Left and right retinal images of an object seen by the 2 eyes can occupy slightly disparate horizontal and/or vertical locations. The role of horizontal disparity (HD) in stereoscopic vision is well established, but the functional contribution of vertical disparity (VD) remains unclear. Various psychophysical studies have shown that HD and VD are used differently by the visual system depending on their location in the visual field, whether near the center of gaze or more peripheral. We show this horizontal/vertical distinction at the cellular level in monkey primary visual cortex (area V1). The range of VD encoding is reduced in central but not in the peripheral representation of the visual field. Moreover, neurons respond selectively to particular combinations of both types of disparities depending on the coded orientation as predicted by the disparity energy model. The preferred orientations of neurons near the fovea present a vertical bias that is well suited for stereopsis based on HD selectivity alone. In the periphery, instead, preferred orientations are radially biased, which allows a peripheral detector to convey the same depth signal based on either HD or VD. Such an organization has functional implications in both the perceptual and oculomotor domains.

Keywords: central and peripheral V1, disparity energy model, extracellular recordings, horizontal and vertical disparities

Introduction

Due to the lateral separation between the eyes, an object lying in the binocular field of view can form images in disparate locations in the left and right retinas, along both the horizontal and vertical dimensions. Because the eyes are displaced horizontally, there is an anisotropy between horizontal disparity (HD) and vertical disparity (VD), both in their natural range of occurrence and in the information they carry. This is reflected by the fact that stereo images with disparate horizontal positions create a perception of depth when they are fused (Wheatstone 1838; Julesz 1971), whereas stereo images with disparate vertical positions will not produce any depth percept when presented alone (Nielsen and Poggio 1995).

To understand this functional anisotropy, it is useful to consider the geometry of binocular vision. The horizontal separation between the eyes means that, for a given feature in the left retinal image, its possible matches in the right retina lie along a line (epipolar line), with an orientation close to horizontal (Fig. 1, epipolar lines for a gaze straight ahead, in black, or in tertiary position, dotted lines). For this reason, HD is generally considered as the main, or unique, signal for stereoscopic vision. However, VD also appears as retinal eccentricity increases and is mainly expressed as a vertical shift of the epipolar lines that depends on the eyes position. The pale gray areas in Figure 1 show the range of VD that can be encountered at various retinal locations for a range of gaze azimuth (±25°), elevation (±25°), and fixation distance (from 10 cm to +∞) along epipolar line segments extending ±1° horizontally (see Materials and Methods for details). It is clear that, even with the large range of binocular fixation conditions considered in this simulation, VD is usually very weak close to the fovea (for a special case where VD can be created in the central field by placing vertical occluders in front of oblique lines, see Farell 1998) and increases with increasing retinal eccentricity.

There are psychophysical evidences that the visual system does not strictly follow the epipolar constraint and search for corresponding features along both the horizontal and vertical dimensions (Stevenson and Schor 1997; Farell 1998; Schreiber and others 2001). In the central part of the visual field, binocular search zones are elliptical, with a horizontal elongation axis (Ogle and Prangen 1953; Tyler 1991). In the peripheral field, their shape is not documented, but the preceding geometrical considerations would suggest a relative increase of their vertical dimension. Interestingly, VD can also play a role in stereoscopic vision, even if it is not traditionally thought of as a depth signal. Such influence has been demonstrated for large stimuli extending into the peripheral field of view, where VD can be as effective as HD in driving a stereoscopic depth percept (Ogle 1938; Rogers and Bradshaw 1993; Backus and others 1999; Howard and Rogers 2002). In the central field, VD can also influence the depth percept, but its effect is generally weaker and can be observed only for oriented stimuli, not broadband stimuli such as random dot surfaces (Matthews and others 2003). This suggests that neurons in charge of processing disparity in the central and peripheral representations of the visual field have distinct characteristics. In a recent model, Matthews and others (2003) have proposed that a radial organization of the disparity detectors in periphery could account for this effect assuming that disparity is encoded in an orientation-dependent manner. Although a radial organization of the receptive fields (RFs) has been reported in the superficial layers of central V1 (Bauer and Dow 1989), in peripheral V4a (Pigarev and others 2002) of the monkey and in cat extrastriate areas (Leventhal 1983; Rodionova and others 2004), no link between this organization and disparity coding has been demonstrated so far.

From an oculomotor point of view, corrective vergence eye movements (horizontal, vertical, or cyclorotational) are used to keep the eyes accurately aligned and thus constrain positional disparity in a range allowing fusion. Input signals for these vergence eye movements are respectively HD, VD, or particular combinations of both (cyclodisparities) (Howard 2002). Whereas horizontal vergence exhibits a gain that is already maximal for small stimuli (same gain for a central stimulus 0.75°
or 65° in diameter), the gain for vertical and cyclovergence increases as the stimulus diameter increases up to 20° (Howard and others 1994, 2000). Altogether these observations lead to the conclusion that HD and VD are exploited differently by the visual system and as a function of the eccentricity at which they appear.

The primary visual area (V1) is the first cortical site where monocular signals emanating from the left and right retinas converge onto single cells. Some of these cells are positional disparity detectors in the sense that they are optimally activated by binocular stimuli that fall in slightly disparate retinal locations due to the existence of slight mismatches between their left and right RF locations (Barlow and others 1967; Nikara and others 1968; Joshua and Bishop 1970) and/or internal structure (Tsao and others 2003). As the first binocular stage, V1 is of prime importance for computing the signal used by both the stereovision and the oculomotor control systems. However, very few studies have tackled the issue of the functional organization of V1 for disparity encoding as it relates to the geometrical and functional considerations described above. In trying to reveal the neural basis of stereoscopic vision, most previous studies have focused on HD encoding in the central visual field representation, and very little is known about VD encoding (Poggio 1995; Trotter 1995; Gonzalez and Perez 1998; Cumming and DeAngelis 2001). Pioneering works performed in the primary visual cortex of anesthetized paralyzed cats revealed the existence of both horizontal and vertical positional disparities but suffered from an inherent imprecision due to the acute preparation in which the exact vergence state of the animal is not controlled (Barlow and others 1967; Nikara and others 1968; Joshua and Bishop 1970).

