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V1 responses to transparent and nontransparent motions

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Abstract It is well known that a stimulus composed of two independent sets of random dots moving in opposite directions produces a percept of two overlapping transparent surfaces moving across each other, while a counterphase grating composed of two identical sine wave gratings drifting in opposite directions does not. We recorded from the directionally selective V1 cells of behaving macaque monkeys using these two types of stimuli in order to investigate the physiological basis of transparent motion perception. Previous single-unit recording experiments from our laboratory indicated that many V1 cells respond well to transparent random dot patterns, while MT cells' responses to the same patterns are strongly suppressed in comparison with their preferred direction responses. This observation alone would seem to suggest that V1 activity could better explain transparent motion perception than MT activity. However, one could argue to the contrary based on the psychophysical observation that there is a motion threshold elevation under the transparency condition. We decided to determine the correlation between V1 activity and the transparent motion perception directly by recording from V1 cells using both transparent random dot patterns and nontransparent counterphase gratings. It is found that V1 cells on the average could not reliably tell the two types of patterns apart. Our results further the idea that additional processing beyond V1 is involved in transparent motion analysis.

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Introduction

Our visual system can represent more than one motion in the same part of visual space. For example, when we look at a display composed of two independent sets of random dots moving in opposite directions, we see two transparent surfaces, one defined by each set of dots, moving continuously across each other. This phenomenon is an example of transparent motion perception. Transparent motion occurs frequently in the natural environment due to either partial occlusions of moving objects (for example, an animal moving behind bushes) or motion of overlapping semitransparent surfaces (such as when looking through a car window). Other examples include shadows moving across textured backgrounds or stationary specular reflections from turning objects. While we can effortlessly perceive transparent motion, it turns out to be a rather difficult problem from a computational point of view, since most machine vision algorithms fail to solve it (Horn and Schunck 1981; Heeger 1987; Wang et al. 1989; Grzywacz and Yuille 1990).

In order to investigate the physiological basis of multiple motion representation, transparent random dot displays, composed of two independent sets of randomly distributed dots moving in opposite directions, have previously been used in our laboratory in recording experiments from primary visual area (V1) and middle temporal area (MT) cells in behaving monkeys (Snowden et al. 1991). It was found that the response of a typical MT cell to such a stimulus, with one set of dots moving in its preferred direction and the other in its antipreferred direction, was significantly reduced compared with a single set of dots moving in its preferred direction alone. This result indicates a strong suppres-

sion in MT between the preferred and the antipreferred directions of motion. This type of suppression was found to be much weaker in area V1, and many V1 cells respond to transparent patterns quite well compared with their preferred responses. While MT is usually considered to be a major site for motion analysis, the above observation would seem to suggest that the subpopulation of directionally selective V1 cells, whose responses to transparent displays are not much suppressed, could better solve the problem of motion transparency. Snowden et al. (1991) have argued to the contrary based on the fact that there is an elevation of the psychophysically measured motion thresholds under the transparency condition (Snowden 1989). The stronger suppression between opposite directions of motion (i.e., weaker responses to transparent patterns) in MT might better account for the motion threshold elevation.

We decided to determine more directly whether V1 activity could explain transparent motion perception. Our experiments are based on the observation that not all stimuli composed of two overlapping components moving in opposite directions give a percept of motion transparency. We thus recorded from V1 cells using stimuli of very different degrees of perceptual transparency and examined whether V1 responses could account for the perceptual differences. Specifically, we used two types of stimuli: perceptually transparent random dot patterns and nontransparent counterphase gratings. As we have already mentioned, a transparent random dot pattern is composed of two independent sets of random dots moving in opposite directions. Looking at such a pattern one sees two transparent surfaces moving coherently across each other. A counterphase grating is made of two identical sine wave gratings drifting in opposite directions with equal speed. Perceptually, however, one does not see in a counterphase gratings two sine wave gratings sliding across each other. Instead, the pattern looks more like flicker or oscillation.

Our results indicate that V1 responses of these two types of patterns do not correlate well with their perceptual transparency. Specifically, we found that V1 cells respond well to both the transparent random dot patterns and the nontransparent counterphase gratings and that as a population they could not reliably distinguish the two types of stimuli. We will show in a separate publication that MT activity correlates well with our perception of transparent motion (Qian and Andersen 1994). Some of the results reported here have been presented previously in an abstract (Qian et al. 1991).

Materials and methods

Preparation of animals

The data reported in this paper were obtained from two male rhesus monkeys (*Macaca mulatta*). Details of the training and experimental procedures have been published previously (Snowden et al. 1991). Briefly, the animals were trained to fixate for several seconds in a dimming-detection reaction-time task. The animals' heads were fixed throughout the experiments and their eye positions were monitored during the fixation period by the magnetic search coil technique (Robinson 1963). The eye position resolution of our system is about 2 min. During data collection, if the animals' eyes moved at a speed above 15°/s, the trial was aborted. The standard deviations of the horizontal and vertical eye positions on the successful trials for the first monkey were 3.5 min and 4.9 min, respectively. Those for the second monkey were 3.8 min and 4.0 min, respectively. Recording chambers were surgically placed over areas V1 for the two monkeys.

