the eye position was performed daily by requiring the monkey to fixate sequentially nine LEDs placed in a 3x3 grid (see Fig. 4), where each row was placed in iso-vergence plane (-15°,0°, +15° in version) and each column in isoversion plane (18°, 13°, 8° in vergence). From the two individual calibrated eye position signals we derived the mean of the two eyes (the conjugate or version signal), and the difference between the two eyes (the disconjugate or vergence signal).

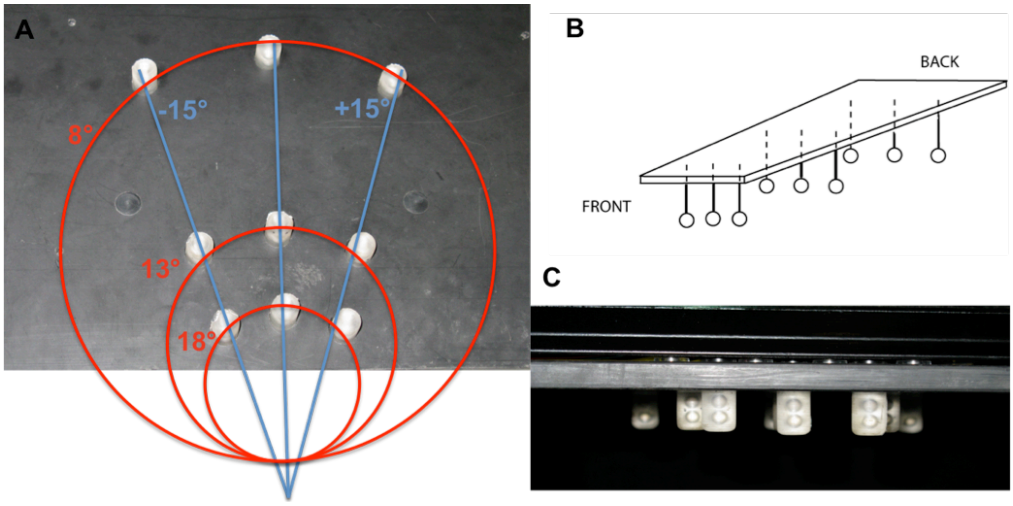

Fig 4: The calibration device.
A) Bottom view of the device superimposed with isoversion (blue) and isovergence (red) lines. B) General prospect of the device. C) Frontal view of the device (as seen from the monkey side).

3.2 Data analysis

Eye movements in the wrong direction, anticipatory movements (latency shorter than 100 ms), and slow movements (latencies longer than 600 ms), or movements contaminated by blinks were discarded.
Mean discharge rate was quantified in several time epochs (Fig. 5):

- 'visuomotor': from 40 ms after LED presentation till 50 ms before the onset of the saccade
- 'perisaccadic': from 50 ms before the onset of the saccade till 50 ms after the end of the saccade. The onset and the offset of a saccade were defined as the time points where the version velocity exceeded or dropped below 15% of the peak velocity, respectively.
- 'fixation': from 50 m after the end of the saccade till 1050 ms after saccade offset. The fixation epoch was further subdivided into two periods, the 'early fixation', the first 500 ms, and 'late fixation', the last 500 ms.

