The Nature of V1 Neural Responses to 2D Moving Patterns Depends on Receptive-Field Structure in the Marmoset Monkey

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Tinsley, Chris J., Ben S. Webb, Nick E. Barraclough, Chris J. Vincent, Amanda Parker, and Andrew M. Derrington. The nature of V1 neural responses to 2D moving patterns depends on receptive-field structure in the marmoset monkey. *J Neurophysiol* 90: 930–937, 2003. First published April 23, 2003; 10.1152/jn.00708.2002. A plaid pattern is formed when two sinusoidal gratings of different orientations are added together. Previous work has shown that V1 neurons selectively encode the direction and orientation of the component gratings in a moving plaid but not the direction of the plaid itself (Movshon et al. 1985). We recorded the responses of 49 direction-selective neurons to moving gratings and plaid patterns in area V1 of the anesthetized marmoset monkey (*Callithrix jacchus*). The responses of V1 neurons to rectangular patches of varying lengths and widths containing gratings of optimal spatial frequency were used to measure size and aspect ratio of the receptive-field subunits. We measured responses to plaid patterns moving in different directions and graded the magnitude of the response to the direction of motion of the plaid and the response to the direction of motion of the component gratings. We found significant correlations between receptive-field structure and the type and strength of its response to moving plaid patterns. The strength of pattern and component responses was significantly correlated with the interrelated properties of direction tuning width (Spearman's $r = 0.82$, $P < 0.001$), and receptive-field subunit aspect ratio (Spearman's $r = -0.79$, $P < 0.001$). Neurons with broad direction tuning and short, wide receptive-field subunits gave their greatest response when the plaid moved in their preferred direction. Conversely, neurons with narrow direction tuning and long, narrow receptive-field subunits gave their greatest responses when the plaid moved in a direction such that one of its components moved in the preferred direction.

INTRODUCTION

Neurons in the primary visual cortex of cat and monkey encode the direction of motion of elongated or oriented stimuli, such as lines, edges, and sinusoidal gratings (Cooper and Robson 1968; Hubel and Wiesel 1962, 1968). However, when they are presented with plaids or 2D patterns, made by adding together moving sinusoidal gratings of different orientations, their responses show selectivity for the direction of motion of the component gratings (*component selectivity*), but not for the direction of motion of the plaid (Gizzi et al. 1990; Movshon et al. 1985). Neurons with selectivity for the direction of motion of plaid patterns (*pattern selectivity*) occur in area MT in macaque visual cortex, although many MT neurons are component selective (Movshon et al. 1985).

The speed and direction of motion of a plaid pattern can be calculated from the motion of its components using the intersection of constraints (IOC) computation shown graphically in Fig. 1*D* (Adelson and Movshon 1982). If each component's motion is represented as a vector, the constraint line that is the line at right angles to the component vector through its endpoint passes through the endpoints of the vectors representing all the possible velocities of patterns containing that component. The only velocity vector that is compatible with both component velocities is the one that ends at the intersection of the constraint lines of the two components.

The finding that direction-selective neurons in V1 show only component selectivity, whereas some neurons in monkey MT show pattern selectivity and others show component selectivity, has led to the suggestion that the intersection of constraints is calculated in area MT. Consistent with this suggestion, Pack and Born (2001) report that, when presented with a pattern of 3° bars of the same orientation moving in a direction 45, 90, or 135° different from the contour orientation, MT neurons initially respond to the component of motion perpendicular to the contour's orientation and later respond to the actual movement of the pattern.

There is a good deal of psychophysical data consistent with the hypothesis that the visual system computes the motion of plaid patterns from the motion signals generated by their components (Derrington and Suero 1991; Movshon et al. 1985; Stone et al. 1990; Welch 1989). However, it is also possible that V1 neurons with short, wide receptive fields could extract a "pattern-motion" signal without any IOC computation (Derrington and Badcock 1992). The process is illustrated schematically in Fig. 2, *C* and *D*, which shows two plaid patterns. Each of them moves upward and to the right and is made from one component grating that moves horizontally to the right and one that moves vertically upward. Superimposed on the patterns are schematic receptive fields oriented vertically and obliquely to represent responses for the direction of motion of the component gratings (component motion) and for the direction of motion of the pattern (pattern motion), respectively. The receptive-field subunits are drawn as black or white oval outlines to indicate regions in which luminance has excitatory or inhibitory effects, respectively.

