Exp Brain Res (1992) 88:389–400

Experimental Brain Research

The response of neurons in areas V1 and MT of the alert rhesus monkey to moving random dot patterns

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Received November 14, 1990 / Accepted October 23, 1991

Summary. We studied the response of single units to moving random dot patterns in areas V1 and MT of the alert macaque monkey. Most cells could be driven by such patterns; however, many cells in Vl did not give a consistent response but fired at a particular point during stimulus presentation. Thus different dot patterns can produce a markedly different response at any particular time, though the time averaged response is similar. A comparison of the directionality of cells in both V1 and MT using random dot patterns shows the cells of MT to be far more directional. In addition our estimates of the percentage of directional cells in both areas are consistent with previous reports using other stimuli. However, we failed to find a bimodality of directionality in V1 which has been reported in some other studies. The variance associated with response was determined for individual cells. In both areas the variance was found to be approximately equal to the mean response, indicating little difference between extrastriate and striate cortex. These estimates are in broad agreement (though the variance appears a little lower) with those of Vl cells of the anesthetized cat. The response of MT cells was simulated on a computer from the estimates derived from the single unit recordings. While the direction tuning of MT cells is quite wide (mean half-width at half-height approximately 50°) it is shown that the cells can reliably discriminate much smaller changes in direction, and the performance of the cells with the smallest discriminanda were comparable to thresholds measured with human subjects using the same stimuli (approximately 1.1°). Minimum discriminanda for individual cells occurred not at the preferred direction, that is, the peak of their tuning curves, but rather on the steep flanks of their tuning curves. This result suggests that the cells which may mediate the discrimination of motion direction may not be the cells most sensitive to that direction.

Key words: Motion perception – V1 – MT – Random dot patterns – Response variance – Direction discrimination – Alert monkey

Introduction

Complex patterns such as visual noise and random dot patterns have been widely used in the psychophysical research of motion perception because they contain no features which can be tracked from frame to frame, thus allowing the isolation of the motion system (Nakayama and Tyler 1981). Their use for single cell recording has also proved fruitful (e.g. Hammond and MacKay 1975; Gulyás et al. 1987; Skottun et al. 1988) but has mostly been limited to the anesthetized cat. While these studies are most valuable, it is often difficult to compare such data with psychophysical studies of motion perception in humans. Two major factors seem relevant. Firstly, when a psychophysical task is performed the subjects typically attempt to fixate a point. The exact point of fixation will vary from trial to trial (as we will demonstrate for the monkey), and there will be microsaccades and slow drifts even when "fixation" occurs (Motter and Poggio 1984; Snodderly and Kurtz 1985). Secondly, striate cortex in the cat and monkey cannot be regarded as functionally identical. For example the proportion of directionally selective cells is different in the two areas (around 70% in the cat and 30% in the monkey and in addition, they have different layering characteristics (Gilbert 1977; Hawken et al. 1987). It therefore is of great interest to collect data on the response of single cells in the alert primate and to compare these data with relevant studies of human psychophysics, the physiology of cat cortex, and with previous reports on monkey cortex using both anesthetized and alert animals. One notable exception to the studies cited above is a recent report by Newsome et al. (1989). They recorded from neurons in MT/V5, an area believed to be important for the perception of motion (Zeki 1974; Newsome and Paré 1988), while a mon-

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key viewed moving, partially correlated random dot patterns. They were able to show that individual neurons can, with certain assumptions, distinguish opposite directions of motion at similar correlation levels to the animal itself.

In order to ascertain the relationships between psychophysical performance and the response properties of single cells we have recorded from single units in areas MT and V1 of the alert, behaving monkey. The stimuli employed were patterns of randomly placed dots of high luminance, whose direction, density and speed were under experimental control. We have also quantified the variance of eye movements while the animals fixated in the presence of the stimuli. The response variance of area V1 and MT cells was measured for different mean levels of activity and the direction tuning of area MT neurons was quantified.

Using the data from single MT cells relating the mean response to the direction of motion, and the response variance to the mean response, we modelled the ability of individual MT neurons to discriminate different directions of motion. Direction discrimination thresholds for human observers were also measured using the same stimuli employed in the single cell studies. To anticipate the results, our data indicate that a small number of MT neurons can discriminate changes in direction with a similar precision to human observers. Interestingly, the minimum discriminanda occur on the flanks rather than on the peaks of their curves. Since Newsome et al. (1989) showed that detection of motion direction is mediated by cells with peaks in their tuning curves in that direction, these experiments suggest that different populations of MT neurons are responsible for *detection* and *discrimination* of direction of motion.

Material and methods

Overview

A detailed description of our recording methods has appeared elsewhere (Snowden et al. 1991) and this section will therefore be limited to a brief overview and a more detailed description of the stimuli used.

Two male rhesus monkeys were trained to fixate a small fixation point, while ignoring the test motion stimuli, and to signal the dimming of the fixation point by releasing a key. Using a scleral search coil technique (Robinson 1963) the animals' eye movements and point of fixation were closely monitored. Visual stimulation was provided to the receptive field of individual neurons during this 4–6 s period of fixation. Electrode penetrations were made through a chamber implanted over area V1. This placement allowed us to sample cells from V1, V2 and MT. Over the course of many penetrations topographic maps of each area were compiled and these were used as an aid to assigning each recording site to an area. During the final 6 penetrations of one monkey marking lesions (all occurring within the 2 weeks prior to the animal being sacrificed) were placed at relevant sites and these were used to help reconstruct recording sites after histological reconstruction.

Stimuli and data analysis

Stimuli consisted of bright dots (30 ft. lambert) randomly plotted upon a dark background. Each dot was approximately 1 mm in diameter, and subtended 6 min arc. The pattern was circular and subtended 3 deg at the viewing distance of 57 cm. Under most conditions to be reported a total of 64 dots were used which corresponds to a dot density of 7% or 9.2 dots/deg. This type of pattern is similar to that used by Skottun et al. (1988) but somewhat different from that used by some previous investigators (e.g. Hammond and MacKay 1975, 1977) where the texture was made by assigning each pixel black or white (50% dot density).

Movement was created by displacing the X and Y coordinate of each element by a certain amount. Dots which would have fallen outside the 3 deg circle were wrapped to the opposite side of the display. Each element had a limited point lifetime of 500 ms, after which it was randomly replotted on some other part of the screen. The rate of screen refresh was 60 or 35 Hz. Each trial commenced with the onset of the fixation point. After 1 s the stimulus appeared if the animal was successfully fixating. This stimulus was extinguished after 1 s, and another stimulus appeared for 1 s after a 1 s delay. The fixation point dimmed 0.2–2.0 s after the end of the last stimulus; thus a complete trial lasted 4.2–6 s. In this manner we were able to present two stimuli per trial. This was the case for most of our data; however, for the earliest recordings (consisting of approximately 20% of V1, and 40% of the MT recordings) a single stimulus was presented for 3–5 s.

The response to the stimulus was calculated for a 1 s period whose commencement was aligned with response onset. For each stimulus condition 6–10 trials were completed and the mean response and standard deviation were calculated. Only cells whose activity could be significantly modulated by random dot patterns are included in this study. To test for a significant response modulation we performed a t-test between two conditions (A and B) via the formula:

$$(A_{mean} - B_{mean})/\mathrm{sqrt}((A_{sd}^2/N_a) + (B_{sd}^2/N_b))$$

where sd is the standard deviation and N_a and N_b the number of trials run on conditions a and b respectively. Any cell that scored > 5.0 on any such test was included in the study.