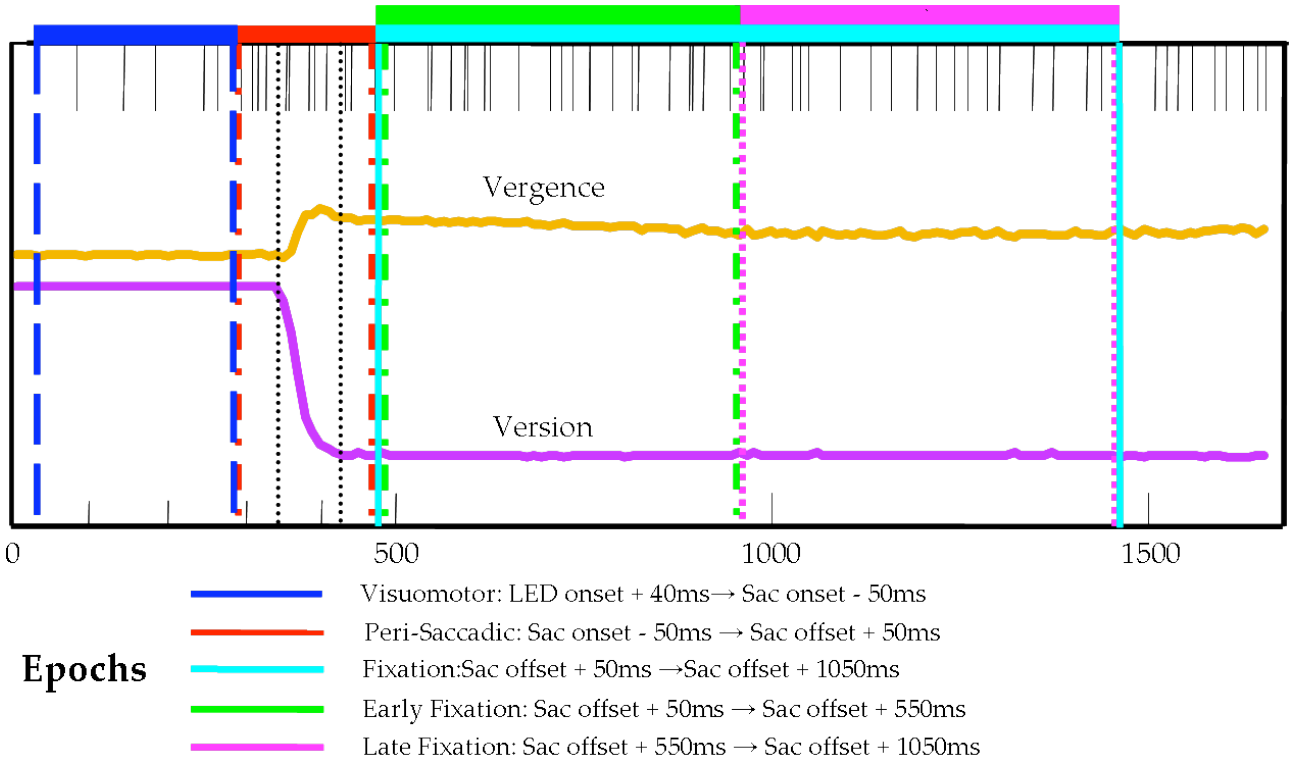

Fig.5: Behavioural epochs in which the neural activity has been divided to quantify mean frequency rate.

Neural activity in the different epochs was compared by a Kruskal-Wallis test ($p < 0.05$).
A spike density function (SDF) was calculated (Gaussian kernel, halfwidth 40 ms) for each neuron that was found significantly modulated by LED position (Kruskal-Wallis test). SDFs were averaged across all trials for each tested condition. We found the peak discharge rate in the behavioral epochs of interest and used it to normalize the SDF. The normalized SDFs were then averaged to derive population responses (Marzocchi et al., 2008).
To quantify the selectivity of the recorded neurons we computed a preference index (*PI*). The *PI* takes into account the magnitude of the neuron response to each LED position. It was computed as:

$$PI = \left(n - \frac{\sum_i r_i}{r_{pref}} \right) / (n-1)$$

where n is the number of positions, r_i is the activity in position i, and r_{pref} is the activity in the preferred position. The *PI* ranges between 0 and 1. A value of 0 indicates the same magnitude of response for all positions, whereas a value of 1 indicates a preference for only one position.
In addition, we calculated the depth of the preference index (*dPI*) which is given by the formula:

$$dPI = (r_{pref} - r_{nonpref}) / (r_{pref} + r_{nonpref})$$

were r_{pref} is the activity in the preferred position and $r_{nonpref}$ that in the nonprefered position. *dPI* index ranges from 0 to 1 and measures the intensity of modulation of neural activity by the LED position.

4- Results

Two-hundred ninety seven neurons were studied from area V6A (91 from monkey A, 206 from monkey B) while the monkey was required to make disconjugate and/or conjugate eye movements

to one of the ten different targets in depth. Up to now the quantitative analysis has been performed only for monkey A. For statistical purposes, cells with less than five samples for each of four (or more) LEDs positions were discarded from analysis. Of the 91 neurons tested, 65 yielded useful quantitative data that were used for further analysis.
The neural activity of 14 (22%), 29 (45%) and 39 (61%) of V6A neurons was significantly modulated by LED position in the visuomotor, perisaccadic and fixation epoch, respectively (Kruskal-Wallis, $P<0.05$). When the same analysis was performed in the two periods of the fixation epoch, namely the early and late fixation period, 39 and 30 neurons were found to be modulated, respectively. The discharge pattern of 14 out of 69 cells was not affected by LED position in any epochs. These results are reported in Table 1.

Table 1: Neural discharge modulations by eye movements in depth in cells of area V6A

Time Epoch	**Number of modulated cells**	***Percentage***
Visuomotor	14	*22*
Peri-saccadic	29	*45*
Fixation	39	*61*
Early fixation	39	*61*
Late fixation	30	*47*
Non-modulated	14	*22*

The neurons modulated by eye-movements in depth can be grouped in 2 sets: neurons modulated during the dynamic phases of the task (perisaccadic and visuomotor), and neurons modulated during the constant one (fixation).
Figure 6 shows an example of a neuron modulated in visuomotor and perisaccadic epochs; in the upper part of the figure, the responses of the neuron are illustrated while the monkey gazed to the five LEDs of the row located contralateral to the recording hemisphere. This neuron responds clearly in both the perisaccadic and visuomotor epochs when the gaze is directed to the nearest targets (left responses in Fig. 6). The neuron responds much less, or not at all, for the intermediate and farthest LEDs (right in Fig. 6). In the lower half of Fig.5 the activity of the same neuron is shown when the monkey fixated the LEDs of the central row. Here the cell is less sensitive to eye-signals in depth.
In Fig. 7, the activity of the same cell shown in Fig. 6 has been plotted for each epoch as a function of the LED position in space, to better highlight its neural encoding of different targets in 3D space. Fig. 7 shows more clearly that the mean activity during the visuomotor and perisaccadic epochs is higher for the two nearest LED positions compared to the other positions. This tuning is pronounced in the contralateral row and weakly present in the central row. In addition, it is evident that targets located on the right hemifield and near the frontoparallel level of the eyes evokes higher activity during the visuomotor and perisaccadic epochs.