In the central visual field representation of V1, of the 3 studies performed in behaving primates, 2 offer indirect evidence (Gonzalez and others 1993, 2003) and one gives direct proof (Cumming 2002) of a specialization for HD processing, with a wider range of encoding along the HD than along the VD dimension. We have recently reported VD selectivity in peripheral V1 (Durand and others 2002) with tuning curve profiles similar to those found for HD at the same retinal eccentricities.

Because these studies suggest a difference in VD processing between the central and peripheral representations, our first objective was to compare the tuning of central and peripheral disparity detectors in the same monkeys and with the same stimuli and experimental conditions. A second objective was to study the potential link that exists between HD/VD encoding and orientation tuning in V1. The disparity energy model (Freeman and Ohzawa 1990) predicts a strong link for V1 disparity detectors between their preferred orientation for contours and their disparity sensitivity, with a higher sensitivity orthogonal to the preferred orientation. Surprisingly, such a relationship has not been reported in central V1 (Cumming 2002; Gonzalez and others 2003). In Cumming’s study, a horizontal elongation of the disparity response surfaces (visual responses as a function of HD and VD) is reported for a majority of cells, irrespective of their preferred orientation. This was interpreted by the author as another expression of the HD specialization in V1. Thus, we were also interested to know if, in the peripheral representation where such a specialization is not expected, this cornerstone prediction of the disparity energy model could be verified.

Materials and Methods
A detailed description of the general methods has been reported elsewhere (Trotter and Celebri, 1999; Durand and others 2002). All experimental protocols, including care, surgery, and training of animals, were performed according to the Public Health Service policy on the use of laboratory animals. Three monkeys (Macaca mulatta) were trained, with their heads restrained, to fixate a target in total darkness on a video screen located 50 cm from the head. Eye position was monitored using scleral search coils implanted in both eyes.

Visual Stimulation
Steroscopic stimulation was performed using dynamic random dot stereograms (dRDS) generated through ferroelectric stereo glasses (60 frames per second per eye), size 6° × 6°, dot density 20%, and dot size 3.5 min of arc. Generally, HD and VD were varied within the range [−0.6°, +0.6°], with a sampling step of 0.2°. For cells with very fine disparity tuning, the disparity range was set to [−0.3°, +0.3°] with a 0.1° step size. For cells with very coarse disparity tuning, the disparity range was set to [−1.2°, +1.2°] with a 0.4° step. Orientation selectivity was tested using square-wave gratings (circular window 6° diameter) with a spatial frequency of 2 cycles/degree in 8 steps of 22.5° for a 180° range. The different stimuli were flashed binocularly for 500 ms, centered on the RF, and presented 5 times randomly interleaved. Spike activity was collected from 300 ms before the appearance of the fixation target (spontaneous activity) until 500 ms after the stimulus onset (visual evoked activity).

Simulation of the Natural VD Range
We used simulation to estimate the range of naturally occurring VD as a function of retinal eccentricity in our experimental conditions but...
also over a broad range of binocular fixation conditions. Helmholtz coordinate system was used to specify eye position (positive directions clockwise, right and up). The torsional state of the eyes was calculated using an intermediate between L2 and Listing's law, similar to the one used by Schreiber and others (2001), where the cyclorotational state of the left and right eyes ($C_l$ and $C_r$) is specified by $C = -L_2 + V/2 + 0.15\Delta V$ and $C_r = -L_2 + V/2 - 0.15\Delta V$. $H_l$ and $H_r$ are the horizontal angles of the left and right eyes, $V$ is their common vertical angle, and $D$ is the vergence angle ($H_l - H_r$). We used a planar projection plane situated at one unit distance from the eyes projection center to calculate the positional disparities arising in the left eye for fixed points on the right retina using the equations given in Garding and others (1995). The only addition to the left-to-right-eye transformation matrices was a rotational term accounting for the relative cyclorotational state of the 2 eyes. For each point on the right retina, positional disparity was calculated for an object situated slightly in front and slightly behind the horizontal horopter (position of the points in space projecting without HD). The epipolar line was then defined as the line segment passing through their projections on the left eye projection plane and extending ±1° horizontally (which is an approximation of the fusion range for HD). This was repeated over a broad range of fixation distance (vergence distance from 17° to 0°), gaze azimuth (±25°), and elevation (±25°). Monkey interocular distance was set to 3 cm.

### Data Analysis

#### Spatial Analysis

The criterion for disparity (horizontal and vertical) and orientation selectivity was a P value < 0.05 in a 1-way analysis of variance (ANOVA). We computed an ANOVA-based selectivity index to quantify its strength. This index corresponds to the mean intercondition variance of the visual responses divided by the mean inter- plus intracondition variance. The maximum value this index can reach is 1, if the response strength varies when changing the condition (disparity or orientation) while remaining constant for repetitions of the same condition (Prince, Pointon, and others 2002).

Disparity tuning curves were fit with a Gabor function. We followed the method described by Prince, Pointon, and others (2002) to set the disparity frequency parameter according to the frequency spectrum obtained from the mean raw tuning curve before Gabor fitting. Preferred disparity was the disparity value evoking the most extreme response level (peak or trough) relative to the baseline level of activity. Orientation tuning curves were fitted with a Gaussian function, and the peak of the Gaussian bell was used as an estimate of the preferred orientation. Only cells for which the fit accounted for more than 75% of the intercondition variability were used in this analysis.

