Exp Brain Res (1989) 75: 53–64

Experimental Brain Research

Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT)

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Summary. The middle temporal visual area (MT) in macaque extrastriate cortex is characterized by a high proportion of neurons selective for the direction of stimulus motion, and is thus thought to play an important role in motion perception. Previous studies identified a population of cells in MT that appeared capable of coding the motion of whole visual patterns independent of the motions of contours within them (Gizzi et al. 1983; Movshon et al. 1985). These "pattern-motion selective" neurons are unlike motion sensitive cells that have been observed at earlier stages of the visual system. Using very different criteria, we have also previously indentified an apparently functionally distinct group of MT neurons (Albright 1984). We predicted that these "Type II" neurons correspond to the pattern-motion neurons. In the present study, we have applied both sets of criteria to individual neurons in MT and found that these two differently defined sets of cells actually form the same population. These results support the idea that MT contributes to a specialized type of motion processing which reflects the integrity of normal perception.

Key words: Area MT – Extrastriate cortex – Direction selectivity – Motion perception – Monkey

Introduction

Area MT of the macaque is a small, topographically organized, striate-recipient cortical zone located in the posterior bank of the superior temporal sulcus (Zeki 1974; Ungerleider and Mishkin 1979; Gattass and Gross 1981; Van Essen et al. 1981). Among extrastriate visual areas, MT is notable for the selectivity of its cells for direction and speed of motion (Maunsell and Van Essen 1983a; Albright 1984). Lesion studies have shown that area MT plays a role in the detection and discrimination of visual motion (Newsome and Pare 1986; Siegel and Anderson 1986) and in maintaining foveal pursuit of targets of interest (Newsome et al. 1985; Wurtz et al. in press).

The visual environment of an animal is likely to be made up of patterns considerably more complex than the oriented slits and edges traditionally used in neurophysiological experiments. The pioneering studies of Hammond and colleagues (e.g. Hammond and MacKay 1977; Hammond 1978) began the search for directionally selective responses to more complex patterns and began to dissociate direction and orientation sensitivity. However, until recently, virtually all of the direction selective responses that had been described in cortical cells remained explicable in terms of their concomitant orientation selectivity. In monkey (and also cat) striate cortex, cells are typically orientation tuned and preferentially responsive to movement in a direction perpendicular to the preferred orientation (Hubel and Wiesel 1968; Henry et al. 1974; Emerson and Gerstein 1977; DeValois et al. 1982). The majority of cells in area MT are identical to striate neurons in this respect (Maunsell and Van Essen 1983a; Albright 1984). However, two recent sets of results have found a small population of neurons in MT which may be capable of coding whole pattern motion, independent of the motions of constituent contours.

To study the motion selectivity of MT neurons, Movshon et al. (1985) employed plaid patterns formed by the intersection of two moving sinusoidal gratings, each at a different orientation. Under certain conditions of relative contrast, spatial frequency and direction of motion of the gratings, the

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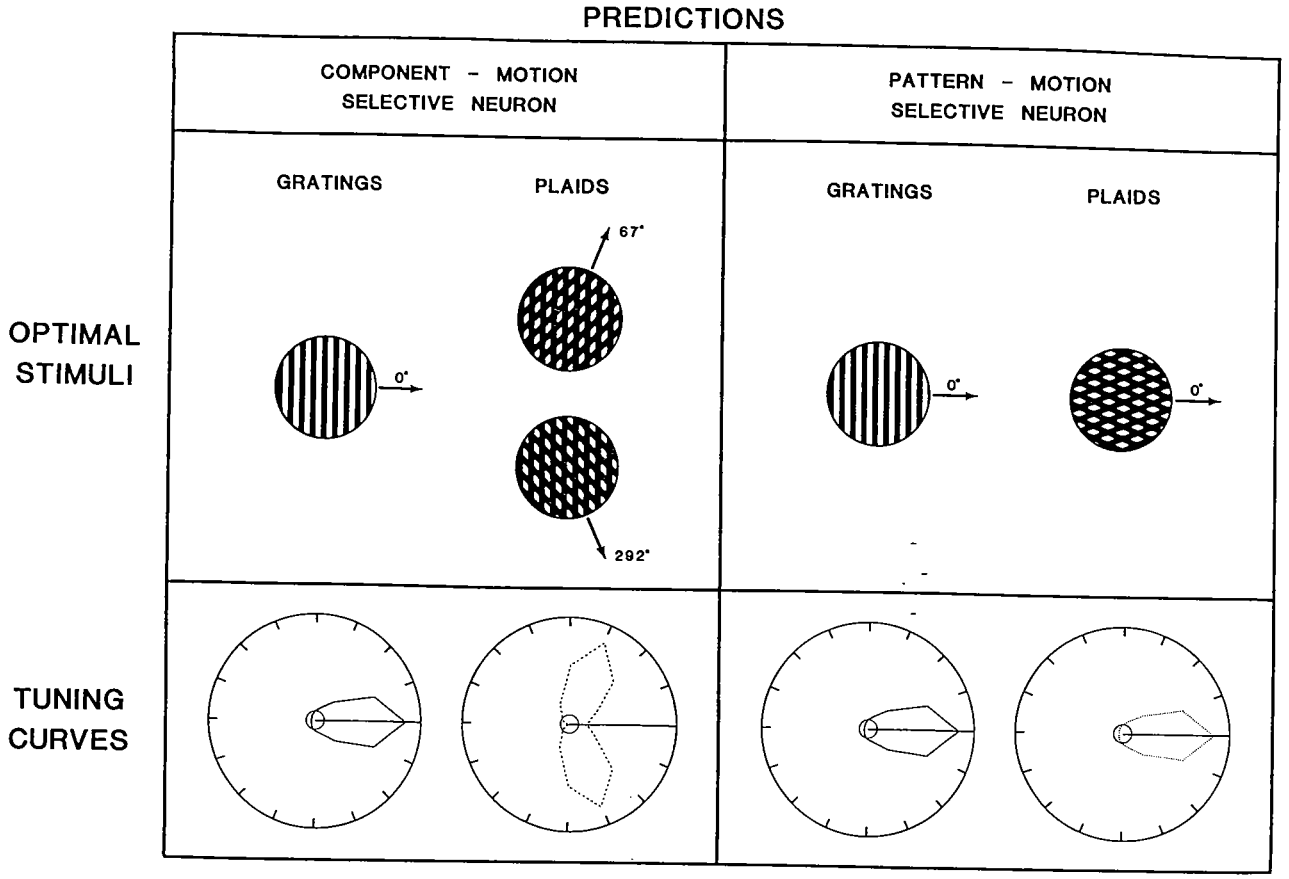