Psychophysics

In addition to the neurophysiological studies described above we also collected human psychophysical data using the same stimuli so that more direct comparisons could be made than would be afforded by using data from other laboratories. A single random dot pattern was presented on each trial. On half the trials the pattern moved "upward" and on half "downward" in order to prevent aftereffects. The pattern did not move vertically but with an angle slightly to the left or right of the vertical, and the subject's task was to indicate which of these had been presented via a button box press (binary forced choice). No feedback on performance was given. In order to help the subject maintain a good sense of the vertical, a stationary dot was placed 0.5 deg above and below the pattern along the vertical axis. Nine subjects took part in the experiment. Seven subjects were given a very brief (2–4 min) practice session to familiarize themselves with the task, and two of the subjects were well practiced. The method of constant stimuli was employed. Twenty stimuli (ten up, ten down) were presented 20 times each in pseudorandom order and the proportion judged moving to the right of vertical was plotted as a function of angle (Fig. 9B; 90° = vertical) separately for the upward and downward conditions. The data were fitted by an integrated Weibull function and the discrimination threshold was taken as the angle change from a probability of 0.5 to one of 0.25. The two discriminanda were averaged for upward and downward motion for each subject.

Results

Eye position

In the introduction we suggested that the alert animal has differences in eye movement over the paralysed animal.

was the lateral nucleus. We have recently demonstrated using the anterograde tracer *Phaseolus vulgaris* leucoagglutinin (PHA–L) that at least some portions of the lateral nucleus contribute a substantial projection to the basal nucleus (Pitkänen and Amaral 1991). Our present results would indicate that a component of this intrinsic connection may be excitatory.

Acknowledgements. This work was supported by NIMH grant MH 41479. We would like to thank Mr. Rama Ranaganathan and Ms. Janet Weber for help with the initial stages of the analysis, and Mr. Kris Trulock for photographic assistance.

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Table 1. Standard deviations of eye positions from trial to trial (in min arc)

Monkey number	Horizontal eye position	Vertical eye position
34	5.9	6.3
49	4.3	8.2

To quantify this for our monkeys we recorded the point of eye position fixation from trial to trial over a series of 100 successive trials. The eye position at the time of the fixation point dimming was taken as the measure of the point of fixation. Table 1 presents the standard deviations for both vertical and horizontal position of the eye for each monkey. Both animals showed variation in fixation of only a few min of arc in good accord with previous measurements (Motter and Poggio 1984; Snodderly and Kurtz 1985). It should be noted that some of the scatter found in the position might be attributable to the inherent noise in the measuring system. We attempted to estimate this by collecting eye position data using a coil, similar to the one implanted in the monkey's eye, placed in the magnetic field. The standard deviation in the output was around 1 DAC (digital to analogue conversion) unit, which corresponds to 0.80 min in the vertical axis and 0.87 min of monkey 34, and to 1.3 min in both axes of monkey 49. Thus the standard deviation measured for the monkey's fixation contained a small component due to noise in the measuring system.

While the trial to trial variability in eye position is quite small this represents a substantial fraction of receptive field size for area V1 neurons. At the eccentricities we recorded from in V1 (1–3 deg) receptive fields vary in size from about 10 min to around 1 deg (Dow et al. 1981).

Response properties

Grain of response. Nearly all the cells we formally tested were driven to some extent by random dot patterns. It is hard; however, to know the percentage of cells which were unresponsive to such stimuli as much of our searching and mapping of receptive fields was performed using these patterns. Hence, there is a systematic bias towards finding this type of cell.

While nearly all V1 cells tested were driven by the random dot patterns it was clear that different types of response could occur. Many cells did not respond in a uniform manner during the stimulus presentation time (see Fig. 1A). Instead these cells tended to fire at a certain time (and not at other times) during stimulus presentation. As the same pattern was presented on each trial this is consistent with the cell firing to some particular feature or phase relationship within the dot pattern. Such a result has been previously reported for cat V1 cells (Hammond and MacKay 1975; Gulyás et al. 1987) where this type of response was termed a "grain" response. Other V1 cells (e.g. Fig. 1B) gave responses which were much more consistent over the time course of the stimulus. Gulyás et al. (1987) term this a "field" response. Nearly all MT

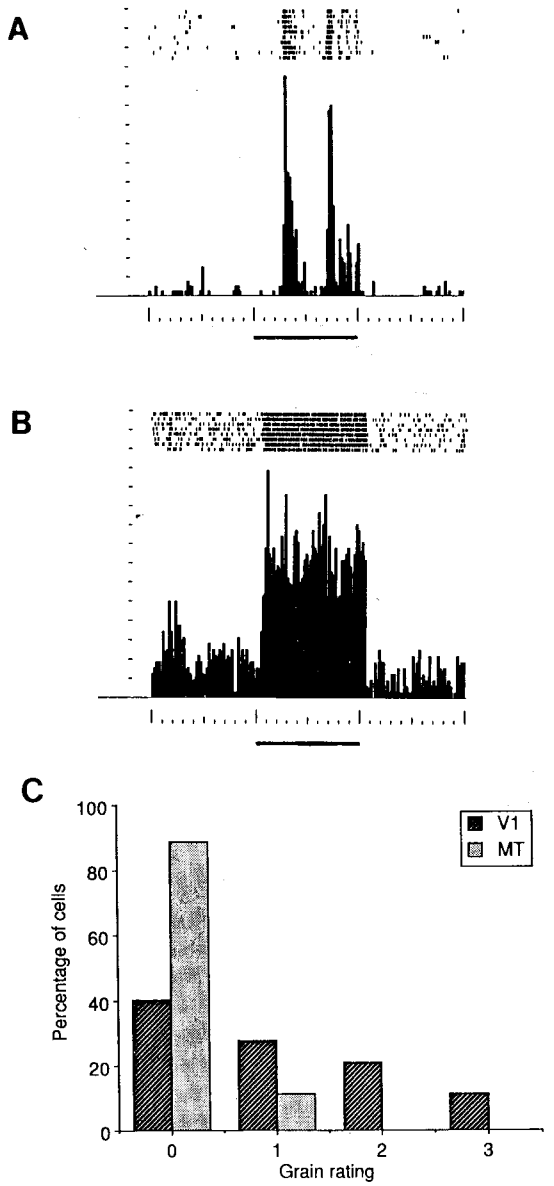

Fig. 1A–C. Responses of a V1 cell to a moving random dot pattern. **A** The upper part of the figure shows the response rasters. Each raster indicates a trial, and each dot represents a spike elicited from the cell. Below this is the response histogram constructed by assembling the number of spikes within 20 ms bins and averaging across trials. The presence of the stimulus is indicated by the dark bar under the histogram. The ticks on the Y axis represent 20 spikes/s/tick, and those of the X-axis 100 ms/tick. The stimulus was of 1000 ms duration. It can be seen that this cell had a tendency to fire at discrete points during stimulus presentation, rather than in a continual manner. It was thus given a grain rating of 3 (see text). **B** Another V1 cell. This cell fired in an almost continuous manner and was given a grain rating of 0. **C** Frequency histogram of the type graininess of response in areas V1 and MT

cells gave responses that were similar to this "field" response. Quantifying the "graininess" of the response is not a trivial operation (as the response is very much tied to the exact pattern used) and so in order to give some impression of the relative amounts of graininess in each area we rated (3 {very grainy} – 0 {no grain}) the graininess of each cell (the observer did not know from which

area the cell came). The result is displayed in Fig. 1C and shows that very grainy response types were confined to area V1.