Visual responses evoked by various HD/VD combinations were recorded for 78 cells to build disparity response surfaces. For the majority of cells ($n = 42$), 49 combinations were tested with at least 5 repetitions: 7 HD × 7 VD, both between -0.6° and 0.6° (some cells were tested with very fine, ±0.3°, or coarse, ±1.2°, disparity ranges). For the other cells ($n = 36$), we used a reduced protocol in which VD selectivity was measured for several (3–5) HD values after measurement of the HD tuning curve.

Prior to the 2-dimensional (2D) Gabor fitting, a 2D fast fourier transform was used to obtain the surfaces' frequency spectrum after removal of the DC component (i.e., mean overall visual response), and the zero-frequency component was shifted to the center of spectrum. Disparity frequency was then set to the distance between the peak of highest energy and the spectrum center. The disparity modulation axis (perpendicular to the parallel stripes of the Gabor function) was set to match the orientation of the axes passing through the spectrum center and the peak of highest energy. A 2D Gabor function of the form

$$R(b, v) = B \cdot \text{Aexp} \left( - \frac{m^2 + e^2}{2\sigma^2} \right) \cos(2\pi m f + \phi)$$

where

$$m = (b - b_0)\sin\theta + (v - v_0)\cos\theta$$

and

$$e = (b - b_0)\cos\theta + (v - v_0)\sin\theta$$

was then used to fit the data. Visual response $R$ is expressed as a function of HD ($b$) and VD ($v$), relative to the disparity along the modulation ($m$) and elongation ($e$) axis through rotation by the angle $\theta$ (the orientation of the disparity modulation axis set by the method described above). $A$ is the amplitude of the Gabor relative to $R$, its baseline level. The Gaussian envelope is defined by its width, $\sigma$, and its peak position ($b_0$, $v_0$). The $\gamma$ is the aspect ratio that specifies how elliptical the Gaussian envelope is ($\gamma = 1$ for a spherical envelop). The cosine term is defined by its frequency, $f$, and its phase, $\phi$, relative to the peak of the Gaussian envelope. Preferred disparity and surface elongation axis were determined from the fitted surface. Preferred disparity was the HD/VD combination eliciting the most extreme response relative to baseline (this could be a peak, for a “tuned excitatory” [TE] cell, or a trough, for a “tuned inhibitory” [TI] cell).

To determine the disparity elongation axis following the method proposed by Cumming (2002), the main response peak was kept (i.e., the level of activity higher than half the peak amplitude relative to baseline) from which was measured the orientation of the long axis. Note that for this analysis, disparity frequency and modulation axis extracted from the 2D spectrum were used as starting parameters but not fixed for the fit, in order to allow direct comparison of the results.

The treatment described so far was also applied to a set of 999 synthetic surfaces generated from each experimental surface by parametric bootstrap (Efron and Tibshirani 1993) to assess the 95% confidence intervals of the various parameters.

#### Temporal Analysis

Visual onset latency was determined from the visual responses evoked by the optimal disparity (or orientation). A mean poststimulus time histogram (PSTH) was constructed and smoothed with a Gaussian kernel (sigma between 3 and 8 ms, depending on the overall response strength) in order to compensate for the relatively weak number ($N$) of responses (Lu and others 1995). Distribution of spike counts in the 1-ms bins before stimulus onset (from -200 to 0 ms) was fitted with a Poisson distribution and visual onset was set to the first of 20 subsequent poststimulus bins for which the probability of belonging to the baseline Poisson distribution was <0.001. Because the smoothing can lead to an underestimation of visual response onset, it was corrected by sliding this first visual bin on the smoothed PSTH until inflexion of the first visual response peak (the peak of its first derivative). Selectivity appearance was then calculated. The Poisson term was omitted from the unsmoothed PSTH by running successive ANOVA tests in a temporal window starting from the visual response onset and iteratively incremented by 1 ms. Selectivity onset was set the first of 10 successive bins for which the ANOVA $P$ value < 0.05.

### Results

#### General Results

Data were obtained from 3 monkeys. In total, 633 cells were recorded in area V1 for at least one of the following tests: orientation, HD, or VD selectivity. Two regions of area V1 were explored: 1) central V1 (cV1; $N = 319$), corresponding to the operculum, in which cells were recorded within 7° of the visual field center (median RF eccentricity, 3.2° [0.5°–6.3°]) and had RF size ranging from 0.5° to 1.5° and 2) peripheral V1 (pV1; $N = 314$), lying along the bank of the calcarine sulcus where RFs are slightly larger (from 1° to 4°) at retinal eccentricities ranging from 7° to 27° (median 14.8°) (Fig. 2A,B); see (Daniel and Whitteridge 1961;Gattass and others 1981; Van Essen and others 1984) for a detailed visual topography. Orientation- and disparity-selective cells were encountered across the whole range of retinal eccentricities we explored (Fig. 2C), and we did not observe any difference in the proportions of selective cells between central and peripheral V1 either for orientation (about 90%) or for disparities (about 55%). Only disparity-selective cells for which the Gabor fit accounted for at least 75% of the tuning curve variance were kept for further analysis (93% of the

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total population of disparity-selective cells). Similarly, 86% of the orientation-selective cells for which the Gaussian fit described at least 75% of the tuning curve variance were kept (Table 1).

**Spatial Analysis: Encoding of Central and Peripheral Disparities**

**Categories of HD and VD Detectors**

In their pioneering works performed with behaving monkeys, Poggio and others (Poggio and Fischer 1977; Poggio and others 1985, 1988) introduced the idea of categories of HD-selective cells: “Tuned” cells have sharp tuning profiles with a preferred disparity close to 0° for TE and TI cells and more far away from 0° for the “tuned near” (TN) and “tuned far” (TF) cells. “Reciprocal” cells exhibit symmetric profiles often centered on 0°, with a preference for positive versus negative disparities (“far” cells) or the opposite (“near” cells).

