Exp Brain Res (1991) 84:1–11

Experimental Brain Research



# Quantitative study of striate single unit responses in monkeys performing an orientation discrimination task

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Received February 12, 1990 / Accepted August 20, 1990

**Summary.** Contour orientation discrimination accuracy is determined by the orientation bandwidth, response variance and response strength of single units that code for orientation. We measured the latter three properties for V1 cells of monkeys which were performing an orientation discrimination of the grating stimulating the cell under study. We recorded from 285 cells, of which 76% responded to the grating. The orientation bandwidth, measured as full width at half height of the tuning curve, varied over a wide range amongst cells. The median bandwidth was 41 degrees. The response variance of the cells also varied considerably between cells; on average it was about two times the response strength. We also studied the temporal properties of the responses. Most of our cells had a latency between 40 and 100 ms. The response variance was found to be smaller in the initial phases of the response than at the later response stages. In some cells the orientation tuning varied in successive stages of the response, while in others the orientation bandwidth and preferred orientation remained stable throughout the response. However, all orientation sensitive cells were orientation tuned from the start of the response, a property which contribute to the fast and reliable coding of contour orientation. These results provide for the first time an estimation of the orientation tuning properties of V1 cells during visual orientation discrimination. They will be very useful to compare single cell properties of other areas to as well as in simulation studies of models of primate visual discriminations.

**Key words:** Single cell recording – Striate cortex – Orientation discrimination – Orientation selectivity – Behaving monkey

## Introduction

Primates are able to discriminate orientation differences smaller than 2 degrees (deg), the exact value depending on the reference orientation, the psychophysical task, and the amount of practice (Orban et al. 1984; Vogels and Orban 1985, 1986; Vogels and Orban, in press). These small just noticeable differences (jnds) in orientation indicate that orientation is coded with a relatively high accuracy. In contrast to the relatively small orientation bias of cells at earlier stages of the visual system (Levick and Thibos 1982; Vidyasagar and Urbas 1982), many V1 cells are strongly selective for the orientation of contours. Since orientation selectivity is such a salient property of primary visual cortical cells (Hubel and Wiesel 1968), several models have been formulated concerning the link between striate cortical orientation tuning properties and jnds in orientation (Barlow 1972; Howard 1982; Regan and Beverley 1985; Orban 1984; Westheimer et al. 1976; Paradiso 1988, Orban et al. in press, Vogels in press).

The accuracy with which a single cell represents the stimulus orientation is determined by its orientation tuning, response strength and response variance (Vogels and Orban, in press). The degree to which these three single cell properties determine discrimination performance will depend on the particular model used to establish the link between single cells and jnds. However, irrespective of the details of the model, all three characteristics are essential variables since they determine the accuracy of the coding of orientation at the single cell level.

Anaesthesia (Ikeda and Wright 1974; Livingstone and Hubel 1981), the animal's behavioural state (Haenny and Schiller 1988), attentional factors (Wurtz et al. 1980) and eye movement related factors (Noda et al. 1972) may influence the response of striate neurons and hence their coding accuracy. Hence, in order to relate single cell responses and visual discrimination accuracy, a first and necessary step is to measure the single cell properties while the subject is performing a discrimination task. Indeed in such a task the subject has to use stimulus orientation to guide his behaviour. This is precisely what we have done for orientation discrimination: we have recorded from striate single cells while monkeys were actually performing an orientation discrimination of the stimuli stimulating the receptive field (RF) of the cell under study. The

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monkeys had to discriminate the orientation of two gratings which were presented in succession. The orientation of the first grating of a pair varied between trials, and, hence the responses to this grating could be used to determine the response strength, response variance and orientation tuning of the cell. The presentation of the second grating of a pair had a behavioural goal: the monkey had to discriminate it from the first one and hence to pay attention to both stimuli. As such we could determine quantitatively the response properties of V1 cells while the monkey was engaged in an orientation discrimination of the very stimulus which stimulated the cell recorded from.

Orientation discrimination is a fast process: response latencies in primates can be as short as 220 ms (Vogels and Orban, in press). Since orientation discrimination is such a temporally restricted phenomenon, it is also important to know how the orientation tuning and response variance vary in the course of the response. This is an important issue given the recent report by Dinse et al. (1988) in which they describe neurons in the cat visual cortex that are initially unoriented and become orientation selective in the course of the response to the stimulus. This would increase the time needed for a single cell to reliably code the orientation of a stimulus. Hence we also determined whether orientation selective V1 neurones of monkeys engaged in an orientation discrimination task, are tuned for the orientation of the stimulus from the beginning of the response. The same question can be asked about the variability of the response: is the variability of the response smaller at the initial, critical phases of the cell's response than during the later phases of the response that contribute less to the behavioural response.