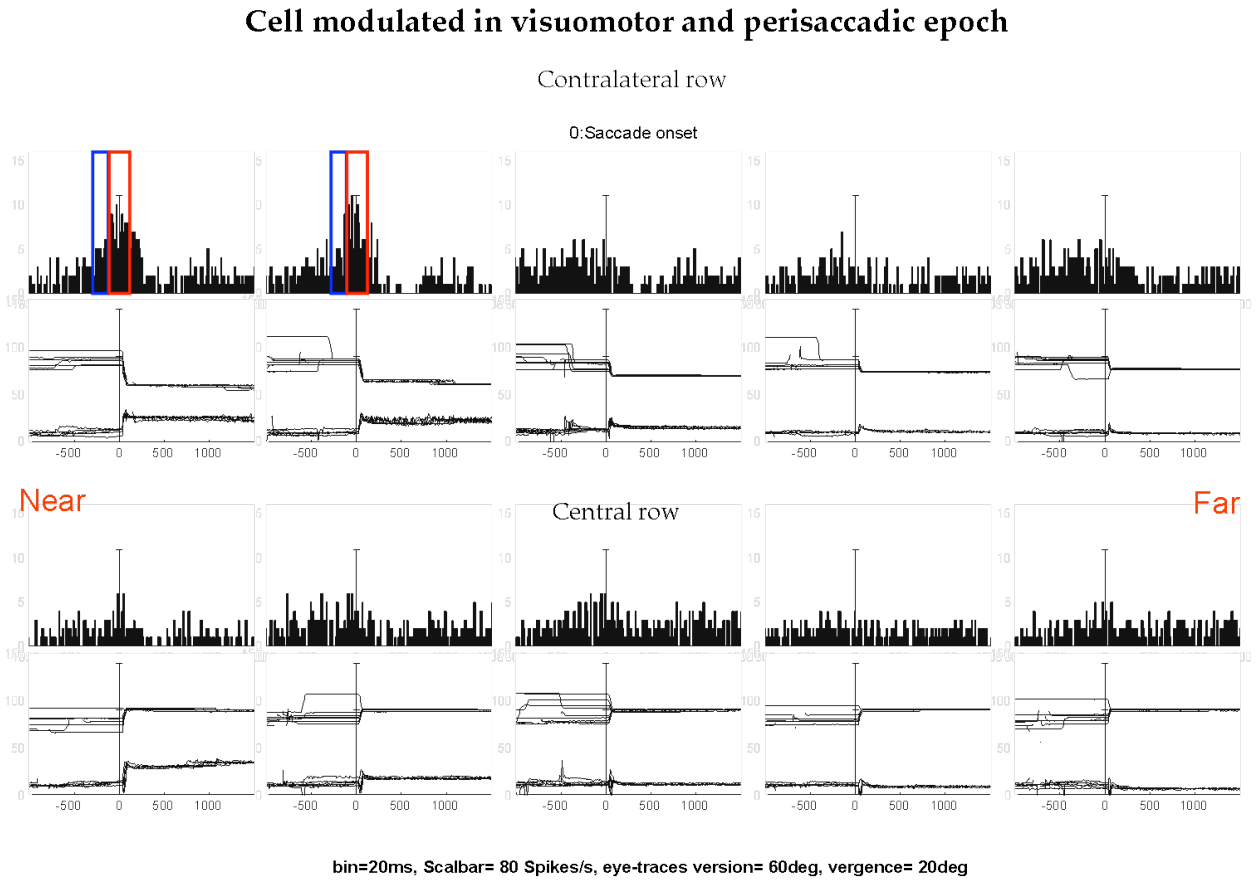

Fig. 6: Neuron modulated by LED position in the visuomotor and perisaccadic epochs.
Upper/lower half: spike histograms and eye traces (version and vergence, repsectively) to the five LEDs of the contralateral and central rows, respectively, arranged from near (left) to far (right) space. Spike histograms and eye traces are aligned to the saccade onset. Blue rectangle: visuomotor epoch; red rectangle: perisaccadic epoch. Scale bars for spike histograms are 80 sp/s, and version and vergence traces are 60 deg and 20 deg, respectively.

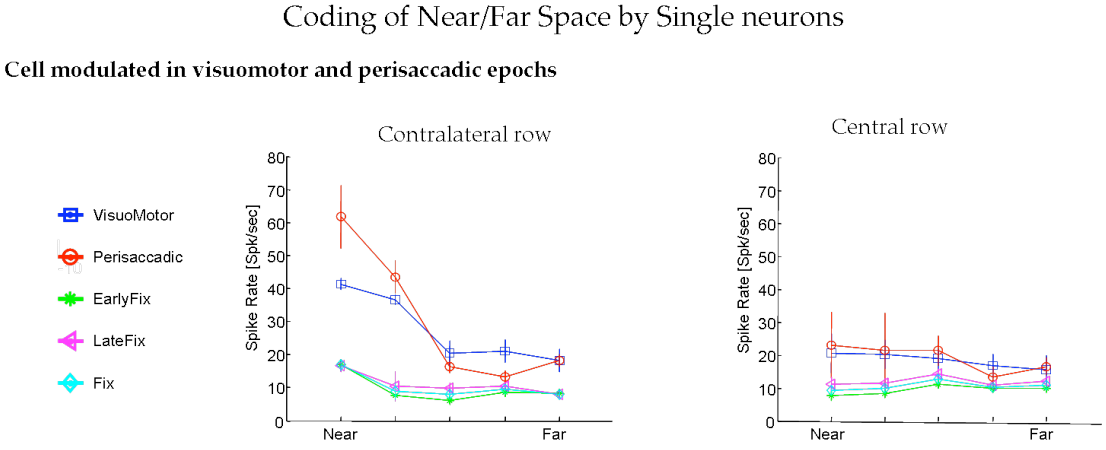

Fig 7: Tuning of the same neuron of Fig. 6 for all the epochs and for the 10 target positions in depth.
Mean±SE discharge rates are shown for each target position of the contralateral (left) and central (right) row for the 5 epochs in which the neuronal activity was quantified.

