Ning Qian - Richard A. Andersen

V1 responses to transparent and nontransparent motions

Received: 21 January 1994 / Accepted: 20 September 1994

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 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.

Keywords: Motion transparency - Behaving monkey physiology - Random dot patterns - Counterphase gratings - Directional selectivity - Monkey

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 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; Greweze and Yiltle 1990).

In order to investigate the physiological basis of multiple motion representation, transparent random dot displays, composed of 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-
vision in MT between the preferred and the antiprefered directions of motion. This type of suppression was found to be much weaker in area V1, and many V1 cells responded to different 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. Snowdon (1976) has pointed out that the neural basis of the fact that there is an elevation of the psychophysical strength of motion thresholds under the transparency occurred in the area V1 of the monkeys. We also investigated the effects of motion direction on the visual responses in area V1 of the 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 SGI graphics board installed. The visual refresh rate of the bar was 60 Hz computerized. The output of the board was sent to two video monitors simultaneously. The monitor (a) was in front of the monkey in a closed and dimly lit room, and the other in the control area for the experiments. The monitor stimulus was calibrated for linear response with an FTA 1015 Monitor (Colorimeter Model 456)-a colorimeter with a white light source. The colorimeter was used to monitor the stimulus when the monitor was turned off, and the visual stimuli were all under the control of a Microview mouse and could be moved to any location on the monitor screen. Using various mouse and keyboard combinations, we could also change the size of the fixation point. The stimuli and mobility add to, and are, 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, we obtained a good visual angle of the stimuli.

All stimuli were generated by an origin 3.0 volunteer, and were displayed on the computer and printed. For display purposes, the initial location of a dot was chosen randomly inside the 3°×3° display area. When the dot moved off the edge of the window, it was wrapped around and replotted on the opposite 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 stimuli are used to test the cells' responses to one horizontal, and two at 45° oblique angles. We then generated four transparent stimuli, where the position, pulling, and release of the keys, sent the PG for displaying the fixa-
tion point, and signal the direction of the motion. After a cell was isolated, we presented a series of patterned stimuli to each of the three V1 recordings. We then performed a series of trials, in which one of the three V1 recordings was presented in each recording session.

Sine wave and counterphase gratings were generated using the technique outlined above. It should be noted that the responses of V1 cells were primarily low spatial frequency, and that the spatial frequency of a V1 cell with a spatial frequency of 2 Hz, which was the frequency used by most V1 cells, was normally below 0.5 cycles per degree, considerably smaller than the spatial frequency of the bar.

Data collection and analysis

A total of 92 V1 cells were recorded. The data were collected in the periods when the monkeys were fixating and various displays were shown in the cell's receptive fields. The times intervals between two successive spikes were recorded. In each trial, the collection started after the monkeys established fixation. 500 ms later, a 1-s stimulus was shown, lasting for 500 ms, and the monkey had to track interval of 1 s and the other 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 offline analysis on a Macintosh computer. The first 200 ms of the 1-s stimulus were used for the quantitative data collection. This delay was chosen to avoid the bias of the transient effects and to take the response delays into account. We also collected the data for the 1-s stimulus, and the monkey was trained to follow a yellow line across the screen. The stimuli were presented in pairs, with one offset to the left and the other to the right of the fixation point. The orientation of the two stimuli was identical. The stimuli were presented in random order. In each trial, the collection started after the monkeys established fixation. 500 ms later, a 1-s stimulus was shown, lasting for 500 ms, and the monkey had to track interval of 1 s and the other 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 offline analysis on a Macintosh computer. The first 200 ms of the 1-s stimulus were used for the quantitative data collection. This delay was chosen to avoid the bias of the transient effects and to take the response delays into account. We also collected the data for the 1-s stimulus, and the monkey was trained to follow a yellow line across the screen. The stimuli were presented in random order.
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 resonance technique (Cohen and Josephson 1963). The eye position resolution of our system is about 2 min. During data collection, if a class of trials in which no suppression was observed. The standard deviations of the horizontal and vertical eye positions were about 3° and 2°, respectively. The data from the two monkeys was recorded separately at 4 mm and 4.9 mm, respectively. Recording diaphragms 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 SGI graphics board installed. The vertical refresh rate of the bar was 60 Hz refresh rate. The output of the board was sent to two video monitors simultaneously, one (Monotronic) 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 Monotronic monitor was calibrated for linearity with an LS Monitor/Scientific lightmeter (Model 4650) with a fiber optic probe. The input to the monitor's refresh rate to obtain time-averaged images. The lightmeters were placed on the same horizontal plane as the eyes of the monkey, and the visual stimuli were all under the control of a Microsight mouse and could be moved to any location on the monitor screen. Using various mouse and keyboard combinations, we could also change the size of the fixation point and the stimuli, and modulate the width, height, and orientation of the bar. In all our experiments, the monkey was 60 cm away from the monkey's eyes. At this distance, the angular size of the white bar was about 0.3°.