Stimuli

We developed an integrated software package for our physiological experiments. All displays (motion stimuli, a fixation point, and a bar for mapping receptive fields) were generated on an AST 386 PC with a Number Nine SGT graphics board installed. The vertical refresh rate of the board was 60 Hz noninterlaced. The output of the board was sent to two video monitors simultaneously, one (Monitronix) in front of the monkey in a closed and dimly lit experiment room, and the other outside in the control area for the experimenters. The Monitronix monitor was calibrated for linearity with an EG&G Gammer Scientific photometer (Model 450-1) with capacitors added across the output resistors in order to integrate over the monitor's refresh period to obtain time-averaged readings. The fixation point, the bar for receptive field mapping, and the visual stimuli were all under the control of a Microsoft mouse and could be moved to any location on the monitor screen. Using various mouse and keyboard combinations, we could also change the sizes of the fixation point and of the stimuli, and modify the width, height, and orientation of the bar. In all our experiments, the monitor was 57 cm away from the monkey's eyes. At this distance, each pixel subtends a visual angle of 0.056°.

All stimuli covered an area of 3° by 3°, and each lasted for one second. For random dot stimuli, the size of each dot was 1 pixel and the initial position of a dot was chosen randomly inside the $3° \times 3°$ display window. When a dot moved off the edge of the window, it was wrapped around and replotted on the other side of the window. In order to measure the directional tuning of the cells, we generated a set of eight unidirectional random dot stimuli; each consisted of 200 dots moving in one of the eight directions. These eight directions defined four axes of motion, one vertical, one horizontal, and two at 45° oblique angles. We then generated four transparent random dot stimuli along the same axes of motion. There were 400 dots in each of these patterns, with 200 of them moving in one direction and the other 200 moving in the opposite direction. For control purposes (see Results) we also generated four transparent random dot patterns with the numbers of dots in each direction halved. The above 16 random dot stimuli (8 unidirectional stimuli, 4 transparent stimuli at high dot density, and 4 transparent stimuli at halved dot density) formed a single block of trials during recording experiments and were presented to the monkeys in a pseudorandom order.

Sine wave and counterphase gratings were generated using a gray scale of 8 bits/pixel. The monitor nonlinearity was properly taken into account through calibration (see the above). A sine wave grating has the luminance profile:

$$L_{\sin}(x, t) = L_0[1 + c \sin(2\pi f_x x + 2\pi f_t t)] \quad (1)$$

along the axis perpendicular to the orientation of the grating. Here L_0 and c represent the mean luminance and the contrast of the grating respectively, and f_x and f_t stand for the spatial and temporal frequencies. The luminance profile of a counterphase grating can be obtained by adding together two identical sine wave gratings moving in opposite directions:

$$\begin{aligned} L_{cp}(x,t) &= L_0[1 + c \sin(2\pi f_x x + 2\pi f_t t)] \\ &\quad + L_0[1 + c \sin(2\pi f_x x - 2\pi f_t t)] \quad (2) \\ &= 2 L_0[1 + c \sin(2\pi f_x x)\cos(2\pi f_t t)]. \quad (3) \end{aligned}$$

Note that the resulting counterphase grating has a mean luminance twice as large as each of the constituent sine wave gratings while the contrast remains the same. We used drifting sine wave gratings of mean luminance 2 ft-lamb (fL), contrast 0.5, spatial frequency 2 cycles/deg, and temporal frequency 4 Hz. The speed of these gratings was thus 2°/s, identical to those of the random dot patterns we used. We made eight such sine wave gratings moving alone the same eight directions as in the random dot case for obtaining directional tuning of the cells. We then made four counterphase gratings along the same four motion axes. Since the mean luminance of these counterphase gratings was equal to twice that of the constituent sine wave gratings while their contrast remained the same, according to Eq. 3, we also generated four counterphase gratings with their mean luminance halved as a control. These 16 gratings (8 drifting sine wave gratings, 4 counterphase gratings at high mean luminance, and 4 counterphase gratings at halved mean luminance) formed a single block of trials during the experiments and were presented to the monkeys in a pseudorandom order.

A counterphase grating can have a spatial phase parameter ϕ, as shown in the following equation:

$$L_{cp}(x,t) = L_0[1 + c\ \sin(2\pi f_x x + 2\pi f_t t + \phi)] + L_0[1 + c\ \sin(2\pi f_x x - 2\pi f_t t + \phi)] \quad (4)$$

$$= 2L_0[1 + c\ \sin(2\pi f_x x + \phi)\cos(2\pi f_t t)]. \quad (5)$$

In our early experiments, we recorded counterphase responses at one spatial phase only. We later generated, for each axis of motion, four counterphase gratings with different spatial phases: 0, 45, 90, and 135°, in order to test the phase sensitivity of the cells. In this case, the mean of the four responses was used as the counterphase response in the data analysis. We did not generate counterphase gratings with phases in the range 180–360° because they are equivalent to those in the range 0–180° except a half cycle time delay. The phase parameter for the drifting sine wave gratings is not essential also because it is equivalent to a small time delay. Since we excluded the first 200 ms of the cells' responses in our data analysis (see below), these time delays will not affect the results.

Recording procedure

The experiment was controlled by a PDP-11 computer, which monitored the monkey's behavior (eye position, pulling, and releasing of the key), sent signals to the PC for displaying the fixation point and the stimuli, collected data, and gave juice reward to the monkey. All V1 recordings were performed with the glass-coated platinum-iridium electrodes. After a cell was isolated, we first attempted to map its receptive field with mouse-controlled bars of different sizes, orientations, and speeds while the monkey performed the fixation task. For a small proportion of cells that could not be well driven by the bar stimuli a mouse-controlled small random dot pattern with adjustable size was used instead. After the receptive field border was approximately determined the display window of the stimuli was positioned in its center. Then, a series of blocks of trials were presented until all experiments were completed or until the cell was lost. For the V1 cells we recorded, the receptive field diameters were normally below 0.5°, considerably smaller than our stimuli.