Figures 8 and 9 show an example of a cell modulated in fixation epochs, analyzed in the same way as the cell shown in Figs. 6 and 7. The only difference here is that here the spike histograms and the eye traces are aligned with the offset of the saccade. This neuron responds more strongly when the monkey fixates the nearest targets, in particular in the contralateral row. The modulation of its neural activity occurs during the perisaccadic epoch, the early and late fixation epochs. Most of its response is contained in the fixation epochs and it gradually declines going from the nearest LED (left) to the farthest one (right).

The tuning of the activity for each epoch of the neuron of Fig. 8 is shown in Fig. 9. In the contralateral row (Fig. 9, left) a peak shaped tuning of activity with a maximum at the second nearest target is present in the perisaccadic and fixation epochs. In the central row, the neural discharge shows a monotonic increase towards near target positions even more than in the contralateral row (Fig. 9, right).

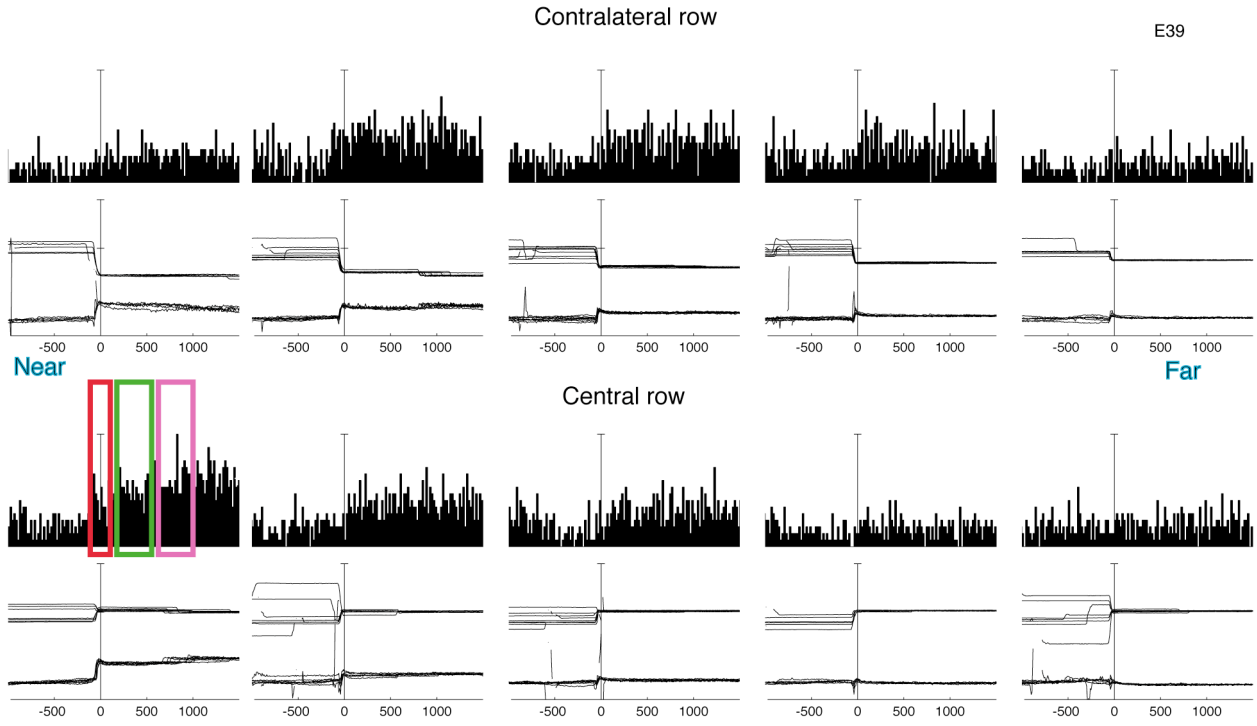

Fig. 8: Example of a neuron modulated by depth in the perisaccadic (red rectangle), early fixation (green rectangle) and late fixation (magenta rectangle) epochs.
Alignement at saccade end. Conventions are the same as in Fig. 5. Scale bars for spike histograms are 70sp/s, and version and vergence traces are 60 deg and 20 deg, respectively.

