

Clustering of selectivity for optic flow in the ventral intraparietal area

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The presence of a columnar or clustered organization for some property often denotes that this property is important to the local information processing in a cortical area. To determine whether self-motion is systematically organized in the ventral intraparietal area (VIP), we made long electrode penetrations, recording both multi-unit and single-unit tuning for horizontally varying heading stimuli at frequent intervals. Single units were well correlated with

the tuning of multi-unit activity at the same location and multi-unit activity was more correlated with tuning at nearby locations than it was with tuning at locations beyond ~ 0.5 mm. From this, we conclude that heading information is represented in a clustered, and possibly columnar, fashion in VIP. *NeuroReport* 15:1941–1945 © 2004 Lippincott Williams & Wilkins.

Key words: Architecture; Columns; Heading; Monkey; Navigation; Self-motion; Topography

INTRODUCTION

Mountcastle first introduced the idea of a cortical column based on observations made in somatosensory cortex [1], and it has proved to be a powerful tool in making inferences about the functions of cortical areas. Columns or similar modular structures have now been described in nearly every cortical area [2]. Columns are defined by local similarity of neuronal properties spanning cortical layers, and these common properties derive from shared input to a local area, as well as dense, vertical connectivity within a region of cortex [3]. In addition to the classic vertically organized columns, a number of other cortical modules have been described, including the blobs of primary visual cortex [4], barrels in rodent somatosensory cortex, and many others (for review, see [5]). In all of these cases, the presumed function of such discrete local structures is to bring together related information so that local processing within an area can take place. Therefore, the presence of such organization is a profound clue as to what features are important to an area.

The ventral intraparietal area of macaque monkeys (VIP) does not have a single, obvious function. It is multimodal, with responses to somatic, visual, and auditory stimuli [5]. Visual inputs largely derive from motion-processing areas of dorsal extrastriate cortex [6,7], and bestow upon VIP directional responses to visual stimuli [8]. Interestingly, the responses to somatic stimuli are often also directional, and the preferred directions for visual and somatic stimuli often align [9]. This has led to the speculation that VIP might be important in the processing or guidance of the trajectories of objects in near extrapersonal space [10]. A related suggestion has been made on the basis of a recent electrical stimulation experiment [11]. From the movements evoked, it

was suggested that VIP might be involved in the organization of defensive motions in peri-personal space. However, other observations suggest a role for VIP in more far-field motion processing. VIP neurons are often selective for optic flow stimuli, not unlike those for which the medial superior temporal area (MST) is selective [12,13]. VIP is also clearly involved in directional detection, since neuronal activity in VIP is clearly correlated with decisions on a motion detection task [14,15]. It seems likely, on the basis of these relatively restricted observations, that VIP might be involved in a multiplicity of perceptual roles.

To better constrain what information is being importantly processed in VIP, we studied the local organization of selectivity for optic flow in area VIP. The presence of local clusters or columns of similarly tuned neurons would suggest that afferents or local circuitry is organized with respect to optic flow, and this would in turn lead to the conclusion that optic flow processing is a particularly important function for this multimodal area.

These results have previously appeared in abstract form [16].

MATERIALS AND METHODS

The methods used in these experiments were standard, and have been described in detail in previous publications [17,18]. Accordingly, they will be described only briefly here. Two female rhesus macaques (*Macaca mulatta*) were implanted with scleral search coils, head restraint posts, and chronic recording cylinders, all under deep surgical anesthesia. The cylinder was placed over the parieto-occipital border, and was positioned in a parasagittal plane over the posterior end of the intraparietal sulcus. In one

monkey, the cylinder was inclined at an angle of 30° above horizontal; in the other the angle was 45° .

In both monkeys extensive physiological mapping to localize VIP preceded the collection of the data reported in this paper. Our monkeys were trained on a standard delayed saccade task, to allow us to observe delay-period and saccade-related activity typical of the lateral intraparietal area, which adjoins VIP dorsally and laterally. Reach-related activity characteristic of the medial intraparietal area could be observed as the animal reached for treats. VIP was identified on the basis of its ventral location in the sulcus and by brisk, visually driven activity, which was nearly always directionally selective. While we did not systematically explore somatosensory responses, these were frequently observed, and helped to confirm our recording locations as being in VIP. Both monkeys are still alive and being used in related experiments; histological confirmation will be obtained once these are complete. Our mapping methods are described in greater detail in another publication [17].