We used similar terminology for VD-selective cells, without any a priori functional meaning (see preliminary data in Durand and others 2002). Examples of VD tuning profiles illustrating these six categories are shown in Figure 3 with their corresponding raster displays.

Disparity tuning curves were parameterized using 1D Gabor functions and quantitatively classified according to both disparity frequency and preferred disparity. Tuning measures did not reveal clusters (Fig. 4A,B), in agreement with previous studies reporting that these categories (at least for HD selectivity) do not represent distinct cell populations but rather prototypes along a continuum of tuning profile shapes (Levay and Voigt 1988; Prince, Cumming, and Parker 2002). Nevertheless, it remains a convenient way to characterize the tuning profiles and to compare results with other studies because this classification has been widely used in the field. Disparity tuning sharpness, estimated by the frequency parameter of the Gabor fitting, was not significantly broader in the periphery than in the central representation either for HD or for VD (Wilcoxon rank

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**Table 1**

<table>
<thead>
<tr>
<th>Selectivity</th>
<th>Central V1 (n = 319)</th>
<th>Peripheral V1 (n = 314)</th>
</tr>
</thead>
<tbody>
<tr>
<td>HD (n = 202)</td>
<td>VD (n = 91)</td>
<td>Orientation (n = 193)</td>
</tr>
<tr>
<td>Sel 57% (n = 115)</td>
<td>54% (n = 49)</td>
<td>92% (n = 178)</td>
</tr>
<tr>
<td>Sel and GF 92% (n = 106)</td>
<td>92% (n = 45)</td>
<td>87% (n = 155)</td>
</tr>
<tr>
<td>Sel index 0.87 (0.68-0.92)</td>
<td>0.84 (0.68-0.91)</td>
<td>0.92 (0.80-0.98)</td>
</tr>
<tr>
<td>1D disparity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disp freq (cpd) 0.94 (0.73-1.69)</td>
<td>1.03 (0.83-1.73)</td>
<td>—</td>
</tr>
<tr>
<td>Disp pref (SD, °) 0.24</td>
<td>0.10</td>
<td>—</td>
</tr>
<tr>
<td>TE/TI 55% (n = 58)</td>
<td>84% (n = 38)</td>
<td>—</td>
</tr>
<tr>
<td>TN/TF 16% (n = 17)</td>
<td>2% (n = 1)</td>
<td>—</td>
</tr>
<tr>
<td>NE/FA 29% (n = 31)</td>
<td>13% (n = 6)</td>
<td>—</td>
</tr>
<tr>
<td>2D disparity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disp freq (cpd) 0.98 (0.85-1.45)</td>
<td>—</td>
<td>0.96 (0.77-1.35)</td>
</tr>
<tr>
<td>Disp pref (SD, °) 0.25</td>
<td>0.09</td>
<td>—</td>
</tr>
<tr>
<td>Orientation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orientation sigma (°) —</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Both disparity frequency (Disp freq) and preferred disparity (Disp pref) are given for the 1D tuning curves and the 2D response surfaces. The 66% interquartile range is reported within parentheses. TE, tuned excitatory; TI, tuned inhibitory; TN, tuned near; TF, tuned far; NE, near; and FA, far cells; GF, Gabor/Gaussian fit (see text); cpd, cycles per degree.
This sharpness parameter was used to distinguish the tuned from the reciprocal cells (frequency above and below 0.75 cycles/degree, respectively), in conjunction with the preferred disparity, which was used to distinguish the TE/TI from the TN/TF cells for the first class and the near/far cells for the second class (limit was set to ±0.15'). The distributions in Figure 4 show that the cells of the TE/TI type are about twice as common in cV1 as in pV1 (55%/30%) for HD-selective cells. This central overrepresentation of TE/TI (like) categories is even more pronounced for VD (84%) but again not found in the periphery (43%) (see Table 1).

When comparing the disparity encoding ranges (Fig. 4 A B top histograms), it appears that preferred VDs are essentially concentrated around 0° in the central field and are distributed over a much wider range in the periphery (standard deviation [SD] ratio = 2.70; F-test; P < 0.0001). This same trend was also apparent for HD in peripheral V1 (SD ratio = 1.33; P < 0.005). In central V1, the range of preferred HDs was more than 2 times broader than that for VDs (SD ratio = 2.40, P < 0.0001), whereas no such anisotropy was found in peripheral V1 (SD ratio = 1.18, P > 0.05).

To evaluate the competency of the same disparity detectors to encode both horizontal and vertical components, we show in Figure 5, the distribution of preferred disparities, for a subset of 78 cells for which we recorded disparity response surfaces. In that case, the preferred disparity is a 2D parameter (combination of HD and VD) extracted from the 2D Gabor fitting of the response surfaces. It confirms a specialization for HD coding in central V1 (SD ratio = 2.78, P < 0.0001), as shown by the horizontal shape of the scatter plot also reported in previous studies (Cumming 2002; see also Fig. 4 C in Pack and others 2003). By comparison, in peripheral V1, the dispersion of the data points is similar in both horizontal and vertical dimensions (SD ratio = 1.20, P > 0.05).

We calculated the VD that would naturally occur in these cells’ RFs for a gaze straight ahead and a fixation distance of 50 cm (experimental conditions; see Materials and Methods for details), in order to compare with the VD actually preferred by the same cells. Naturally occurring VD ranged between ±0.005° and ±0.30° for the central and peripheral populations of V1 cells, respectively. The VD encoding range was significantly higher than the range of naturally occurring VD (F-test, P < 0.0001 both in cV1 and pV1), and significant correlation was found between these 2 measures neither in cV1 (r = 0.34, P > 0.05) nor in pV1 (r = 0.25, P > 0.05). This can be interpreted as indicating that VD tuning is not set to match the VD naturally occurring for a particular gaze configuration but rather across a wider range of viewing conditions.