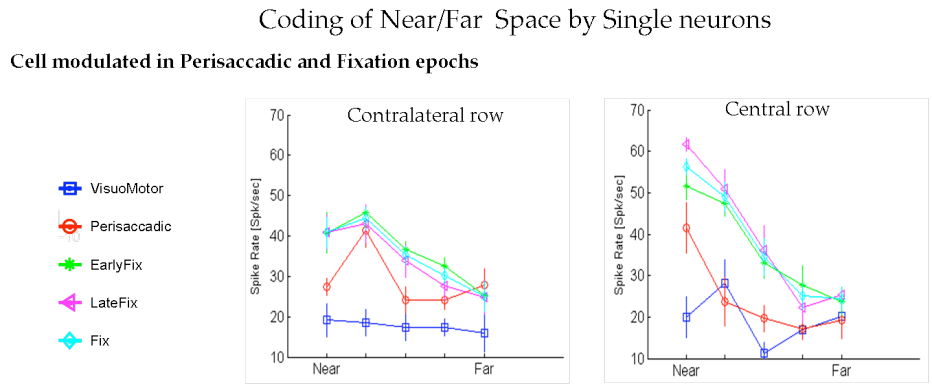

Fig. 9: Tuning of the neuron shown in Fig. 8 in all epochs for the 10 targets in depth.
Conventions are the same as in Fig. 8.

More examples of neurons modulated by depth in the visuomotor and perisaccadic epochs can be found in Fig. 10, whereas Fig. 11 shows the tuning of 3 cells modulated mainly in fixation epochs. From these examples, it is clear that there are several types of neural modulations in V6A, with some neurons strongly modulated in early parts of the trials and others in the late phases, when the target is already fixated. Often, neurons show modulations for depth in more than one epoch. In all cases analyzed so far, the nearest target positions evoke the highest activity from the neurons, and the farthest the weakest, as it is shown by population data reported in Fig. 12.

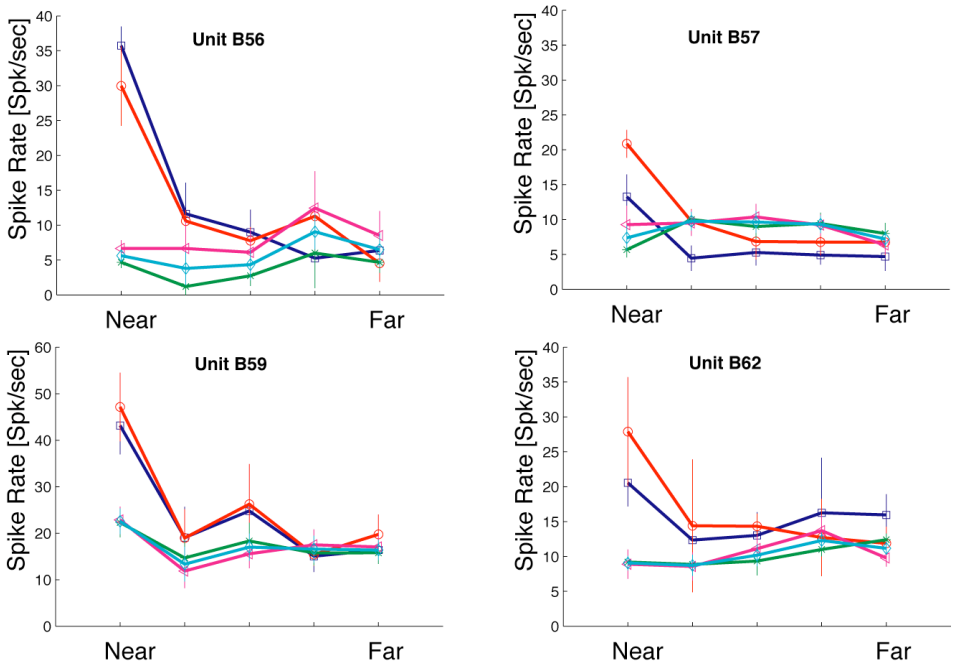

Fig 10: Tuning of four neurons modulated in visuomotor and perisccadic epochs
Conventions are the same as in Fig. 8.

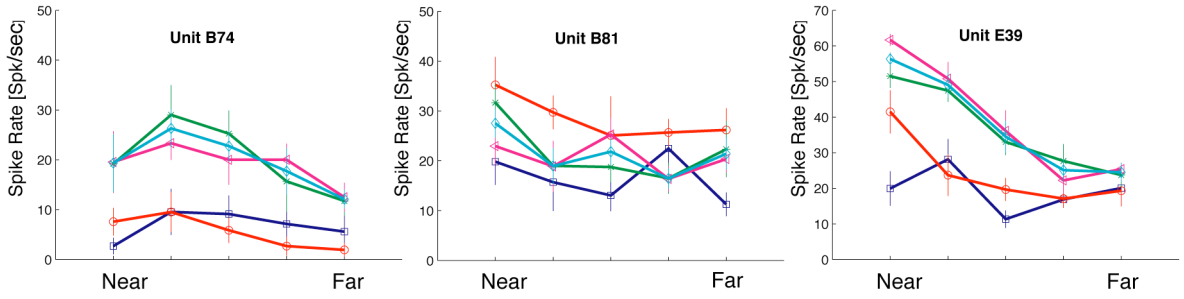

Fig. 11: Tuning of three neurons modulated in perisccadic and fixation epochs
Conventions are the same as in Fig. 8.