A long, thin receptive field, like that shown in Fig. 2*C*, can respond to the component gratings but not to the plaid. The illustration shows that when the receptive field is aligned so

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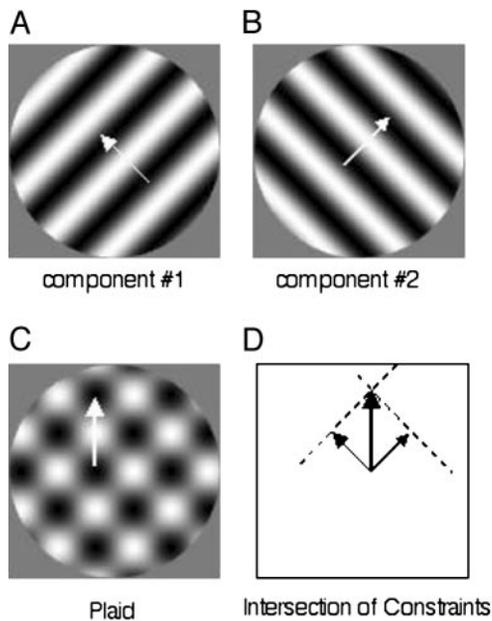
FIG. 1. *A–C*: plaid pattern and its constituent gratings. *D*: intersection of constraints computation. Gratings *A* and *B* add together to form plaid *C*. Each grating has direction and speed of motion indicated by white arrows. Plaid *C* has direction and speed of motion that can be calculated from intersection of constraints (IOC). See text for further explanation.

that a white bar of the vertical component grating falls on its white subunit, giving it a high mean luminance, and a dark bar falls on its dark subunit, giving it a low mean luminance, the average luminance within each subunit matches its selectivity so the neuron responds, giving a component response. However, in the oblique receptive field the average luminance within each subunit will be approximately equal to the mean luminance of the pattern, regardless of the location of the pattern on the receptive field. Clearly the neuron will not respond: it will not produce a "pattern response."

On the other hand, neurons with short receptive fields can respond both to the component gratings and to the local features of the plaid. The subunits of the short, fat receptive field in Fig. 2*D* are about the same width as the pattern features and not much longer; thus the receptive field can be aligned either horizontally or obliquely so that the luminance distribution in the pattern matches the selectivity of the receptive field. Consequently we would expect this neuron to give optimal responses when the plaid is moving in its preferred direction. Another prediction of the hypothesis outlined above is that broadly tuned neurons would be more likely to produce strong responses to the pattern motion of moving plaid patterns. This is because neurons with broad direction tuning tend to have short, wide receptive fields (Lampl et al. 2001).

In this study we aimed to test the hypothesis proposed above, that V1 neurons with short, wide receptive fields give large responses to the direction of motion of a moving plaid pattern. A preliminary version of this report was previously published in abstract form (Tinsley et al. 2001).

METHODS

Electrophysiological recording

Single neurons were recorded with epoxy-coated electrodes (FHC) in area 17, primary visual cortex, in 2 male and 3 female common

marmosets (*Callithrix jacchus*). Extracellular electrical signals were amplified and filtered between 300 Hz and 5 kHz before being sampled at 44 kHz by a Macintosh computer that extracted the action potential waveform.

Surgery

Anesthesia was induced with intramuscular Saffan (alphadalone/alphaxalone acetate, 24 mg/kg) and ketamine (8 mg/kg). After cannulation of a tail vein and of the trachea, anesthesia was maintained with fentanyl citrate (20 μg kg^{-1} h^{-1}) and a mixture of NO$_2$-O$_2$ (67:33). Vecuronium bromide (0.2 mg kg^{-1} h^{-1}) was administered to prevent eye movements. The electrocardiogram and the electroencephalogram were monitored to assess the depth of anesthesia, which could be increased with supplementary isoflurane. All procedures were in accordance with the UK Animals Scientific Procedures Act (UK).

Visual stimuli

Stimuli were generated by a Macintosh computer and displayed at a resolution of 4.6 pixels/deg on a tangent projector screen (800 × 600 pixels at 120 Hz), which was used to plot receptive-field locations. Neuronal responses were tested for each eye, the eye that produced the weaker response was occluded, and the receptive field was projected onto a Sony color monitor (model GDM 200PST, 56 pixels/deg) using a mirror. The size and location of the receptive field were determined using a rectangular patch of moving sinusoidal grating. The length and width of the patch were reduced to the smallest dimensions that produced the maximal firing rate of the neuron. We determined the preferred spatial frequency, temporal frequency, and direction of each
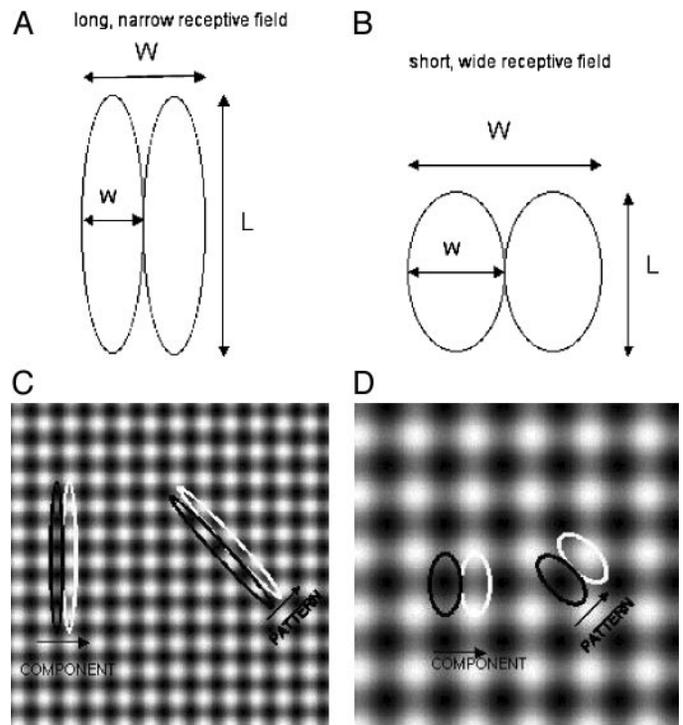

