



Tuning of Orientation Detectors in Human Vision

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A new method to study the tuning of orientation detectors in the human visual system is proposed. The stimulus consists of a sequence of flashed sinusoidal gratings of random orientations and spatial phases shown at a fast presentation rate. The subject's task is to report, as fast as possible, when the presence of a particular orientation (horizontal, vertical, or oblique) is seen in the stimulus sequence by pressing a button. The data are analyzed by calculating the empirical distribution of orientations present in the stimulus sequence within an optimal time-window before the button was pressed. The resulting orientation distributions show a "Mexican hat" shape, which resembles the distributions obtained in some single neurons of monkey primary visual cortex using a similar method (Ringach *et al.*, 1997). The findings are consistent with the idea of "lateral inhibition" between neighboring detectors in the orientation domain. © 1998 Elsevier Science Ltd. All rights reserved.

Orientation detectors Lateral inhibition Visual cortex

INTRODUCTION

Soon after the discovery of orientation tuning in single cells of primary visual cortex by Hubel and Wiesel (1962, 1968) a number of psychophysical results suggesting the presence of interactions between orientation tuned detectors in human vision were reported (Andrews, 1965; Wallace, 1969; Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Lennie, 1971; Bouma & Andriessen, 1968; Bouma & Andriessen, 1970; Thomas & Shimamura, 1975; Georgeson, 1976; Georgeson, 1980). One specific proposal was that orientation detectors are driven by two components: a tuned excitatory component and a more broadly tuned inhibitory component centered at the same orientation (Andrews, 1965; Andrews, 1967; Blakemore *et al.*, 1970). Linear combination of these components would cause the effective orientation tuning curve to resemble a "Mexican hat" in the orientation domain. A possible functional role of the inhibitory component would be to sharpen the orientation tuning obtained with the excitatory component alone (Andrews, 1965). Mexican hat shaped tuning profiles may explain systematic errors in visual angle judgments, such as the perceptual expansion of acute angles and the contraction of obtuse angles, which seem to underlie the optical effects seen in the Zöllner, Ponzo, and Poggendorff illusions (Wallace, 1969; Lennie, 1971; Heywood & Chessell, 1977; Virsu & Taskinen, 1975; Kurtenback & Magnussen, 1981; Hotopf & Robertson, 1975; Tolhurst & Thompson, 1975; Oyama, 1975; Weale, 1978; Wenderoth, Beh, & White, 1978; Lovegrove, 1976; Carandini & Ringach, 1997).

Two early neurophysiological findings demonstrated that the interactions between orientation-selective detectors are evident at the single cell level (Benevento, Creutzfeld & Kuhnt, 1972; Blakemore & Tobin, 1972). More recently, masking, visual evoked potentials, and single-cell recording techniques have revealed the presence of inhibitory interactions between orthogonal orientations (Burr, Morrone & Maffei, 1981; Morrone, Burr & Maffei, 1982; Burr & Morrone, 1987; Morrone, Burr & Speed, 1987; Bonds, 1989; Speed, Morrone & Burr, 1991; Snowden & Hammett, 1992; Snowden, 1994; Ross & Speed, 1996). There seems now to be ample support for the idea that interactions between oriented neurons play a crucial role in shaping their orientation tuning (Nelson, 1991; Sillito, Kemp, Milson & Berardi, 1980; De Valois, Yund & Hepler, 1982; Sillito, Grieve, Jones, Cudeiro & Davis, 1995; Somers, Nelson & Sur, 1995; Vidyasagar, Pei & Volgushev, 1996; Sato, Katsuyama, Tamura, Hata & Tsumoto, 1996; Ringach, Hawken & Shapley, 1997). However, the issue remains controversial (Reid & Alonso, 1995; Ferster, Chung & Wheat, 1996).

Here, a psychophysical method to expose the average tuning of orientation detectors in human visual cortex is presented. The main idea behind the technique is to attempt to mask a grating at a target orientation by embedding it in a fast sequence of gratings having randomly chosen orientations. The data are analyzed by searching for correlations between the probability of target detection and the presence of specific orientations in the stimulus. The method is very similar to the one we have previously used in the study of orientation tuning dynamics in macaque visual cortex (Ringach *et al.*, 1997); it also resembles, in some aspects, the rapid serial

