Neurons in Parafoveal Areas V1 and V2 Encode Vertical and Horizontal Disparities

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INTRODUCTION

The retinal disparity of a physical point in space corresponds to the difference in location between its left and right retinal projections. It can be quantified as the angular difference between the two monocular visual directions associated with this point. In this way, its horizontal disparity (HD) is the difference between its left and right monocular azimuths, and its vertical disparity (VD) is the difference between the monocular elevations (Ogle 1962). Because the eye separation is in the horizontal dimension, HD and VD do not contain the same kind of information about the three-dimensional (3D) world. The horizontal component of the binocular disparity carries information about relative distances between points in space. Stereoscopic vision mainly relies on the HD signal, which is sufficient to drive a stereoscopic perception of depth (Julesz 1960). However, HD also varies as a function of the position of the viewed object relative to the head. VD carries information that theoretically permits disambiguation of the HD signal, and several models have been proposed to explain how HD and VD could interact to recover the 3D space with or without an extraretinal source of information on the position of the eyes in their orbit (Gårding et al. 1995; Koenderink and van Doorn 1976; Mayhew and Longuet-Higgins 1982; Weisshall 1990). Psychophysical experiments have since confirmed the functional role of VD on stereoscopic vision (Backus et al. 1999; Berends and Erkelens 2001; Bradshaw et al. 1996; Howard and Kaneko 1994; Kaneko and Howard 1997; Rogers and Bradshaw 1993, 1995; Stenton et al. 1984). HD and VD signals are also used to drive horizontal and vertical vergence eye movements to move the gaze in 3D space and to correct errors in eye alignment. Horizontal vergence occurs when the gaze is shifted from one depth plane to another and vertical vergence occurs when the fixation is oblique, toward a target in a tertiary position (Howard et al. 1997). Gain for vertical vergence increases as the stimulus area increases around the fovea (Howard et al. 2000).

Thus far, neurophysiological studies have mainly focused on the neural substrate for HD sensitivity in the foveal representation of the visual field, while neural basis for VD selectivity has drawn less attention (for review, Gonzalez and Perez 1998), probably because HD implication in stereoscopic vision is not as straightforward as HD. In the behaving monkey, only two studies have addressed the question of the VD selectivity in the earliest cortical visual areas: Gonzalez et al. (1993) in V1-V2 and Poggio (1995) in V3-V3A. Their results cannot account for a functional role of VD but rather suggest that VD disturbs the horizontal binocular matching (Poggio 1995). Failure to find a real encoding of VD could be due to the fact that VD is naturally weak in the central part of the visual field and increases with retinal eccentricity. This explanation seems also valid to explain why some psychophysical studies, using small displays in the central part of the visual field, did not find any effect of VD on the viewing distance estimation needed for the scaling of a stereoscopic surface (Cumming et al. 1991; Sobel and Collett 1991). In the present study, we looked for the presence of HD and VD detectors in the areas V1 and V2 at parafoveal retinal eccentricities (10°). The results, in part, have been presented briefly elsewhere (Durand et al. 2001).
METHOIDS

A macaque Rhesus monkey, with normal refractive indices for both eyes, was trained to perform a fixation task. After surgical implantation of a head holder, scleral coils in both eyes, and a recording chamber, extracellular recordings were carried out in both hemispheres in the calcarine part of V1 and in the part of V2 located just below. All the procedures complied with guidelines of the European Ethics Committee on Use and Care of Animals. While the monkey maintained an accurate binocular fixation on a small target without disparity in the center of the video screen (controlled with the magnetic scleral search coil technique), at a distance of 50 cm, the visual stimulus was presented in the cell’s receptive field during 500 ms. The stimuli used to test HD and VD sensitivity were dynamic random dot stereograms (dRDS, 6° of visual angle, dots of 0.1°, density of 50%) presented with crystal shutter glasses at a frequency of 60 Hz per eye. For some V2 cells with larger receptive fields (≥4° of visual angle), the stimulus size was set to 12° to cover the whole receptive field. Disparity was added between the right and left stereograms by shifting them in opposite horizontal and/or vertical directions. For positive (or uncrossed) HD values, the left stereogram is presented to the left eye and the right stereogram to the right eye and conversely for negative (or crossed) HD. While the RDS appears to be floating in front of the screen in the first case and behind the screen in the second one, VD does not induce a stereoscopic depth percept per se and the terms of crossed and uncrossed disparities are meaningless. By convention, a positive VD value corresponds to the right eye seeing the upper stereogram and the left eye seeing the lower one. Both HD and VD selectivities were tested between −0.6° and 0.6°. Generally, HD sensitivity was tested first and then VD was added on the preferred HD value. In preliminary sets of experiments, VD selectivity has been tested on several HD values and then characterization of the HD selectivity was done for the optimal condition (i.e., the more selective HD tuning curve).