FIG. 2. *A*: structure of long, narrow receptive field. *B*: short, wide receptive field. Length of receptive field is denoted "L" and width is denoted by "W." Width of receptive-field subunit is "w." *C* and *D*: how differences in receptive-field structure may account for component responses (*C*) and pattern responses (*D*) to plaid patterns. Plaid patterns of differing spatial frequency are depicted in *C* and *D*. Superimposed on these patterns are putative receptive fields. Subunits are oriented along the axes of pattern motion and component motion. See introduction for further explanation.

neuron using high-contrast sinusoidal gratings of differing spatial frequencies, temporal frequencies, and orientations presented to the receptive field of the neuron.

Plaid patterns were constructed from two sinusoidal gratings added together on each frame using a mixed-color lookup table that allocated 15 luminance levels (4 bits) to each component (each component was set to half the contrast of the gratings used in the experiments outlined above). The stimuli used to determine direction preference and test the neuron's response to the moving plaid were presented moving at the optimal temporal frequency within a Gaussian time window with a sigma of 1.25 periods of the optimal temporal frequency, truncated to a duration of ±2 sigma. The gratings used to test direction and the plaid patterns were presented on the classical receptive field of the neuron and were matched to it in size. Single gratings were presented within a rectangular aperture with dimensions set to those previously determined. Plaids were presented within a circular aperture with a diameter that was the larger of the width or length of the receptive field. A plaid composed of gratings with an orientation difference of 90° was presented; each component grating had a spatial and temporal frequency that matched the neuron's preferred frequency. During the experiments great care was taken to align the center of the plaid with the center of the receptive field (see the second half of the METHODS section for further discussion of this topic). Directionally selective neurons, defined as having a response to the optimal direction that was at least twice the response to the opposite direction, were selected for testing with plaids.

Histology

Electrolytic lesions were placed at points along the electrode track by passing a 5-μA, 5-s DC current through the electrode. At the end of the experiment the animal was killed with an overdose of barbiturate and was perfused through the left ventricle with phosphate buffer followed by fixative (4% formalin in 0.1 M phosphate buffer). Frozen sections were cut at 60 μm and stained with cresyl violet. Recording sites were then histologically reconstructed.

Analysis of neuronal responses

The response of individual neurons to different directions of motion of the grating and plaid patterns were analyzed. The directions tested ranged from the preferred direction −120° to the preferred direction +120°, in 15° steps.

An objective assessment of the dimensions of each receptive field was achieved by measuring the response to moving sinusoidal gratings matched to the neurons' preferred spatial frequency, temporal frequency, and direction, and differing in length and width. The dimensions of the grating that produced the neurons' maximum firing rate in response were assumed to equal the receptive-field dimensions.

The preferred spatial and temporal frequency tuning were measured by fitting difference of Gaussian curves to the responses at differing frequencies and finding the frequency that elicited the maximum response. The receptive-field subunit aspect ratio was calculated by multiplying the neuron's preferred spatial frequency by twice the length of its receptive field. Our justification for doing this for complex cells is on the assumption that complex cells derive their input from subunits that act in an approximately linear way (Movshon et al. 1978). The direction tuning width was measured by fitting a Gaussian curve to the responses at different directions and measuring the half-width at $1/\sqrt{2}$ of the peak height.

Neurons were classified as simple or complex using an index generated by dividing the response at the frequency of the moving grating (calculated by fax fourier transform (FFT) of the peri-stimulus time histogram) by the response at zero frequency (DeValois et al. 1982). This index was measured using responses to gratings of optimal size, spatial frequency, and temporal frequency. Neurons with an index of one or more were classified as simple and those with an index of less than one were classified as complex. For complex cells mean firing rates were used to analyze neuronal responses to moving gratings and plaids. For simple cells the modulation in firing at the stimulus frequency was used.

Exclusion criteria for neurons

Gaussian curves were fit to the direction tuning curves of the neurons. Neurons were excluded from further analysis if the fit accounted for <80% of the variance in mean firing rate at different directions. Likewise, for measures of spatial and temporal frequency difference of Gaussian curves were fit to the tuning data and neurons were excluded if the fit accounted for <80% of the variance. All measures of plaid responses were made with the center of the plaid pattern placed over the center of the receptive field of the neuron. This is important in simple cells because the plaid must be presented with both components in the same phase to assess the relative preference for component and pattern motion. In principle this matters less for complex cells in which subunits are distributed throughout the receptive field (Movshon et al. 1978). (For further discussion on phase effects in visual cortical neurons see Carandini et al. 1997.) To check the centering of plaid stimuli we calculated an index of symmetry from the responses of simple cells to plaid patterns as follows. First, we fit a sum of Gaussian curves to the neuronal responses to the plaid pattern. Neurons were excluded if this curve fit accounted for <85% of the variance. In theory neurons that produce a symmetrical response to plaid patterns of this type would be responding to components with roughly the same relative phase. Conversely, neurons that produce an asymmetric response to plaid patterns would be responding to components with different relative phases. We calculated an index of symmetry from the curve fit to see whether the neurons' response to different directions of motion of the plaid was symmetrical. We used the following formula, where 1) Dp is the neurons' response to the plaid moving in its preferred direction of motion (as determined by its responses to single gratings); 2) Dc1 is the smaller of the two response values obtained when the plaid moved in a direction such that one of the component gratings moved in the neuron's preferred direction; and 3) Dc2 is the response when the plaid moved so that the other component grating moved in the neuron's preferred direction. The symmetry index (SI) ranged between 0 and 1