Recordings were made through trans-dural guide tubes positioned in a plastic grid secured inside the recording cylinder [19]. Epoxy-insulated tungsten wire electrodes of 0.5–1.0 Mohm impedance (FHC, Inc.) were lowered through the guide tube to record neural activity. Signals were amplified and passed to a dual time/amplitude window discriminator (Bak Electronics) for the isolation of single- and multi-unit activity. For the isolation of single units, very strict criteria were applied; no false positives were allowed. Occasionally, recordings contained a small percentage (<5%) of false negatives; these will not greatly affect the shapes of tuning functions. For multi-unit activity, the second window was lowered until it was near the top of the amplitude distribution of the undifferentiated hash of activity. An upper window was applied to ensure, if necessary, that the single unit and multi-unit criteria were non-overlapping. Because we kept the multi-unit window in the upper quartile of the activity, we probably biased our sampling towards larger, nearby cells.

The stimuli used for the tuning measurements in this paper consisted of random dot patterns presented on the face of a monitor (Mitsubishi Diamond Pro, 21 inch) kept at a distance of 28 cm in front of the monkey. The dots were moved to simulate motion through a cloud of bright points (not unlike the opening sequence of the film, *Star Wars*). Overall, the stimulus subtended 72° horizontally by 56° vertically. Dots were white (60 candelas/m² per square meter) on a dark background (<0.5 candelas/m²). The simulated motion trajectory varied horizontally from trial to trial, but always simulated a speed corresponding to 10% of the depth in the scene (e.g. 1 m/s towards a cloud of points 10 m across). We termed the angle of the simulated trajectory, relative to dead ahead, the heading angle. The monkey was required to fixate during the stimulus presentation, though on some trials, the fixation point was moved horizontally at 10° /s, and the monkey was required to track it with smooth pursuit eye movements. A complete set of data consisted of all combinations of 13 heading angles and three different eye movement conditions (stationary, left and right pursuit); this was used for all the single-unit data. For the correlation across distance measurements, we wanted to maximize the number of sites we could record from in a penetration, and therefore removed the pursuit trials.

RESULTS

We measured the local organization of tuning for heading stimuli in two complementary ways. First, we measured the similarity between the tuning of single units with that of the local multi-unit activity. Secondly, we measured the similarity between multi-unit tuning measurements along single electrode penetrations spanning VIP. These data were collected from a total of 37 penetrations in two monkeys.

Single unit vs multi-unit correlation: Single cells tended to be tuned very similarly to the surrounding multi-unit activity, as shown in the example in Fig. 1. Like the majority of VIP cells [17], the single unit at this location (Fig. 1a) was well-tuned for heading, and compensated well for smooth