**Temporal Analysis**

Because differences were found concerning spatial tuning characteristics between central and peripheral disparity detectors,
Figure 4. Horizontal and VD tuning. (A) Disparity frequencies (in cycles per degree, cpd) of HD-selective cells in central V1 (dark) and peripheral V1 (white) are plotted as a function of the preferred disparity. Horizontal line delimits cells with coarse tuning profiles (frequency < 0.75 cpd, near and far cells) from those with fine-tuning profiles (>0.75 cpd, tuned cells). Among the tuned categories, neurons are classified as TE or TI if their preferred disparity is within ±0.15° (vertical lines). Beyond these limits are cells with TN- or TF-tuning profile types. (B) Same as (A) for VD-selective cells. (C) Distributions of the different categories of HD-selective cells for central (dark) and peripheral (white) fields. (D) Same as (C) for VD.

Figure 5. Scatter plots of neurons’ preferred in central (A) and peripheral fields (B) with corresponding marginal distributions on top and at right. This was determined from cells for which a disparity response surface was recorded. In each case, the preferred disparity is a 2D parameter (combination of HD and VD) extracted from the Gabor fit to the disparity response surface (see Materials and Methods).
we assessed possible differences in the temporal domain by analyzing both response latencies and selectivity onsets to random dots stimuli and to oriented gratings (see Materials and Methods and Table 2). Some cells (9%) were discarded from this analysis because of a too low level of response to compute response latencies.

The distributions of visual latencies in response to HD, VD, and orientation, for central and for peripheral V1 cells, are shown in Figure 6A. No difference was found between the central and peripheral representations of V1 (Wilcoxon rank sum test, $P > 0.05$) either for HD and VD or for orientation (Table 2). Similarly, for the time needed by individual cells to show a disparity- or orientation-selective response, no difference was observed between the cells with central versus peripheral RFs. Thus, similar temporal characteristics were found for the central and peripheral population of cells. Moreover, no difference was found among the categories of disparity-selective cells, either for the visual latency (median latencies are 49 ms for TE/TI cells, 49 ms for TN/TF cells, and 50 ms for near/far cells) or for the selectivity onset (respectively, 77 ms, 86 ms, and 83 ms; Wilcoxon rank sum test, $P > 0.05$). The only significant difference was found between onsets for disparity selectivity and orientation selectivity, in both regions (Fig. 6B). Selectivity for grating orientation appears very rapidly after the beginning of the visual responses (median of 8 and 9 ms for central and peripheral V1), confirming previous studies (Vogels and Orban 1991; Celebrini and others 1993; Pugh and others 2000; Mazer and others 2002). In contrast, selectivity to binocular disparity in dRDS appears on average much later (between 77 and 84 ms) with a very wide range. This probably reflects the fact that V1 neurons need to integrate disparity information over a succession of dot patterns in order to build a reliable disparity-selective response (Chen and others 2001).

### Orientation/Disparity Relationship

#### Central and Peripheral Distributions of Preferred Orientation

RF orientation of disparity-selective neurons is an important issue because theoretically, the current model for disparity selectivity (binocular energy model; Ozhawa and others 1990) explicitly requires an orthogonal relationship between orientation and disparity axes, implying that disparity detectors in V1 should be most sensitive to disparities introduced orthogonal to their preferred orientation. To address this issue, we first asked,
at the population level, if the differences we found in disparity coding between central and peripheral regions were reflected in the orientation distribution as well. Second, we studied at the level of individual neurons (n = 51), the relationship between RF orientation and disparities coding (by comparing their preferred orientation with the orientation of their disparity response surface). Among the cells that were tested for orientation and at least one disparity dimension in cV1 (n = 86)/pV1 (n = 107), 49%/48% were selective to both, 35%/29% were only orientation selective, 6%/9% only disparity selective, and 10%/14% were neither orientation nor disparity selective. No difference was observed concerning the orientation tuning bandwidth, assessed by the Gaussian fit parameters, between central and peripheral V1 cell populations (Wilcoxon test, P > 0.05, see Table 1).

We defined 2 angles to quantify the preferred orientation coded by V1 neurons. The first one (Φ_H) is classically determined relatively to the horizontal axis and the second one (Φ_p) is relative to the polar axis passing from the visual field center to the cell's RF center. An example of orientation-selective cell is displayed in Figure 7A with a preferred orientation angle of −53° and a polar axis of −45°. Thus, this peripheral V1 neuron was oriented obliquely relative to the horizontal axis (Φ_H = −53°) but nearly parallel (or radial) relative to the polar axis (Φ_p = −8° (−53° − (−45°))). The distribution of Φ_H and Φ_p is shown in Figure 7B for central (top row) and peripheral (bottom row) cells. We found that, at the population level, the previously shown specialization of central V1 for HD coding is accompanied by a vertical bias of the distribution of preferred orientation (Φ_H, the bias is just below significance with a Rayleigh test of uniformity, P = 0.065, but it reaches significance when uniformity is tested against the alternative of an expected nonuniform distribution with 90° mean, Vtest/0°, P < 0.05; Fischer 1993; Zar 1998) (Fig. 7B top left). Others (Mansfield 1974; Poggio and Fischer 1977; Bauer and others 1980; De Valois and others 1982; Celebrini and others 1993) have already described this vertical bias. We did not find such vertical bias in the peripheral representation of the visual field (Vtest/90°, P = 0.24) (Fig. 7B top right).

Furthermore, we observed a significant radial preference in the peripheral field (Φ_p Rayleigh test, P < 0.05, Vtest/0°, P < 0.01) (Fig. 7B bottom right) but not in central V1 (Vtest/0°, P = 0.42) (Fig. 7B bottom left). Such a radial organization of the RFs, reported once in the superficial layers of central V1 (Bauer and Dow 1989), has also been reported in the periphery of area V4a (Pigarev and others 2002) of the monkey and in the cat extrastriate areas (Leventhal 1983; Rodinova and others 2004). This distribution allows these cells, which are not located along both horizontal and vertical meridians, to encode both disparity components.