Data collection and analysis

A total of 92 V1 cells were recorded. The data were collected from the periods when the monkeys were fixating and various displays were shown in the cells' receptive fields. The time intervals between successive spikes were recorded. In each trial, the collection started after the monkeys established fixation; 500 ms later, a 1-s stimulus appeared, followed by a blank interval of 1 s, and the another 1-s stimulus. During data collection, a spike raster was displayed after the completion of each trial and the corresponding histogram was updated. The data were saved in a file after each block of trials for off-line analysis on a Macintosh computer. The first 200 ms of the responses to stimuli were excluded from quantitative analysis to avoid the bias of the transient effects and to take the response delays into account. In most blocks there is also a class of trials in which no stimulus was shown. The activities of the cells during these "fixation alone" trials were used to calculate their spontaneous rates of firing. For a small number of cells from which we did not collect data with fixation point alone, we used the activities in the last 0.5 s of the blank interval between the two stimuli in all trials to calculate the background rate. The cells were first screened based on their reliability to fire above the spontaneous rate in at least one direction of motion for both unidirectional random dot patterns and the sine wave gratings. A two-tailed t-test with a significance level of 5% was used in the screening process. For each cell that passed this test, two preferred directions were determined. They are the directions with the highest firing rates for the unidirectional random dot patterns and the sine wave gratings, respectively. The opposite directions of the preferred directions were defined as the antipreferred directions for the two types of stimuli, respectively. The cells were then tested for their directionality by comparing their firing rates along the preferred and the antipreferred directions for the two types of stimuli. Again, a two-tailed t-test with a significance level of 5% was used. With this procedure, 21 V1 cells were found to be directionally selective to both types of patterns. They were analyzed further for comparing the degrees of suppression under the two conditions. Among them 90% (19/21) have their preferred directions for the two different types of stimuli differ by less than 45°, the sampling step we used for directional tuning.

Results

V1 responses to random dot patterns and counterphase gratings

As we mentioned in the Introduction, if V1 activity could account for the perception of transparent motion, then a correlation should be found between the V1 responses and the degrees of perceptual transparency of the stimuli. This does not turn out to be true in general. We recorded the responses of isolated V1 cells using both the perceptually transparent random dot patterns and the nontransparent counterphase gratings. Both types of patterns are made of two components moving in opposite directions, but their degrees of perceptual transparency are quite different. An example of the responses of a directionally selective V1 cell is shown in Fig. 1. Figure 1a shows the cell's responses to a single set of 200 dots moving in its preferred and antipreferred directions, respectively. The response of the cell to the transparent random dot pattern with 200 dots moving in its preferred direction and 200 dots its antipreferred direction is shown on the right of Fig. 1b. Similar responses of the same cell to the sine wave and counterphase gratings are shown in the rest of Fig. 1. Figure 1c shows the cell's responses to a single sine wave grating drifting in its preferred and the antipreferred directions. Its response to the counterphase grating with luminance equal to the sum of the two sine wave gratings in Fig. 1c is shown on the right of Fig. 1d.

It is clear from these figures that the cell is directionally selective, as tested with either the unidirectional

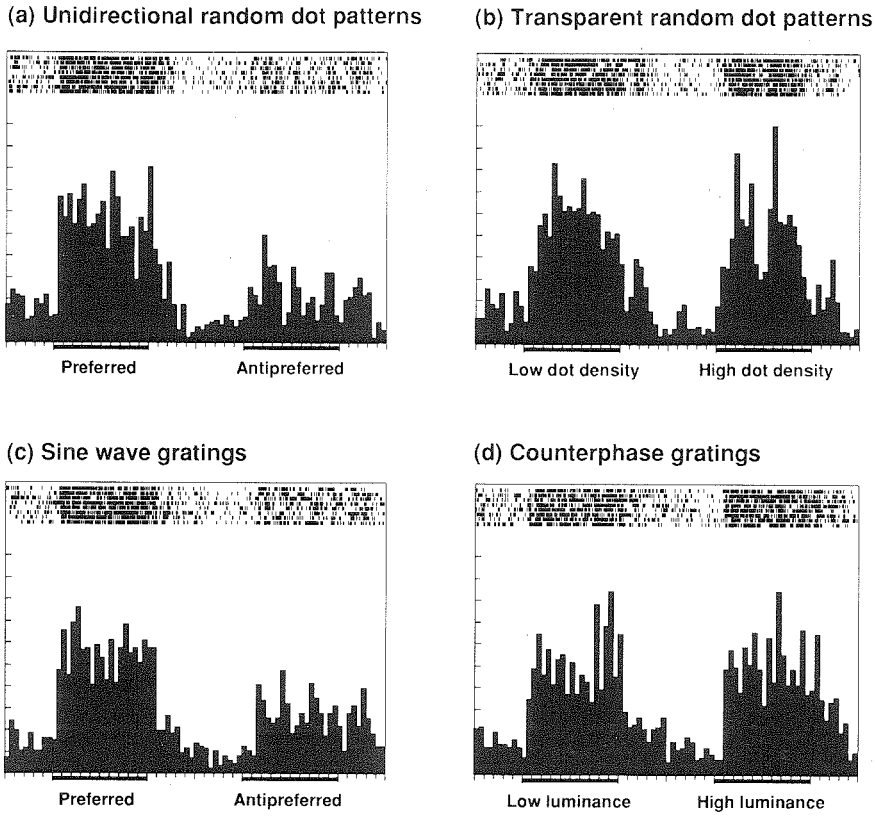

Fig. 1a–d Responses of a V1 cell to unidirectional and transparent random dot patterns, and to sine wave and counterphase gratings. This cell does not show much suppression between opposite directions of motion for both types of stimuli. The directional indices of the cell for the dot and grating patterns are 0.85 and 0.66, respectively. *Each small dot in the rasters* represents the occurrence of a spike and the different *lines* present responses from repeated trials. The time periods of stimuli presentation are indicated by the *black bars below the histograms*. **a** Responses to a single set of dots (200 dots) moving in its preferred and the antipreferred directions. **b** Responses to the corresponding transparent dot patterns with 100 and 200 dots per direction, respectively. **c** Responses to a single sine wave grating moving in its preferred and the antipreferred directions with a mean luminance of 2 fL. **d** Responses to the corresponding counterphase gratings with mean luminance of each component sine wave grating equal to 1 fL and 2 fL, respectively. One *small vertical division* represents 21.8 spikes/s (*sps*); one *small horizontal division* represents 100 ms