4.1 Population data

Fig. 12 shows the average spike density functions (SDF) of the population of V6A neurons that were modulated in the 5 epochs considered for the analysis: visuomotor, perisaccadic, early fixation, late fixation and fixation, respectively. Data plotted in the figure refer to the analysis of the 5 positions of the central row. The darkest and ligthest blue colors represent the normalized discharges for the nearest and farthest LEDs, respectively. The spike density function is a continuous function that shows the temporal evolution of the neural activity (Richmond et al., 1987). At the population level, it measures how well the activity of a number of cells distinguishes between the different experimental conditions, in our case the different fixation depths. For the cells modulated in the visuomotor (n=14) and perisaccadic (n=29) epoch, the SDF traces are aligned at LED onset and saccade onset, respectively. For the cells modulated in the 3 fixation epochs (n=39, 39, and 30, respectively) SDF traces are aligned with saccade end. It is well evident that for all epochs and all neurons, the nearest LED evoked the strongest activity, the two intermediate LEDs, an intermediate activation, whereas the farthest LED showed a weaker response. In summary, the SDF analysis showed that the modulated V6A neurons can, as a population, discriminate between the different depths of fixation and confirms by the strong preference for the near space shown from single neurons.

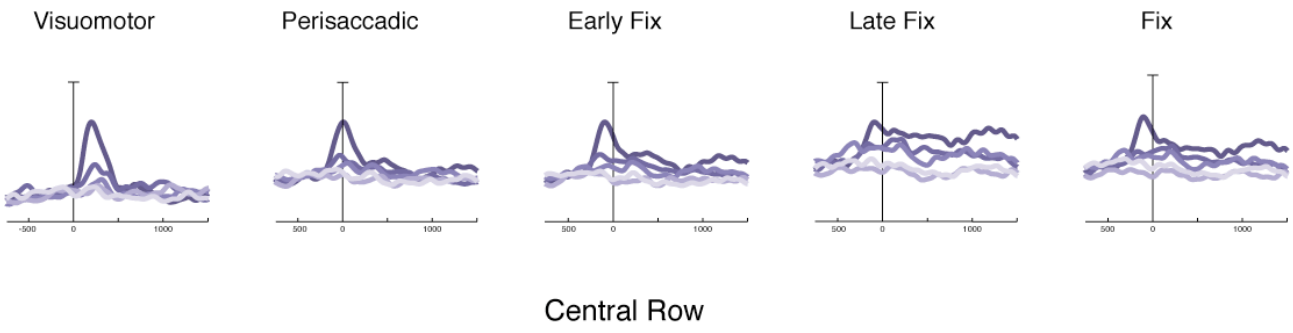

Fig 12: Population responses in V6A for fixating targets at different depths.
Activity is expressed as averaged normalized SDFs. Activity is aligned with LED onset for the neurons modulated in the visuomotor epoch, with saccade onset for the neurons modulated in the perisaccadic epoch, and with saccade end for neurons modulated in the fixation epochs.

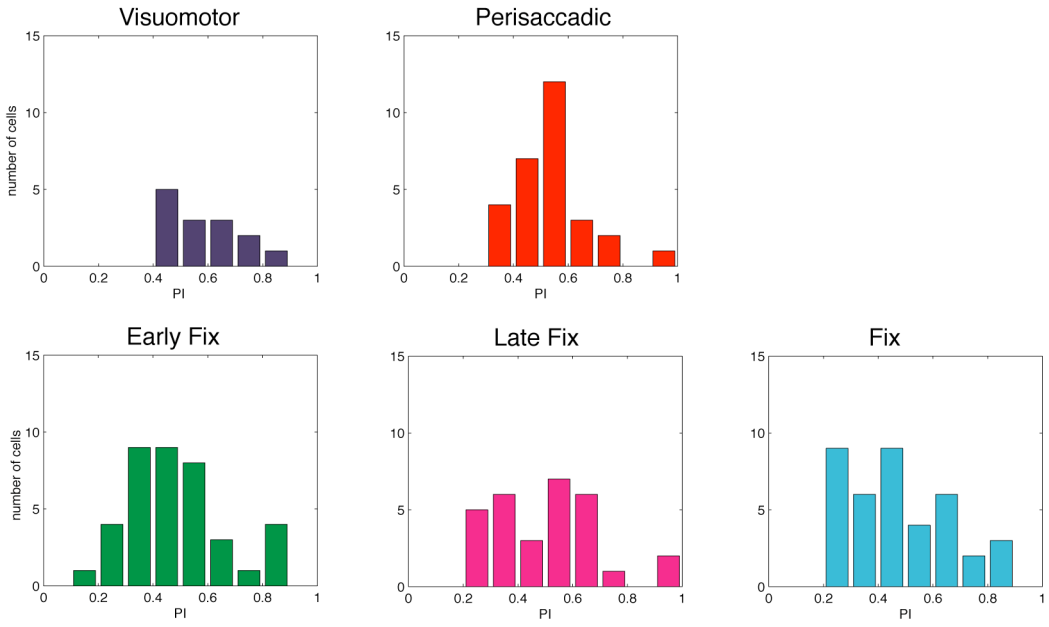

Fig. 13: Distribution of Preference Index (*PI*) in the analyzed V6A population.
Ordinate, number of neruons; Abscissa, PIs in the different epochs analized, as indicated on the top of each histogram.