Effects of dot density. One possible explanation of our finding of a greater grain type of response in area V1 is that, since receptive fields are much smaller in area V1 as compared to MT (Gattass and Gross 1981), our stimuli often extended beyond the boundaries of the V1 receptive fields. This leads to a smaller *mean* number of dots in the receptive field which would increase the variability of how many dots actually were within the receptive field at any given time. At the extreme end would be a receptive field so small that it would either contain one dot or no dot at all. Such effects might account for the greater incidence of grain type responses in V1 cells than in MT cells. We investigated this issue by systematically recording the response of cells as a function of dot density of the pattern. We found that cells that gave a grain type response did so even with a sixteen-fold increase in dot density and we therefore suggest that it is not the scarcity of dots which induces this graininess (clearly if very low dot densities are used then a graininess can be induced in any cell). It was also noticeable in most cells that changes in dot density seemed to make little difference to firing rates. To quantify this we normalized the response of each cell to its maximum firing rate and calculated the mean response and the standard deviation at each dot density tested in each area. Fig. 2A and B plots these curves for areas V1 and MT respectively. Both functions show a rapid rise with increasing dot density and a saturation at a fairly low dot density. There are no obviously differences between areas V1 and MT. It should be further noted that our normal number of dots (64) lies in the area which produces a saturated response.

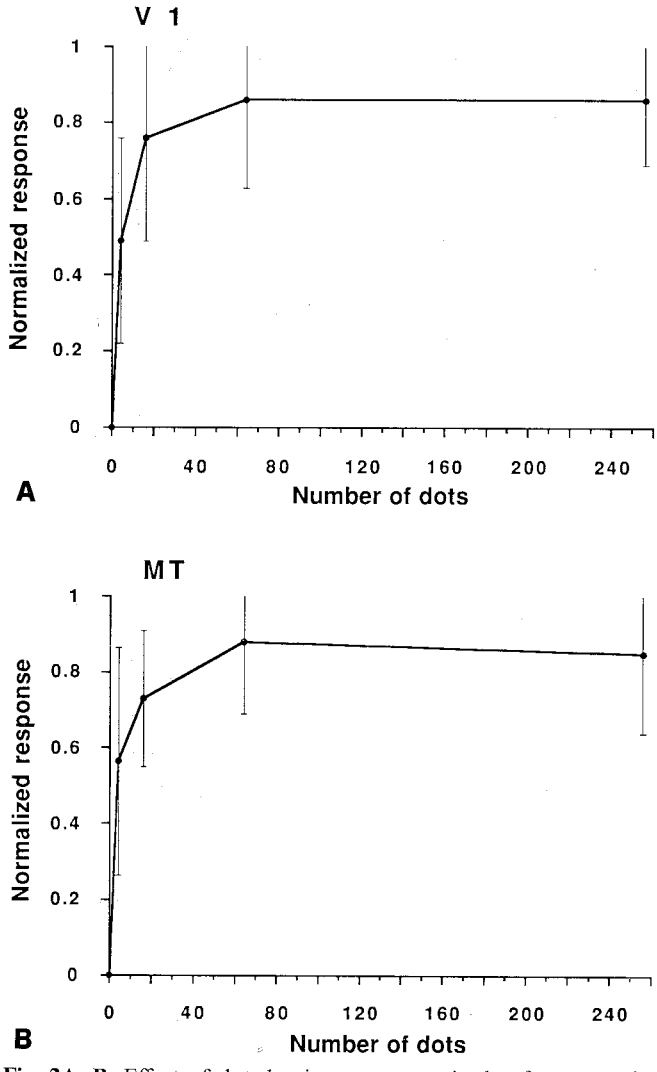

Fig. 2A, B. Effect of dot density upon magnitude of response in areas V1 (**A**, $N=37$) and MT (**B**, $N=42$). The response from each cell was normalised with respect to its maximum response, and the mean and standard deviation of the population are plotted as a function of the dot density of the pattern

Direction tuning. In order to compare our results with previous estimates of the directionality of cells in the cortex it is necessary to derive an index which can be used across studies. Unfortunately a standard index has not yet been adopted by all laboratories and this complicates our attempts to compare indices derived with random dot patterns with those obtained using other stimuli. The direction index (I_d) we chose to use was:

$$I_d = 1 - A/P \quad (1)$$

where P stands for the firing rate in the preferred direction and A the firing rate in the opposite (antipreferred) direction. This index was calculated *after* the spontaneous rate (obtained when the animal was fixating an otherwise blank screen) had been subtracted. Values near 0.0 indicate no difference between these directions (a non-directional cell), and increasing values indicate greater and greater directionality. With this index it is also possible to quantify when motion in the antipreferred direction causes the cell to be suppressed below the spontaneous rate (values > 1.0).

Figure 3 plots the occurrence of I_d in both V1 and MT. As has been noted by many other authors (Zeki 1974; Albright 1984; Mikami et al. 1986) the cells of MT show a far greater directionality than those of V1 (median V1 = 0.44; median MT = 1.01; Mann-Whitney U: $p < 0.0001$).

We have considered a cell to be directional if it gave a response which was three times greater for the preferred direction than for the null direction. About 32% of the V1 cells, and 93% of MT cells, gave such a response. These figures are in excellent agreement with previous studies on the monkey (Schiller et al. 1976; De Valois et al. 1982a; Hawken et al. 1988) using bar and grating stimuli, suggesting that such estimates are relatively independent of the type of stimulus used.

De Valois et al. (1982a) presented data suggesting a bimodal distribution of directionality within the macaque V1 with many cells showing just a weak preference for direction and a few cells showing a strong preference with essentially no response to the anti-preferred direction. Our data exhibit no sign of this bimodality. The reason for this discrepancy may lie in the different stimuli employed in this study (dot patterns) and their studies

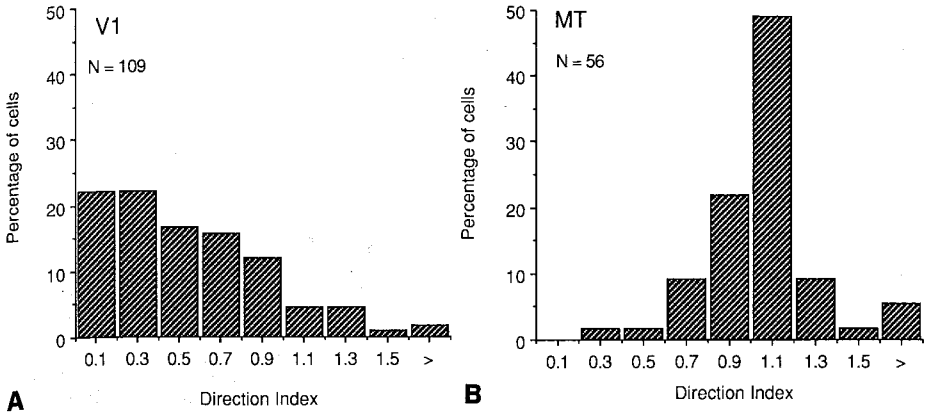

Fig. 3. Frequency of index of directionality for cells in area V1 and MT

(lines and gratings); however, other factors such as anesthesia may also be involved. The direction index used by De Valois et al. (1982) (antipreferred/preferred response) is very sensitive to small changes in firing rate for low responses in the antipreferred direction. The use of anesthetics has been previously shown to reduce the activity of cells (Livingstone and Hubel 1981). This reduction could serve to increase the number of cells with extreme direction indices, generating their bimodal distribution. It should be noted that the data of Hawken et al. (1988), who performed experiments very similar to those of De Valois et al. (1982a) but used another directionality measure, show no bimodality.