random dot patterns or the drifting sine wave gratings. More importantly the response of this cell to the transparent random dot pattern is similar to its preferred response to the unidirectional random dot pattern, and the cell's responses to the counterphase grating is similar to its preferred response to the drifting sine wave grating.

In the above, we did not directly compare the cell's response to the transparent random dot pattern and its response to the counterphase grating, because these two types of stimuli are different not only in their perceptual transparency but in other aspects (such as the presence and the absence of a spatial orientation) as well. Instead, we compared two relative responses: the transparent random dot response relative to the preferred direction random dot response, and the counterphase response relative to the preferred direction sine wave response. In other words, we made the comparison after normalizing the cell's responses to the transparent random dot patterns and the counterphase gratings by the corresponding preferred responses to the unidirectional stimuli. In the following, when we talk about cells' responses in the context of comparing the two types of stimuli, we always mean the normalized responses.

The transparent random dot pattern described above contains twice as many dots as in the unidirectional random dot patterns. Similarly, the mean luminance of the counterphase grating is twice that of the unidirectional sine wave gratings (see Materials and methods). As a control we also recorded from the same cell using a transparent random dot pattern and a counterphase grating with the number of dots or the mean luminance in each direction of motion halved, so that the total number of dots or the total mean luminance is the same as in the corresponding unidirectional stimuli. The results are shown on the left sides of Fig. 1 b and d, respectively. For this cell, reducing the number of dots or the mean luminance does not affect the results significantly.

We also found cells that responded to the two types of patterns differently. Examples are shown in Figs. 2 and 3. Figure 2 shows a case in which the cell responded better to transparent random dot pattern than to non-transparent counterphase gratings, while Fig. 3 shows

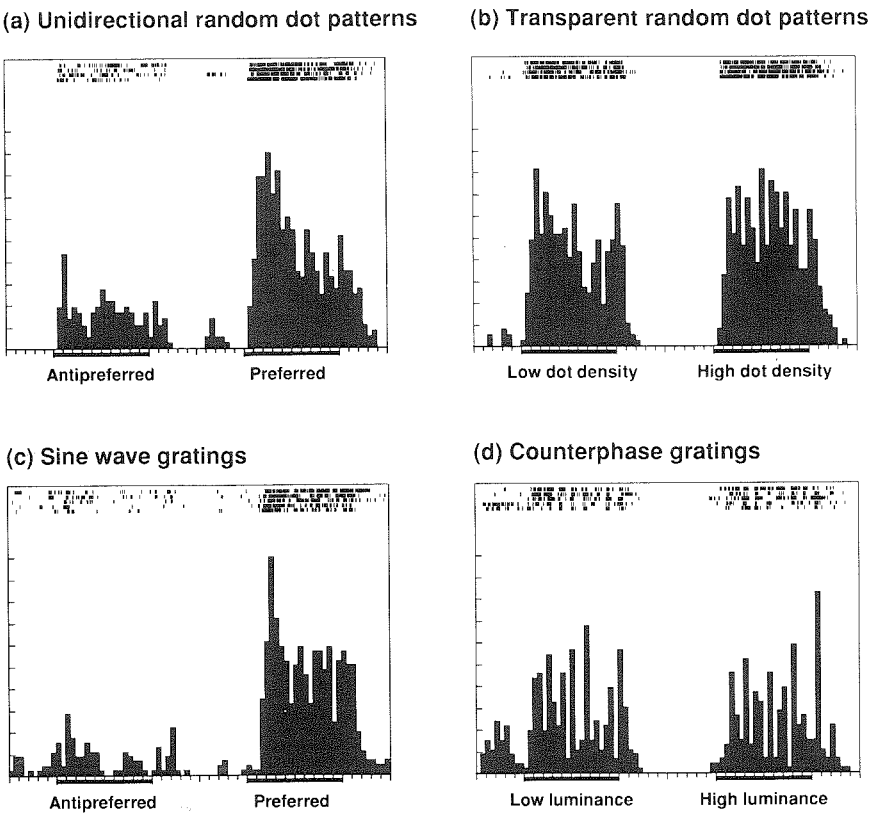

Fig. 2a–d Responses of a V1 cell to unidirectional and transparent random dot patterns, and to sine wave and counterphase gratings. This cell shows stronger suppression between opposite directions of motion in the counterphase case than in the random dot case. The directional indices of the cell for the dot and grating patterns are 0.89 and 1.0, respectively. The presentation format of this figure is same as that of Fig. 1. One *small vertical division* represents 18.4 spikes/s (*sps*); one *small horizontal division* represents 100 ms