Fig. 1. *Left:* optimal stimuli (top) and direction tuning curves (bottom) for a hypothetical component-motion selective neuron in MT. In each of the polar direction tuning curves, radius corresponds to magnitude of response and polar angle corresponds to direction. Spontaneous firing rate is indicated by the dashed circle. The response to the single grating is best for movement directly to the right. From the moving grating curve, moving plaid component and pattern predictions are generated (see text for details). The predicted optimal plaid stimuli and plaid tuning curve reflect the cells' sensitivity to both oriented components in the plaid. *Right:* optimal stimuli (top) and direction tuning curves (bottom) for a hypothetical pattern-motion selective neuron. The predicted optimal plaid stimulus and plaid tuning curve reflect sensitivity to only the composite appearance of the plaid

intersection of the gratings forms an unambiguously moving and coherent "plaid", as reported by human subjects (Adelson and Movshon 1982). The direction and speed at which the plaid appears to be moving is different from that of either of the gratings alone. A cell sensitive only to the motion of the oriented components of the plaid should respond well only when the pattern stimulus contains one component moving in the preferred direction (see Fig. 1). On the other hand, a cell truly sensitive to the motion of a pattern independent of its oriented components should respond to the motion of the whole plaid in the same way it would respond to an isolated component. In other words, for a pattern-motion selective cell, the optimal speed and direction of a coherent plaid would be the same as the optimal speed and direction of a single grating or bar. Movshon et al. showed that while virtually all neurons tested in cat and monkey striate cortex and in cat superior colliculus and lateral suprasylvian area are component-motion selective, about 25% of the neurons in MT show pattern-motion selective behavior.

Using more traditional stimuli, Albright (1984) identified a population of neurons in MT that may correspond to Movshon et al.'s pattern-motion cells. While 60% of MT cells selective for both direction of a moving spot or random dot pattern and orientation of a slit shown direction selectivity perpendicular to the preferred orientation (Type I) (Fig. 2), another 30% are selective for the direction of spot motion parallel to the preferred bar orientation (Type II) (Fig. 3). The behavior of Type II cells corresponds to that of a pattern-motion detector that receives inputs from an array of orientation- and speed-selective component-motion detectors. An oriented contour viewed through an aperture (such as a receptive field) will appear stationary within a moving pattern

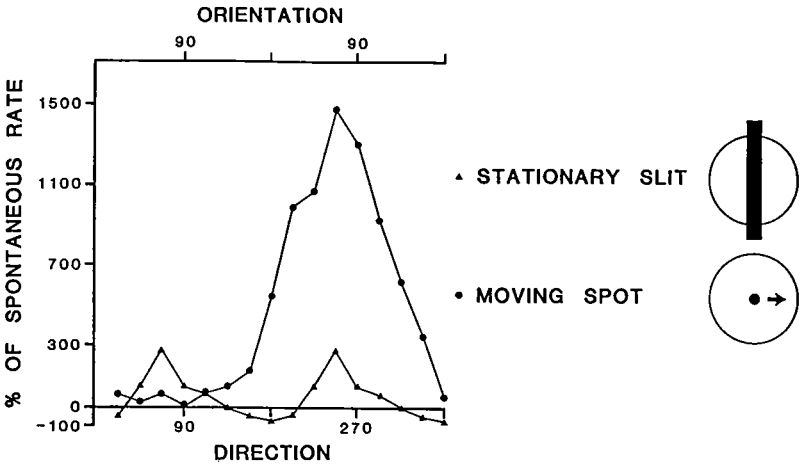

Fig. 2. Direction and orientation tuning curves from a typical Type I MT neuron illustrating the relationship between optimal direction and optimal orientation. Responses are plotted at left as a function of direction for the moving spot and as a function of orientation for the stationary slit. Two cycles of orientation tuning are plotted to facilitate comparison with direction tuning. (Although orientation varies over only 180°, for each "orientation" of the moving spot there are two directions of motion and the direction parameter varies over 360°.) The alignment of peaks for the moving and stationary stimuli reflects an orientation preference that is perpendicular to direction preference. This relationship is illustrated schematically at right

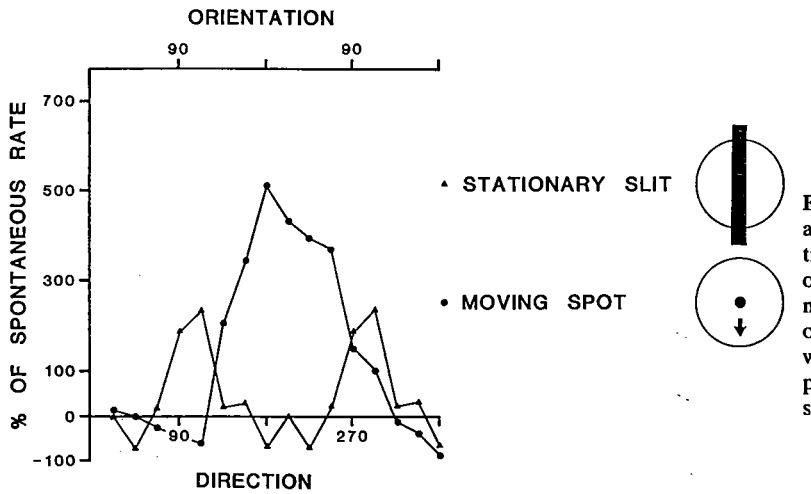

Fig. 3. Direction and orientation tuning curves from a typical Type II MT neuron illustrating the relationship between optimal direction and optimal orientation. The optimal orientation for the stationary slit is shifted approximately 90° away from the optimal direction of motion. This relationship, which reflects an orientation preference that is parallel to direction preference, is illustrated schematically at right. See also legend to Fig. 2

only when the pattern is moving parallel to the axis of the oriented contour. Thus, when a stationary slit is presented alone, it presumably activates component-motion detectors which provide input to only those pattern-motion detectors that are selective for movement along the axis of the preferred orientation – as are Type II cells.

Thus, we predicted that Type II cells and Movshon et al.'s pattern-motion selective neurons in MT constitute a single population involved with pattern-motion processing. However, the tests for the two classifications have not previously been applied to the same cells, and it is conceivable that the two populations are actually functionally distinct. In order to illuminate the unusual properties of Type II neurons and lend support to the notion of MT as the locus of a pattern-motion processing mechanism, we investigated the overlap of the Type II and pattern-motion selective populations by testing MT neurons with the stimuli relevant to both of the classifications and identifying them accordingly.