**Figure 7.** Preferred orientation distributions. (A) An example of orientation-selective cell from peripheral V1. From left to right are displayed its RF location and polar axis (dashed line, with an orientation of 135°), its orientation tuning curve (with Gaussian fit, 127°), and the 2 measures of preferred orientation axes that were computed (from horizontal, Φ_H, and from polar axes, Φ_p). The preferred orientation obtained from the fit (thick line in the middle and right polar plots) is equal to −53° relative to the horizontal (Φ_H = −53°) and equal to −8° (−53° − (−45°)) relative to the cell’s polar axes (Φ_p = −8°). B. Distributions of preferred orientation (left column for Φ_H and right column for Φ_p) for the central (top row) and peripheral (bottom row) orientation-selective cells (radius scale N = 25 cells). The asterisks indicate significant nonuniform distributions (Rayleigh test and V test).

**Link between Orientation and HD/VD Encoding**
To test more specifically the disparity energy model, we studied the relationship between 2D disparity encoding and orientation selectivity on the same cells by recording disparity response surfaces for 51 (23 in cV1 and 28 in pV1) orientation-selective cells. Three examples are shown in Figure 8A.

In order to compare the orientation of these disparity response surfaces with the preferred orientation of the same cells, we defined the disparity modulation axis as the axis along which the visual response varies maximally for changes in angular disparity values. According to the disparity energy model (Freeman and Ohzawa 1990), this axis of finest disparity tuning should be orthogonal to the preferred orientation. It was computed on the mean raw data expressed in the frequency domain as the axis passing through the center and the peak of the 2D power spectrum (Fig. 8B, see Materials and Methods). Thus, the disparity modulation axis was extracted directly from the disparity response surface, without a priori mathematical assumptions as to the shape of this surface. The relationship of these modulation axes with the preferred orientations obtained for the tested cells are shown for these example of cells in Figure 8C and for the entire population of cells in Figure 9A, B. In these scatter plots, it can be seen that most of the cells are concentrated around the dashed diagonals that indicate an orthogonal relationship between modulation axis and preferred orientation. Sixty five percent of the cells in the central field (Fig. 9A) and 61% in the peripheral field (Fig. 9B) overlap the dashed diagonals (black symbols), against 0% and 14% of cells overlapping the solid diagonals of parallel relationship (white symbols). The remaining cells (in gray) overlapped none or both of these diagonals. This significant orthogonal relationship was confirmed by considering the distribution of angular differences.
between modulation axes and preferred orientations for the central and peripheral cell populations (Rayleigh test, \( P < 0.001 \) in central and \( P < 0.01 \) in the periphery, with mean angles ±95% confidence interval of 84.8° ± 24.3° in cV1 and of 91.1° ± 27.7° in pV1). Because this result contradicts a previous study performed in central V1 (Cumming 2002), we also used parametric fits to the disparity response surfaces, as was done in this previous study. This method involves fitting a 2D Gabor to the surfaces to extract the disparity elongation axis from the main surface peak or trough (red axes in Fig. 8C). This axis, corresponding to the orientation of the response surface, theoretically reflects the RF orientation and should thus be parallel to the preferred orientation and orthogonal to the disparity modulation axis according to the disparity energy model. Again a significant parallel relationship between the preferred orientation and the elongation axis was found for
Figure 9. Relationship between disparity axes and preferred orientation. (A, B) Disparity modulation axes as a function of preferred orientations in central V1 (A, left column) and peripheral V1 (B, right column). Vertical and horizontal error bars represent the 95% confidence interval for the modulation axes and preferred orientations, respectively. Diagonal black lines represent parallel relationships and dotted lines represent orthogonal relationships. Black symbols are for the cells with orthogonal relationships, white symbols for cells with parallel relationships, and gray symbols for cells without any relationship (neither orthogonal nor parallel) between modulation axis and preferred orientation. (C, D) Same representation for the disparity elongation axes as a function of preferred orientation in foveal (C) and peripheral V1 (D). (E, F) Number of cells with orthogonal (black), parallel (white), or no relationship (gray) between disparity axes (modulation on left, elongation on right) and preferred orientation in foveal (E) and peripheral V1 (F). (G, H) Distributions of angular differences between disparity axes (modulation on left, elongation on right) and preferred orientations in foveal (G) and peripheral V1 (H). **p < 0.01, ***p < 0.001; \chi^2 test in (E, F); Rayleigh test in (G, H).
a majority of cells in both central (61%) and peripheral (64%) field representations (Fig. 9C,D). This relationship was also confirmed at the population level by considering the angular differences between the axis of elongation and the preferred orientation (Rayleigh test, $P < 0.001$ in both cV1 [Fig. 9E,G right part] and pV1 [Fig. 9F,H right part], with mean angles of $9.2^\circ \pm 33.6^\circ$ and $17.5^\circ \pm 25.2^\circ$, respectively).

These results are in agreement with the predictions of the disparity energy model (Freeman and Ohzawa 1990).

**Discussion**

The main objective of this study was a quantitative comparison of retinal disparity encoding in the central and peripheral visual field representations of primary visual cortex. We measured neuronal selectivity for both HD and VD, as well as the relationship between their joint encoding and the preferred orientation.

Our results confirm the existence of V1 neurons in the peripheral field representation (up to $30^\circ$) selective for both orientation (Battaglini and others 1993) and disparity (Durand and others 2002). They are similar in proportion, strength, tuning bandwidth, and also regarding their temporal characteristics (response and selectivity onsets) to the neuronal selectivity found in the central field representation (about $7^\circ$). In contrast, marked differences were found in the spatial organization of disparity and orientation coding between the center and the periphery: differences in the coding range for disparities and in the distributions of preferred orientation. We also gave clear evidence of a relationship between neuronal sensitivity to disparities and orientation coding, in line with the prediction of the disparity energy model. On the basis of this result, we propose a functional organization of V1 disparity detectors that is retinal eccentricity dependent.