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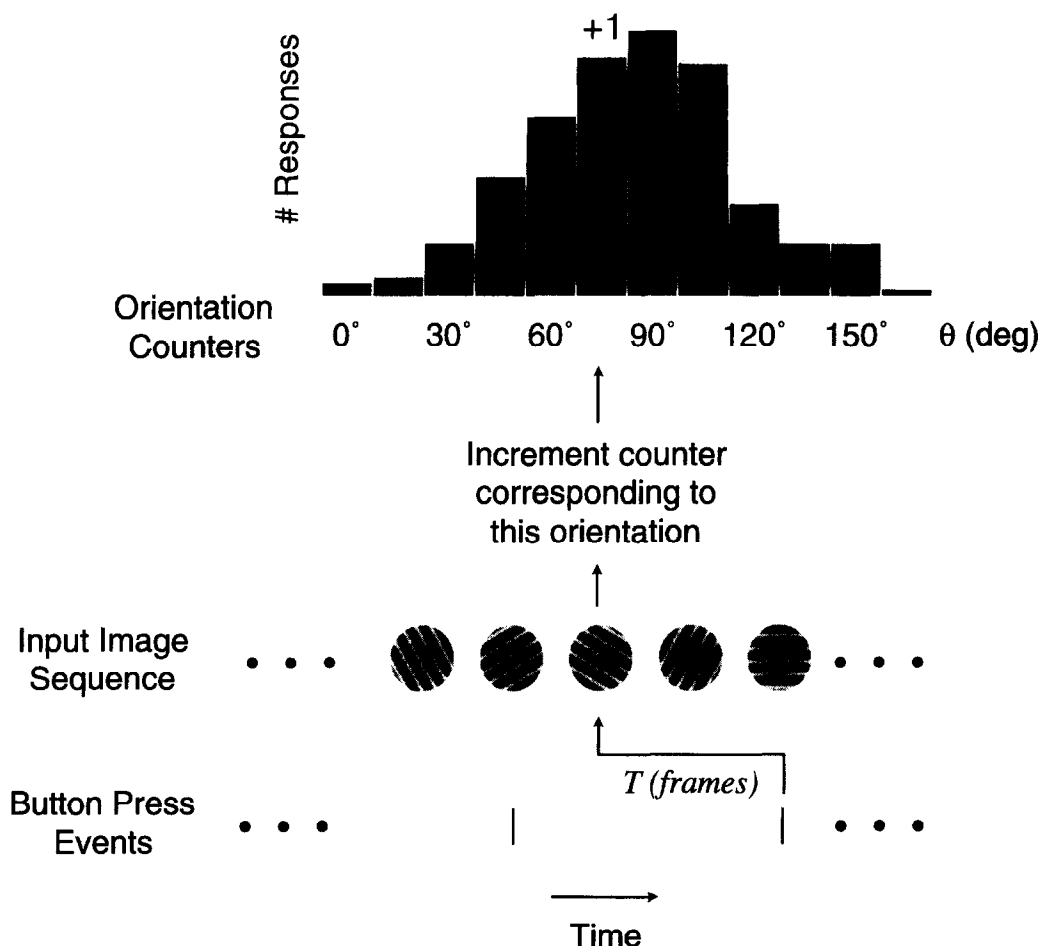


FIGURE 1. The method. A fast sequence of gratings with a fixed spatial frequency but random orientations and spatial phases is presented to the subject. A segment showing five consecutive frames in such a sequence is shown in the figure. The number of times a particular orientation was present in the stimulus sequence T frames before a key press occurred is shown by the histogram. Normalizing the histogram by the total number of responses provides an estimate of the probability that a grating with orientation θ was present in the stimulus T frames before a response was recorded.

presentation technique employed by Reeves and Sperling (1986) to study attentional and short-term visual memory mechanisms.

METHODS

The stimulus was generated by a Silicon Graphics R4000 Elan computer. A set S of sinusoidal gratings of a fixed spatial frequency but different orientations and spatial phases was first calculated and stored in memory. In these experiments, S contained a total of 40 gratings having one of 10 possible orientations (spaced 18 deg apart) and one of four possible spatial phases (spaced a quarter of a cycle apart). A stochastic image sequence (the stimulus) was generated by randomly selecting, at a rate of 30 frames/sec, a new image from S . The video refresh of the monitor was 60 Hz. The gratings appeared within a circular window of 3 deg in diameter centered on the screen, had a spatial frequency in the range of 1–4 cycles/deg, and a contrast of 99.8%. The mean luminance of the display was 59 cd/m². The screen was calibrated using a Photo Research PR-703A spectral scanner (Chatsworth, California, U.S.A.). A trial consisted of 1-

min-long sequences. Subjects were instructed to report, as fast as possible, every time they saw a grating at a particular orientation (horizontal, vertical, or one of the obliques) embedded in the sequence by pressing a button. A block for one target orientation consisted of 20–25 trials. Experiments for the three target orientations, horizontal, vertical, and one of the obliques, were run in separate blocks. For the stimulus at the oblique orientation the entire set of ten angles was rotated by 45 deg. A bite bar was not used, but subjects were instructed to maintain a stable head position during the experiment. No fixation point was present in the stimulus. The monitor was 34.3 cm × 27.4 cm; the viewing distance was 60 cm. Five subjects (four male and one female) participated in the experiment. They all have normal or corrected to normal vision. Presentation was binocular.