To quantify how selective are the modulated neurons for their preferred LED and to measure how broad is their tuning for different fixation depths, we calculated the preference index (PI) and the depth of preference index (dPI), respectively (see Materials and methods). The frequency distributions of the PIs and dPIs for all groups of modulated neurons are shown in Figs. 13 and 14. All distributions are uniform and have a similar range of values. The PIs range from 0.14 to 0.92 (average±S.D., 0.51±0.17) across all types of modulated neurons, thus indicating a medium degree of selectivity (Fig.13). Concerning the values of the dPIs (Fig.14) of the modulated cells, they vary between 0.19 and 1 (average±S.D., 0.63±0.21). This means that on average the response of the population of the modulated V6A neurons for their preferred target is four times that for their least preferred one (dPI=0.6).

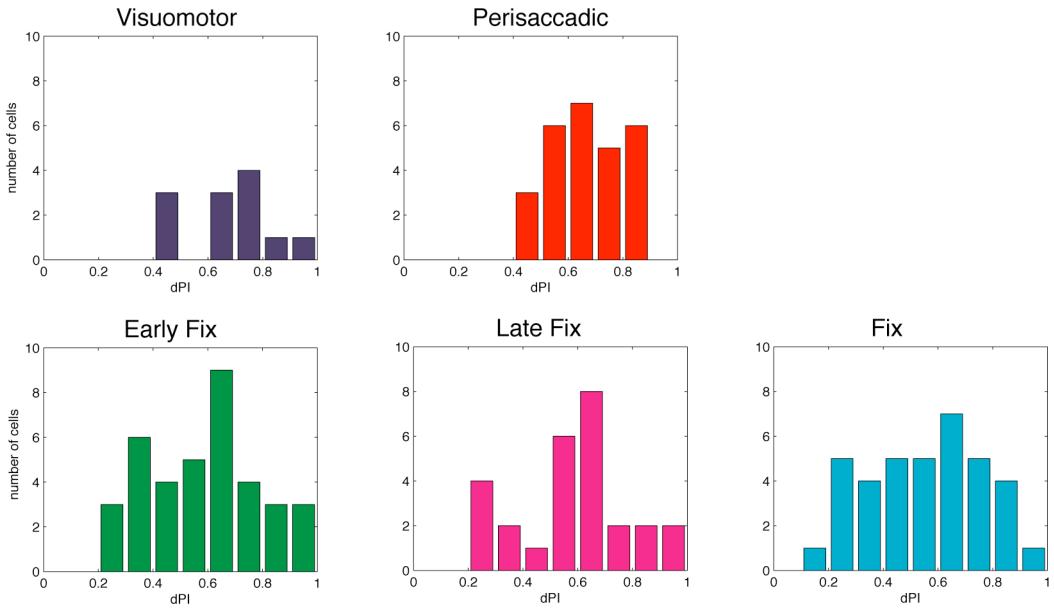

Fig. 14: Distribution of the depth of preference index (dPI) in the analyzed V6A population
Conventions are the same as in Fig. 13.

5- Conclusions

These data demonstrate that an high percentage of neurons in medial parieto-occipital cortex about 80%) are tuned to ocular spatial parameters in the three dimensional space. In addition, the data so far collected and analyzed indicate that in area V6A there is a far-to-near gradient of activity both at single cell level and at population level (as shown in Fig.12). For the majority of the neurons, the preference for near space is evident in both the initial (visuomotor and/or perisaccadic) and late (fixation) epochs. This means that V6A prefers near space in both visuomotor and oculomotor domains.
Given the well established role of V6A in arm reaching movements (Fattori et al., 2001; Fattori et al., 2005), the present data show that this area also carries the appropriate neural signals in terms of vergence angle, eventually supporting the reaching behaviour. In fact, during reaching, vergence signals is a useful information indicating the location in space of the foveated object.
Our results suggest that V6A neurons carry signals well suited to form a representation of the peripersonal/reachable space. Visual, oculomotor and fixation activity in area V6A could construct a representation of the visual world with a strong emphasis on the near, peripersonal space, in line with functional imaging data on the human parieto-occipital cortex (Quinlan and Culham, 2007). These functional MRI studies showed that in the putative human homologue of macaque V6A the BOLD signal is related to the viewing distance of gazed objects. This region of the human brain had near-space preference: activation was highest for near viewing, moderate for arm's length viewing, and lowest for far viewing (Quinlan and Culham, 2007). The authors reporting these data concluded that this medial parieto-occipital area could provide the areas of the dorsal visual stream with spatial information useful for guiding actions toward targets in depth. Similarly, we suggest that macaque area V6A is able to link perception to action in the 3D space and to provide to dorsal stream areas these information for the purpose of organizing hand actions in the 3D space.

5.1 Next steps

From these preliminary results, V6A seems to be a cortical region able to perform the sensory-to-motor transformations underlying the visually guided reaching movements in depth. It will be the next step of our research to find experimental data to support (or discard) this hypothesis.
Specifically, we will study the relative influence of vergence and version signals on the neural discharges of V6A cells in a context of pure iso-vergent or iso-version eye movements.
In addition, we will investigate whether the depth influences the reach-related discharges in this cortical sector, and if these modulations interact with those related to eye movements in depth.
To do so, we have planned a device and a task where the same visual target in 3D space can be the goal of a reaching movement or of an eye movement, in a well controlled sequence trial, as summarized in Fig. 15.