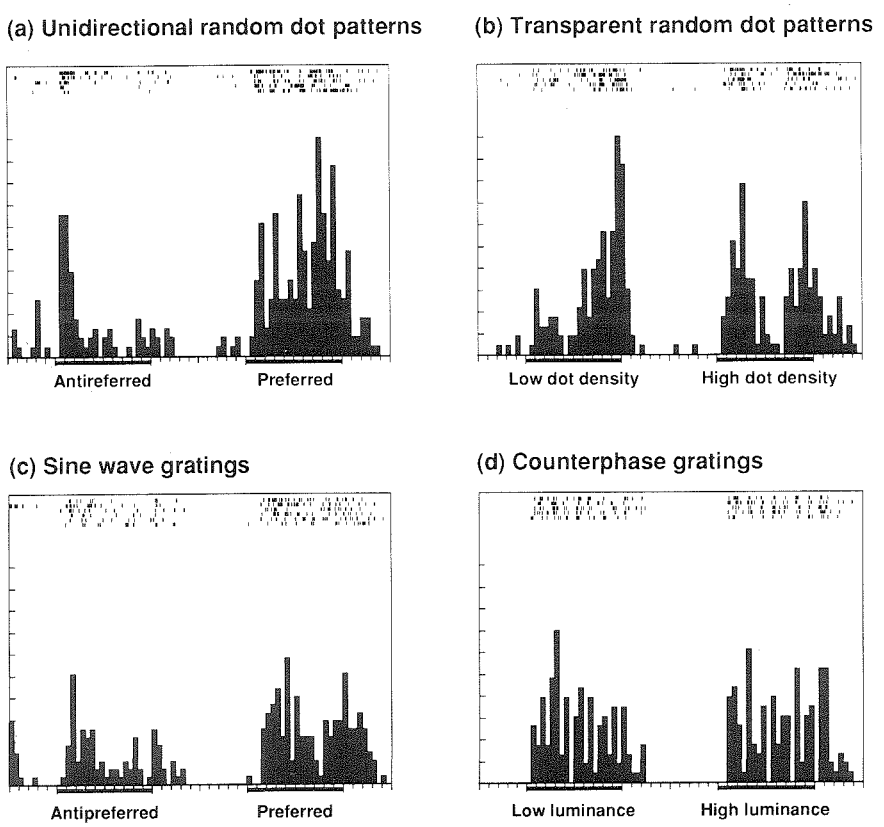

Fig. 3a–d Responses of a V1 cell to unidirectional and transparent random dot patterns, and to sine wave and counterphase gratings. This cell shows stronger suppression between opposite directions of motion in the random dot case than in the counterphase case. The directional indices of the cell for the dot and grating patterns are 0.90 and 0.63, respectively. The presentation format of this figure is same as that of Fig. 1. One *small vertical division* represents 9.2 spikes/s (*sps*); one *small horizontal division* represents 100 ms

an opposite situation (again, we are comparing the normalized responses; see above). The presentation format of these figures is the same as that in Fig. 1.

In order to see how a population of cells respond to these patterns, we have recorded 92 V1 cells from two monkeys. Among them, 38 were found to be directionally selective (see Materials and methods) for at least one of the two types of stimuli; 21 of them were tested on both the random dot patterns and the gratings stimuli *and* were directionally selective for the two types of stimuli. To quantify the behaviour of the cells, we computed two suppression indices for each cell, one for each type of stimuli, and then compared the two indices. These are defined as:

$$SI_{dot} = 1 - \frac{\text{transparent dot response}}{\text{preferred dot response}}, \quad (6)$$

$$SI_{grating} = 1 - \frac{\text{counterphase response}}{\text{preferred sine response}}. \quad (7)$$

The background firing rates were subtracted from all responses before calculation. Note that these definitions are equal to one minus the normalized responses. SI_{dot} ($SI_{grating}$) represents the percentage reduction of a cell's response to the transparent random dot pattern (counterphase grating) in comparison with its preferred direction response to the unidirectional random dot pattern (sine wave grating). The indices therefore measure the degrees of suppression between the preferred and antipreferred directions of motion. An index near zero indicates no suppression, a large value indicates strong suppression, and a negative value means that enhancement instead of suppression has occurred.

The population results are shown in Fig. 4. This figure plots, for each cell, the random dot suppression index, SI_{dot}, against the grating suppression index $SI_{grating}$. Cells with similar normalized responses (thus similar degrees of suppression) for the random dot and the grating stimuli lie near the diagonal line. Those falling well below the diagonal line show stronger suppression for the gratings than for the random dot patterns. Finally, cells well above the diagonal line have the opposite behavior: they show stronger suppression for the random dot patterns than for the gratings. Figure 4 indicates that the cells we recorded distribute fairly evenly on both sides of the diagonal line without a significant bias in one way or the other (Wilcoxon signed-rank test, $P=0.88$). Also note that V1 cells on the average do show a significant amount of suppression between opposite directions of motion, whether measured with the random dot patterns or the gratings. This can be seen by projecting the dots in Fig. 4 along either coordinate axis and note that there is a bias toward the positive axis. This result is different from that of Snowden et al. (1991), who found that on the average V1 cells show no directional suppression. This difference is probably caused by the fact that the directional indexes were higher overall for the V1 population in the current study. However, the suppression for V1 cells in Fig. 4 is much weaker than that for MT cells found by Snowden et al. (1991).