Cells were classified as visually responsive for RDS when the mean visual response was significantly higher than the spontaneous activity (t-test, P < 0.05) and the criterion for the disparity selectivity was a P value < 0.05 in a one-way ANOVA. The tuning index (Ti) was calculated with the method developed by Prince et al. (2002b), with

\[ Ti = \frac{MS_{\text{between}}}{(MS_{\text{within}} + MS_{\text{within}})} \]

where \( MS_{\text{within}} \) and \( MS_{\text{between}} \) are the one-way ANOVA terms representing the response variance (mean squares) within the conditions and between the conditions, respectively. Values of Ti near 1 are found when the variability intrinsic to the visual response is negligible relative to the one induced by the change of disparity value. For the disparity selective cells, tuning curves have been fitted with a Gabor function (the product of a Gaussian envelope and a cosine function) of the form

\[ f(d) = A \times \exp\left(\frac{(d-d_0)^2}{\sigma^2}\right) \times \cos(2\pi f(d-d_0) + \phi) + B \]

representing the visual response as a function of the disparity value, \( d \). The Gaussian envelope is characterized by its baseline, \( B \), its amplitude, \( A \), its width, \( \sigma \), and its peak location, \( d_0 \), \( f \), and \( \phi \), respectively, correspond to the frequency and phase of the cosine term. For the fitting, data points were the mean visual responses for each condition and had been weighted with SE.

RESULTS

Seventy-four cells were tested in the calcarine V1 (60 cells) and in V2 (14 cells) for their selectivity to HD and VD. Their receptive field eccentricities ranged from 8 to 22° (14.2 ± 2.5°, mean ± SE, median 14.1°). In total, 47% of the cells were selective to both HD and VD (HD/VD cells), 8% were HD selective only (HD cells), 23% VD selective only (VD cells), and the last 22% were nonselective to binocular disparities (NS cells, see Table 1). V2 cells were found to be selective to binocular disparities in higher proportions, with 86% (12/14) of HD/VD cells against 38% (23/60) in V1. According to the phase parameter (\( \phi \)) of the Gabor fit (Prince et al. 2002b), cells were classified into the classical categories described for HD selective cells (Poggio et al. 1988), with Tuned Excitatory (TE), Tuned Inhibitory (TI), Near, and Far cells. Cells with sharp tuning peaks around 0° of HD, including the tuned near (TN) and tuned far (TF) cells, were included in the TE category. Since we found similar profiles for VD sensitivity, the same classification was used, even if, in this case, terms of Near and Far cells make no sense. We have named the VD categories TE-like (including TN-like and TF-like), TI-like, Near-like, and Far-like, by analogy with the HD cells categories. Results of this classification are reported in Table 1.

Four examples of VD tuning profiles are shown in Fig. 1A, corresponding to the four HD categories described (TE-like, TI-like, Near-like, and Far-like). In Fig. 1, B and C, two examples of cells tested for VD selectivity on several HD values are presented. The first example (Fig. 1B) is a cell selective for both HD and VD, with a peak on 0.4° of HD and −1° of VD. The second example (Fig. 1C) is a non-HD selective cell for a VD value of 0°. However, this cell is HD selective for a VD value beyond 0.4° and, conversely, is VD selective beyond 0.6° of HD. Distributions of the principal Gabor parameters are presented in Fig. 2 for the 41 HD selective cells and for the 52 VD selective cells. Distributions for the width of the Gaussian envelope (\( \sigma \)) and for the cosine frequency (\( f \)) were statistically different between HD and VD (Wilcoxon rank-sum test, \( P < 0.05 \)). Median value for the width of the Gaussian envelope was smaller for VD (0.41 vs. 0.61° for HD) while the median frequency was bigger (0.9 vs. 0.7 cycle per degree for HD). For the Gaussian peak (\( d_0 \)) and cosine phase (\( \phi \)), no statistical difference was found between HD and VD distributions and their median values were both equal (0.1° for the peak and −0.1° for the phase) but the interquartile range (IQR) of the peak distribution was almost half for VD (0.18° vs. 0.34° for HD). HD and VD tunings were compared in our pool of 35 HD/VD cells. HD/VD cells exhibited a high correlation between their HD and VD tuning indexes, with a regression slope near 1 (Fig. 3C). Peak and width of the Gaussian envelope do not directly characterize the disparity tuning of a cell. To assess it more closely, HD and VD tuning peaks for each cell were evaluated as the location of the Gabor local peak (or trough) having the biggest amplitude relative to the baseline, \( B \), and the tuning width was measured.