## Methods

### *Subjects*

Two rhesus monkeys (Macaca Mulatta) served as subjects. Monkey Ronnie was a juvenile male monkey, while Loebas was an older dominant male monkey. During the experiment, the monkeys were on a strict water deprivation schedule but had dry food ad libitum. Monkey Ronnie still is in very good condition and is currently participating in further experiments. Money Loebas, after being used in other experiments, was sacrificed with an overdose of nembutal and perfused with fixative. The recording site was anatomically verified as being V1.

### *Apparatus and set-up*

The monkeys were isolated in a dark, black-painted room (average luminance 0.003 cd/m2). They were restrained in a primate chair with their heads fixed by means of a headholder which was cemented to the skull. Eye positions were measured with the scleral search coila technique (Judge et al. 1980) and sampled at a rate of 200 Hz. The stimuli consisted of square wave gratings and flickering spots. The latter were used to plot the RF of the single unit or background activity, while the former were used to test quantitatively the responses of the cell. These stimuli were generated on a HP1332 CRT (green phoshor) with a Picasso CRT image synthesizer. The corners of rotated images were masked away by means of a plastic plate with a circular hole. This mask assured that the subject was unable to use nearby contours as cues in the discrimination. This mask also contained a series of computer controlled red LEDs, each of which could serve as a fixation point. The RF of the cell was approximately centred on the grating by selecting the appropriate LED as fixation point. The square wave grating had a spatial frequency of 2 c/deg, which is optimal for cells with parafoveal RFs (De Valois et al. 1982). By using square wave gratings instead of sinusoidal gratings the cell's selectivity for spatial frequency will be much reduced (Schiller et al. 1976). The diameter of the grating ranged between 8 to 10 deg, its Michelson contrast and mean luminance were 80% and 7 cd/m2 respectively. The latter was identical to the luminance of the blank CRT screen which was always on. A PDP11/73 controlled the sitmulus presentation and reward, collected the spikes and eye movements, and displayed the eye position and the spike trains.

### *Discrimination paradigm*

The onset of the fixation point marks the start of a trial (see Fig. 1 for a schematic drawing of the paradigm). The monkey has to saccade to the fixation point within 3000 ms after its onset, otherwise the fixation point goes off and the inter-trial interval (2000 ms) starts again. After 1000 ms fixation, a square wave grating (S1) is presented parafoveally for 350 ms, i.e. on the RF of the cell. Then, after an inter-stimulus interval of 300 ms, a grating (S2) is again presented at the same position. If the two successively presented gratings differ in orientation, the monkey has to make a saccadic eye movement towards the grating within 500 ms after presentation of the second grating. When both gratings have the same orientation the monkey was required to continue fixating the LED for 500 ms after the presentation of the second grating. After the monkey's response the

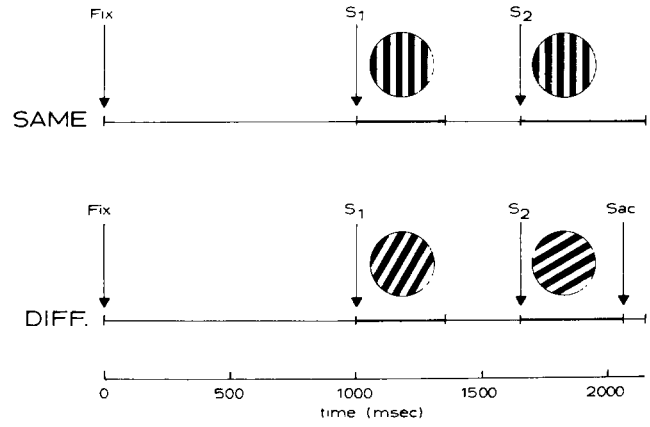


**Fig. 1.** Schematic drawing of the orientation discrimination task. Two different types of trials were presented in random order: SAME trials (above) and DIFFERENT trials (below). Each trial started with the onset of the fixation spot (not shown). The monkey started to fixate this spot at time 0. After 1000 ms a grating, S1, was presented for 350 ms at a location peripheral to the fixation point, i.e. on the receptive field of the cell. Then after an inter-stimulus interval of 300 ms a second grating, S2, was presented at the same spatial position as S1. In case of a SAME trial, S2 had the same orientation as S1; in case of a DIFFERENT trial the orientation of S2 differed from S1. If S2 had the same orientation as S1 (above) the monkey had to keep fixating the spot for 500 ms after presentation of S2. If S2 differed from S1 in orientation (below) the monkey had to make a saccade to the position of the grating within 500 ms (SACC indicates the start of the saccadic eye movement). The orientation of S1 was randomly varied between trials and, as such, was used to measure the response properties of the cell. The presence of the gratings is indicated by the thick lines

inter-trial interval starts. During this period the monkey is allowed to look around in the room.