Methods

Animal preparation and maintenance

Four male *Macaca fascicularis* weighing between 3.6 and 6.0 kg were each recorded from once or twice weekly for up to six sessions. One week prior to the first recording session, a 2.5 cm diameter stainless steel recording well and cap and a stereotaxically oriented headbolt were affixed to the animal's skull with screws and dental acrylic. Surgical procedures were performed under ketamine hydrochloride (Ketaset) anesthesia, using an initial dose of 35 mg/kg and supplemented with 50 mg as necessary. Prior to surgery, atropine sulfate (0.15 mg/kg) was given to reduce mucous secretions. Diazepam (Valium, 2.5 mg) was given to ease recovery.

On the day of the recording session, the animal was given atropine as above, a restraining dose of ketamine hydrochloride (4 mg/kg), and then anesthetized with a 7 : 3 mixture of nitrous oxide and oxygen to which 2% halothane was added. The head was held in a stereotaxic apparatus by means of the head bolt and a holder attached to the apparatus. After the cap was removed from the recording well, a small hole was drilled through the bone, leaving the dura intact. Halothane was then discontinued and anesthesia was maintained by a 7 : 3 mixture of nitrous oxide and oxygen. To prevent eye movements, the animal was immobilized

with an intravenous infusion (0.03 mg/kg/h) of pancuronium bromide (Pavulon) in dextrose-lactated Ringers solution, and subsequently artificially ventilated. Temperature was maintained at 37–38° C with heating pads, and respiratory rate was adjusted to give an end-tidal carbon dioxide level of about 4%. Heart rate was also monitored. The pupils were dilated with cyclopentolate (Cyclogyl, 1%) and the corneas covered with contact lenses selected to focus the eyes on a rear-projection tangent screen 57 cm away. Recording sessions lasted 12–17 h and were separated by a minimum of two days.

Recording

Varnish-coated tungsten microelectrodes with exposed tips of 10 μm or less were used to record extracellular potentials from single isolated neurons. Electrodes were angled 40° from vertical in the parasagittal plane passing dorsoanteriorly to ventroposteriorly. Recordings were made from the portion of MT representing the visual field within approximately 30° of the center of gaze. Spikes were considered to be arising from a single neuron if they were of constant amplitude and waveform.

Visual stimulation and analysis of responses

Once a cell was isolated, preliminary observations were made using a hand-held tungsten-filament projector and an audio monitor of single-unit activity. Stimuli were presented on a tangent screen subtending 60° by 60° with a background luminance of 2 cd/m^2. Stimulus intensity was approximately 1.5 log units above background. First, optimal values of stimulus parameters such as bar length and width, spatial frequency, and speed of motion were estimated using the eye contralateral to the recording site. The optimal stimulus was then used to plot the receptive field (RF).

Quantitative testing was performed using stimuli produced by a PDP-11/34A computer with the aid of waveform generators and an electronic image-rotation device and displayed on an X-Y CRT screen (HP1300A) which could be positioned to subtend a maximum of about 25° × 15° of the visual field. Four types of stimuli were used: moving gratings, moving plaids, moving spots and stationary slits. (In this and previous studies (Albright 1984) a moving spot was used to test pattern motion direction preference. Like a moving random dot pattern, a moving spot contains some energy at every orientation, and local measurements of velocity (e.g. by component-selective neurons viewing small sections of the spot's perimeter) are by themselves ambiguous.) The moving grating, moving plaid, and stationary slit stimuli were generated by modulating the intensity of a uniform raster (100 frames/s, 1000 lines/frame) with signals from the computer. Perceptually coherent moving plaid stimuli were generated by interleaving frames of the moving grating stimulus oriented at an angle of 135° to one another. The CRT screen was centered on the neuron's RF and fitted with an aperture sized to extend about 1 cm beyond the RF borders. The spatial frequency, contrast and, for the moving stimuli, speed of motion of the stimuli were chosen to evoke optimal responses from each neuron tested. Spatial frequencies used for the moving grating and moving plaid stimuli ranged from 1–4 cycles/deg. Speeds used ranged from 4–32 deg/s. For all cells, at least three cycles of these stimuli fit within the RF.

For a given cell, the same speed was used for both moving grating and moving plaid tests. In other words, the speed of the single grating tested alone was equivalent to that of the coherent motion of the plaid in the moving plaid test. In this way, we attemped to present cells with "component" and "pattern" stimuli having identical subjective motions. However, because the oblique components of a pattern necessarily move at speeds less than that of the whole pattern (see Albright et al. 1986), the moving gratings constituting the moving plaid had a speed lower than that of the moving gratings presented alone. Each of the types of moving stimuli was presented in 16 directions of motion with a constant angular deviation (22.5°) separating one direction from the next. For the single moving grating and the interleaved moving gratings used to generate the moving plaid, stimulus orientation was always perpendicular to the absolute direction of movement. The stationary slit was presented in each of 8 orientations with a constant angular deviation of 22.5° between neighboring orientations. The stimuli extended slightly beyond the borders of the aperture (and thus the RF) in all cases. All stimuli were presented for a duration of 2.5 s. For each type of stimulus, a test consisted of a series of 5 pseudorandomly interleaved presentations of each direction or orientation.

Both the moving grating and the moving plaid uniformly stimulated the entire RF for the duration of presentation. The measure of response used for these stimuli was the spike rate averaged over the entire pesentation interval. The moving spot did not stimulate the entire RF during presentation and, thus, the measure of response used was the average spike rate in a time window centered around the peak response for each direction of motion. For stationary stimuli, the measure of response was the average number of spikes per second during the stimulus exposure. (In Figs. 2 and 3, percent of spontaneous spike rate is used as the measure of response. This measure is linearly related to average spike rate and is useful for comparing two or more sets of data on the same graph.)

Histology

At the completion of experimentation, each animal was anesthetized with an overdose of intravenous sodium pentobarbitol and perfused through the heart with saline followed by 10% buffered formalin. The brain was allowed to sink in sucrose formalin, blocked in a stereotaxic apparatus, and sectioned in the parasagittal plane on a freezing microtome. Sections were cut at 50 μm and stained alternately with cresylecht violet or the Gallyas silver myelin stain (1969). Electrode penetrations were reconstructed from sections stained with cresylecht violet. The boundaries of area MT within the superior temporal sulcus were determined from myeloarchitectonic transitions seen in the Gallyas-stained material.

Results

Quantitative testing with all four types of stimuli was carried out for 33 MT neurons recorded along 15 penetrations in the four animals. Additional cells recorded on these and other penetrations through MT in the same hemisphere were not tested with all of the types of stimuli requisite for classification and were thus excluded from the final analysis. This group included cells which became injured or poorly isolated before testing was completed, and, early in the study, cells which were unresponsive to or nonselective for the orientation or direction of motion of one or more of the stimulus types. Later in the study, it was noted that cells which were unresponsive to or nonselective for either or both the moving spot and the stationary slit tended to show

behavior intermediate between pattern- and component-motion selectivity when their responses to the moving grating and moving plaid were compared (see below). Subsequently, all cells which responded to the moving grating and moving plaid stimuli were tested fully and included in the analysis, even if they did not respond selectively to one or both of the stimuli used for the Type I/Type II classification.