The data were analyzed to determine the dependence of the subject's button presses on the past history of oriented gratings presented on the screen (see Fig. 1). First, an array of counters corresponding to each of the orientations present in the stimulus was zeroed. A fixed value of a time-delay parameter T (in frames) was

selected. For each button press recorded we went back T frames and obtained the orientation of the grating that was present at that moment in the image sequence. The counter corresponding to that orientation was incremented by one. Gratings at the same orientation but different spatial phases shared the same counter. Thus, this procedure averaged across spatial phases. When all button presses were distributed in the counters we normalized the resulting histogram by their total number and thereby obtained an estimate of the probability that an orientation θ was present in the stimulus image sequence T frames before the subject pressed the button. This probability is denoted by $r_T(\theta)$. For a fixed value of T , $r_T(\theta)$ represents a probability distribution on the orientation angles present in the stimulus set. $r_T(\theta)$ was computed for $T=0, \dots, 30$ frames, which at 30 Hz corresponds to time delays going from 0 to 1 sec.

Clearly, when $T=0$, one does not expect to see any influence of the input on the subject's response due to visual delay and reaction time. Therefore, $r_0(\theta)$ should be a uniform distribution on the orientation domain. Similarly, for very large values of T one also expects to obtain a uniform distribution; this is because subjects respond within a short time window after the detection of the stimulus. For intermediate values of T , one expects an orientation distribution which has a mode at the orientation that the subject was instructed to detect. The largest departure of $r_T(\theta)$ from the uniform distribution will occur at an "optimal" delay time T that includes the delay in visual processing, the time required to make a decision, and the reaction time to press the button. This optimal value of T is denoted by T' . Due to variability in this delay time, the responses will be scattered around T' . To increase the signal to noise, the average distribution in a symmetric time window centered at T' , was computed:

$$\hat{r}(\theta) = \frac{1}{2m+1} \sum_{q=T'-m}^{T'+m} r_q(\theta), \quad (1)$$

where the window size, controlled by m , is increased until $r_{T'-m}(\theta)$ or $r_{T'+m}(\theta)$ are no longer significantly different from the uniform distribution ($p > 0.1$ using Kuiper's test) (Mardia, 1972).

Notice that a uniform distribution would result if subjects pressed the response button at random. It is also reasonable to assume that mistakes made by the subject (for example, pressing the button when there was no real intention) would be uniformly distributed. Therefore, we are interested in studying the *deviations* from the uniform distribution in $\hat{r}(\theta)$. One way to do this is by normalizing $\hat{r}(\theta)$ to lie between zero and one. The *normalized response* is defined by:

$$N(\theta) \equiv \frac{\hat{r}(\theta) - \min_{\theta} \hat{r}(\theta)}{\max_{\theta} \hat{r}(\theta) - \min_{\theta} \hat{r}(\theta)}.$$

In these experiments the mean frequency at which subjects pressed the response button was 0.5 Hz. In contrast, the target orientation appeared in the stimulus with a frequency of 3 Hz. Thus, subjects are detecting, at most, 17% of the total available targets.

RESULTS

Figure 2 depicts the results obtained when subjects were instructed to report the appearance of horizontal gratings embedded in the sequence. The left column in the figure contains plots of $N(\theta)$, the normalized deviations from a uniform distribution in the subject's response. The right column illustrates the raw data (normalized between zero and one) for each subject as a density plot of the two-dimensional distribution $r_T(\theta)$, with θ along the x-axis and T along the y-axis, with increasing time delays going from the top to the bottom of the plot. The arrows to the right of these plots represent the boundary of the time-window employed in calculating the average response $r(\theta)$. Additional results in the remainder of the paper are shown in the same format.

Subjects responded with a mean reaction time (average T') of 420 ± 50 msec (1 SD). From the peak of the normalized deviation curves it is clear that subjects pressed the button more frequently when a horizontal grating appeared embedded in the stimulus (as they were instructed). More significantly, we observe that the curves have a "Mexican hat" shape. In other words, subjects responded *least frequently* when gratings at $\approx \pm 40$ deg off the horizontal were present in the recent past history of the stimulus. "Mexican hat" profiles can also be measured when subjects are instructed to detect the appearance of a vertical or oblique grating in the sequence (Fig. 3). Finally, preliminary data seem to indicate that the effect diminishes when the spatial frequency of the grating is increased while the aperture size is kept constant (Fig. 4). It is not clear if the determining factor is spatial frequency, the number of cycles within the aperture, or the relationship between spatial frequency and the separation in orientation between the gratings in the stimulus set. This will require a parametric study of the dependence of the effect magnitude on the spatial frequency, aperture size, and angular density of the stimuli.

DISCUSSION

A new psychophysical method to study orientation tuning detectors in human vision was proposed. The results indicate that the probability of an orientation being flashed within a "reaction-time window" before a button press deviates from uniform. The deviation has a "Mexican hat" (or "center-surround") shape in the orientation domain, with its peak usually located at the orientation the subject was instructed to report (for the oblique orientation, subjects MJH and RS showed a bias towards the horizontal). This means that observers either tend to miss the target when other gratings with similar orientations appear in close temporal contiguity, or that the presence of gratings at orientations orthogonal to the target orientation enhances its detection, or both. Another possibility is that a (rotational) motion signal generated by having gratings at different orientations separated in time is masking or enhancing the detection of the target