$$SI = (Dc1 + Dp)/(Dc2 + Dp)$$

Any simple cells with a symmetry index of <0.85 were excluded from the sample.

Analysis of neuronal response to plaids

Partial correlations were calculated between the responses of each neuron and the responses of an idealized component neuron and an idealized pattern neuron (Cohen and Cohen 1983; Mante 2000). This involved the generation of simple model predictions for pattern-selective and component-selective responses of each neuron to plaid patterns (Movshon et al. 1985). For the calculation of the component prediction, the spontaneous firing rate was subtracted from the responses to gratings before they were added together, and added back after the prediction had been computed (Movshon et al. 1985). The predictions were generated from the response of the neuron to gratings and were then compared with the response of the neuron to plaid patterns. Partial correlations between the measured response to the plaid pattern, the predicted pattern response, and the predicted component response were calculated. The partial correlations for the pattern (R_p) and component predictions (R_c) were calculated as follows

$$R_p = r_p - r_{pc}/\sqrt{(1 - r_c^2)(1 - r_{pc}^2)}$$

$$R_c = r_c - r_{pc}/\sqrt{(1 - r_p^2)(1 - r_{pc}^2)}$$

where r_c is the correlation of the component model with the response to the plaid pattern, r_p is the correlation of the pattern model with the response to the plaid pattern, and r_{pc} is the correlation of the component model with the pattern model.

To compare the receptive-field subunit aspect ratio and breadth of direction tuning of neurons with their response to plaid patterns, it was necessary to produce a *pattern* index that reflected the strength of their response to the *1)* the pattern motion and *2)* the component motion of the plaid patterns. Two indices were produced. One, the *pattern correlation* index, was based on the correlations between the pattern of responses to a plaid moving in different directions and the pattern model or component model prediction (Movshon et al. 1985). This correlation index is useful for calculating the extent to which the response to a plaid differs from what would be expected from the responses to gratings. However, we also wished to address the simpler question of whether the neuron's responses signaled the motion of the plaid pattern or the motion of its component gratings. To test this we calculated a different index, the *pattern response* index, based on comparing the responses to the plaid when the motion of the plaid was aligned with the preferred direction, with the average response when one of the components was aligned with the preferred direction of motion of the neuron.

The pattern correlation index used the correlations r_p and r_c used in the calculation of the partial correlation of neuronal responses. However, because the individual correlations are not additive the correlation coefficients r_p and r_c were converted with a version of Fisher's transformation (http://www.fon.hum.uva.nl/praat/manual/Correlation_Confidence_intervals_.html), for example

$$Z_p = 0.5 \left(\frac{\ln\,(1 + r_p/1 + r_p)}{\sqrt{1/n - 3}} \right)$$

where ln denotes the natural logarithm and n is the number of neurons in the correlation. The transformed correlation values were used to produce an index, the pattern correlation index (PCI)

$$PCI = (z_p - z_c)/(z_p + z_c)$$

The pattern response index (PRI) used direct measures of neuronal activity

$$PRI = (i_p - i_c)/(i_p + i_c)$$

where i_c is the firing rate of the neuron in response to the plaid moving in a direction that that one of its component gratings was moving in the preferred direction of motion of the neuron. It was calculated as the average of the responses for the two plaid orientations that aligned one of the two components with the receptive field. The other constituent, i_p, was the firing rate in response to the plaid pattern moving in the direction that was optimal for grating motion. Both indices produced negative values for neurons with strong responses to component motion and positive values for neurons with strong responses to pattern motion.

RESULTS

We recorded from 252 neurons in the primary visual cortex of 3 female and 2 male marmoset monkeys. Of these, 49 (19%) were direction selective (i.e., the responses to opposite directions of motion were at least a factor of 2 different in magnitude). Twenty-eight of the direction-selective neurons were classified as simple cells and 21 were classified as complex cells. The responses of 18 simple cells were excluded from the analysis because they were judged to have been stimulated by plaid patterns in which the phase of the component gratings was different (see METHODS section). This left 10 simple cells in the sample.