Classification as Type I or II

Cells were categorized as Type I or Type II by determining the angular difference between the preferred direction of motion (moving spot test) and the preferred orientation for the stationary contour (stationary slit test). A difference of 0° between tuning curve peaks reflects a stationary oriented contour preference that is exactly perpendicular to the preferred direction of pattern motion (the relationship that one would expect from a component-motion detector). Type I MT neurons (15/33, 45%) were defined as those having a difference measure of less than 30° (Fig. 2). On the other hand, a difference measure of 90° between the moving spot and stationary slit tuning curve peaks reflects an oriented contour preference that is exactly parallel to the preferred direction of pattern motion (the relationship one would expect for a pattern-motion detector). Type II MT neurons (8/33, 24%) were defined as those having a difference measure of 60–90° (Fig. 4). Neurons with difference measures between 30° and 60° were designated as Type 0, as were neurons that were unresponsive to or nonselective for either the stationary slit or moving spot or both (10/33, 31%).

Classification as component- or pattern-motion selective

Procedures for this portion of the analysis followed those of Movshon et al. (1984). Briefly, for each neuron, a "component prediction" and a "pattern prediction" for the pattern motion stimulus (moving plaid) were generated from the component stimulus data (moving grating) and compared with the actual moving plaid responses, as follows. The predicted tuning curve of a component-motion selective neuron to the moving plaid is the sum of the responses to each of the components presented separately, and appears as a bilobed curve with peaks straddling the single peak of the moving grating tuning curve (Fig. 1, left). With a plaid made up of components oriented at 135° to each other, the predicted peaks for the moving plaid data are shifted from the moving grating preference (here 0°) by 67° in each direction. The neuron responds optimally when the direction of motion for the moving plaid is either 67° or 292°, since these plaid stimuli each contain a vertically oriented, rightward moving component. The predicted moving plaid tuning curve for a pattern-motion selective neuron, on the other hand, is unimodal and identical to that derived from the moving grating data, since by definition the neuron is viewing only the overall direction of motion, and not that of the components (Fig. 1, right).

The "component prediction" was generated by taking the responses to each of the directions of motion that make up the moving grating tuning curve and adding them to the same set of responses to the 16 directions of motion shifted by 135°. The "pattern prediction" was simply the set of responses to each of the directions of motion of the moving grating. Thus, each prediction consisted of a set of 16 response values in spikes/s, one for each direction of plaid motion. Component and pattern predictions were then correlated with the actual responses of the cell to the sixteen directions of plaid motion, using the procedure developed by Movshon et al. A partial correlation coefficient was calculated as follows:

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

where:

R_p = partial correlation for the pattern prediction

r_c = raw correlation of the data with the component prediction

r_p = raw correlation of the data with the pattern prediction

r_{pc} = correlation of the two predictions

A partial correlation coefficient R_c for the component prediction was similarly calculated by exchanging r_p and r_c. These values were used to classify each neuron as pattern- or component-motion selective or neither. The top left of Fig. 4 shows a data space, adapted from Movshon et al., in which the partial correlation coefficients R_c and R_p can be plotted against each other. The zone marked "component" contains values of R_c that are significantly greater than either R_p or 0. The zone marked "pattern" contains values of R_p which are significantly greater than either R_c or 0. The zone marked "unclassified" contains points for which neither R_c or R_p significantly exceed zero, or for which both do so, but do not differ significantly from one another. For each neuron, R_c and R_p were plotted and the location of the resulting point in the space was used to classify the neuron. Using these criteria, pattern-motion selective cells (10/33) made up 30% of the sample and