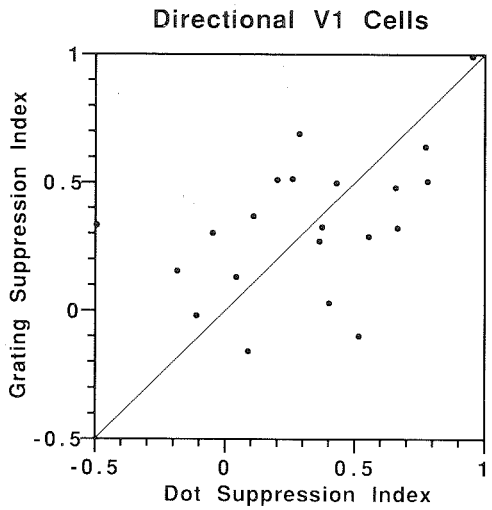

Fig. 4 Population results for directionally selective V1 cells. For each cell, the suppression index for the random dot patterns is plotted against that for the gratings. Cells with identical normalized responses for the two types of stimuli would fall on the *diagonal line*

A cell often shows somewhat different degrees of directionality depending on whether it is tested with the random dot patterns or the sine wave gratings. It is possible that the strength of directional suppression of a cell may be correlated with its degree of directionality. To justify the above comparison between the suppression indices for the two types of stimuli, we need to show that the degrees of directionality of the V1 cells under the two types of stimuli are similar. For this purpose we define two directional indices for each cell as follows:

$$DI_{dot} = 1 - \frac{\text{antipreferred dot response}}{\text{preferred dot response}}, \quad (8)$$

$$DI_{grating} = 1 - \frac{\text{antipreferred sine response}}{\text{preferred sine response}}. \quad (9)$$

Again, the background firing rates were subtracted from all responses before calculation. Figure 5 plots for each cell the directional index measured with the random dot patterns against that measured with the sine wave gratings. We see that the cells we recorded show similar directionality under the two different types of stimuli (Wilcoxon signed-rank test, $P=0.36$).

In the above experiments, we kept the numbers of dots in the preferred direction and the antipreferred direction of a transparent random dot pattern equal to those in the unidirectional patterns moving in either one of the two directions. The total number of dots in the transparent random dot pattern is thus twice as many as those in the unidirectional patterns. Similarly, the mean luminance of the counterphase gratings we used is twice as large as that of the sine wave gratings. As a control,

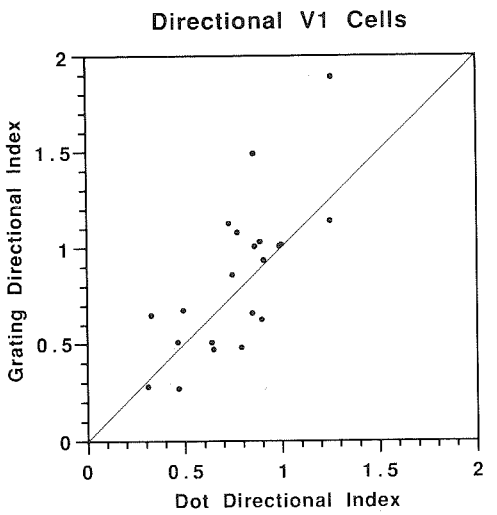

Fig. 5 For each cell, the directional index for the random dot patterns is plotted against that for the sine wave gratings. Cells with identical degrees of directionality for the two types of stimuli would fall on the *diagonal line*

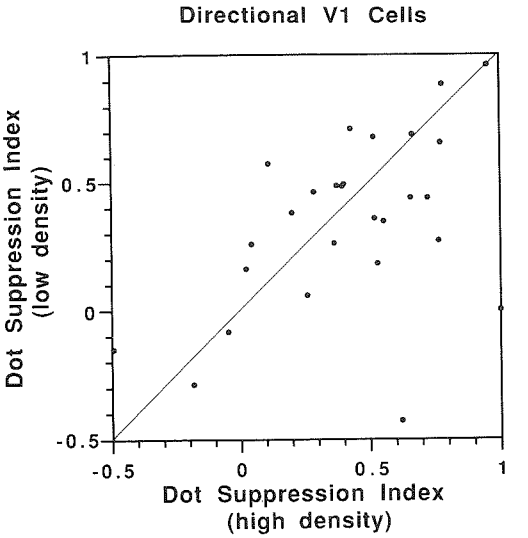

Fig. 6 For each cell, the suppression index for the random dot patterns with high dot density is plotted against that with halved dot density. Cells with identical responses for the two types of stimuli would fall on the *diagonal line*

we also used transparent random dot patterns with the numbers of dots in each direction halved and the counterphase gratings with the mean luminance halved. We have already presented example cells above showing that our results are not affected by these changes in dot density or grating luminance. The population results supporting this claim are shown in Figs. 6 and 7. Figure 6 plots the suppression index for the random dot patterns with high dot density against that with the halved dot density. Similarly, Fig. 7 plots the suppression index for the counterphase gratings with high mean luminance against that with the halved mean luminance. As can be seen from these figures, the cells are distributed approximately evenly around the diagonal lines. These results indicate that cells' behavior under the two conditions are not significantly different from each other (Wilcoxon signed-rank test, $P=0.55$ for the random dot patterns; $P=0.58$ for the gratings).

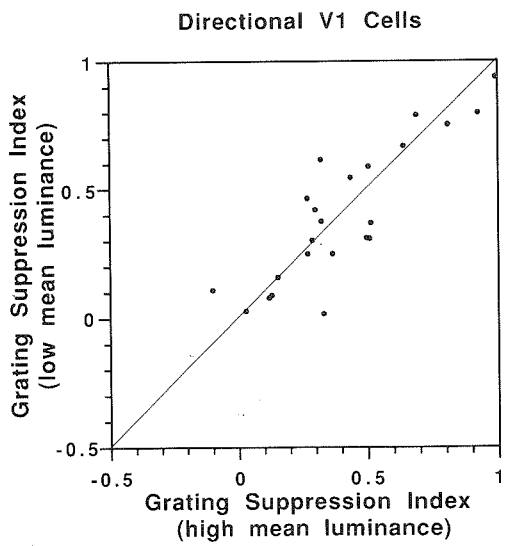

Fig. 7 For each cell, the suppression index for the gratings with high mean luminance is plotted against that of the gratings with halved mean luminance. Cells with identical responses for the two types of stimuli would fall on the *diagonal line*