Variance

Neurons of the visual cortex fire in a probabilistic fashion. That is to say that identical stimuli do not produce exactly the same response from trial to trial. This variability of the response to a stimulus (and in the cells' spontaneous rate) has been of tremendous interest (Heggelund and Albus 1978; Rose 1979; Tolhurst et al. 1981; 1983; Dean 1981; Parker and Hawken 1985; Bradley et al. 1987; Scobey and Gabor 1989; Vogels et al. 1989; Zohary et al. 1990) because it helps determine and constrain the capacity of a cell to signal the presence or absence of features/information in the world.

The majority of the studies cited above recorded the response of cells in striate cortex of anesthetized cats. The effect of anesthetic on response properties is still not totally clear (e.g. Livingstone and Hubel 1981) but must serve to complicate any comparison between performance measures of single neurons, especially when attempts are made to compare this performance with those of the behaviour of an animal. A further complication is that paralysis of the eye muscles is induced. Small eye movements still occur under conditions of strict fixation

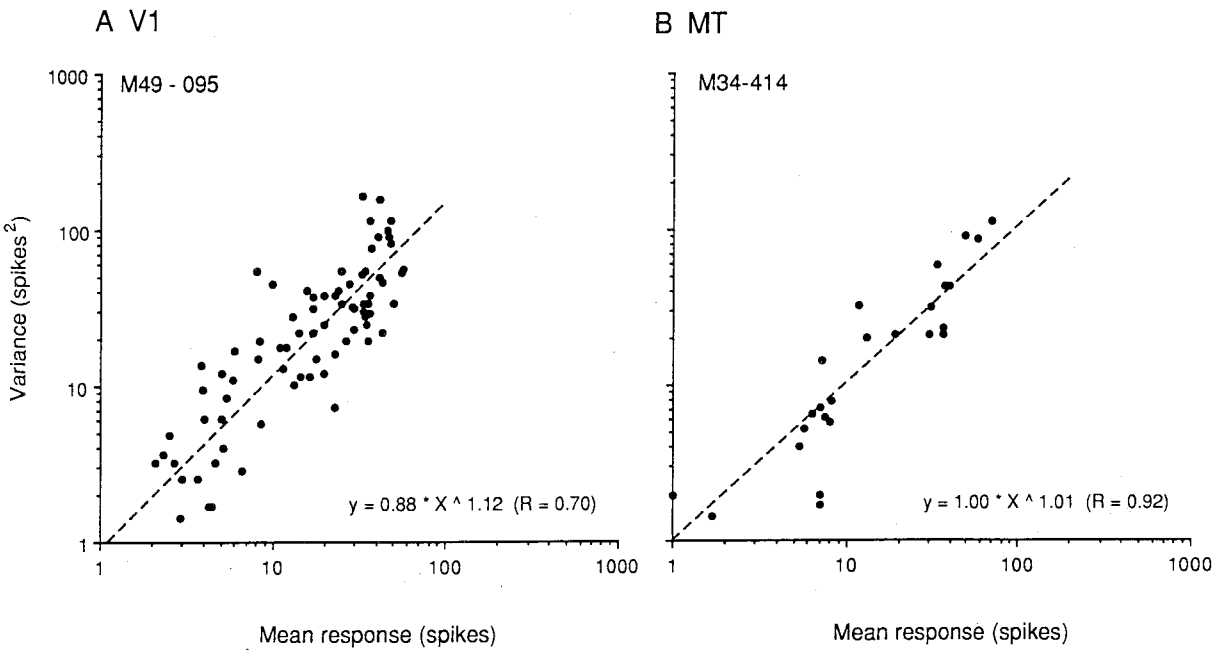

Fig. 4A, B. Variance as a function of mean response for a cell from area V1 **A** and one from MT **B**. The dashed line is the best fitting function of equation 2 (see text), and is indicated at the bottom of the diagram

and there is a limited ability to fixate precisely the same point from trial to trial (see Table 1; Motter and Poggio 1984). This introduces variance into the precise nature of the position of the stimulus with respect to the receptive field of the neuron being examined which is not present for the paralysed preparation, but may be a factor in limiting psychophysical thresholds. Secondly, the functional organization of visual cortex is sufficiently different in cats and primates that we are most wary of comparing these data to human psychophysical performance. Taken together this suggests that the optimal data to compare with human psychophysics are those recorded from an alert, fixating primate performing some psychophysical task.

The first report of such efforts has recently appeared. Vogels et al. (1989) report upon the relationship between response and variability for a population of V1 neurons stimulated with stationary square wave gratings. In this section we extend these data by examining the response to moving random dot patterns. We have also examined the response of MT cells and establish (for the first time) the variability of responses in an extrastriate area.

For neurons where recording was stable for a long enough period we have examined the relationship between variance and mean response. Figure 4 shows the variance (the square of the standard deviation) as a function of mean response on a double logarithmic plot for both representative V1 and MT neurons. The variance increases with increasing mean response for both cells. In accord with previous studies (Tolhurst et al. 1981; Dean 1981; Vogels et al. 1989) we attempted to fit a power function of the form:

$$\text{variance} = x * \text{response}^{y} \qquad (2)$$

where y represents the slope of the straight line on log-log coordinates and x the intercept (i.e. the variance when mean response = 1). In both areas we found such a power law to be an adequate fit to the data, and clearly superior to other relationships (i. e. semilog, linear, exponential).

Such plots were made for all suitable neurons. Figure 5 shows frequency histograms of the power functions (A and C) and intercepts (B and D) encountered in both areas. In area V1 we obtained a mean power of 1.21