Figure 3 shows responses of two direction-selective neurons to gratings and 90° plaids moving in different directions. Figure 3, *B* and *E*, show the response of a component-selective neuron to gratings (*B*) and plaid patterns (*E*) moving in different directions. This neuron is tightly tuned for direction as we can see from its response to moving gratings; it responds only to gratings within 15° of the optimal direction. The neuron gives a strong response when the plaid moves so that the direction of motion of the component gratings is aligned with the optimal component response, whereas it gives no response when the direction of motion of the plaid is aligned with the optimal pattern response.

In Fig. 3, *C* and *F*, we can see the response of a neuron with broad direction tuning to gratings (*C*) and plaid patterns (*F*).
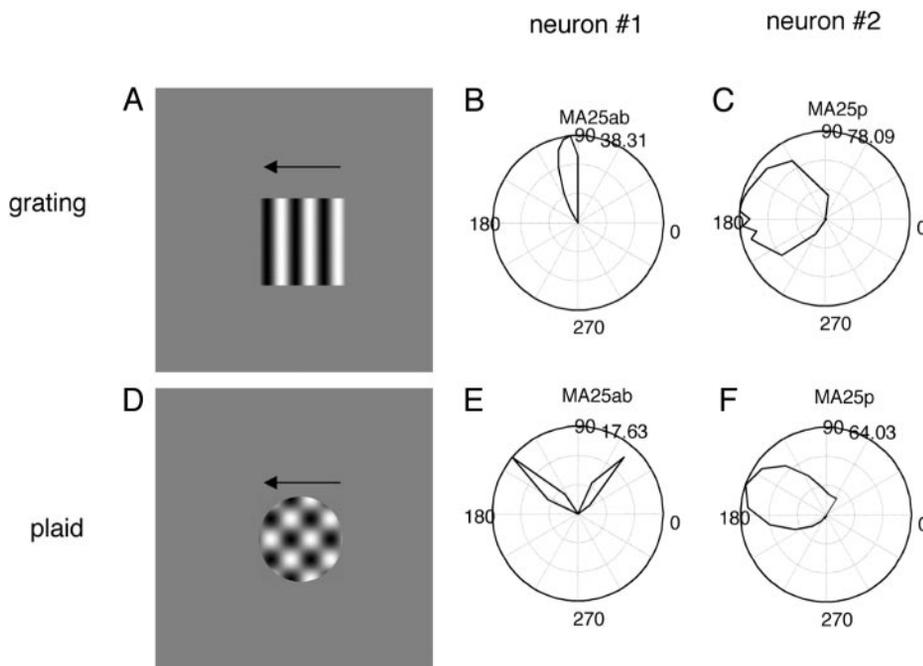

neuron #1　　neuron #2

FIG. 3. Grating and plaid pattern stimuli and responses of two neurons to them. The polar plots show responses of neurons to directions of motion of gratings and plaid patterns. *A*: grating. *B* and *C*: responses to grating in *A*. *D*: plaid pattern. *E* and *F*: responses to plaid pattern in *D*. *E*: response of neuron 1 to the plaid shows clear responses to components. *F*: response of neuron 2 to the plaid is greater in response to preferred direction of motion of the pattern than it is to the components. This response profile is the same when a larger plaid pattern is presented.

This neuron gives a strong response when the direction of motion of the plaid is aligned with the optimal pattern response; it gives a much weaker response when the plaid moves so that the direction of motion of the component gratings is aligned with the optimal component response. The simplest explanation for this is that the direction tuning curves to the individual curves overlap and summate at the direction of pattern motion (Movshon et al. 1985), thus generating the maximum response at this direction (see DISCUSSION section below for further details on this topic).

Direction tuning width and responses to plaid patterns

The responses of a range of neurons selected to illustrate the relationship between direction tuning width and responses to gratings and plaid patterns are shown in Fig. 4. Preferred grating dimensions, which were used for subsequent measurements of receptive-field structure, are depicted in the *top row* (*A–E*) for five neurons (columns). The responses of neurons to gratings and plaid patterns are shown in *row 2* (*F–J*) and *row 3* (*K–O*), respectively. Neurons with short, wide receptive fields (*A* and *B*) display broad direction tuning and have a greater response to the direction of pattern motion of the plaid than to the component motion of the plaid. Conversely, neurons with long, narrow receptive fields (*D* and *E*) display narrow direction tuning and produce a much greater response to the component motion of plaid patterns than to the pattern motion itself. Finally, neurons with receptive-field aspect ratios that are intermediate in dimensions (*C*) display similar responses to both the direction of pattern motion and directions of component motion of a plaid pattern.