Phase dependence of counterphase responses

A counterphase grating can have different spatial phases. In our early recordings we stimulated cells with counterphase gratings of a single phase parameter only ($\phi=0$ in Eq. 5). As our stimuli were much larger than cells's respective fields and we did not chose a specific positional relationship between the counterphase gratings we used and the receptive fields of the cells, we basically recorded from each cell using a counterphase grating of a randomly chosen phase. In order to study the phase dependence of the cell's responses, we later recorded cells using counterphase gratings of four different phase parameters: 0, 45, 90, and 135°. For cells recorded with the four phases, we used the mean of the four responses to compute the suppression index. We found that the cells we recorded are not very sensitive to the phases of the counterphase gratings. An example of a recorded cell is shown in Fig. 8. Figure 8a shows the cell's responses to the sine wave gratings in the preferred and the antipreferred directions, demonstrating the directionality of the cell. Figure 8b shows the cell's responses to the counterphase gratings with the four different phases. These counterphase responses are very similar to each other indicating relative phase-independence of the responses. To quantify the phase dependency of the cell population, we calculated four phase dependence indices for each cell. We first computed the

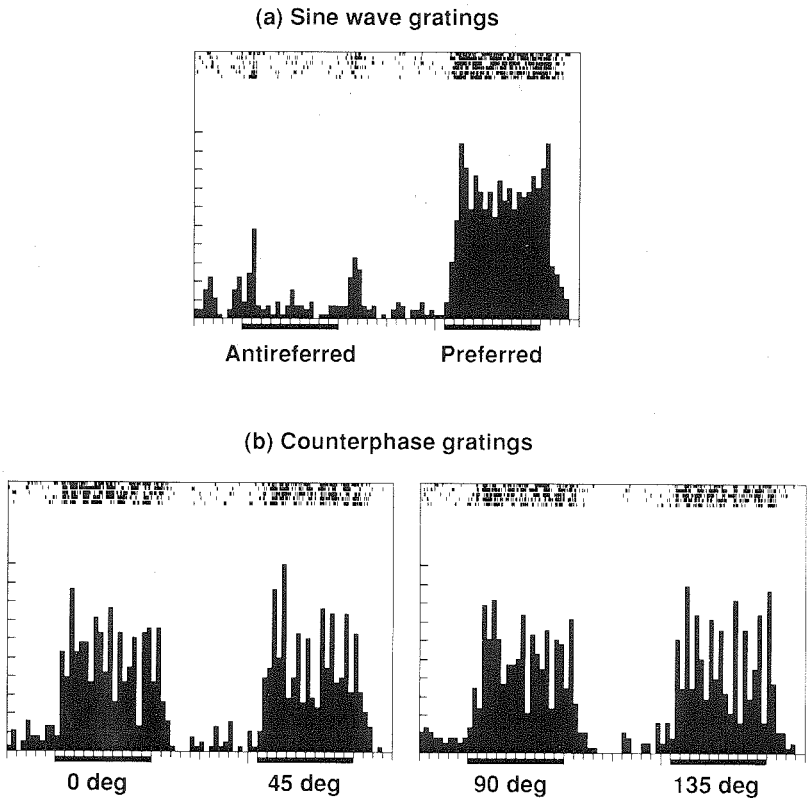

Fig. 8a, b The responses of a directional V1 cell to counterphase gratings of four different phases. **a** Preferred and antipreferred responses to drifting sine wave gratings, **b** responses to counterphase gratings with spatial phases equal to 0, 45, 90, and 135°. One *small vertical division* represents 15.6 spikes/s (*sps*); one *small horizontal division* represents 100 ms

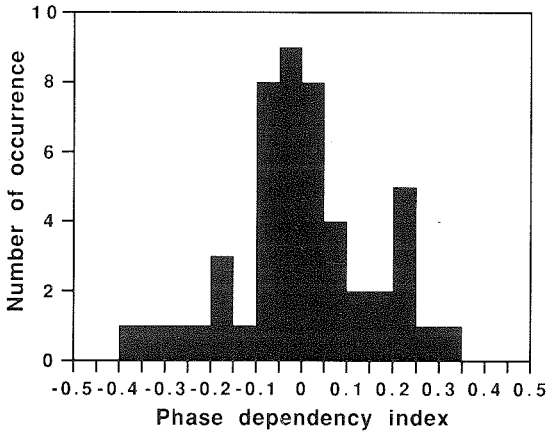

Fig. 9 Phase dependence of V1 cells' responses to counterphase gratings. The histogram of the phase dependence index is shown here with a bin width of 0.05

mean counterphase response over the response at the four phases and then computed four ratios of the responses at the four phases to the mean response. The phase dependence index is defined as 1 minus the ratio. An index near zero means that the response at a particular phase is very close to the mean response and thus indicates little phase dependence. The population histogram compiled from eight cells tested this way are plotted in Fig. 9. We see from this figure that the indices are clustered around zero, indicating weak phase dependence. We also computed for each cell a different index equal to the maximum phase response minus the minimum phase response divided by the mean response. The mean of this index over the eight cells is 29%.