| TABLE 1. Classification of disparity sensitive cells |
|------------|------------|------------|
| V1 + V2 Cells | HD Selectivity | VD Selectivity |
| NS | 22 (16) | TE | 54 (22) | TE-like | 40 (21) |
| HD | 8 (6) | TI | 24 (10) | TI-like | 8 (4) |
| VD | 23 (17) | Near | 10 (4) | Near-like | 25 (13) |
| HD/VD | 47 (35) | Far | 12 (5) | Far-like | 27 (14) |

Values are percentages with number of cells in parentheses; total number of cells was 74 for V1 + V2, 41 for HD selective, and 52 for VD selective. NS, nonselective; HD, horizontal disparity; VD, vertical disparity; TE, tuned excitatory, TI, tuned inhibitory.
at half-height of the peak (Fig. 3, A and B). For both parameters, significant differences were found between HD and VD distributions (Wilcoxon signed-rank test, $P < 0.05$). For the peak location, median values were similar (0.06° for HD and 0° for VD) but the IQR for the VD distribution was less than half (0.15° vs. 0.36° for HD). Tuning widths were smaller for VD than for HD (median values of 0.29° for VD against 0.40° for HD), but a significant correlation existed between the HD and VD widths (Fig. 3B).

**Discussion**

The present results show for the first time that both HD and VD are encoded in the parafoveal calcarine V1, and, in V2, beyond 10° of retinal eccentricity. Cells selective to both HD and VD are the most common (38% in calcarine V1 and 86% in V2). Selectivity to HD at these retinal eccentricities is close to what has been reported in foveal V1. The percentage of HD selective cells is comparable in calcarine V1 (45%) and in dorsal V1 (about 50%) (for review, Trotter 1995) and the Gabor parameters distributions are very close (Prince et al. 2002a). Similarity in the HD encoding characteristics between foveal and parafoveal regions is surprising. Indeed, we could expect changes in the HD encoding at parafoveal eccentricities, due to the lower percentage of selective cells and/or coarser tuning curves, since our ability to evaluate stereoscopic depth decreases quickly with increasing retinal eccentricity (Mckee 1983; Rawlings and Shipley 1969).

The existence of nonhorizontal disparities between the receptive fields of each eye has been reported in areas 17 and 18 of anesthetized cats (Barlow et al. 1967; Joshua and Bishop 1970; von der Heydt et al. 1978). To our knowledge, von der Heydt et al. (1978) were the first to test HD and VD selectivities but only on two cells. In behaving monkeys, Gonzalez et al. (1993) have found two types of VD tuning profiles in foveal areas V1 and V2: TI-like and TE-like. Poggio (1995) reported in V3-V3A a consistent reduction of the visual response to HD when VD was added, with a TE-like tuning profile. Their results can be interpreted as a perturbation of the HD matching process by the VD: the visual response is brought back to its floor level when VD is present. If VD is added to an HD value eliciting a lower visual response than the floor level, the VD tuning profile is TI-like and if VD is added to an HD value giving a high response relative to the floor level, the VD tuning profile is TE-like. This view is in accordance with the known sensitivity to complex cells in V1 for binocular correlation in RDS (Poggio et al. 1985, 1988) and with the deleterious effect of a relative vertical displacement between the stereoimages in a stereoscopic perceptual task (Fender and Julesz 1967; Nielsen and Poggio 1984). In contrast, we found cells, in the parafoveal representation of V1 and V2, selective to VD with the same diversity in the tuning profiles as previously described.
for HD-selective cells (Poggio et al. 1988) and with tuning indexes similar to the HD ones. These results rule out the noise effect attributed to VD on the HD encoding and support the idea of a real encoding of VD, sharing a common neural process with the HD encoding. So far, two-dimensional (2D) disparity encoding has been shown only in area MT of the behaving monkey (Maunsell and Van Essen 1983) and in the Wulst of the behaving barn owl (Nieder and Wagner 2001).