**HD/VD Encoding Range**

In the representation of the peripheral visual field, preferred HD and VD ranges are similar, whereas, near the representation of central vision, the ranges are very different, with preferred VDs tightly clustered around $0^\circ$. This result might be expected by the fact that VDs do not naturally occur in central vision (Fig. 1). This anisotropy in the ranges of HD and VD encoding confirms a previous report from perifoveal V1 (Cumming 2002) and further reveals that this anisotropy is restricted to the representation of the central visual field.

VDs occurring naturally for a monkey fixing straight ahead at 50 cm are within $\pm 0.02^\circ$ in the central visual field (up to $7^\circ$) and cover a larger range of $\pm 0.45^\circ$ in peripheral field (up to $30^\circ$). These ranges increase drastically when considering a wide range of eye positions: up to $\pm 1^\circ$ in the center and up to $\pm 7^\circ$ within the periphery (see Fig. 1). Thus, the HD encoding ranges found for the central and peripheral populations of V1 cells (about $\pm 0.25^\circ$ in central V1 and $\pm 0.60^\circ$ in peripheral V1, see Fig. 5) do not cover the full range of possibly arising VD. However, most of the viewing conditions considered in this simulation are quite uncommon (for instance a gaze directed $25^\circ$ to the right and $25^\circ$ down with a fixation distance of 10 cm). When considering VD arising within $20^\circ$ of retinal eccentricity (our peripheral population was mainly composed of cells with RFs within $20^\circ$) with more common fixation conditions (gaze direction $\pm 10^\circ$ for both azimuth and elevation and fixation distance of 20 cm or more), the VD ranges found in the center and in the periphery are $\pm 0.24^\circ$ and $\pm 1.00^\circ$, respectively, close to the encoding ranges we reported in the central and peripheral field representations of V1 (see Figs 4A,B and 5). It has been reported that binocular fusion (and thus stereoscopic vision) can fail for very eccentric gaze associated with close fixation distance, probably because the VDs generated in such conditions are out of the binocular fusion range (Schreiber and others 2001). This could reflect the fact that V1 disparity detectors are tuned to encode a range of commonly encountered VD (i.e., associated with common viewing conditions) rather than the full range of possibly arising VD.

**Disparity Energy Model**

According to the disparity energy model (Ohzawa and others 1990), the orientation of the disparity response surface of V1 neurons should match their RF orientation, with highest disparity sensitivity orthogonal to the latter. Our results directly validate this prediction as we found precisely this relationship for neurons in the central as well as in the peripheral representations of V1. They are in agreement, although indirectly, with recent observations based on surface responses obtained by reverse correlation technique, which report an orthogonal relationship between V1-oriented subunits and disparity interactions (Pack and others, 2003).

However, our results partly contradict a study reporting a horizontal elongation of the disparity response surfaces irrespective of the cells’ preferred orientation in central V1 (Cumming 2002). To confirm that the apparent discrepancy was not due to a difference in the analytical methods, we reprocessed our data using the same method as in Cumming’s study. When looking at the disparity elongation axis after 2D Gabor fitting of the response surfaces, we still found a clear parallel relationship between the elongation axis of the disparity response surfaces and the preferred orientation in both central and peripheral V1. However, we also found that among the 9 cells in the central field representation that do not exhibit this parallel relationship, 6 have a horizontal elongation axes (Fig. 9C, black arrow). A possible overrepresentation of such cells might have been responsible for the weak relationship reported between disparities and orientation encoding (Cumming 2002). In peripheral V1, we did not observe such a tendency. Thus, if a horizontal elongation of the disparity response surfaces exists, it is likely restricted to the central field representation. Despite the claim that it represents another aspect of the specialization for HD (Cumming 2002; Read and Cumming 2004), its functional advantages remain unclear because it implies a coarser tuning to HD.

Another study reported a lack of relationship between disparity and orientation encodings in central V1 (Gonzalez and others 2003). However, the sampling precision used in this study to investigate VD selectivity was too coarse (steps of $0.45^\circ$) as we have shown that, in central V1, preferred VDs are found over only a narrow range of $\pm 0.25^\circ$ (see also Cumming 2002). This alone explains why these authors failed to find neurons with nonzero preferred VD as well as why they could not demonstrate any relationship with orientation selectivity.

**Distribution of the Preferred Orientation**

An important difference between central and peripheral fields found in our study is the vertical bias of the preferred orientation in the center versus the radial bias in the periphery.
This difference is consistent with the observed encoding ranges in both regions because, according to the disparity energy model, a VD detector will be optimal for HD encoding (DeAngelis and others 1991), whereas an oblique detector will have similar characteristics along the HD and VD dimensions. It should be noted that these biases are also observed with the smaller samples of disparity response surfaces recorded in central (n = 26) and peripheral (n = 52) representations of V1. When comparing the cell populations having disparity axis (modulation/elongation), rather parallel ($0^\circ-30^\circ$), oblique ($30^\circ-60^\circ$), or perpendicular ($60^\circ-90^\circ$) relative to the horizontal and to the RF polar axis, we found a significant horizontal bias of the disparity modulation in cV1 ($\chi^2$ test, $P < 0.05$) and a significant radial bias of the disparity elongation axis in pV1 ($\chi^2$ test, $P < 0.05$).

Our results show that at the first cortical stage of binocular processing, many V1 neurons are selective for both HD and VD and that their responses to these disparity components are tightly related to their RF orientation. In the central part of the visual field, the specialization for HD encoding is reflected by the encoding range anisotropy and the fact that cells with vertically oriented RFs are well suited for encoding HD (Ohzawa and others 1990; DeAngelis and others 1991). In contrast, in the periphery, HD and VD are encoded over similar ranges and disparity detectors have a radial organization. Such an organization has probable implications in both the oculomotor and perceptual domains that are discussed below.