Discussion

The work described in this paper complements a previous study from our laboratory by Snowden et al. (1991). It was found in that study that V1 cells respond better to the transparent random dot patterns than MT cells. This result by itself would seem to suggest that V1 activity could be responsible for our perception of transparent motion. However, as pointed out by Snowden et al. (1991), the reduced responses of MT cells under the transparency condition could better account for the psychophysical observation that motion threshold is higher for transparent stimuli than for the corresponding unidirectional ones (Snowden 1989). An alternative possibility is that cells in V1 may respond very well to all composite patterns with two components moving across each other regardless of their degrees of perceptual transparency. The main purpose of this paper is to show that this is indeed the case. We used two different types of composite patterns: the perceptually transparent random dot patterns and the nontransparent counterphase gratings. It was found that V1 cells on the average respond to both types of stimuli quite well, and, as a population, they could not reliably tell them apart. Our result suggests that additional processing beyond V1 must be involved in transparent motion analysis.

When we were recording responses of isolated V1 cells to the sine and counterphase gratings, we did not first search for their optimal spatial and temporal frequencies and then record at these frequencies. Nor did we look for the best parameters for the random dot patterns. We think that this approach is justified, because here we are not interested in optimal tuning properties of the cells. Instead, we would like to find out how a population of V1 cells respond to two fixed types of stimuli, one of which is perceptually transparent and the other nontransparent. In fact, the degree of perceptual transparency of a stimulus depends on its parameters. Had we changed stimulus parameters from cell to cell, the results would be more difficult to interpret. To ensure that cells included in our analysis were reliably driven by our stimuli, we first screened our cells for the reliability to fire above their background rates (see Materials and methods). Since we used the normalized responses to the two types of patterns for comparison, the absolute firing rates of a cell should have had little effect on our results.

It should be pointed out that the presence of motion transparency in the moving random dot patterns and the lack of it in the counterphase gratings are observations mainly based on human subjects. When interpreting our data, we assumed that monkeys perceive the two types of patterns in the same way as we do. A previous study from our laboratory provides evidence that monkeys do see transparent motion in random dot patterns (Siegel and Andersen 1988). In that study monkeys were trained to detect a transition in some structure-from-motion displays made of overlapping random dots moving in opposite directions. The monkeys had to be able to perceive transparent motion in order to extract the underlining structures in the displays. It was found that the performance of monkeys was remarkably similar to the human performance, suggesting that monkeys' ability to perceive transparent motion in random dot patterns is similar to our own. It is perhaps not surprising that monkeys should be able to see transparent motion, because motion transparency occurs frequently in the natural environment due to the abundance of partial occlusions (for example, a tiger moving behind trees). However, there is yet no direct evidence on whether monkeys, like us, do not see any transparent motion in the counterphase gratings. If they do, the interpretation of our data would be different; the data would then suggest that V1 activity is consistent with *monkeys'* perception of transparent motion. Although we cannot rule out this possibility it is unlikely for the following reason. In a separate study we showed, using a different but related set of stimuli, that MT activity (in monkeys) correlates well with the *human* perception of motion transparency, while V1 activity does not (Qian and Andersen 1994). If one assumes that V1 activity correlates well with *monkeys'* perception of motion transparency, then one has to conclude that MT activity does *not* correlate with *monkeys'* perception of motion transparency. However, a previous study shows that an MT lesion eliminates monkeys' ability to perform the above-mentioned structure-from-motion task with transparent random dot displays (Siegel and Andersen 1986), suggesting that MT is crucial for transparent motion perception in *monkeys*.

There do exist directionally selective V1 cells whose normalized responses to the transparent random dot patterns are much stronger than that to the nontransparent counterphase gratings. An example is shown in Fig. 2. It is therefore possible that the activity of this subpopulation of V1 cells could account for the difference in perceptual transparency of the two types of patterns. However, this possibility could only be true if the brain could selectively "listen" to these cells while ignoring activities of those other directionally selective V1 cells with opposite behavior (i.e., stronger response to the nontransparent counterphase gratings than to the transparent random dot patterns). If, instead, the brain had to use the activities of all cells in an area (or a small region within an area) to make a perceptual judgment, then V1 could not be the physiological basis of transparent motion perception because the numbers of cells that behave in opposite ways are about equal (see Fig. 4). We have shown elsewhere that, unlike V1, mean MT responses to some transparent and nontransparent displays are significantly different (Qian and Andersen 1994). MT activity could thus better explain the phenomenon of motion transparency. Our suggestion that additional processing beyond V1 is involved in transparent motion analysis is also in accordance with a recent psychophysical observation by Watanabe (Watanabe 1993, 1994) who found that motion transparency is strongly influenced by surface decomposition. Since the V1 receptive field sizes are too small for surface representation, the finding also suggests that extrastriate areas with larger receptive fields must be involved.

Since the suppression between the opposite directions of motion is much stronger in area MT than in V1 (Snowden et al. 1991; Qian and Andersen 1994), we suspect that this suppression could play a major role in transparent motion perception. For example, it is possible that while two populations of V1 cells with opposite directional preference will be activated stimultaneously by a counterphase grating, the activities of their projection to MT might cancel each other out owing to the strong directional suppression in MT. MT would thus respond very weakly to counterphase gratings. This would explain the lack of perceptual transparency in these patterns. The question remains as how MT cells could account for the perceptual transparency in the transparent random dot patterns and the lack of transparency in the counterphase gratings at the same time. One possibility is that MT cells might be sensitive to local fluctuations of motion signals in opposite directions. A counterphase grating has well-balanced motion signals in opposite directions and thus they may cancel each other out strongly at the suppression stage in MT, while a transparent random dot pattern contains local dot density fluctuations and therefore may leave some

residual responses after suppression. These ideas together with potential biological functions of motion suppression in MT are fully developed and physiologically tested in a separate study (Qian and Andersen 1994).

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