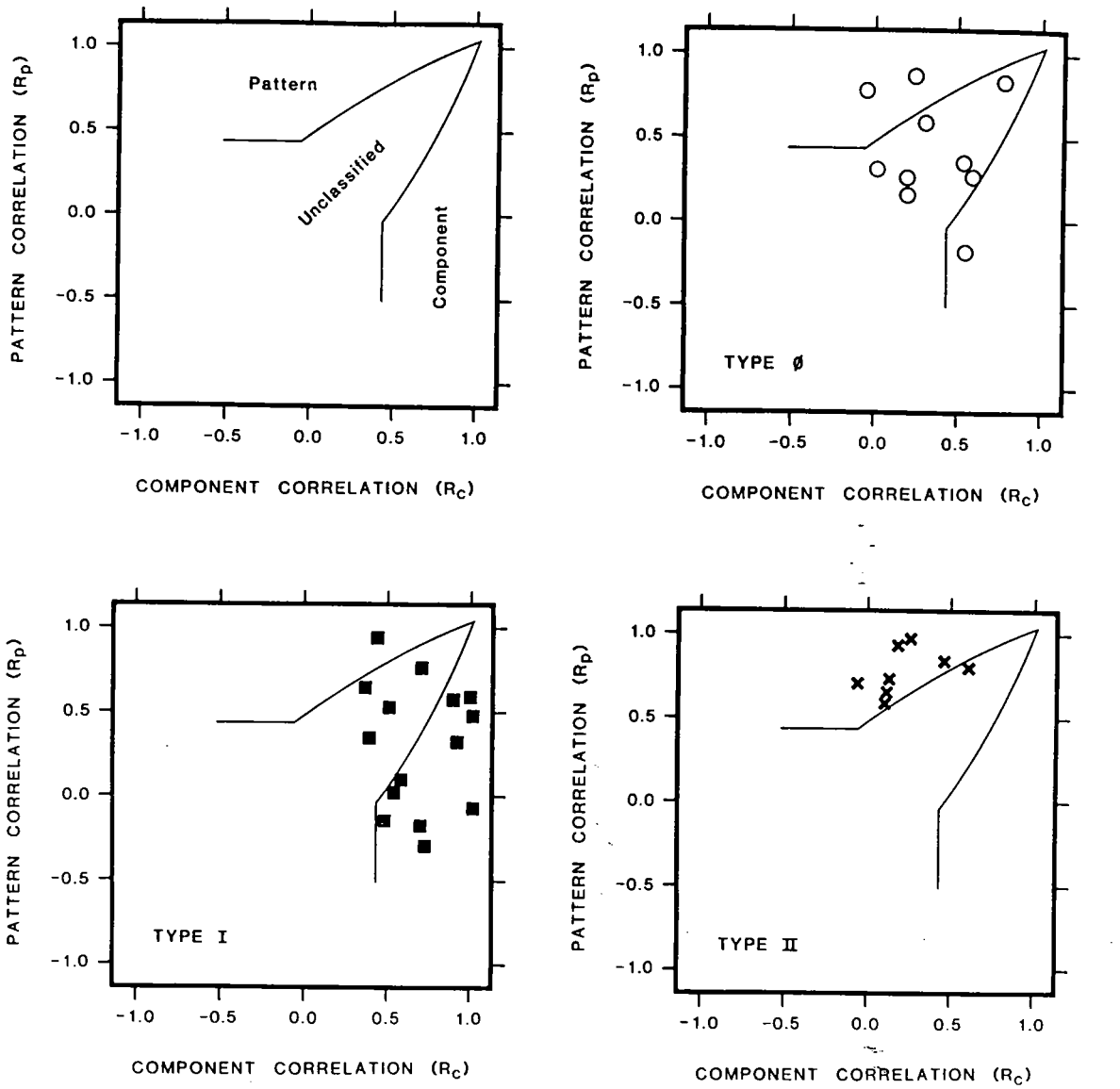

Fig. 4. *Top left:* data space (adapted from Movshon et al. 1985) used to show classifications of component- and pattern-motion selectivity. The degree to which a cell's direction tuning for the moving plaid is correlated with the prediction for pattern-motion selectivity is plotted vs. the correlation for the component-motion prediction. Cells are then labelled as pattern, component or unclassified depending on where fall in the data space (see for details). *Bottom left:* most of the Type I MT neurons are identified as component-motion selective. *Bottom right:* all but one of the Type II neurons are also clearly identified as pattern-motion selective. *Top right:* type 0 neurons (unclassifiable as Type I or II) tend to be unclassifiable as component- or pattern-motion selective as well

component-motion selective cells about 33% (11/33), with the remaining 12/33 (36%) not categorized as either.

Comparisons of classifications

Overall the neurons in our sample form a continuous distribution ranging from those clearly classifiable as component-motion selective to those clearly pattern-motion selective. However, if cells of Types I, II and 0 are considered separately (Fig. 4), groupings do appear. All but one of the Type II neurons (bottom right) fall within the pattern zone, whereas the majority of neurons not classified as Type II fall instead into the component or intermediate groupings. This difference is significant at the 0.001 level ($\chi^2 = 16.4$, df = 1). Similarly, Type I neurons (bottom left) tend to be component-motion selective far more often than do cells classified as Type II or 0

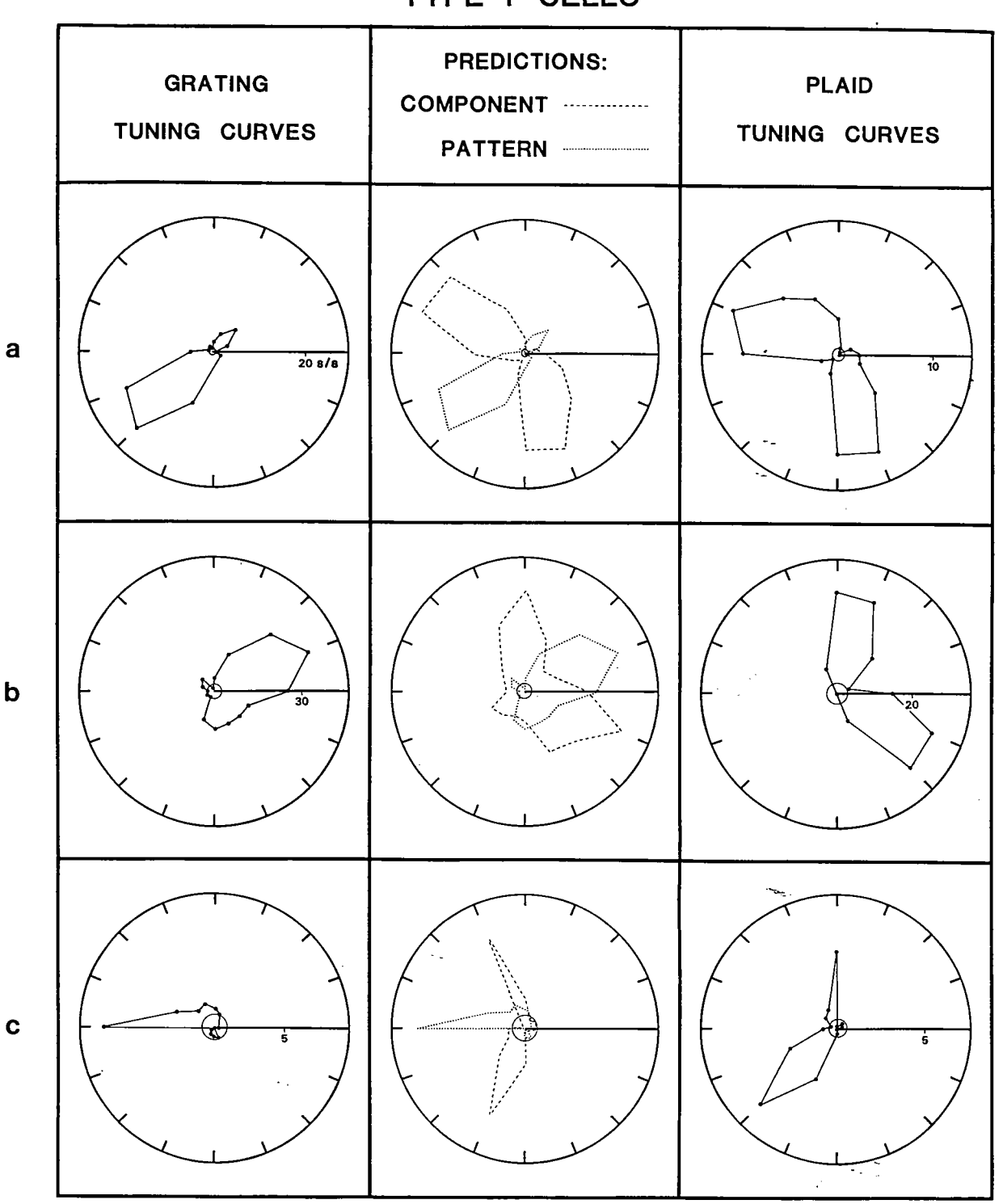

Fig. 5. Examples of direction tuning curves for the moving grating (first column) and moving plaid stimuli (third column) obtained from three representative Type I neurons, along with predicted responses for "component-selective" and "pattern-selective" behavior (column 2). Radius corresponds to response in average spikes/s and polar angle corresponds to direction; spontaneous firing rate is indicated by the small circle. Component and pattern predictions have been drawn to the same scale as the moving grating response. The moving plaid tuning curves have been drawn to the scale which best shows their overall shape and facilitates comparison to the predicted curves. Actual response magnitude is shown on the radius of each plot. For each cell shown here, direction tuning for the moving plaid conforms better to the component prediction than to the plaid prediction. Cell *a:* partial component correlation coefficient (R_c) = +0.90, partial pattern correlation coefficient (R_p) = –0.11; cell *b:* R_c = +0.87, R_P = +0.54; cell *c:* R_c = +0.43, R_p = –0.14