All stimuli covered an area of 3° by 3°, and each was 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 gratings made of two identical sine wave gratings drifting in opposite directions with equal speed. Perceptually, however, one does not see any movement because the two gratings are orthogonal to each other. Instead, the pattern looks more like flicker or oscillation.

Our results indicate that V1 responses of these two types of stimuli are distinct and that this is true even for the motion stimuli, and that the input to the test area of the monkey. All V1 recordings were performed with the glass-coated photodiode probe. After each cell was isolated, we first directed its receptive field to map its receptive field with mouse-controlled cues in 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 stimulus a mouse-controlled small square with adjustable size was used instead. After the receptive field probe was appropriately determined the display window of the stimulus was presented in its center. One or more series of blocks of trials were presented to each cell. The cells were considered to be normal by 0.5° considerably smaller than our stimuli.

Data collection and analysis

A total of 92 V1 cells were recorded. The data were collected from periods when the monkeys were fixating and various displays were shown in their receptive fields. The time intervals between successive trials were randomized. In each trial, the collection started after the monkeys established fixation 500 ms later a 1-s stimulus was presented, the task was to track intervals of 1 s, and the other 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 offline analysis on a Macintosh computer. The first 200 ms of each trial were treated as an anticipatory period to avoid the bias of the transient effects and to take the response delays into account. There is also a time window is shown. The activities of the cells during these "fixation-alone" trials were used to calculate their spontaneous firing rate at cell. For each cell, 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 firing rate. Then cells with a spontaneous rate lower than 5 spikes/s were selected as our study population. For each cell that passed this test, two preferred directions were defined as the directions of maximum response suppression for the single block of trials during which the two stimuli were presented and were compared to the monkeys in a pseudorandom order.

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

\[ L(x, y) = L_0 + \sin(2\pi x / L_x + 2\pi y / L_y + \phi) \]

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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 the case 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 a 0°–180° offset of a half cycle time delay. The phase parameter for the drifting sine wave gratings is now conventionally defined along the range 0°–180° or 0°–360°.

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 perceptual transparency measure and the degree of perceptual transparency of 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 sine wave grating drifting in its preferred direction. The response 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 that of the sine wave gratings in the sine wave gratings in Fig. 1e 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

Materials and methods

Preparation of animals

The data reported in this paper were obtained from two male rhesus monkeys (Macaca mulatta). The details of the experimental procedures have been published previously (Snow et al. 1991). Briefly, the animals were trained to fixate for...
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 0.86, respectively. Each small dot in the ratios represents the occurrence of a spike and the different bars present responses from repeated trials. The time periods of stimulus presentations are indicated by the block 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 2.12. d Responses to the corresponding counterphase gratings with mean luminance of each component sine wave grating equal to 1.12 and 2.12, respectively. One small vertical division represents 21.8 spikes/s (sp/s); one small horizontal division represents 100 ms.

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 (sp/s); 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 pattern and the counterphase gratings by the corresponding preferred responses to the unidirectional stimuli. In the following, 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. 1b 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. 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 any 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 0.88, respectively. Each small dot in the raster presents the occurrence of a spike and the different lines present responses from repeated trials. The time periods of stimulus 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 antiprefered directions. b Responses to the corresponding transparent random 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 2.5L. d Responses to the corresponding counterphase gratings with mean luminance of each component sine wave grating equal to 1.1L and 2.1L, respectively. One small vertical division represents 21.3 spikes/s (sp/s), one small horizontal division represents 100 ms.