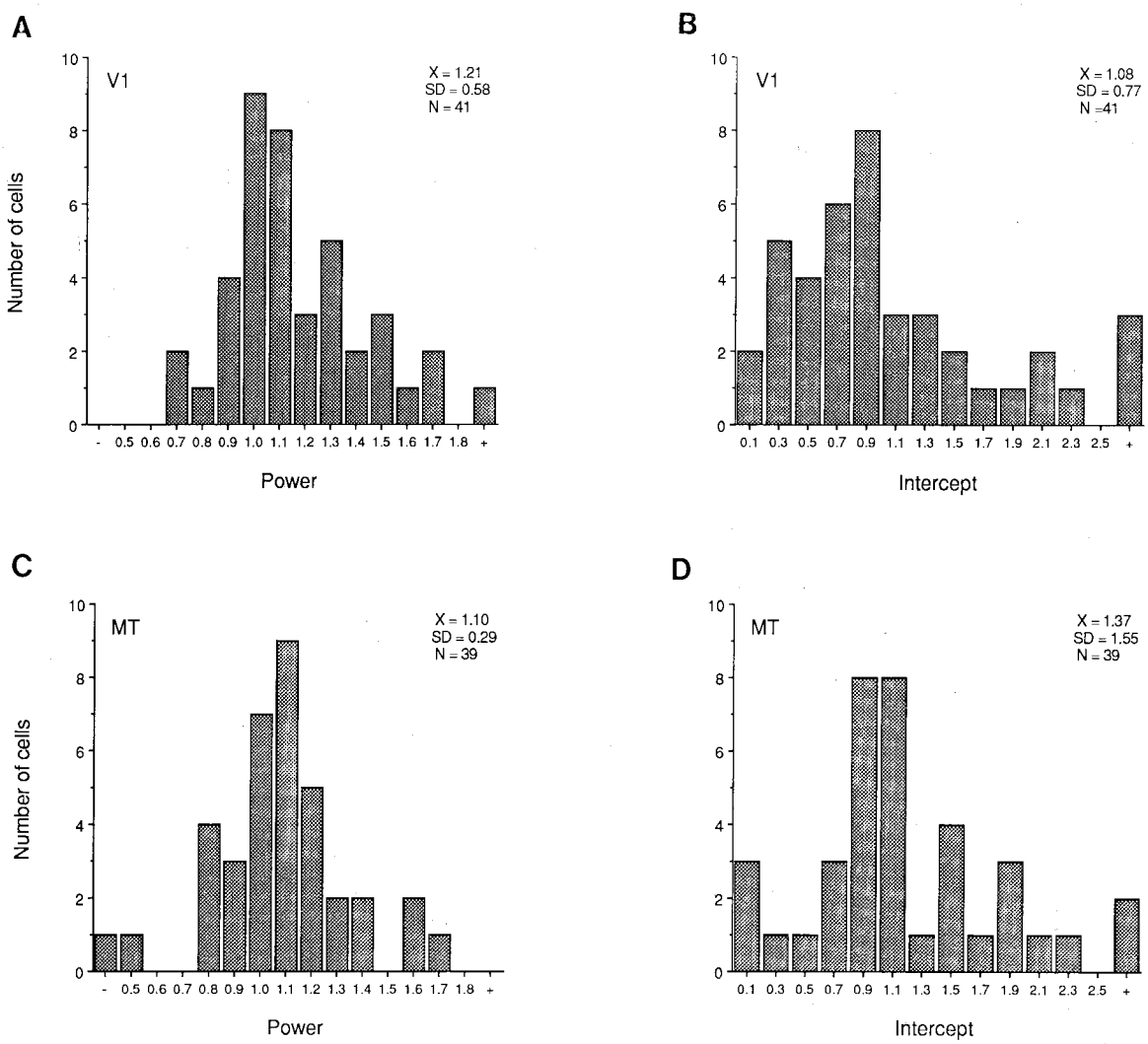

Fig. 5. **A** Distribution of the slope (power of Eq. 2) of the fits to the V1 cells. **B** Distribution of the intercept (constant of Eq. 2) of the fits to the V1 cells. **C** and **D** As for **A** and **B** but for MT cells

($sd=0.28$, $N=41$) and intercept of 1.08 ($sd=0.77$, $N=41$).

The mean slope in area MT was 1.10 ($sd=0.29$, $N=39$) and the mean intercept 1.37 ($sd=1.55$, $N=39$). This is the first estimate of such a parameter for extrastriate visual cortex and is highly suggestive that the variance to response relationship in extrastriate cortex is essentially the same as that found in striate cortex. A non-parametric test (Mann-Whitney U) failed to find any significance in the difference between the data from V1 and MT for the slopes ($p=0.24$) or the intercepts ($p=0.43$) and therefore we have no grounds for believing that the variance in extrastriate area MT is dissimilar to striate cortex.

Each point in the variance-versus-response functions displayed in Fig. 5 was produced by obtaining responses to a certain random dot pattern. In order to manipulate changes in the response level we varied such factors as the direction of movement, speed of movement and dot density. One question of interest is therefore if changes along different stimulus dimensions produce different functions. If they do then clearly we are not justified in pooling across the various stimulus dimensions. Figure 6 demonstrates variance versus response functions from an MT cell produced by changes along the dimensions of speed (open symbols), and direction of motion (closed symbols) separately. In this instance it is clear that both dimensions produced very similar functions. Similar tests were applied to 13 MT neurons and a non-parametric test (Mann-Whitney U) revealed no significant difference between either the slope ($p>0.5$) or intercept ($p>0.5$) when produced by changing the stimulus along these two dimensions. A similar result was found by Dean (1981) who showed that changes along the dimensions of spatial frequency and contrast produce similar functions in cat striate neurons (see also Vogels et al. 1989). Further, the similarity between the slopes produced in the present study using random dot patterns, and those of other studies cited above using gratings, all suggest that it is the mean response level that determines the variance and the amount of variance has little to do with how that mean response level is produced.

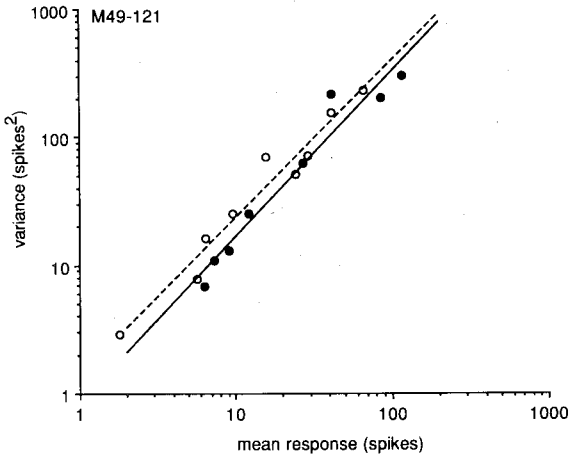

Fig. 6. As for Fig. 4, but the data points represented by open symbols (dashed line) were produced by varying the speed of the pattern, the solid symbols (and solid line) were produced by varying the direction

Direction discrimination by MT cells

In the previous section we addressed the variability of response rate for both V1 and MT cells. The most notable physiological characteristic of MT cells is their different response rates to different directions of motion. Thus these cells have the potential to discriminate the direction of motion of a pattern, and may well play a vital role in determining psychophysical thresholds for the monkey including that of direction discrimination. The ability of a cell to discriminate directions of motion is dependent upon how much its firing rate changes with changes in stimulus direction, and upon the reliability of its response. In theory, if a cell gave exactly the same response to identical stimuli then discrimination would be limited only by the quantum nature of spike genera-

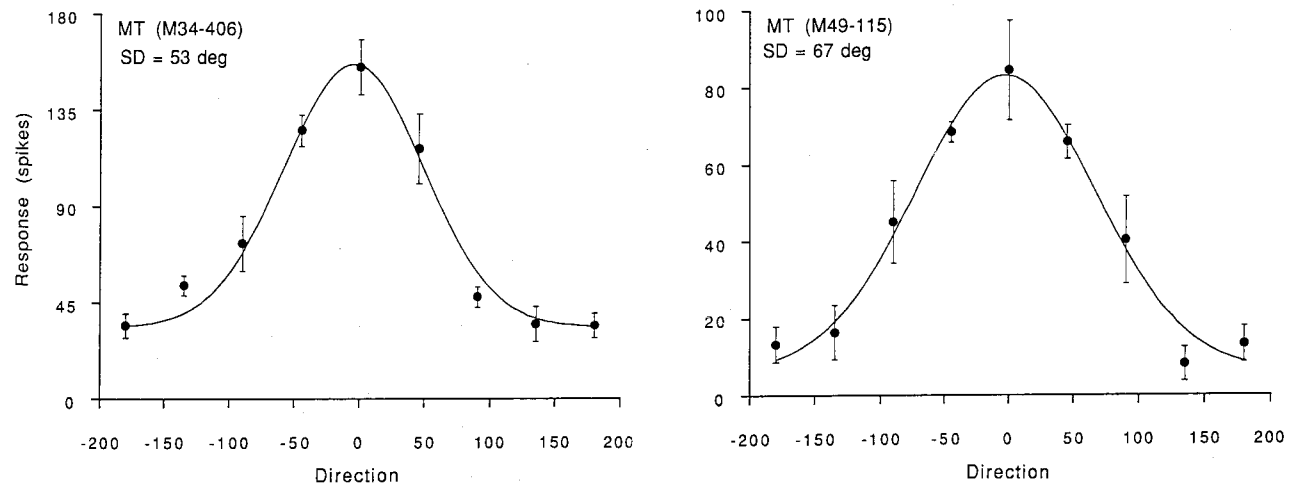

Fig. 7. Direction tuning for two MT cells. The points represent the mean response, and the error bars the standard deviation. The data were fitted by a Gaussian function (see Eq. 3), and the standard deviation of the fitted Gaussian is given in the upper left of the figure

tion. However, as we demonstrated in the previous section, this is far from the case and the variance of a cell is often of the same order as the mean response. In this section we therefore attempt to estimate the capacity of MT neurons to discriminate direction of motion by producing neurometric functions (Tolhurst et al. 1981).