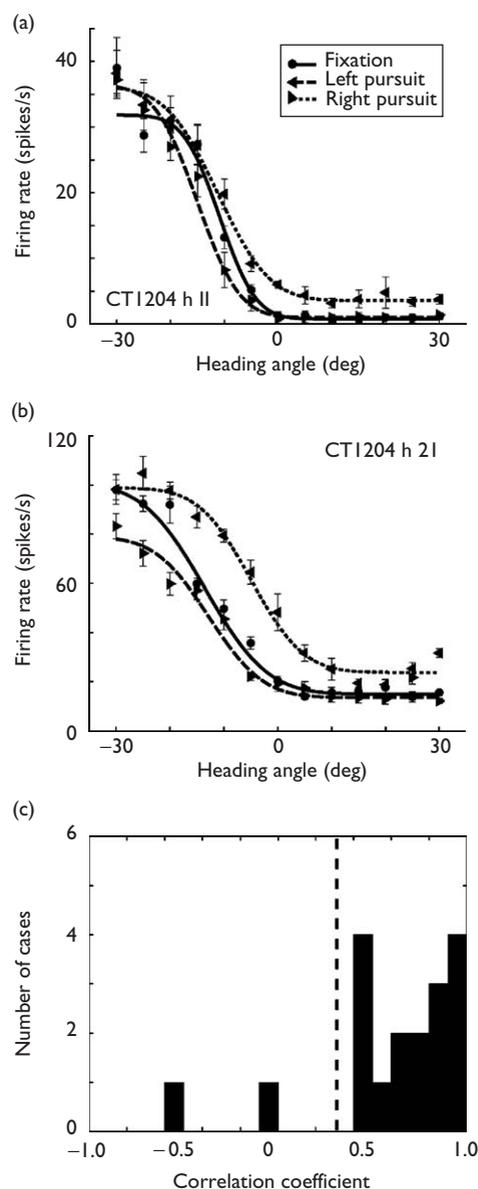


Fig. 1. Correlation of single-unit tuning with simultaneously measured multi-unit activity. (a,b) Raw data from a single case. The same tuning measurements on the single-unit and multi-unit data, from which the correlation coefficient was calculated. (c) Distribution of the correlation coefficients for whole sample of 18 cases.

pursuit eye movements. The multi-unit activity recorded from the same location (Fig. 1b) showed remarkably similar tuning. In making these measurements, we were careful that the thresholds for unit discrimination were set such that spikes from the single cell would never be included in the multi-unit measurement, so the similarity is not a simple consequence of overlapping data. To quantify this similarity, we calculated the correlation coefficient between the responses of the single- and multi-unit data for the same 39 stimuli. If the preference and shape of the tuning functions were similar for both sets of data, the correlation coefficient will be quite high, and will decline as either the shape of the tuning function or the preferred heading changes. Where single neuron and local multi-unit activity were oppositely tuned, the correlation coefficient would become negative. In this case the correlation coefficient was 0.95, indicating near-identity of tuning.

This example case was typical of our data, as shown in the summary histogram in Fig. 1c. This shows the distribution of correlation coefficients for the 18 cases where we were able to maintain isolation for sufficient time to complete the experiment. The vertical dashed line indicates a statistically significant correlation, for the number of points in our data

($p < 0.05$). Data from only one pair fell on the left side of this dashed line. The majority of cases lie to the right of the criterion, indicating significant similarity of tuning. It is noteworthy that in only one case did we observe significant anti-correlation. This might be expected, of course, if the electrode was positioned near the edge of a cluster, or if there were some heterogeneity in tuning. The average correlation in our cases was 0.61, and 89% of cases were significantly correlated. Therefore we can conclude that on average, single-unit tuning and multi-unit activity are both similar and significantly correlated, suggesting a local organization for heading tuning.

Correlation over distance: While the measurements described above strongly suggest a clustered organization for heading tuning, we were also interested in the spatial extent of this organization. To address this question, we measured tuning at closely spaced locations along penetrations spanning VIP. A good example of a penetration spanning VIP is shown in Fig. 2. Figure 2a shows the relative position and trajectory of the electrode, estimated from our physiological mapping of VIP (see Materials and Methods). Because we could not