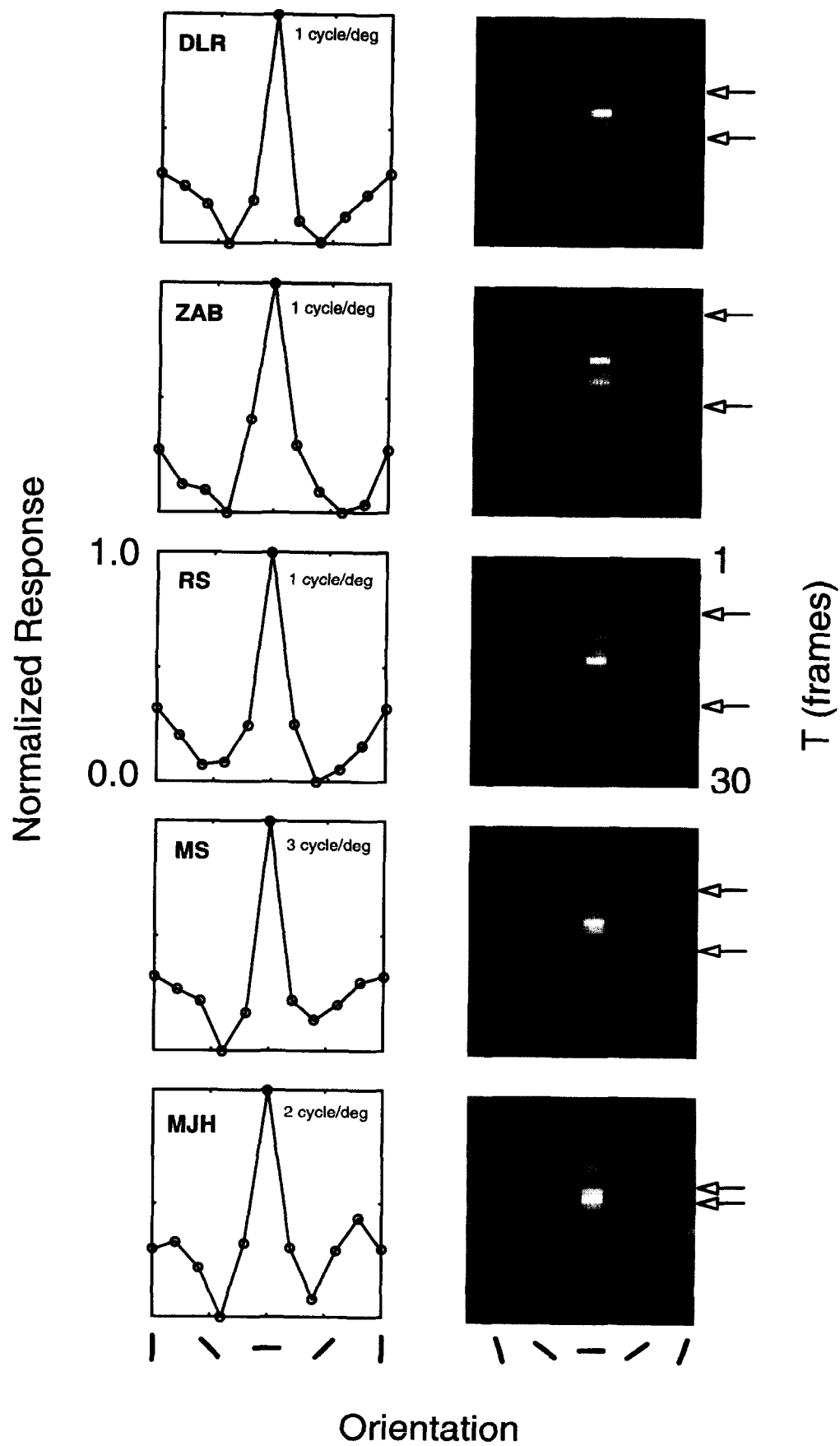


FIGURE 2. "Mexican hat" orientation distributions in human vision. Each row represents a different subject. The column on the right shows the raw data as two-dimensional density distributions of $r_T(\theta)$. The arrows indicate the optimal window of analysis for each subject. The plots on the left show the resulting estimate of $N(\theta)$, the normalized response. The spatial frequency used in each case appears at the inset. In all cases we observe a "Mexican hat" distribution profile.