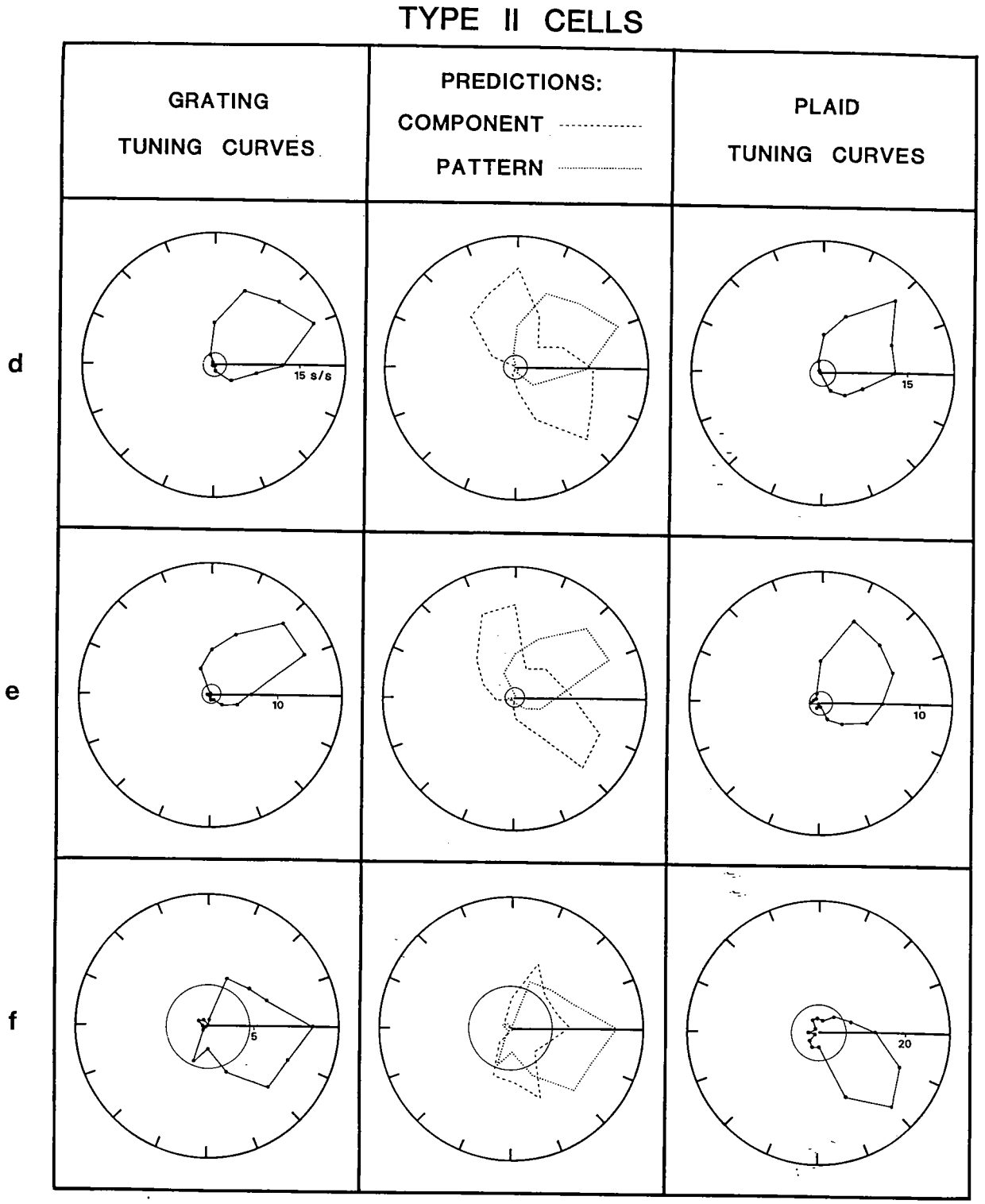

Fig. 6. Examples of direction tuning curves for the moving grating and moving plaid stimuli obtained from Type II neurons, along with component and pattern predictions. For each neuron shown here, direction tuning for the moving plaid conforms better to the pattern prediction than to the component prediction. Cell *d:* $R_c = +0.27$, $R_p = +0.95$; cell *e:* $R_c = +0.18$, $R_p = +0.91$; cell *f:* $R_c = -0.05$, $R_p = +0.70$. See also legend to Fig. 5