Partial correlations of V1 neuronal responses to plaids

To get an idea of the distribution and types of responses generated by different plaid patterns we calculated partial correlations for the component prediction and the pattern prediction (see METHODS section). Figure 5 shows a scatter plot of the partial correlations for all neurons. The partial correlation for the pattern prediction is plotted along the ordinate and the partial correlations for the component prediction are plotted along the abscissa.
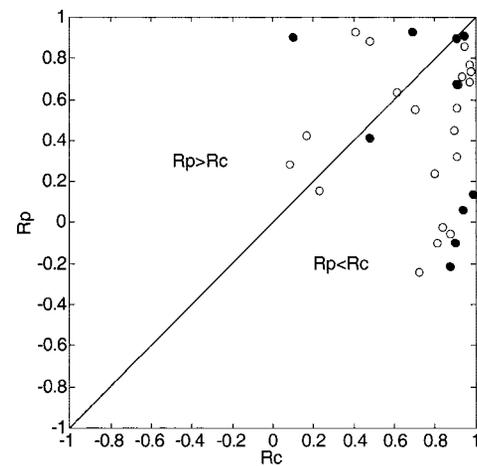

FIG. 5. Scatter plot of partial correlations for component prediction (R_c) and pattern prediction (R_p) of 31 direction-selective V1 neurons. Graph shows partial correlations in response to 90° plaid. Data points belonging to neurons that produced a strong component response are found toward right-hand side of the graph. Data points belonging to neurons with strong pattern response are found toward top of graph. Black circles: simple cells; white circles: complex cells.

along the abscissa. In this plot neurons with a component response that is greater than the pattern response are distributed below the main diagonal. Only 3 of the neurons show both a high pattern response and a low component response, as would be expected of "pattern" neurons. However, many neurons show strong pattern responses. In the next section we consider the receptive-field properties that are associated with component and pattern responses.

Receptive-field properties associated with component and pattern responses

The receptive-field parameters that we expect to be correlated with plaid responses are direction tuning width, receptive-field subunit aspect ratio, and optimal spatial frequency. We calculated correlations between these parameters. We expected that the receptive-field subunit aspect ratio would be inversely related to the direction tuning width of neurons,
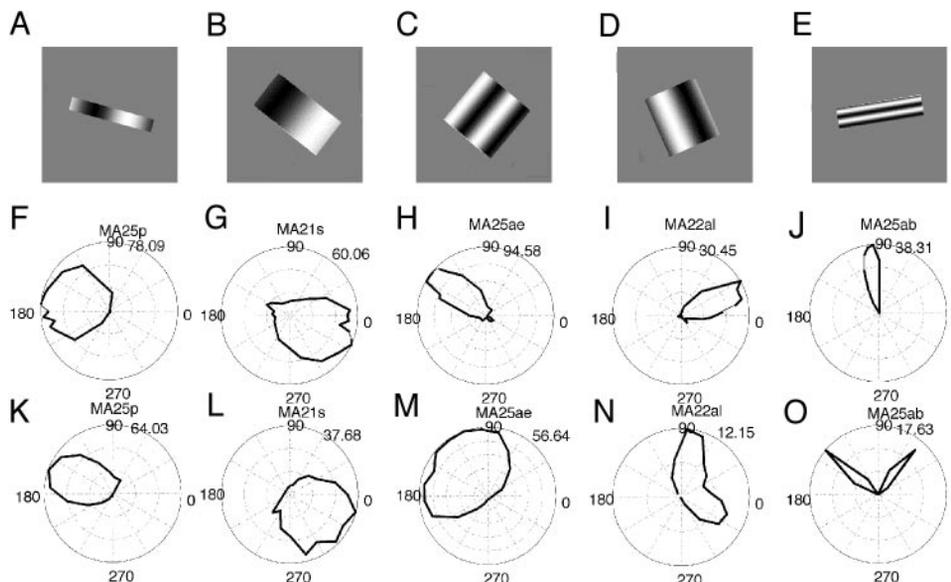

FIG. 4. How the response of neurons to plaid patterns depends on receptive-field aspect ratio. *A–E*: receptive-field aspect ratio and subunit aspect ratio indicated by scale pictures of gratings of optimum dimensions. *F–J*: responses (five V1 neurons) to gratings. *K–O*: responses to plaids. Neurons range from those with short, wide receptive fields and broad direction tuning to those with long, narrow receptive fields and narrow direction tuning. Corresponding responses to plaids range from strong responses to pattern motion (*K*) to strong responses to component motion (*O*).

which proved to be the case. There was a significant inverse correlation between subunit aspect ratio and direction tuning width (Spearman's $r = -0.67$, $P < 0.001$). Optimal spatial frequency of V1 neurons was significantly correlated with both subunit aspect ratio (Spearman's $r = 0.65$, $P < 0.001$) and direction tuning width (Spearman's $r = -0.57$, $P < 0.01$). Optimal temporal frequency was also correlated with the direction tuning width (Spearman's $r = 0.63$, $P < 0.001$). Therefore neurons with a large direction tuning width generally had low values of receptive-field subunit aspect ratio (or short and wide aspect subunits). Neurons with narrow direction tuning generally had higher values of subunit aspect ratio (or long and narrow subunits).

To test our hypothesis that short, fat receptive fields should produce strong responses to pattern motion in the primary visual cortex we looked for correlations between the indices of the pattern/component responses and the relevant receptive-field parameters. Correlations between our pattern/component indices and preferred spatial and temporal frequency were performed using $\log_{10}$ values of frequency. To reduce the risk that they would be dominated by a few neurons with extreme values of parameters, correlations were calculated using Spearman's rank correlation. Table 1 shows Spearman's ranked correlation coefficients for the different comparisons enumerated below.