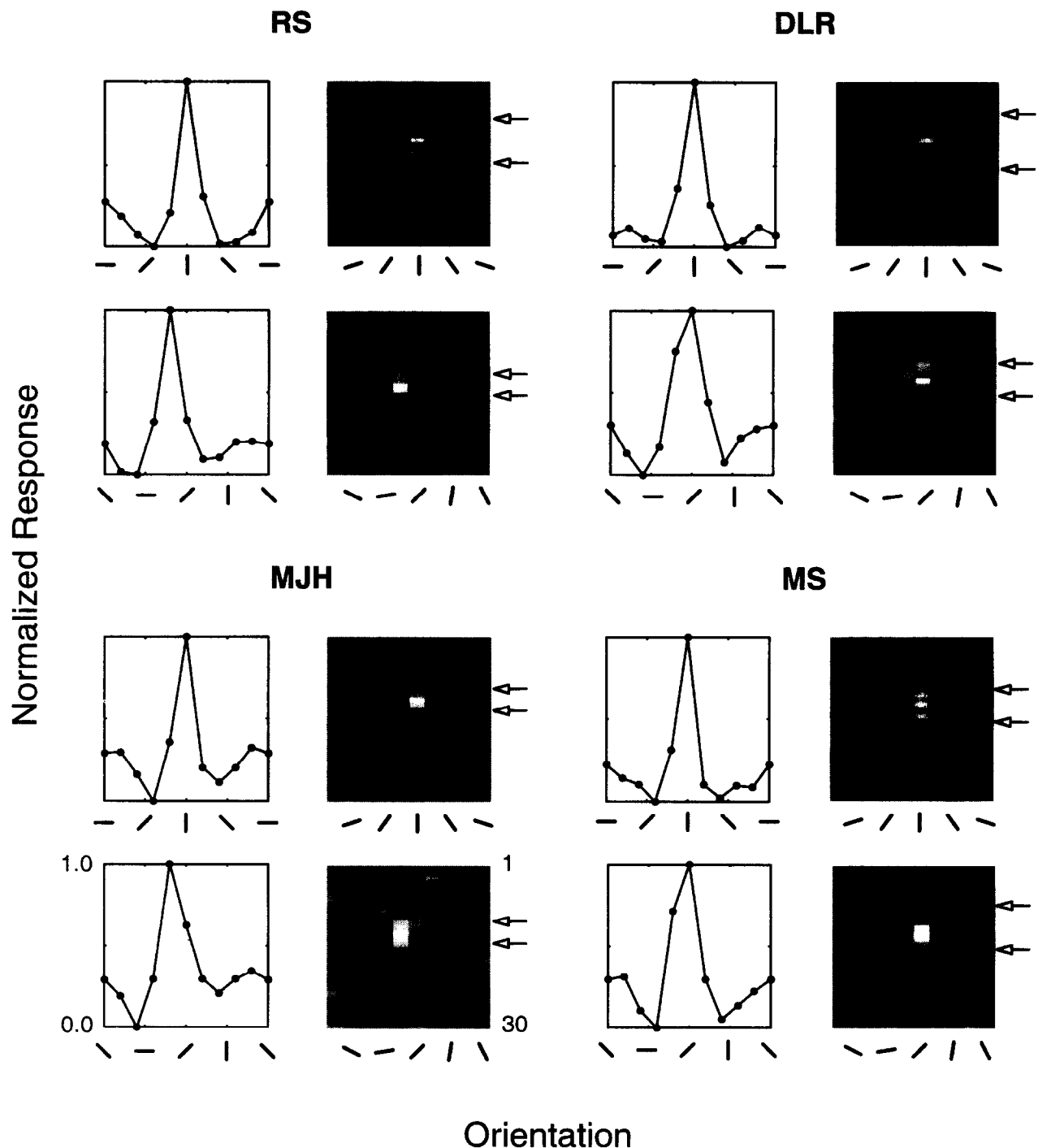


FIGURE 3. Replication of the results when subjects are requested to detect a vertical orientation or one of the obliques. Two subjects (RS and MJH) showed clear biases toward the horizontal meridian when asked to report a grating oriented at 45 deg. The spatial frequency used in this experiment was 1 cycle/deg for RS, 2 cycles/deg for DLR and MJH, and 3 cycles/deg for MS.

orientation*. An analysis of the data aimed at finding correlations between the probability of target detection and a measure of motion strength in the stimulus sequence suggests, however, that this is an unlikely possibility (see Appendix I).

The time-scale of the mechanism generating the Mexican hat profile must be smaller than the spread in time of the responses (the width of the analysis window),

from which one obtains an estimate of ≈ 300 msec. This is about an order of magnitude smaller than a previous estimate by Carpenter and Blakemore (1973). This fast time-scale indicates that the experiment is tapping into early visual mechanisms and that the effect observed is not related to the adaptation of orientation detectors (Gibson & Radner, 1937; Campbell & Kulikowski, 1966; Gilinsky, 1968; Gilinsky & Mayo, 1971; Magnussen & Kurtenbach, 1980), which is known to take much more time (Gibson & Radner, 1937; Gilinsky, 1968). More-

*I am grateful to David Burr for pointing this out to me.