Fixation inaccuracies and the saccades directed toward the stimulus were detected by the computer by means of electronic windows centred on the fixation spot and stimulus respectively. Correct responses were rewarded by means of drops of apple juice.

The orientation of the first stimulus S1 was randomly varied over a series of trials. By this manipulation of the orientation of S1 an orientation tuning function of the neuron can be measured. S1 could have 6 to 12 orientations in steps of 2 to 30 deg, depending on the estimated orientation tuning width of the cell. In monkey Ronnie the orientation difference between the two successive gratings was 15 deg, while in the other monkey, the much less smart Loebas, this orientation difference was 90 deg.

### *Single cell recording*

After the training of the animals, a 19 mm diameter stainless steel chamber was implanted over the left occipital lobe, partly covering the occipital ridge. Inside the chamber a hole, about 1 cm in diameter, was drilled through the skull, leaving the dura mater intact. During the single cell recording sessions, a microdrive holding the electrode was mounted on the steel chamber. We used glass coated Elgiloy microelectrodes (Suzuki and Azuma 1976) with an impedance ranging between 6 and 12 MΩ. The recording chamber was filled with sterile mineral oil and was sealed by the bottom part of the electrode holder. The electrode was advanced more or less perpendicular to the brain using a hydraulic Kopf Micropositioner. After amplification and bandpass filtering, single spikes were isolated using a two level window discriminator. The output of the discriminator was fed into the microcomputer (sampling rate 1000 Hz). On line we could monitor the eye position with respect to the fixation point and stimulus position, spike trains triggered by the stimulus and the stimulus that was actually presented to the monkey. Single cell recordings were done daily for about 5 weeks in each animal. The length of the recording sessions was usually between 3 and 4 h, depending on the monkey's performance. The monkey was performing the orientation discrimination task while we searched for a cell. In this task the orientation of S1 was varied in steps of 15 or 30 deg over a range of 180 deg. Once a spike was isolated, an orientation discrimination task was run in which the range and number of orientations of S1 depended on the estimated orientation tuning of the cell. Usually, the test finished when we had collected 10 trials for each condition.

When the monkey stopped working we demounted the electrode holder apparatus, cleaned the recording chamber with sterile saline, put a few drops of dexamethason and chloromycetin on the dura and then closed the chamber with a plastic cap. The animal was then returned to its home cage.

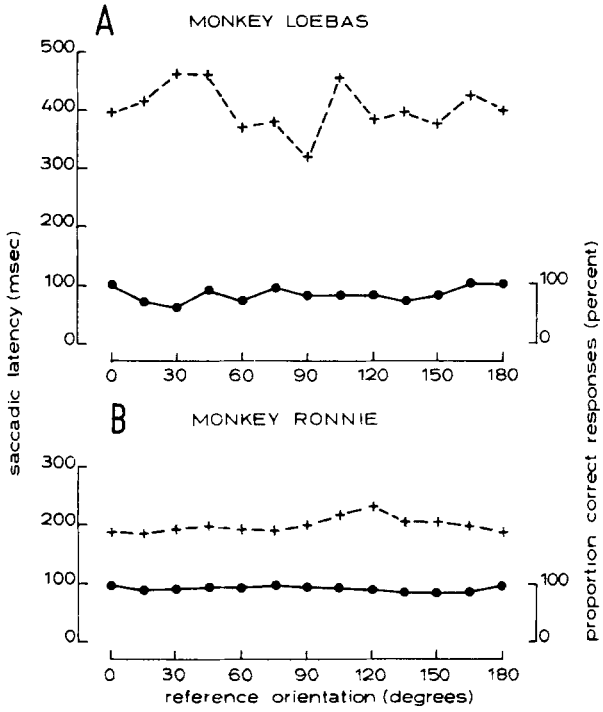


**Fig. 2A, B.** Performance and saccadic latencies in the orientation task for monkey Loebas (**A**) and monkey Ronnie (**B**). Proportion of correct responses and saccadic latencies are shown with a solid and stippled line respectively as a function of the reference orientation, i.e. the orientation of the first stimulus of a pair. The orientation difference between the stimuli within a pair was 90 deg and 15 deg for monkey Loebas and monkey Ronnie respectively. The total number of trials was 120 and 384 for monkey Loebas and monkey Ronnie respectively