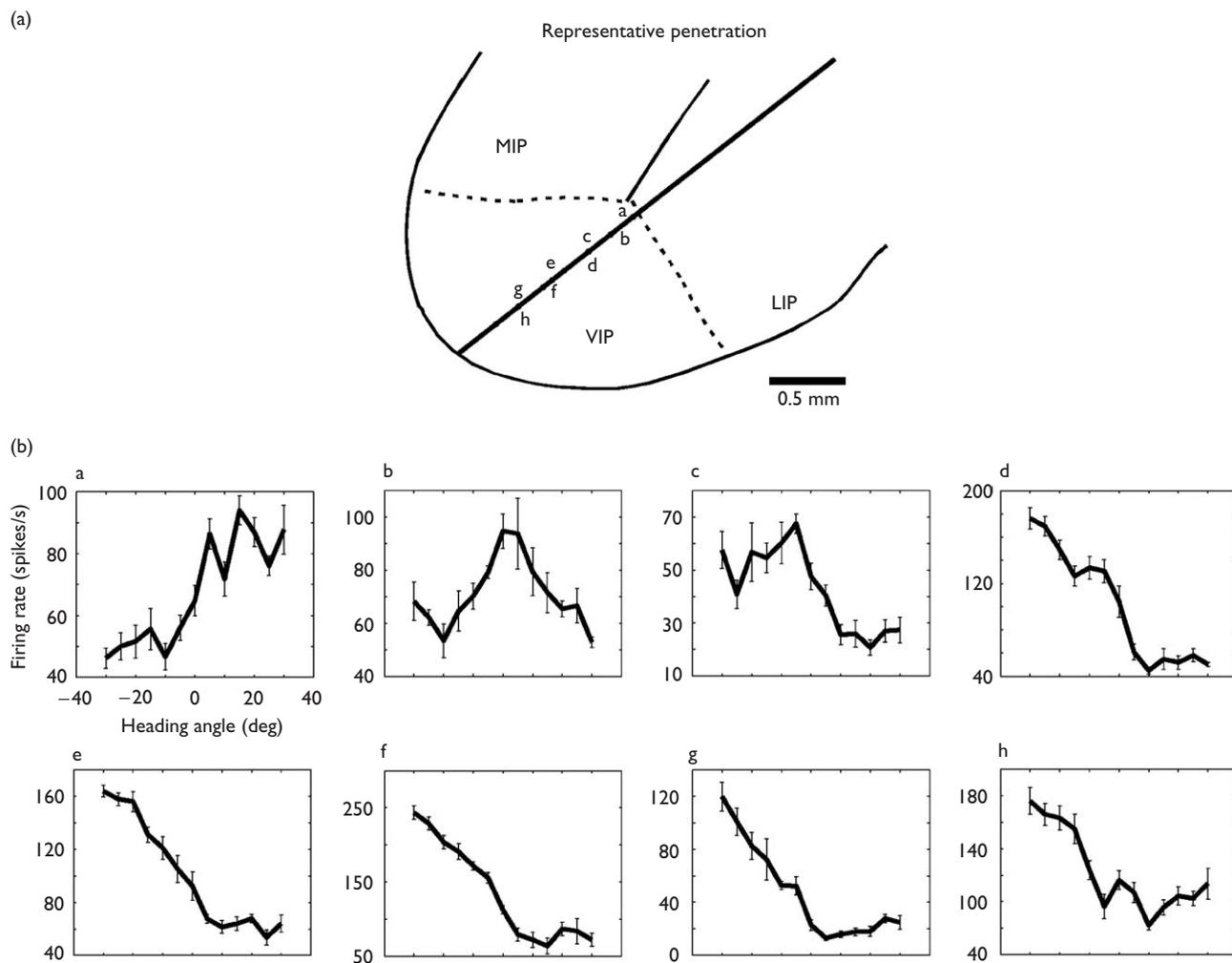


Fig. 2. (a) Schematic illustration of the geometry of a single recording track through VIP, with letters denoting single recording sites. (b) Tuning measurements at the sites along this penetration.

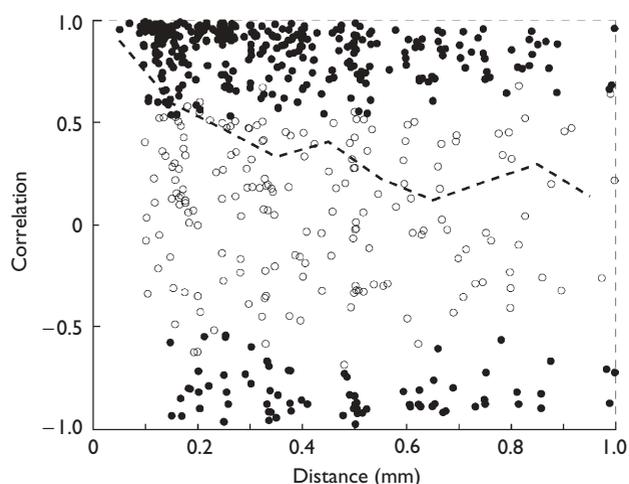


Fig. 3. The relationship of inter-site tuning correlation against track distance. For each pair of recorded sites on a penetration, a correlation coefficient was calculated, and plotted against the distance between the sites.