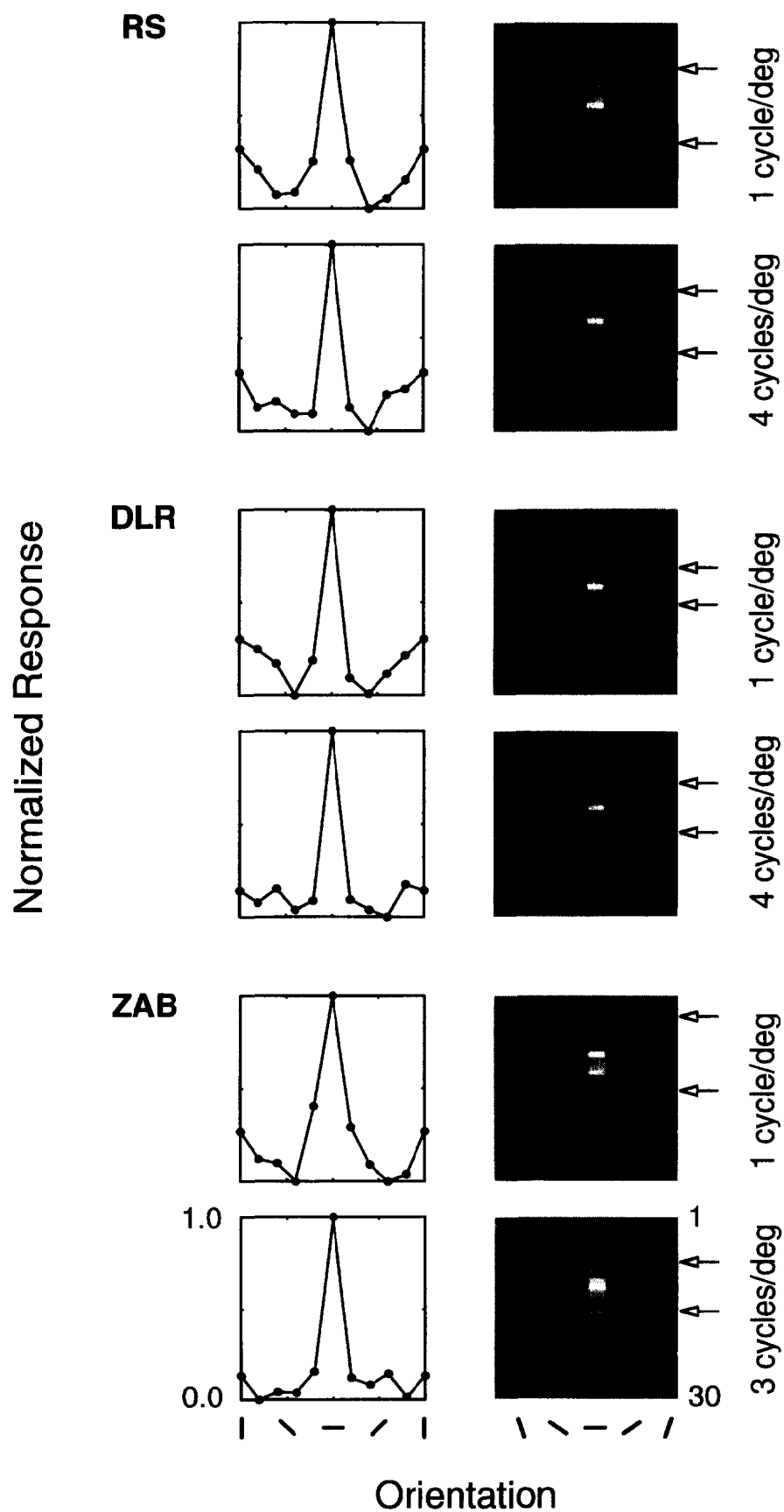


FIGURE 4. Dependence of the responses on spatial frequency. The extent to which one observes a “Mexican hat” profile seems to diminish when the spatial frequency of the gratings is increased while keeping the aperture size constant. The effect is strong in DLR, moderate in RS and is weaker in ZAB.

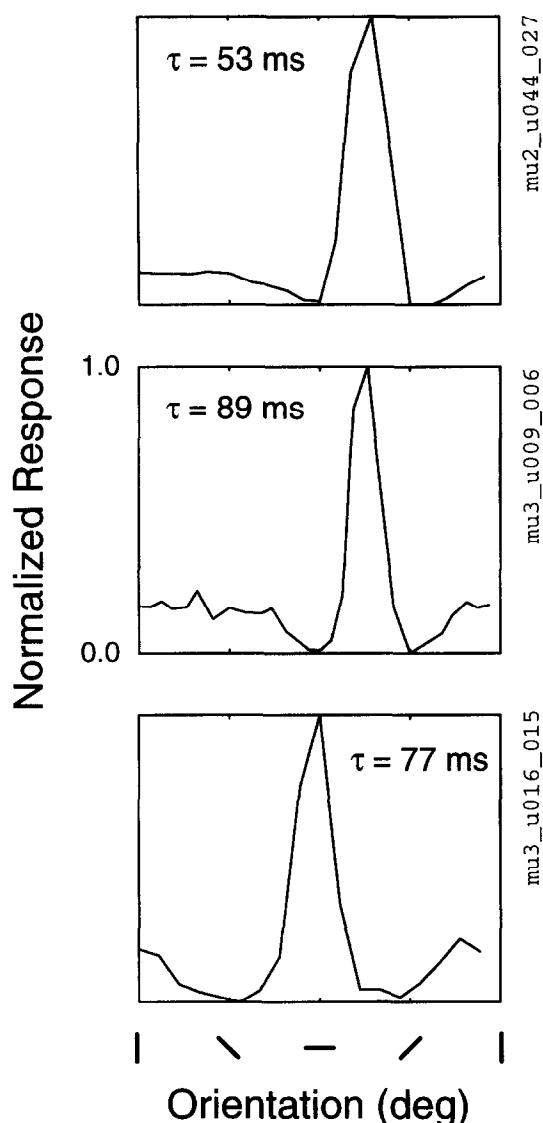


FIGURE 5. Responses of cells in macaque monkey. The graphs show the normalized responses τ msec before a spike occurred. Similar to the results in human observers one obtains “Mexican hat” profiles from experiments in some single cells (Ringach *et al.*, 1997). The results at the top correspond to a cell in layer 4B, the cell in the middle was located in layer 2 + 3, and the one shown at the bottom in layer 5.