The narrower widths of the tuning curves and the narrower range of encoded VD are the only differences found between the HD and VD encoding. This finer VD tuning is coherent with a functional role for this signal, given the fact that, in natural viewing, the VD range is smaller than the HD range. Moreover, the increase of naturally occurring VD with retinal eccentricity could explain the difference found between the HD sensitivity in foveal V1 (Gonzalez et al. 1993), always centered on a VD value of 0°, and the one reported in this study, in parafoveal V1, extended to a larger eccentric angular scale. VD was tested on the preferred HD and not the contrary because it permitted us to rule out the noise hypothesis for the VD on the HD matching and to compare directly the HD encoding in parafoveal V1 to what has been reported in foveal V1 (Prince et al. 2002a; Trotter 1995), but it is unlikely that the observed finer tuning for VD is due to an anisotropy in the orientation preference of the HD/VD cells.

Another issue that remains open is to determine how the HD
and VD sensitivities fit with the predictions of the disparity energy model (Fleet et al. 1996; Ohzawa et al. 1990; Qian 1994). This model, first presented to explain HD encoding, can be extended to the vertical dimension and predicts that a complex cell with a vertically elongated receptive field will have a Gabor-like disparity tuning profile for HD and a Gaussian-like profile for VD and the inverse will be true for a cell with a preferred horizontal orientation (Fig. 3D, top). We have not tested orientation preference in this study, nevertheless we have compared the shape of the HD and VD tuning profiles to look for a possible anisotropy between the HD and VD tuning profile shapes. If HD sensitivity is an artifact of the HD encoding, we should have mainly Gabor-like profiles for HD and Gaussian-like profiles for VD, but the data do not show such anisotropy (Fig. 3D). The fact that Gabor-like profiles are equally present in both horizontal and vertical dimensions also suggests that the finer VD encoding is not due to a given orientation preference anisotropy in our pool of HD/VD detectors but relies on another mechanism that remains to be determined.

To go further in the analysis of the HD and VD encoding, sensitivity to these variables has to be tested systematically in a 2D array. Two preliminary examples of cells tested with such matrix are shown in Fig. 1, B and C, for which it appears that the disparity tuning is closely related to both components of the binocular disparity. The signal encoded by these cells could drive vertical vergence movements, which occur only over a restricted range of HD, suggesting that the same cells encode both horizontal and vertical components of the disparity (Allison et al. 2000).

The disparity detectors found in the present study have small receptive fields (on average 1.5° width in V1 and 4° width in V2) and are tuned for positional disparities (in both horizontal and vertical dimensions). For the extraction of the viewing parameters leading to the reconstruction of the visual space metric structure, a more integrative processing of the VD is required (Bishop 1989, 1996; Mayhew and Longuet-Higgins 1982). However, some models predict that nearness of the parameters leading to the early cortical relief recovery could also theoretically involve an extraretinal eye position signal (Gårding et al. 1995; Koen-derink and van Doorn 1976; Liu et al. 1994; Weinshall 1990). This process leading to the early cortical relief recovery could also theoretically involve an extraretinal eye position signal (Gårding et al. 1995; Koen-derink and van Doorn 1976; Liu et al. 1994; Weinshall 1990). However, some models predict that nearness of the parameters leading to the early cortical relief recovery could also theoretically involve an extraretinal eye position signal (Gårding et al. 1995; Koen-derink and van Doorn 1976; Liu et al. 1994; Weinshall 1990). However, some models predict that nearness of the parameters leading to the early cortical relief recovery could also theoretically involve an extraretinal eye position signal (Gårding et al. 1995; Koen-derink and van Doorn 1976; Liu et al. 1994; Weinshall 1990).

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