Direction tuning width

There was a significant positive correlation ($P < 0.001$) between our indices for pattern/component selectivity and direction tuning width, which occurred for both types of indices (see Table 1). The relationship between direction tuning width and the pattern index is depicted in Fig. 6. The top graphs (*A* and *B*) show that neurons with broad directional tuning have the more positive pattern indices (i.e., have larger pattern responses than component responses). Conversely, neurons with narrow directional tuning produce negative pattern indices (i.e., have larger component responses than pattern responses).

Subunit aspect ratio

We found an inverse correlation between receptive-field subunit aspect ratio and pattern/component index. This correlation was significant ($P < 0.001$) for both pattern response and pattern correlation indices (see Table 1). The relationship between receptive-field subunit aspect ratio and the nature of the response of a neuron to a moving plaid pattern is depicted in the graphs in Fig. 6. The bottom graphs (*C* and *D*) show that neurons with shorter and wider receptive-field subunits (low aspect ratio values) have more positive pattern indices (i.e., have larger pattern responses than component responses). Alternatively, neurons with long, narrow receptive-field subunits (high aspect ratio values) produce negative pattern indices (i.e., have larger component responses than pattern responses).

Receptive-field aspect ratio

Correlations between receptive-field aspect ratio and pattern indices were significant for both indices at the level of $P = 0.01$.

Spatial frequency

There were significant negative correlations ($P = 0.001$) between the preferred spatial frequency of V1 neurons and both the correlation pattern index and the response pattern index.

Temporal frequency

We observed a significant correlation between the preferred temporal frequency of V1 neurons and our indices of pattern/component selectivity. Both the correlation pattern index and response pattern index displayed a positive correlation with temporal frequency tuning ($P < 0.01$).

Similarity of pattern response and pattern correlation indices

To ascertain how comparable the pattern indices were we looked at the correlations between the two indices. There was an extremely high positive correlation of 0.81 ($P < 0.001$) between the pattern correlation index values and the pattern response index values.

DISCUSSION

We found a strong relationship between direction tuning width and subunit aspect ratio, and the relative response of a neuron to the direction of pattern or component motion. The relationship is as hypothesized: neurons with short, wide receptive-field subunits produce strong responses to the pattern motion of a moving plaid pattern. Conversely, neurons with long, narrow receptive-field subunits produce the strongest responses to the component motions of a moving plaid pattern.

TABLE 1. *Correlations between pattern indices and physiological properties of neurons*

Index	Parameter	Direction Tuning Width, deg	SF, cycles/deg	TF, cycles/s	Receptive-Field Aspect Ratio	Subunit Aspect Ratio
PCI (no units)	Spearman's r	0.76*	−0.67*	0.49*	−0.57*	−0.82*
	P-value	<0.001	<0.001	<0.01	0.001	<0.001
	n	31	28	30	31	28
PRI (no units)	Spearman's r	0.82*	−0.61*	0.55*	−0.46*	−0.79*
	P-value	<0.001	0.001	<0.01	0.01	<0.001
	n	31	28	30	31	28

Correlation values of Spearman's ranked correlation coefficient are shown. Significance values testing that the population r is not zero are shown. Two types of correlation are presented: one for the correlation between receptive-field properties and the *pattern response index* (PRI); the other is between receptive-field properties and the *pattern correlation index* (PCI) (the asterisk denotes a significant correlation coefficient at $P < 0.05$).
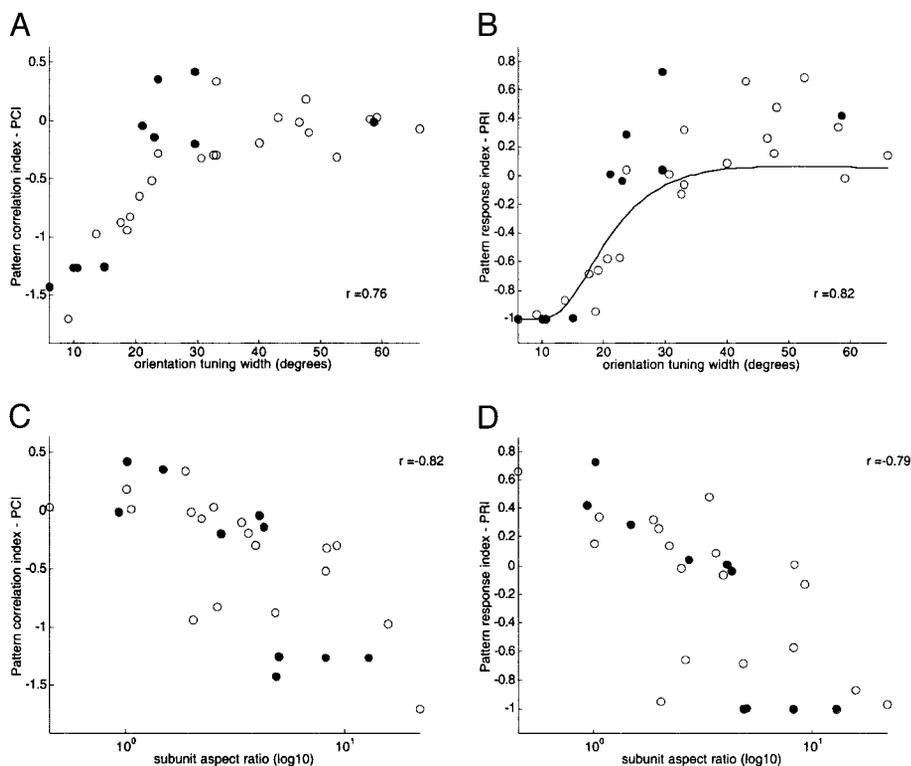
FIG. 6. *A* and *B*: graphs depicting relationship between pattern index and direction tuning width measured at half the peak height. *C* and *D*: graphs depicting receptive-field subunit aspect ratio. Graphs *A* and *C* use pattern correlation index; graphs *B* and *D* use pattern response index. Neurons that produce strong component responses to plaids have long and narrow receptive-field sub-units (high aspect ratios) and small direction tuning widths. Neurons that produce strong pattern responses to plaids have short and wide receptive-field subunits (low aspect ratios) and large direction tuning widths. Correlation values (Spearman's *r*) are shown on each graph. Black circles: simple cells; white circles: complex cells. Curve in *B* shows value of pattern response index predicted simply from summation of direction tuning curves of different widths.