over, meridional differences in contrast sensitivity did not play a role in generating the observed responses; Mexican hat shaped distributions could also be obtained at an oblique orientation (see Fig. 3). Furthermore, it is known that anisotropies in contrast sensitivity are only significant at spatial frequencies larger than 10 cycles/deg, which is well outside the range of spatial frequencies used in the present study (Campbell, Kulikowski & Levinson, 1966).

Andrews (1965) originally suggested that the functional role of the “lateral inhibition” between broadly tuned orientation detectors is to sharpen their selectivity. The idea of “lateral inhibition” is consistent with several psychophysical results related to the perceptual expansion and contraction of angles between line segments (Bouma & Andriessen, 1968, 1970; Carpenter & Blakemore, 1973; Blakemore *et al.*, 1970; Lennie,

1971; Carandini & Ringach, 1997). It has been proposed that these kinds of geometric illusions are only a side effect of the basic mechanism that generates sharp orientation tuning in the brain (Carpenter & Blakemore, 1973). The findings presented here are consistent with these ideas.

The profiles obtained psychophysically are very similar to those we measured in some single cells from the primary visual cortex of macaque monkeys (Ringach *et al.*, 1997). The experimental design for the physiology experiments was essentially the same as the one used in the present study; the stimulus was a fast sequence of randomly oriented gratings with a fixed spatial frequency (optimal for the cell). The neuronal data were analyzed by computing the probability that a particular orientation was present τ msec before a spike was generated by the cell. In other words, spikes played the role of button presses. Figure 5 shows three normalized neuronal responses that exhibited a “Mexican hat” distribution at some time during their response period. We found that, in the monkey, cells with this type of profile are concentrated in the output layers of the cortex (layers 2 + 3, 4A, 4B, 5 and 6). In many cases, the broad inhibitory component is clearly delayed with respect to the excitatory component (Ringach *et al.*, 1997). The delay times can vary, but they are usually in the 10–20 msec range. It is reassuring, and at the same time somewhat surprising, that similar results can be obtained using the same method in single cortical cells and in an entire organism. Our findings, together with previous studies (Benevento *et al.*, 1972; Blakemore & Tobin, 1972; Bonds, 1989; Nelson, 1991; Sillito *et al.*, 1980; De Valois *et al.*, 1982; Sillito *et al.*, 1995), provide evidence that “lateral inhibition” in the orientation domain is present in single visual cells of cat, monkey, and (probably) in human visual cortex.

It is not currently known if the mechanism generating “lateral inhibition” in the cortex is implemented in a feedforward neural circuitry, a feedback circuitry, or a combination of both. This is an important open question, as it is related to the issue of how orientation selectivity arises in the cortex, which has been the subject of renewed experimental and theoretical interest in recent years (Ferster & Koch, 1987; Somers *et al.*, 1995; Ben-Yishai, Bar-Or & Sompolinsky, 1995; Ferster *et al.*, 1996; Reid & Alonso, 1995; Vidyasagar *et al.*, 1996; Ringach *et al.*, 1997; Carandini & Ringach, 1997). One psychophysical study that addressed this point directly argued that non-linear effects in the perceptual expansion of angles is consistent with a “feedback” implementation (Carpenter & Blakemore, 1973). Our measurements of orientation tuning dynamics also suggest that intracortical feedback shapes the dynamics of orientation tuning in the output layers of monkey V1 (Ringach *et al.*, 1997). To what extent the interactions between oriented cells occur within a hypercolumn, involve interactions between cells at different locations in space, or even between cells in different cortical areas are topics for further research. Studying how orientation tuning develops over time

(Volgushev, Pei, Vidyasagar & Creutzfeldt, 1993; Celebrini, Thorpe, Trotter & Imbert, 1993; Eysel & Shevelev, 1994; Ringach *et al.*, 1997; Pugh, Shelley, Ringach & Shapley, 1997) and probing the system with multiple orientations (Bonds, 1989; Carandini & Ringach, 1997) are two promising strategies for investigating these issues.

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APPENDIX

Within the random sequences that comprise the stimulus one can certainly encounter, by chance, segments that will evoke a motion percept. For example, a segment of a sequence like 0, 18, 36, 54, and 72 deg. will induce a strong perception of counterclockwise rotation. It is possible to imagine scenarios in which the activity of motion detectors are the source of the masking or enhancement signal (instead of arising from purely orientation tuned detectors, as we assumed in the Discussion section). This is a relevant point because subjects sometimes perceive rotating patterns in the stimulus. It is worth noting, however, they never report the perception of translational motion. Therefore, in the sequel, I only investigate the possible influence of rotational motion in the outcome of the experiments; the use of the word “motion” will always refer to rotational motion.