reconstruct the exact locations of single penetrations in the alert preparations, this diagram should be considered approximate. However, the distances between recording sites, measured from the microdrive readings, are accurate. The tuning of each site (a-h) in Fig. 2a is shown in Fig. 2b. Just after the electrode passed into VIP, as indicated by the abrupt onset of briskly directional responses, the neurons clearly preferred right headings. Shortly thereafter, the tuning became band-pass, preferring central headings (location b). However, from location 'c' onwards, the tuning consistently favored left headings, until we exited grey matter. In this case, this region of consistent left heading preference spanned about a millimeter of electrode travel. While, in this case, we saw a systematic and progressive shift of tuning that might indicate the existence of some kind of map for heading, this was not typically observed.

To quantify these observations, we again used the correlation coefficient. In this case, we measured correlation between tuning curves made at different distances along single penetrations. The result of this analysis appears in Fig. 3. Each pair appears as a single mark, and filled circles denote significantly correlated sites. The dashed line indicates the binned average correlation coefficient (0.1 mm bins). Several features are apparent in this figure. First, all correlations at distances <0.15 mm are positive, and there is a dense cluster of such cases. Secondly, for all distances less than ~ 0.4 mm, there is a preponderance of positively correlated tuning. This is reflected in the high average correlation at these distances ($r=0.4-0.9$). The average correlation drops considerably at distances greater than about 0.5 mm, which we take as a rough estimate of cluster size. Because the angle of our penetrations with respect to the cortical surface was unknown and variable, we cannot estimate the columnar (vertical) and laminar (tangential) contributions to this clustering. Nonetheless, we take this as evidence that tuning can be quite similar over regions that are similar to reported column dimensions in other cortical areas, and thus heading tuning has a systematic local organization in VIP.

DISCUSSION

The principal finding of this experiment was that tuning for optic flow stimuli in VIP is organized in a clustered or columnar manner, with nearby neurons tuned for similar values of horizontal heading. This was revealed by two related observations: tuning of single units was similar to the nearby background activity, and nearby multi-unit sites tended to have more correlated tuning.

Clustered or columnar organization is by now an extremely widespread finding in many different cortical regions with many different functions. While columns are most easily observed in primary sensory cortices [1,20,21], they have also been described in higher sensory areas [22,23], motor areas [24], and in areas classically considered association areas [5,25]. In all cases where the function of the region is sufficiently well understood, the signals that are brought together are tightly related to the function of the area. This relationship allows one to infer function from the presence of columnar or clustered anatomical organization.

It is important to bear in mind the potential limitations of the present observation as well. The present data do not allow us to conclude whether the organization is truly columnar. This is due to two unavoidable limitations to the approach we used. First, we used alert monkeys, so reconstruction of individual track locations was impossible. Also, the structure of VIP raises problems. It lies at the bottom of the IPS, where cortex curves sharply. Thus, penetrations can neither be aligned directly normal to the cortical surface, nor approximately tangential. We suspect that the organization would be truly columnar, but this awaits direct confirmation.

We also cannot infer the primary visual dimension for which the columns are organized, based on the present results. Our stimuli were chosen to be relatively natural, so they contain a variety of correlated features. As heading varies from left to right, the focus of expansion moves, and the range of horizontal motion vectors systematically changes as well. It would be interesting to repeat these measurements with stimuli in which the different optic flow components could be teased apart, to find out for which the clustered organization would be most robust. We suspect the organization would be most profound for more complex stimuli such as ours, which resemble natural motion. This would directly support the hypothesis that recovering heading is a function for which VIP is specialized.

CONCLUSIONS

There is a systematic local ordering of selectivity for optic flow stimuli in area VIP. This indicates that optic flow processing is probably an important behavioral function of this puzzling, multimodal cortical area. This conclusion does not imply, however, that VIP need be specialized for optic flow processing; it is very likely to be involved in a number of functions. We predict that similar columns will exist for the multiple types of information processed in VIP, and speculate that the proximity of different types of clusters might help to support the flexible visuo-motor behavior typical of primates.

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