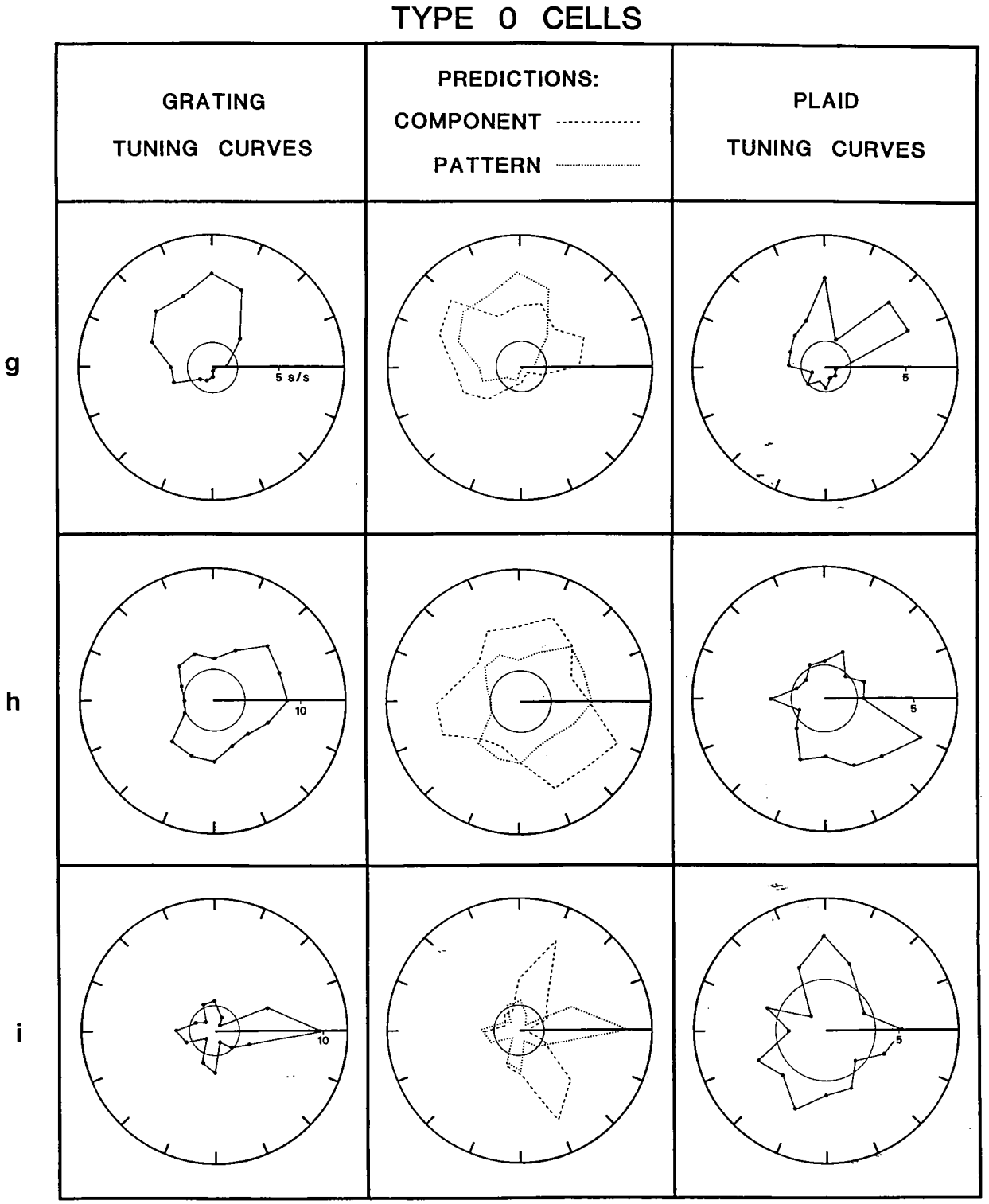

Fig. 7. Examples of direction tuning curves for the moving grating and moving plaid stimuli obtained from several neurons that could not be classified as either Type I or Type II along with component and plaid predictions. For some such neurons (e.g., cells g and i) the moving plaid response does not correlate well with either the component or pattern predictions. For others (e.g., cell h) the moving plaid response correlates moderately well with one or both of the predictions, but the difference between R_c and R_p is not statistically significant. Cell *g:* $R_c = +0.19$, $R_p = +0.19$; cell *h:* $R_c = +0.56$, $R_p = +0.25$; cell *i:* $R_c = +0.16$, $R_p = +0.27$. See also legend to Fig. 5

($\chi^2 = 13.2, p < 0.001$, df = 1). Finally, cells classified as neither Type I nor Type II (Type 0) are likely to be unclassified as component or pattern as well ($\chi = 7.0$ $p < 0.01$, df = 1).

Figure 5 shows polar plots of direction tuning for the moving grating and moving plaid stimuli for three Type I MT neurons from the sample. As in Fig. 1, the component- and pattern-motion predictions for the moving plaid response have been generated from the moving grating response for each neuron. The moving plaid tuning curves shown are typical of the majority of Type I neurons, i.e., of cells whose data fell into the "component" region of the data space shown in Fig. 4. For each, the moving plaid responses conform well to the component prediction, and less well or poorly to the pattern prediction. For each of these cells (and the majority of Type I neurons), the moving plaid direction tuning curve has the bilobed appearance indicative of peak responsiveness to the two directions of the moving plaid containing the preferred component, i.e., the optimal moving grating. Neurons a and b have peaks in the moving plaid tuning curve which match up well with those of the component predictions, and thus have high partial component correlations (R_c). Neuron c has peaks in the moving plaid tuning curve which are slightly offset from those of the component prediction. Thus, the partial component correlation for the cell's moving plaid data is considerably lower than that for neurons a and b; however, the partial *pattern* correlation coefficient (R_p) is actually slightly negative.

Figure 6 shows direction tuning curves for the moving grating and moving plaid stimuli for three representative Type II neurons. These tuning curves illustrate the behavior of neurons whose data fell into the "pattern" region of the data space in Fig. 6. For each of these neurons, the moving plaid response correlates well with the pattern prediction and less well or poorly with the component prediction. For each of the neurons illustrated here the moving plaid direction tuning shows a single peak which approximates the pattern prediction, indicative of responsiveness to overall motion of the pattern as a whole. For each of these cells, the partial pattern coefficient is high and the partial component correlation low (cells d and e) or negative (cell f).

Figure 7 shows direction tuning curves for the moving grating and moving plaid stimuli for three neurons that could not be classified as either Type I or Type II. Most of the neurons in this category demonstrated behavior falling into the "unclassified" region of the data space shown in Fig. 6. For such neurons, the moving plaid tuning curve either correlated well with neither the pattern nor component predictions or correlated similarly with both. A few

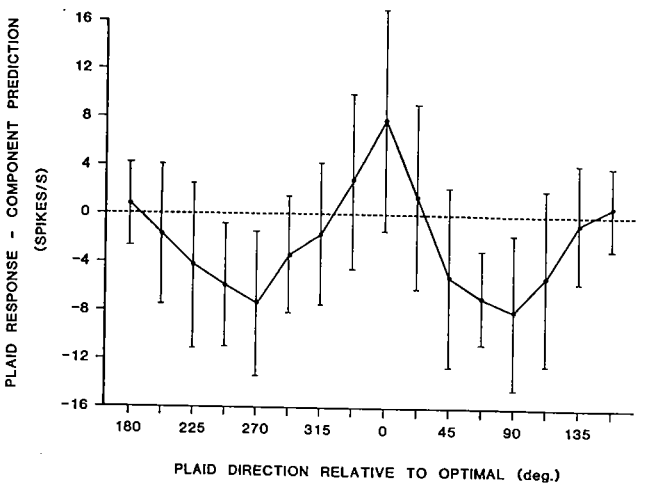

Fig. 8. Difference between actual plaid response and response predicted from linear summation of responses to component gratings ("component prediction") as a function of plaid direction relative to optimal plaid direction. Data points represent mean values for all pattern-motion cells in the sample. The component prediction for each cell was generated by linearly summing the responses of the cell to the gratings that make up the plaid. Preferred plaid direction has been normalized to 0° for all cells. Facilitation is greatest for the optimal moving plaid, whereas suppression is maximal at about directions 90° and 270°, each of which contains a single component grating moving in the preferred direction

Type I neurons and one Type II (see Fig. 4) showed this type of moving plaid tuning as well. As Movshon et al. have also found, many of the neurons in our sample which could not be classified as either component- or pattern-motion selective had broad and/or ragged direction tuning curves for the moving grating (e.g., cells g and h). Some, but not all, of these cells exhibited ragged and/or very broad tuning curves to the moving spot as well.