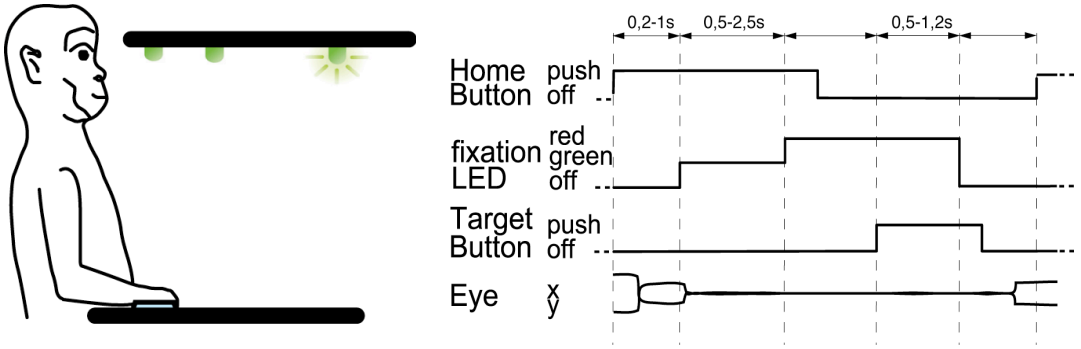

Fig. 15: Timing sequence of the reach-in-depth task to be used to study V6A neural discharges in depth.
Left: sketch of the experimental set-up; right: summary of the main events and monkey behaviours in a typical reaching trial.

6- References

Brain, W R (1941) Visual disorientation with special reference to lesions of the right cerebral hemisphere. Brain 64:244-272.

Breveglieri R, Kutz DF, Fattori P, Gamberini M, Galletti C (2002) Somatosensory cells in the parieto-occipital area V6A of the macaque. Neuroreport 13:2113-2116.

Fattori P, Gamberini M, Kutz DF, Galletti C (2001) 'Arm-reaching' neurons in the parietal area V6A of the macaque monkey. Eur J Neurosci 13:2309-2313.

Fattori P, Kutz DF, Breveglieri R, Marzocchi N, Galletti C (2005) Spatial tuning of reaching activity in the medial parieto-occipital cortex (area V6A) of macaque monkey. Eur J Neurosci 22:956-972.

Fattori P, Breveglieri R, Marzocchi N, Filippini D, Bosco A, Galletti C (2009) Hand orientation during reach-to-grasp movements modulates neuronal activity in the medial posterior parietal area V6A. J Neurosci 2009 29:1928-1936.

Fattori P, Raos V, Breveglieri R, Bosco A, Marzocchi N, Galletti C (2010) The dorsomedial pathway is not just for reaching: grasping neurons in the medial parieto-occipital cortex of the macaque monkey. J Neurosci 30:342-349.

Galletti C, Battaglini PP, Fattori P (1995) Eye position influence on the parieto-occipital area PO (V6) of the macaque monkey. Eur J Neurosci 7:2486-2501.

Galletti C, Fattori P, Kutz DF, Battaglini PP (1997) Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. Eur J Neurosci 9:410-413.
Galletti C, Fattori P, Kutz DF, Gamberini M (1999) Brain location and visual topography of cortical area V6A in the macaque monkey. Eur J Neurosci 11:575-582.
Galletti C, Fattori P, Battaglini PP, Shipp S, Zeki S (1996) Functional demarcation of a border between areas V6 and V6A in the superior parietal gyrus of the macaque monkey. Eur J Neurosci 8:30-52.
Galletti C, Kutz DF, Gamberini M, Breveglieri R, Fattori P (2003) Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. Exp Brain Res 153:158-170.
Gamberini M, Passarelli L, Fattori P, Zucchelli M, Bakola S, Luppino G, Galletti C (2009) Cortical connections of the visuomotor parietooccipital area V6Ad of the macaque monkey. J Comp Neurol 513:622-642.
Genovesio A, Ferraina S (2004) Integration of retinal disparity and fixation-distance related signals toward an egocentric coding of distance in the posterior parietal cortex of primates. J Neurophysiol 91:2670-2684. Epub 2004 Feb 2611.
Gnadt JW, Mays LE (1995) Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. J Neurophysiol 73:280.
Holmes G (1919) Disturbance of visual space perception. Br Med J 2:230-233.
Holmes G, Horrax G (1919) Disturbances of spatial orientation and visual attention with loss of steroscopic vision. Archives of Neurology and Psychiatry 1:385-407.
Kutz DF, Fattori P, Gamberini M, Breveglieri R, Galletti C (2003) Early- and late-responding cells to saccadic eye movements in the cortical area V6A of macaque monkey. Exp Brain Res 149:83-95.
Marzocchi N, Breveglieri R, Galletti C, Fattori P (2008) Reaching activity in parietal area V6A of macaque: eye influence on arm activity or retinocentric coding of reaching movements? Eur J Neurosci 27:775-789.
Perenin MT, Vighetto A (1988) Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. Brain 111:643-674.
Quinlan DJ, Culham JC (2007) fMRI reveals a preference for near viewing in the human parieto-occipital cortex. Neuroimage 36:167-187.
Richmond BJ, Optican LM, Podell M, Spitzer H (1987) Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. I. Response characteristics. J Neurophysiol 57:132.
Sakata H, Shibutani H, Kawano K (1980) Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. J Neurophysiol 43:1654-1672.