Neurometric functions can be estimated in at least two ways. The first is via the receiver operating characteristic (ROC) curve (e.g. Bradley et al. 1987). Typically two stimuli are presented and the probability that the cell gives a greater response to one of the stimuli is observed. From this the cell's ability to discriminate small changes can be calculated. This method requires a very large number of trials and is not particularly suited to work on the alert animal. The second method is to measure the underlying characteristics of the cell, such as its tuning along a particular dimension and its response variability, and then use these measurements to model the response of the cell to various stimuli (e.g. Scobey and Gabor 1989). The latter method requires many fewer trials and is therefore more suited to experiments on the alert animal. We therefore chose this method.

Direction tuning curves were determined by measuring the response of each neuron at 8 different directions of motion for 6–10 trials per direction (see methods) and plotting the mean response as a function of direction (e.g. Fig. 7). The data were then fitted by a Gaussian function of the form:

$$\text{response} = r_{min} + r_{max} * \exp^{(-0.5*d^2/\sigma^2)} \quad (3)$$

where d is the angle of motion away from the preferred direction (degrees), r_{min} is the minimum firing rate, r_{max} the maximum firing rate, and σ the standard deviation of the Gaussian. We found this function to be an excellent fit to all but two of our sample of neurons ($N=32$). The cells which were poorly fit appeared to be so due to a significant bi-directionality in their response, and we eliminated them from further analysis. The finding that a Gaussian provides an excellent fit to MT direction tuning curves is in agreement with Albright (1984) who sampled at 16 different directions of motion. For our population of cells the mean standard deviation was 46.5 deg (sd = 18.2, $N=30$) which is slightly larger than that obtained by Albright (who reported a full bandwidth at half height of 85 deg, which is equivalent to a sd of 36.3 deg).

Knowing the relationship between direction of motion and mean response (Eq. 3), and the function relating mean response to variance (Eq. 2), we were in a position to simulate the response of an MT cell to a stimulus moving in any direction. We ran simulations in which 36

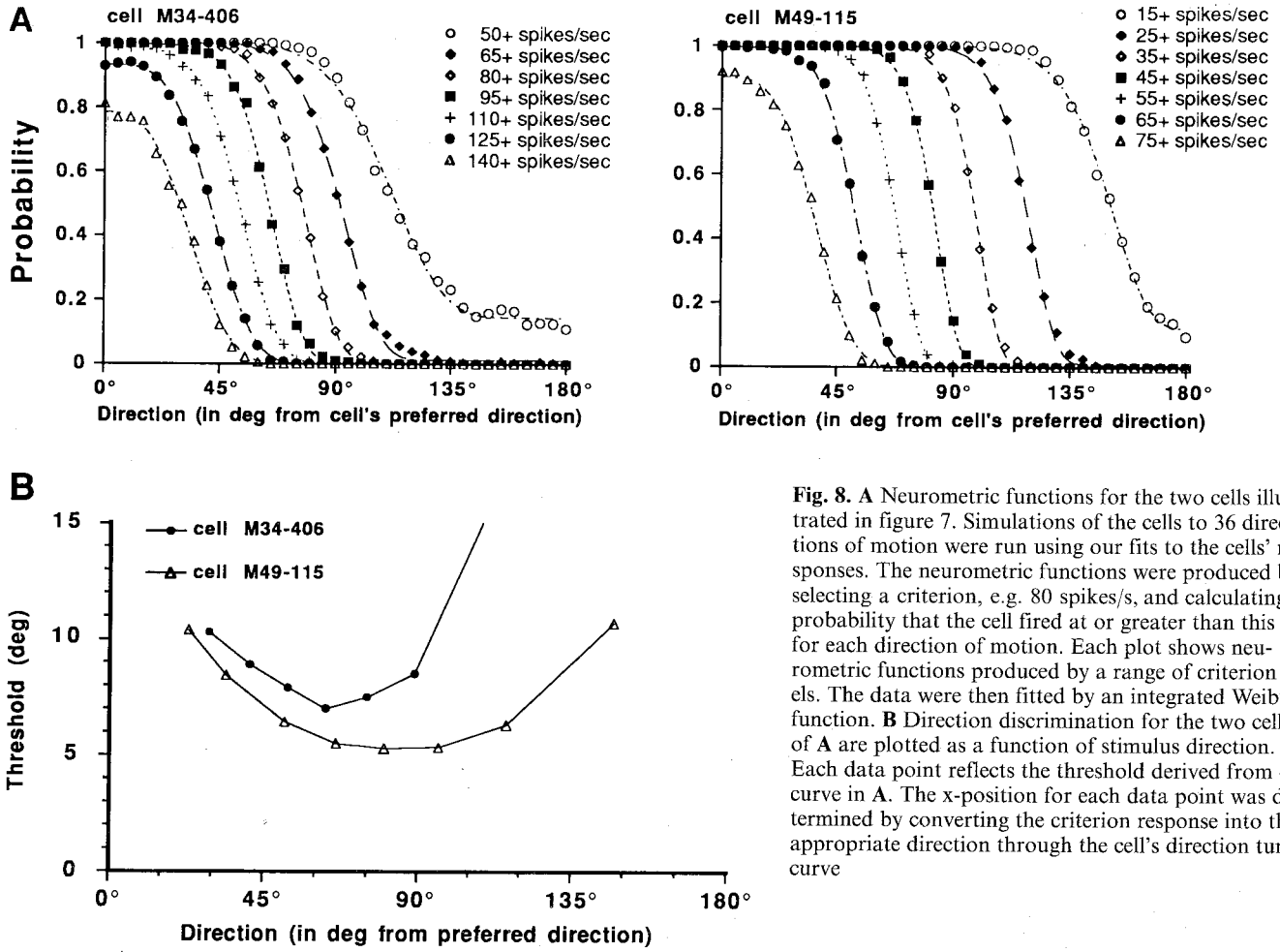

Fig. 8. A Neurometric functions for the two cells illustrated in figure 7. Simulations of the cells to 36 directions of motion were run using our fits to the cells' responses. The neurometric functions were produced by selecting a criterion, e.g. 80 spikes/s, and calculating the probability that the cell fired at or greater than this rate for each direction of motion. Each plot shows neurometric functions produced by a range of criterion levels. The data were then fitted by an integrated Weibull function. **B** Direction discrimination for the two cells of **A** are plotted as a function of stimulus direction. Each data point reflects the threshold derived from one curve in **A**. The x-position for each data point was determined by converting the criterion response into the appropriate direction through the cell's direction tuning curve