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 consists of two 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. 1b and d, respectively. For this cell, reducing the number of dots or the mean luminance does not affect the results significantly.

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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 simultaneously and were directionally selective for the two types of stimuli. To quantify the behavior of the cells, we computed two suppression indices for each cell, one for each type of stimulus, and then compared the two indices. These are defined as:

\[
S_{\text{IA}1/2} = 1 - \frac{\text{transparent dot response}}{\text{preferred dot response}} \tag{6}
\]

\[
S_{\text{SI}1/2} = 1 - \frac{\text{counterpreferred response}}{\text{preferred sine response}} \tag{7}
\]

The background firing rates were subtracted from all responses. Note that calculation of these definitions are equal to one minus the normalized responses. \(S_{\text{IA}1/2} (S_{\text{SI}1/2})\) represents the percentage reduction of a cell’s response to the 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 degree 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. \(S_{\text{IA}1/2}\) against the grating suppression index \(S_{\text{SI}1/2}\). Cells with similar normalized responses (thus similar degrees of suppression) form a cluster 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, \(P = 0.27\)). Also note that V1 cells on the average do not 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 consistent with 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).

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 to measure the strength of directional suppression of a cell that may be correlated with its degree of directionality. To study this, we examined the suppression indexes for the two types of stimuli for each cell. We found that the degrees of directionality of the V1 cells under the two types of stimuli are similar. For this purpose we define two directional indexes for each cell as follows:

\[
D_{\text{IA}1/2} = 1 - \frac{\text{antipreferred dot response}}{\text{preferred dot response}} \tag{8}
\]

\[
D_{\text{SI}1/2} = 1 - \frac{\text{antipreferred sine response}}{\text{preferred sine response}} \tag{9}
\]

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 patterns 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, 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 data for 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).

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’ 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 \(135^\circ\). 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 phase responses are very similar to each other indicating relative phase-independence of the responses. To quantify the phase dependence of the cell population, we calculated four phase dependence indices for each cell. We first computed the
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 behavior of the cells, we computed two suppression indices for each cell, one for each type of stimulus, and then compared the two indices. These are defined as:

\[ S_{\text{trans}} = 1 - \frac{\text{translucent dot response}}{\text{preferred dot response}} \]  
(6)

\[ S_{\text{suppres}} = 1 - \frac{\text{counterphase response}}{\text{preferred sine response}} \]  
(7)

The background firing rates were subtracted from all responses. Note that the definitions are equal to one minus the normalized responses. \( S_{\text{trans}} \) (\( S_{\text{suppres}} \)) represents the percentage reduction of a cell's response to the random dot pattern compared with its preferred direction response to the unidirectional random dot pattern (sine wave grating). The indices therefore measure the degree of suppression between the preferred and an antipreferred direction 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. \( S_{\text{trans}} \) against the grating suppression index \( S_{\text{suppres}} \). 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, \( P > 0.05 \)). Also note that V1 cells on the average 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 consistent 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).

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:

\[ D_{\text{directional}} = 1 - \frac{\text{preferred dot response}}{\text{antipreferred dot response}} \]  
(8)

\[ D_{\text{suppres}} = 1 - \frac{\text{antipreferred sine response}}{\text{preferred sine response}} \]  
(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 patterns 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, 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 the results of 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.

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 (\( \theta = 0 \) in Eq. 5). As our stimuli were much larger than cells' 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 for the four phases, we used the mean of the four responses to compute the suppression index.
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 (Andersen, 1986). We used 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 too 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 of firing 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 is an observation 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 underlying structure in the displays. It was found that the performance of monkeys was remarkably similar to that of human subjects, 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 perceive 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. If the two types of patterns are not well matched, the human perception of motion transparency, while V1 activity does not (Qian and Andersen, 1994). If one assumes that V1 activity corresponds to monkeys' perception of motion transparency, 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 exist directionally selective V1 cells whose normalized responses to the transparent random dot patterns are much stronger than those 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 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 preferences will be activated simultaneously 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 cells might then respond very weakly to counterphase gratings. This would explain the lack of perceptual transparency in transparent random dot patterns. The opposite will be true for stimulus onsets that are not well matched, the human perception of motion transparency, while V1 activity does not (Qian and Andersen, 1994). If one assumes that V1 activity corresponds to 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. 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 responds to two fixed types of stimuli, one of which is perceptually transparent and the other nontransparent (Andersen, 1986). We used 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 too 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 of firing 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.