### *Data analysis*

We made a series of offline analysis programs which constructed histograms and yielded spike counts triggered by different events (e.g. start of fixation, S1, S2). In this paper, the results are based on analysis of the response to the first stimulus of a sequence, i.e. S1. As stated in the introduction, S2 had a behavioural role: it assured that the monkeys attended the stimuli and were engaged in an orientation discrimination. It should be stressed that in our task the monkey's visual system has to code the orientation of S1 as well as that of S2 in order to perform correctly. This approach made it possible to obtain sufficient data for a large number of cells. Indeed much fewer trials had to be presented in order to measure the response properties for S1 than for S2, since the latter was on average identical to S1 in half of the trials and different from S1 in the other trials.

## Results

### *Behavioural performance*

Figure 2 shows representative examples of the performance in the orientation discrimination task for monkey Loebas (Fig. 2A) and monkey Ronnie (Fig. 2B) respectively. The proportion of correct responses as well as the mean saccadic latency (correct responses only) are plotted as a function of the orientation of the first stimulus of a pair. The difference in orientation between the two successive gratings was 15 deg and 90 deg for monkey Ronnie and Loebas respectively, the values used during the recording sessions. Monkey Loebas responded more slowly than Ronnie and his performance was poorer than Ronnie's. Nevertheless, both monkeys perform rather well in this task which is quite difficult for monkeys. Indeed in order to obtain this performance the monkeys had to be trained for several months in this task. Note that the performance level, well above chance, indicates that the monkeys used S1 as well as S2 in their decision. Indeed, since a particular orientation of the grating can correspond to S2 of a different trial was well as to S2 of a same trial, the monkey has to take into account the orientation of S1 in order to perofrm above chance.

A drawback of the good performance of the monkeys in this task is that, due to the small number of errors,

we were unable to make a valid comparison of the single cell responses to correctly and incorrecltly discriminated stimuli.

*Single cell recording: global statistics*

We made 28 successful penetrations in the left hemisphere of monkey Ronnie, and 34 penetrations in the left hemisphere of Loebas. A total of 285 well isolated units were studied, 107 in monkey Ronnie and 178 in monkey Loebas. The cells had parafoveal receptive field (RF) positions, ranging between 4 and 6 deg eccentricity, below but close to the horizontal meridian.

*Response types*

We obtained a wide variety of responses to the grating stimulus, ranging from inhibitory responses to very strong excitatory responses. We also observed a similar variety of responses when the monkey started fixating the LED, i.e. before grating onset. These responses at the onset of fixation are very likely due to stimulation of the RF by the homogeneous CRT screen. 13% of our cells responded neither to the grating nor to the CRT screen at the start of fixation. Several examples of the responses of single cells in our paradigm are shown in Fig. 3. Since these histograms serve to illustrate the different response types we encountered we pooled the responses over the different orientations of S1 and of S2. Figure 3A shows a typical example of a cell that responds to the grating but did not fire before or after the grating presentation. 31% of the cells in our sample belonged to this response type. 38% of our cells responded to the grating onset and also fired when the monkey started fixating the LED (Fig. 3B). A number of cells (8%) were inhibited when the monkey fixated the CRT screen but nonetheless responded well to the grating (Fig. 3C). A few cells (2%) showed an increase in response when the CRT stimulated the receptive field and were inhibited when the grating appeared (Fig. 3D). Some cells did not respond to the grating pattern but were either excited (6%; Fig. 3E) or inhibited (2%; see Fig. 3F for a dramatic example) by the CRT screen during fixation. In some trials the monkey made a saccade to a position close to the fixation point followed by a corrective saccade to the fixation point. This explains the presence of a response in some histograms (e.g. Fig. 3E) 300 ms before fixation, i.e. before entering the fixation window. Overall 76% of the cells responded to the grating stimulus, while half of the cells responded before grating onset while the monkey was fixating. All response types were obtained in each monkey, but some response types were recorded from more frequently in Ronnie than in Loebas.