### V1 Disparity Detectors and the Oculomotor Control of Binocular Fixation

Poggio (1995) proposed an involvement of the TE/TI cells in the fine oculomotor control of horizontal eye alignment. Extending this idea to the TE/TI-like cells for alignment control in the vertical dimension could explain the predominance of these categories in the central visual field representation (because horizontal and vertical vergence eye movements exhibit maximum gain for central stimuli). The fact that VD will rarely occur in central vision for reasons other than error in vertical alignment can explain why it is in the vertical dimension that these categories are the most prominent.

A notable difference between horizontal vergence and vertical vergence is that the gain of horizontal vergence is already maximal for small stimuli, whereas the gain for vertical vergence increases with increasing stimulus size up to $20^\circ$ in diameter (Howard and others 2000). Because we have shown that the VD encoding range is narrow in the central field representation and increases quickly with increasing retinal eccentricity, it is possible that larger stimuli will recruit populations of peripheral disparity detectors that are more suited to encode the range of VD ($\pm0.5^\circ$) used to elicit vertical vergence in the study of Howard and others (2000).

The third type of alignment error (torsional) generates cyclo-disparity, which arises along isocentricity circles centered on the fovea and increases with increasing retinal eccentricity. Theoretically, a radial organization of the disparity detectors is suited to deal with cyclo-disparity because it provides both a better tolerance to cyclo-disparity and a finer encoding to control cyclo-vergence eye movements. Our results show that such a radial bias is actually found at peripheral eccentricities (but not in the central field representation), where it is accompanied by an isotropic HD/VD encoding range.

### V1 Disparity Detectors and Stereoscopic Vision

Stereoscopic vision is preferentially expressed in central vision, where HD drives the stereoscopic percept, whereas VD generally disturbs or cancels it. The vertical bias found for the preferred orientations in central V1 is compatible with a higher sensitivity to HD than to VD and, in combination with the wider HD encoding range, creates a specialization for HD coding in the central visual field. The very narrow VD encoding range is useful in reducing the binocular correspondence search zone in the nonpertinent vertical dimension, thus reducing the chances of false matching. It can also explain the elliptical shape of the Panum’s binocular fusion area observed in the central visual field (Ogle and Prangen 1953; Tyler 1991) and the weak tolerance to an artificially added VD in a stereoscopic stimulus (with the deleterious effect of this signal on central stereoscopic vision; Nielsen and Poggio 1984; Prazdny 1987; Stevenson and Schor 1997).

For large stereoscopic stimuli extending into the peripheral visual field, VD has been shown to contribute to stereoscopic depth perception. The “induced effect” documented by Ogle (1938, 1962) was the first demonstration of such an influence. When a vertical magnifying lens is put in front of one eye while looking straight ahead at a large frontoparallel surface, this surface appears to be slanted in depth about its vertical axis, away from the eye with the lens. This effect defies any explanation of stereoscopic vision based only on a HD signal because the vertical magnifying lens produces only VD.

Because VD is insensitive to local depth variations but varies with distance and direction of the gaze, it can theoretically be used to recover these viewing parameters (Mayhew and Longuet-Higgins 1982; Gillam and Lawgren 1983), which are required for a correct interpretation of HD in terms of stereoscopic depth. However, if the models proposed so far are mathematically valid and fit with psychophysical observations for large stereoscopic surfaces (Rogers and Bradshaw 1993; Howard and Rogers 2002), none of them has received physiological support. For instance, neurons decoupling the HD and VD signals and integrating VD globally or regionally across the visual field have not yet been documented.

More recently, Matthews and others (2003) have proposed a model accounting for stereoscopic depth perception from VD based on disparity encoding by V1-like neurons. In this model, a vertically oriented disparity detector will not produce any depth signal from VD, whereas an oblique detector will produce a depth signal with a local sign (near/far) that depends on its radial/perpendicular orientation. The model assumes that the disparity energy model is valid and thus that the neuronal response evoked by VD is a function of the disparity detector’s RF orientation. To account for the induced effect, a radial organization of the disparity detectors is also assumed to prevent a cancellation of the depth signal produced by disparity detectors at all orientations for stimuli with no dominant orientation. Our results directly demonstrate both assumptions of this model for the peripheral representation of V1: the validity of the disparity energy model and the radial organization of the peripheral disparity detectors. Because our results also show that disparity detectors in central V1 are not organized radially but rather vertically, they can also explain why only weak effects of VD are encountered in the central field representation (because vertically oriented detectors are not suited to encode VD) and only from oriented stimuli (because...
radial/perpendicular detectors are equally represented). Thus, the functional organization of disparity encoding in V1 can account for at least a part of the effects of VD in stereoscopic vision. However, it does not rule out the possibility of further processing of VD, notably its regional and/or global pooling, in order to gather information about absolute distance and azimuth of visual objects or to extract the viewing parameters (fixation distance and gaze direction).

In conclusion, this study reveals distinct functional organizations for the encoding of binocular disparity within the central and peripheral representations of the visual field. In addition, our results confirm the previously reported specialization for HD processing in V1 (Cumming 2002) while revealing that this specialization is confined to the central field representation. In the periphery, we show a radical organization of disparity detectors and an isotropic encoding along the HD and VD dimensions over a range consistent with naturally occurring VDs at the retinal eccentricities considered. Finally, we demonstrate experimentally one of the cornerstone assumptions of the disparity energy model that predicts a relationship between disparity and orientation encodings. Overall, these results show that area V1, the first binocular stage in visual processing, is organized according to the geometrical characteristics of binocular vision in the central and peripheral field and that this organization can explain various functional features associated with the perceptual and oculomotor aspects of binocular vision.

Notes
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Conflict of Interest None declared.

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