directions of motion were presented. For each stimulus a mean response was calculated according to the parameters obtained from equation 2, and then a number was picked from a Gaussian distribution[1] (mean = 0, $sd = 1$ unit) and scaled according to equation 1. These two numbers were then added to produce the response on that trial. In total 20,000 trials were simulated for each cell. From these data neurometric functions could be produced (e.g. Fig. 8A + B). For a certain criteria (e.g. number of spikes on a trial) we calculated the probability that more than this number of spikes was elicited for each direction. These data points were fitted by the formula:

$$P = \gamma - (\gamma - \delta) * \exp^{(-1*(d/\alpha)^{\beta})} \quad (4)$$

where d is the direction of motion, α the direction at which a criterion probability is reached, β the parameter governing the slope of the function, δ the asymptotic value of P (i.e. when d = 0), and γ the probability of reaching criterion for the antipreferred direction (i. e. d = 180). This equation is the integral of the Weibull function. These neurometric functions are equivalent to psychometric functions in that they describe the cell's ability to respond differentially to different directions of motion. Thus the range of directions over which the cell can change the probability of a criterion response by 25 percent is equivalent to a direction discrimination threshold. We chose the range of directions that changes the probability from 0.5 to 0.25 since that covers the steepest portion of the curve.

As can be seen in Fig. 8A and 8B such a function can be generated for any arbitrary criterion. Each of these functions yields a direction discrimination threshold and these are plotted in Fig. 8C as a function of stimulus direction for the cells illustrated in Fig. 8A and B. Discrimination thresholds follow a U-shaped function with a broad base over which discrimination is finest and almost constant. The position of this shallow minimum is for criteria which fall at some distance away from the peak firing rate, and therefore the preferred direction, of the cell. This is because near the peak of the Gaussian function the slope is reduced and, as firing is near maximum, the variance is the greatest.

We used the region of the U-shaped threshold criterion plot (Fig. 8C) to estimate the discrimination ability for each cell[2]. Since we are determining a cell's ability to discriminate different directions of movement, rather than simply detect the presence of movement, we used stimuli that evoked large responses when they moved in the preferred direction of the cell. This is desirable since the shape of the response distribution deviates markedly from a Gaussian for low response values (Dean 1981; Scobey and Gabor 1989; Tolhurst et al. 1983; Bradley et al. 1987). Thus as responses are high, and we are comparing stimuli which are producing similar response levels (and therefore response distributions) this issue is diffused. Clearly, a similar analysis on a detection task, like the estimation of contrast thresholds would be less valid as response rates would be low. In such a situation one would need to employ signal detection theory.

Figure 9A plots the frequency of occurrence of direction discrimination thresholds for our population of MT cells. In addition we measured direction discrimination thresholds for nine human observers (see methods) using the same stimuli as were employed during the recording sessions. Figure 9B plots a psychometric function for an individual observer. The data points have been fitted by

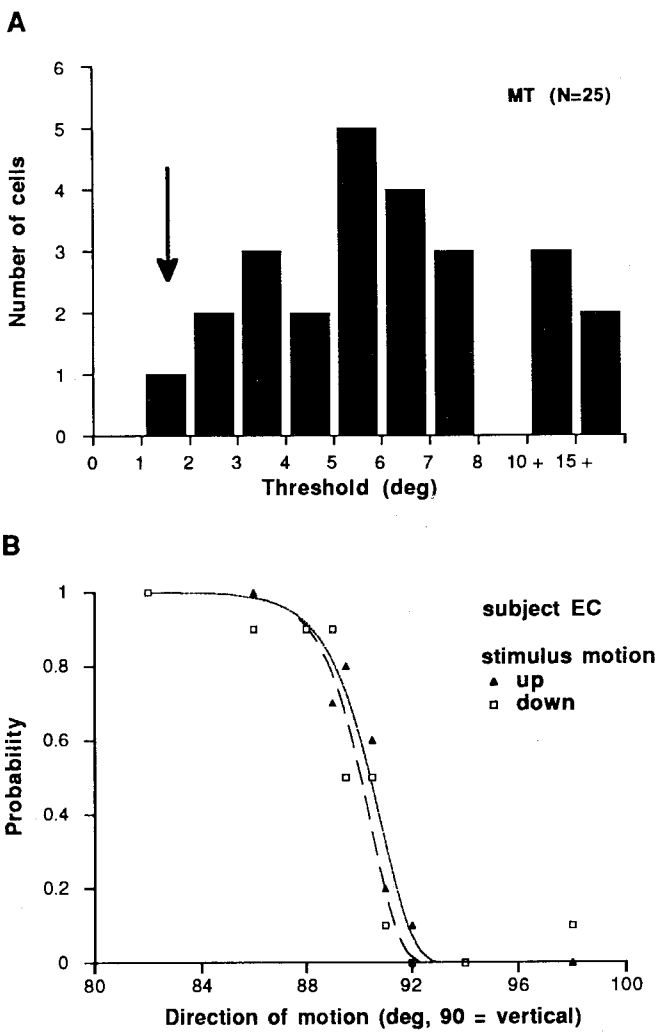

Fig. 9. A Minimum discrimination thresholds for 25 MT cells, determined as illustrated in Figure 8. The arrow indicates the mean direction discrimination from a population of 9 human subjects. **B** Psychometric functions for one human observer. The probability of a "rightward" response is plotted as a function of direction. The open symbols are for downward motion and solid for upward motion (see Methods). The data were also fitted by an integrated Weibull function

[1] The distribution of responses to a particular stimulus is not a perfect Gaussian (Bradley et al. 1987; Dean 1981; Scobey and Gabor 1989). However, the deviation from a Gaussian distribution is not great at high firing rates, the Gaussian distribution is mathematically convenient, and it has been used successfully in similar modelling attempts (Scobey and Gabor 1989)

[2] This approach is supported by psychophysial evidence which suggests that some discrimination thresholds are determined by cells which respond maximally to stimuli other than the ones to be determined (Regan and Beverley 1983)

the same integrated Weibull function as was employed for the neurophysiological data. As can be seen, the thresholds are approximately 1 deg. As a population the mean discrimination threshold was 1.1 (sd = 0.4; $N = 9$) which is similar to the figures provided by De Bruyn and Orban (1988) and Ball et al. (1983) when corrected to the same criterion. Comparison of this figure (indicated by the arrow in Fig. 9A) with the results portrayed in Fig. 9A shows that while there is considerable scatter in the thresholds of individual neurons there appear to be cells whose discrimination abilities are of the order of that of human observers.

Discussion

The nature of the response to random patterns in V1

Cells of area V1 show a range of response types to drifting random dot patterns. Many cells respond in an intermittent manner showing several irregular bursts of firing over the time course of the stimulus. One possibility is that the response of these cells is not a true "texture" response, but rather a response to a particular feature or phase relationship within the pattern. Such a response can only be identified if the same stimulus is used from trial to trial; therefore those studies which refresh the noise pattern between trials would miss this. In addition the position of the eyes must also be stable from trial to trial and could be missed due to slow drifts in eye position in the paralysed animal. Our ability to show this grain-type response testifies to the ability of our monkeys to fixate the same point in a consistent manner from trial to trial. Whether a cell responds with a grain-like response or with a field-like response may depend upon the acuity of the cell and the fineness of the texture employed (Hammond and Pomfrett 1989). While we found no obvious changes in graininess by a sixteen fold increase in dot density (1.75–28%), this is still different from the "visual noise" employed by Hammond and colleagues (e.g. Hammond and MacKay 1975) and by Orban and colleagues (e.g. Gulyás et al. 1987) where each pixel is assigned black or white (i.e. 50% dot density). However, Gulyás et al. (1987) using such a pattern (pixel size = 2.4 min) still classified cells into 3 classes depending upon their response to texture, no response (22%), grain response (55%), and field response (22%). So it appears grain responses can still exist at high dot densities. Our results from monkey striate cortex are in broad agreement with this study since we find cells which failed to respond, those giving a grainy response, and those giving a sustained response (Fig. 1).