Receptive-field interactions in pattern-motion cells

Pattern-motion cells often gave responses to the optimal plaid that were greater than the sum of the responses to the plaid's components. Likewise, non-optimal plaids often produced responses smaller than the sum of the component responses. Figure 8 illustrates this nonlinearity as a function of plaid motion relative to the optimal plaid direction. Values on the Y-axis were generated by taking the mean, across all pattern-motion cells, of the difference between the actual plaid response and the response predicted by a linear summation of the responses to the constituent gratings ("component prediction"). Facilitation is maximal for the optimal moving plaid direction, and falls off sharply as direction deviates

from this optimal. Suppression appears to be maximal near the direction of plaid motion which contains one component *grating* moving in the preferred direction.

The gratings used to make up the plaid stimuli had a speed somewhat less (and less optimal) than the gratings used for the moving grating test (see Methods), from which the component prediction was generated. Thus, the component prediction is probably a slight overestimate of what the cell's response would be if it linearly summed responses to the plaid components. Accordingly, the difference measure plotted on the Y axis in Fig. 8 is probably a slight *underestimate,* and should be taken as only a relative index of the average nonlinearity of the pattern-motion cell's computation as a function of pattern direction. It is worth noting that while the relative roles of inhibition and facilitation cannot, therefore, be deduced from Fig. 8, evidence has been found for both processes in pattern-motion selectivity (Movshon et al. 1984).

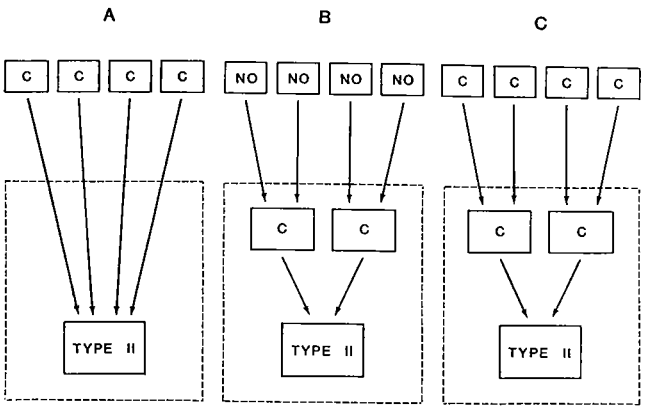

Fig. 9A–C. Possible schemes for the wiring of a pattern-motion detector in MT. Area MT is represented by the dashed rectangle. **A** Direct convergence from component-motion selective neurons outside MT onto pattern-motion (Type II) neurons. **B** Inputs from non-orientation-selective (NO) cells outside MT converge onto component-motion selective cells (Type I) in MT, which then project to pattern-motion neurons. **C** Component-motion selective inputs from outside MT converge onto component-motion selective cells in MT, which in turn provide inputs to Type IIs. In each scheme, facilitatory and inhibitory interactions are permitted between the members of the component-motion selective population which provide inputs to pattern-motion MT neurons

Discussion

This experiment was designed to test the hypothesis that the unusual properties of Type II MT neurons, described previously by Albright (1984), can be explained by their selectivity for the motion of whole patterns. Using the stimuli and classification scheme devised by Movshon and his colleagues (Adelson and Movshon 1982; Gizzi et al. 1983; Movshon et al. 1985), we have confirmed that a small proportion of the neurons in MT are selective for the motion of patterned stimuli rather than for the motion of oriented components within those patterns. Moreover, we have found that a) Type II neurons are pattern-motion selective neurons; b) Type I neurons are component-motion selective neurons; and c) neurons unclassifiable as Type I or II are, more often than not, also unclassifiable as either pattern- or component-motion selective. Finally, we have presented evidence that facilitatory and/or inhibitory RF interactions are important in the generation of pattern-motion selectivity.

Figure 9 illustrates several possible schemes for how pattern-motion detectors in MT might be wired up from component-selective ("oriented") inputs. One possibility (scheme A) would be for pattern-motion MT neurons to receive converging oriented inputs directly from structures outside of MT. The other two possibilities require initial convergence of inputs from outside MT upon component-motion selective (Type I) neurons in MT, which then provide the direct input to pattern-motion neurons. Component selectivity might be generated at the inital stage in MT from unoriented inputs (scheme B); alternatively, inputs to the initial stage in MT might come from oriented cells from structures outside MT (scheme C). Some evidence exists to support each possibility. Antidromic experiments (Movshon and Newsome 1984) indicate that most of the striate cortex input to MT is from component-motion selective neurons, specifically supporting schemes A and C. Movshon et al. (1985) report some laminar segregation of their cell types in MT, with neurons falling into the pattern-motion group found more often in layer II, III, and V, and component-motion neurons found more often in layers IV and VI. Since most of the striate projections to MT terminate in layer IV (Ungerleider and Desimone 1986), it is likely that striate inputs, at least, converge on component-motion cells rather than contacting pattern-motion neurons directly. This evidence supports schemes B and C over scheme A.

However, MT receives projections from visual structures other than striate cortex, in particular from the superior colliculus via the inferior pulvinar (Benevento and Fallon 1975; Maunsell and Van Essen 1983b). We have recently shown that, for at least some MT neurons, visual responsiveness and direction selectivity per se are not dependent upon the integrity of striate cortex (Rodman et al. 1985). The residual responsiveness is obliterated by a superior colliculus lesion (Rodman et al. 1986). Since

inferior pulvinar neurons lose their direction selectivity following striate cortex removal (Bender 1983), visual information reaching MT from the colliculus through the inferior pulvinar following a striate lesion is probably nonoriented. Thus, it appears likely that MT is capable of generating component direction selectivity locally on the basis of even unoriented input (scheme B). It remains to be seen whether such input is also sufficient for the generation of pattern-motion selectivity or whether oriented input from striate cortex or elsewhere is necessary.

Acknowledgements. We wish to thank C. Gross for his assistance and for valuable discussions of the significance and presentation of this material. We also wish to thank J. A. Movshon, C. Colby, S. Fenstemaker and G. Stoner for their comments on earlier drafts, M. Hess for work on the histology and figures, and D. Flowers and M. Rosengarten for typing. Support was provided by N.I.H. grant MH-19420, N.S.F. grant BNS-8200806, and an N.S.F. predoctoral fellowship to H.R.

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Received January 4, 1988 / Accepted September 19, 1988