We also found significant correlations between our pattern indices and preferred spatial and temporal frequency tuning of the V1 neurons in our sample. These correlations are likely to be related to the relationship between these parameters and direction tuning width; both preferred temporal and spatial frequency were correlated with direction tuning width. We also recorded from a small number of neurons that displayed the characteristic high pattern response and a low component response of pattern direction selective neurons. The response of these neurons cannot be explained by receptive-field structure alone; therefore it is seems likely that other mechanisms may be responsible for the responses of a small number of V1 neurons.

The idea that receptive-field structure is important for the detection of motion of moving plaid patterns as well as gratings has been suggested before. Geisler et al. (2001) found that parallel motion (i.e., 90° from the preferred direction of the neuron) of moving plaid patterns can be detected by V1 neurons in the cat and monkey. This result was explained by the alignment of neuronal receptive fields with the motion tracks of the elements of moving plaid patterns. Our analysis of neuronal responses did not involve the analysis of parallel motion of moving plaid patterns. The pattern response we analyzed using both our pattern indices referred to the motion of the plaid that was perpendicular to the alignment of the neurons' receptive field (as opposed to parallel).

The gradient between pattern-responsive neurons and component-responsive neurons

In this study we have deliberately avoided classifying neurons as pattern-selective or component-selective. This is because we were keen to investigate not only the neurons that are clearly classified as "pattern-selective" or "component-selec-

tive" because of their high correlation with the pattern or component prediction but also those whose responses were correlated with both models. In previous studies such neurons would have been labeled "unclassed" (i.e., neither pattern- nor component-selective) (Gizzi et al. 1990; Movshon et al. 1985). The significant correlations presented here between our pattern response index and receptive-field subunit aspect ratio, and receptive-field aspect ratio and direction tuning width, reveal that neurons with intermediate receptive-field properties will also produce intermediate responses to moving plaid patterns. Furthermore, these relationships indicate that there is a gradient of V1 responses to plaid patterns, rather than separate groups, and that this spectrum of responses is based on the variation in receptive-field structure of these neurons.

Pattern neurons and component neurons

In comparison to previous studies, we found clear component-selective neurons (see neuron no. 1, Fig. 3) that were described previously (Gizzi et al. 1990; Movshon et al. 1985). We also found neurons with greater responses to the pattern motion than to the component motion of moving plaid patterns (see Fig. 4, *row 2* and *row 3*, *column 1* and *column 2*). This type of neuronal response is also consistent with the idea of component selectivity. This is because the peak response to the direction of motion of the plaid pattern is consistent with a simple summation of overlapping direction tuning curves in the case of neurons with broad directional tuning (see curve in Fig. 6*B*). The responses of these neurons can also be explained by considering the similarity between the shape of the local features in the plaid pattern and the subunits of the receptive field. These neurons could be described as both *component responsive* and *local-feature responsive*.

The significance of responses to pattern motion in areas V1 and MT

Previously it was postulated that area MT is the primary area responsible for pattern responses to plaid motion and that this area produces these responses by performing an intersection of constraints like calculation on component responses from V1 neurons (Movshon et al. 1985; Movshon and Newsome 1996). Here we emphasize that area V1 may also have an important part to play in detecting the pattern motion of plaid patterns, even though the responses of neurons to such motion may not be purely pattern-selective. We hypothesize that neurons with short, wide receptive-field subunits may be able to contribute to the detection of pattern motion of a plaid by responding to the local features of the plaid (Derrington and Badcock 1992). Such neurons are likely to be part of the first stage of motion analysis, generating signals to be combined with the responses to component gratings to solve the aperture problem using the IOC. It seems more than likely that neurons that respond to pattern motion in area V1 may provide input to neurons that are pattern-selective in area MT. Simultaneous recording of such neurons in these areas may help to answer this question.

DISCLOSURES

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