Field-type responses could occur from the neural convergence of signals from many grain-type cells in a manner similar to that suggested for how the phase *invariant* complex cell could be produced by the averaging of many phase *variant* simple cells (Holub and Morton-Gibson 1981; De Valois et al. 1982b). Such a hierarchical process from phase-dependent to phase-invariant responses has been argued to be of great importance in motion processing (Borst and Egelhaaf 1989) and is consistent with several recent models of human motion perception (van Santen and Sperling 1985; Adelson and Bergen 1985). For example the motion-energy model of Adelson and Bergen (1985) has several stages, with each stage predicting a particular type of response to random dot patterns. At the first stage of the model (separable responses) the response to random dot patterns is phase sensitive and non-directional. The response to random dot patterns is therefore grainy and non-directional for a time averaged response (though at any particular moment in time it could appear directional). The next stage (oriented linear response) gives a greater response to motion in a particular direction (for a time averaged response). However, as this stage is linear it is still phase sensitive (gives a grainy response to random dot patterns) and has two undesirable effects: 1) it has opposite preferred directions of motion for stimuli of opposite contrast (e.g. Albus 1980) and 2) at any particular instance it is hard to determine directionality due to the grain type response to random dot patterns. The next stage of the model (oriented energy) is produced in the model by summing the squared output of two directional filters whose phase preference is shifted by 90°. This stage is phase independent and gives a constant output throughout time. The final stage of the Adelson and Bergen model (the opponent energy stage) consists of differencing the output from "oriented energy" cells of opposite preferred direction. Interactions between different directions of motion have previously been demonstrated (Snowden et al. 1991) and are much more prevalent in area MT than in area V1.

Dot density

Figure 2 shows that dot density has a relatively minor role in changing response strength. In both area MT and V1 responses rise quickly with dot density and saturate at low dot densities (though there is considerable variability between neurons). This is in accord with psychophysical results which show that dot density has very little effect in determining the upper and lower displacement limits of apparent motion (Baker and Braddick 1982) or in determining signal to noise ratios for detecting motion (Downing and Movshon 1988).

Variance

Our results (Figs. 4–6) show that the variance of a cell to a particular stimulus is proportional to (and just a little greater than equal to) the mean response. The average slope of the function was 1.21 for V1 cells and is in very good agreement with previous studies of the anesthetized cat (Dean 1981; Tolhurst et al. 1981, 1983; Scobey and Gabor 1989) and of the alert monkey (Vogels et al. 1989). However, our estimation of the average intercept parameter (1.08) is around half those previously cited (above references). This may arise from using alert animals. Many previous studies (e.g. Tolhurst et al. 1983)

have noted that the observed response variance may be an overestimation due to slow changes in the responsiveness of the cells over time.

MT cells are thought to receive an excitatory drive from many V1 cells. If many of these V1 cells are driven by a stimulus, and their response/variance characteristics are as described above, then it should be possible for each MT cell to derive a much lower variance to mean response as the noise associated with each V1 cell should cancel while the signal should add (assuming the noise is uncorrelated from cell to cell). However, our estimates of the variance to mean response characteristics of MT cells is very similar to that of V1 cells; that is the variance is nearly proportional to the mean response. Hence our results show no sign of improvement due to pooling. This result suggests that noise associated with the response of a MT cell may arise from mechanisms inherent in the cell itself, rather than being inherited from its inputs. Similar response variance ratios have been found elsewhere in cortex (Werner and Mountcastle 1963).

Direction discrimination

By using the fits to the functions relating mean response to direction, and relating variance to mean response, we were able to simulate the response of MT cells to different motion directions. The analysis shows that the cells can discriminate directions of motion which are but a small fraction of the tuning bandwidths. A similar result has been found for orientation discrimination and orientation bandwidths (Parker and Hawken 1985; Bradley et al. 1987; Scobey and Gabor 1989). While the above analysis is suggestive of the information processing capacity of MT neurons it should not be taken as a *fait accompli*. There are certainly some problems in applying these estimates directly to psychophysics. The first is that the analysis is based upon counting spikes over a time period of 1 s (the duration of the stimulus). This time period is somewhat arbitrary and it is unclear over what time period the spike count should be taken. While we made sure our psychophysical studies used the same duration stimulus as the physiological recordings, it has been demonstrated that thresholds for direction discrimination in humans asymptote in around 100–200 ms of stimulus duration (De Bruyn and Orban 1988). It is therefore clearly possible that information is not gathered throughout the whole 1 s period of stimulus presentation. As duration is lengthened the total number of spikes will increase and the variance will decrease resulting in an increase in the signal to noise ratio (defined by the mean divided by the standard deviation) will decrease allowing better performance. This effect of increasing duration of presentation upon a cell's ability to reliably detect a stimulus configuration has been recently demonstrated in monkey striate cortex (Zohary et al. 1990). Secondly, psychophysical experiments usually employ a technique in which two stimuli are presented and compared; thus the variability in determining the direction of *each* stimulus must be considered. This contrasts with the normal physiological practice of presenting just one stimulus. We chose to use a psychophysical technique of presenting just one stimulus in order to complement the single cell recordings. However, other researchers (e.g. Bradley et al. 1987) have chosen to compare the responses of a cell to two stimuli closely spaced in time. Under these conditions they found that thresholds (of orientation and spatial frequency discrimination) for individual neurons are improved when compared to similar estimates compiled by the comparison of responses to stimuli which were presented at intervals over a period of several minutes (a situation similar to the present study). This difference is accounted for by the fluctuations in a cell's responsiveness over the course of a few minutes, a well documented finding (e.g. Tolhurst et al. 1981) which adds to the estimate of a cell's variance. As our data were also collected over a similar time period our calculation of variance, and therefore discrimination, may also underestimate the cells' abilities. On the other hand the reasons for these fluctuations over time are poorly understood, and may have some connection to the preparation of the animal (anesthesia and paralysis) which would be avoided in our experiments.

Peak direction discrimination in these cells (as determined by our analysis) does not occur at the direction to which the cell is tuned (i.e. the one to which it gives the greatest response), but to a direction which is away from the preferred direction. While researchers have shown the variation coefficient to be at a minimum at the response peak (Heggelund and Albus 1978) this seems to be outweighed by the steeper rate of change of response evident on the response flanks. A similar result has been reported after analysing the response of cat striate neurons to changes in orientation (Bradley et al. 1987; Scobey and Gabor 1989) and is implicit in the results of Parker and Hawken (1985). If it is assumed that detection of motion of a random dot pattern is mediated by cells which are tuned to the direction in question (e.g. Newsome et al. 1989) then this implies different cells mediate threshold detection and suprathreshold discrimination of direction of movement.

Acknowledgements. The work was supported by NIH grant EY07492. R.J.S. was supported by a postdoctoral fellowship from Whitaker College, MIT. We thank Gail Robertson, Joseph Goddard, Richard Keough and Stephen Marchetti for technical assistance, and Catherine Cooper for editorial assistance.

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