First, a general measure of “motion strength” is defined. The basic idea of the analysis is to measure the correlation between the motion strength signal and the probability of target detection in the experimental condition and to compare it with the correlation one would expect at random. This will determine if motion had any effect on the subject’s performance.

Measures of “motion strength”

Given a sequence of oriented gratings we can define an associated “motion strength” sequence. Consider a sliding window of length $2l + 1$. We can center this window at time n and obtain a list of the orientations in this subsequence: $(\theta_{n-1}, \dots, \theta_n, \dots, \theta_{n+1})$. We will define a “motion strength” signal, $M(n)$, for this subsequence by considering the angular separation between all possible pairs of gratings within the subsequence. The general form of the expressions we will consider is the following:

$$M(n) \equiv \left| \sum_{i=n-l}^{n+l} \sum_{j=i+1}^{n+l} m(\theta_j - \theta_i, j - i) w\left(\frac{\theta_i + \theta_j}{2}\right) \right|,$$

where $m(\Delta\theta, k)$ is a measure of the strength of motion between two

gratings separated by $\Delta\theta$ in orientation and by k frames in time, and $0 \leq w(\theta) \leq 1$ will be used to weight the motion by the location of the mean angle between the orientations (at this point I should remark that all the angular arithmetic between orientation angles is defined modulo 180 deg).

We will assume that $m(\Delta\theta, k)$ is zero when $\Delta\theta = 0$ deg or $\Delta\theta = 90$ deg and peaks somewhere in-between. That is, there is no motion between two identically oriented or orthogonal gratings. Two forms of m will be used:

Linear. We define:

$$m(\Delta\theta, k) = \frac{\sin(2\Delta\theta)}{2l + 1 - k}.$$

Notice that $m > 0$ when induced rotation is counterclockwise and $m < 0$ when the rotation is clockwise. The optimal separation in orientation that will induced maximum motion is 45 deg. The denominator normalizes the measure by the total number of pairs separated by k frames in the subsequence. The rationale behind this definition is the assumption that the underlying motion mechanism is linearly integrating the motion induced between frame pairs.

Non-linear. We define:

$$m(\Delta\theta, k) = \left| \frac{\sin(2\Delta\theta)}{2l + 1 - k} \right|.$$

In this case the absolute values of the elementary motion signals are added together. The rationale for this definition is the assumption of an underlying apparent motion mechanism that could pick up the motion between two gratings separated by k frames without the influence of the other gratings within the sequence.

Two possible choices for the weighting function $w(\theta)$ will be considered:

Uniform. We define $w(\theta) \equiv 1$. The rationale behind this definition is the idea that motion centered at any orientation has a global masking effect (no matter which target orientation we are considering).

Tuned. We define $w(\theta) = \sin^2(\theta - \theta_T + \phi)$, where θ_T is the target orientation and ϕ is a phase offset. The idea behind this definition is that motion centered around the target orientation ($\phi = 0$), near the orthogonal orientation ($\phi = 90$), or the obliques ($\phi = \pm 45$), could be the signals masking the detection of the target. This weighting factor allows one to selectively pick motion signals at different locations in the orientation domain.

All the possible motion strength measures were used: Linear–Uniform, Linear–Tuned, Non-linear–Uniform, Non-linear–Tuned. In the tuned cases four different values of the phase offset were selected: $\phi = 0, \pm 45, 90$ deg.

Analysis

Once a particular motion strength measure was selected the following analysis may be performed:

1. Obtain the empirical distribution of $M(n)$ values in the window centered at the optimal delay time, T' , for one particular experiment (T' is defined in the Methods section).
2. Randomly generate a number of subsequences of length $2l + 1$ in which the distribution of orientations is matched to those obtained experimentally. The number of subsequences generated should be the same as the total number of button presses obtained in the experiment. Then we can calculate the distribution of motion strength values in this simulated experiment.
3. Bin these two distributions and compare them. If motion has any masking effect one would expect to see the empirical distribution shifted to the left (towards smaller motion strength values) relative to the simulated distribution. If motion has the effect of enhancing the detection of a target, one expects the empirical distribution shifted to the right relative to the the simulated distribution. One can test if these distributions differ by using a Chi-Square test.

Results

The above analysis was performed for the experiments presented in Fig. 2 when the window size was 5 frames (166 msec, $l = 2$). In all

cases but one (DLR, Non-linear-Tuned, $\phi = 0$, p -value = 0.01) we obtained a p -value larger than 0.05. The only significant result obtained seems to have occurred by chance: repetition of the test ten additional times gave p -values larger than 0.05 for that same condition. Thus, we

find no evidence that motion had any influence on the results. This should be considered only partial evidence, as it can always be argued that the motion measures considered here are not the “appropriate” ones.