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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 (Quan and Andersen 1994).

Acknowledgements: We would like to thank Dr. Ted Adelson for many helpful discussions and Gail Robertson, Drs. Stefie True and Peter Theur for their help with the early recording experiments. The research is supported by NIH grant E130749 and Office of Naval Research contract N00014-89-J-3336, both to Richard Andersen. N.O. was supported by a McGeown-Pew postdoctoral fellowship during the early phase of this work.

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Original Paper


Reduced postischemic expression of a glial glutamate transporter, GLT1, in the rat hippocampus

Received: 27 September 1994 / Accepted: 31 October 1994

Abstract Perturbations of the synaptic handling of glutamate have been implicated in the pathogenesis of brain damage after transient ischemia. Notably, the ischemic episode is associated with an increased extracellular level of glutamate and an impaired metabolism of this amino acid in glial cells. Glutamate uptake is reduced during ischemia due to breakdown of the electrochemical ion gradients across neuronal and glial membranes. We have investigated, in the rat hippocampus, whether an ischemic event additionally causes a reduced expression of the glial glutamate transporter GLT1 (Pínes et al. 1992) in the postischemic phase. Quantitative immunoblotting, using antibodies recognizing GLT1, revealed a 20% decrease in the hippocampal contents of the transporter protein, 6 h after an ischemic period lasting 20 min induced by four vessel occlusion. In situ hybridization histochemistry with [3S]labeled oligonucleotide probes or digoxigenin labelled riboprobes directed to GLT1 mRNA showed a decreased signal in the hippocampus, particularly in CA1. This reduction was more pronounced at 3 h than at 24 h after the ischemic event. We conclude that the levels of GLT1 mRNA and protein show a modest decrease in the postischemic phase. This could contribute to the delayed neuronal death typically seen in the hippocampal formation after transient ischemia.

Key words Hippocampus - Ischemia - Glial glutamate transporter - In situ hybridization - Immunoblotting

Introduction

It is now well established that transient global ischemia is followed by a delayed death of certain neuronal populations, including the pyramidal cells of the CA1 field of hippocampus (review: Schmidt-Kastner and Freudenthal 1991). Many attempts have been made to unravel the mechanisms underlying this type of selective neurodegeneration, as its restricted course should offer possibilities for therapy. The delayed neuronal death is not an obligatory consequence of the acute ischemic event since the pathological changes may be alleviated by pharmacological intervention in the recovery phase (review: Meldrum 1992). Several lines of evidence suggest that glutamate receptors figure prominently in the pathogenesis of postischemic cell death (Albers et al. 1992; Choi 1992; Diemer et al. 1992; Meldrum 1992; Nellgärd and Wiech 1992; Pellegrini-Giampietro et al. 1992), although the relative contribution of the different receptor subclasses remains an issue of debate. In CA1, currents through N-methyl-D-aspartate (NMDA) receptor channels are potentiated after anoxia or ischemia (Hor et al. 1991; Crepel et al. 1993), in agreement with earlier data demonstrating a postischemic augmentation of Ca2+ influx in CA1 pyramidal cells (Andnæs et al. 1988, 1991). These and other changes (Pellegrini-Giampietro et al. 1992) impose an increased Ca2+ load on the postsynaptic cells which may contribute to their vulnerability (Van Rees et al. 1986; Siesjö 1993; Choi 1994). The potentiation of NMDA receptor currents after an ischemic or anoxic insult may be due to altered properties of the receptor channel itself (Szatkowski and Astwood 1994). Alternatively, or in addition, it could reflect an increased release or a reduced uptake of glutamate. It is well known that the extracellular glutamate concentration, which is increased severalfold under the ischemic insult, rapidly returns to near normal levels upon reflow (Bennett et al. 1984; Torp et al. 1993). However, microdialysis experiments have demonstrated elevated levels of both aspartate and glutamate 5-8 h after ischemia (Andnæs et al. 1991). These changes, while not nearly as