*Orientation tuning*

To quantify the orientation tuning of the cells we computed the net response to the stimulus S1, i.e. the response

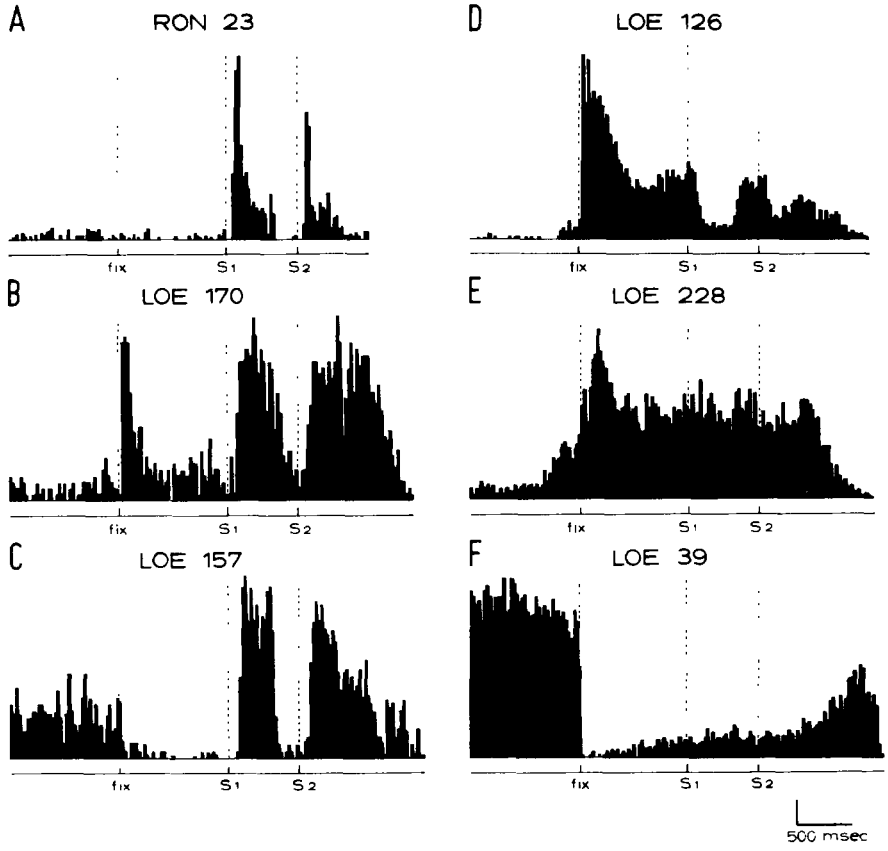


**Fig. 3A–F.** Examples of responses in our paradigm. In each histogram the start of fixation (Fix), the onset of the first stimulus (S1) and the onset of the second stimulus (S2) are indicated by vertical lines. The vertical calibration mark (lower right corner) corresponds to 6.6 spikes/s, 2.7 spikes/s, 6 spikes/s, 19 spikes/s, 11 spikes/s and 9.6 spikes/s for figures **A–F**, respectively. The responses were pooled over orientation of S1 and S2. The grating responses in **A–C** would be 2 to 4 times stronger when considering only the preferred orientation

after subtraction of the activity before grating onset. Since a number of cells showed a 'fixation response' (see preceding section), we subtracted the number of spikes within a bin of 400 ms immediately before grating onset from the number of spikes collected 400 ms after grating onset. The average net response was then plotted as a function of the orientation of the stimulus.

Examples of orientation tuning curves are shown in Figure 4. These examples show that there is a wide variety in orientation tuning of V1 neurons, ranging from narrowly tuned neurons (Fig. 4A) to very broadly tuned orientation sensitive cells (Fig. 4B), and non-oriented cells (Fig. 4C). In some cells we observed inhibition at non-preferred orientations (Fig. 4D), while in others, although very similar in orientation bandwidth (Fig. 4E), no inhibition was evident. Instead of inhibition, some cells showed a second excitatory peak at orientations orthogonal to the preferred one (Fig. 4F). We took the width of the tuning curve at half the maximum net response (a–b in Fig. 4A) as an index of the orientation bandwidth of the cell. This is the index most commonly used to describe quantitatively parameter tunings. However, as all simple quantitative measures it captures only parts of the aspects of the tuning curve. This issue of the usefulness of this measure as a description of monkey V1 orientation tuning curves is critically discussed in De Valois et al. (1982). For those cells that showed more than one peak (Fig. 4F) we measured the bandwidth for the peak with largest response. We restricted our sample to those cells (N = 189) that showed an excitatory response to S1 and for which we had collected sufficient trials at all orientations. The distribution of the orientation bandwidths of this sample of cells is shown in Fig. 5A. The median orientation bandwidth is 41 deg (first quartile: 25 deg; third quartile: 71 deg). 15% of the cells had a width at half height larger than 90 deg. Although we had relatively more narrowly tuned cells in monkey Ronnie's sample (filled bars in Fig. 5A) than in monkey Loebas' sample (stippled bars), their was no significant difference between the median orientation bandwidths of the two monkeys. Cells which responded

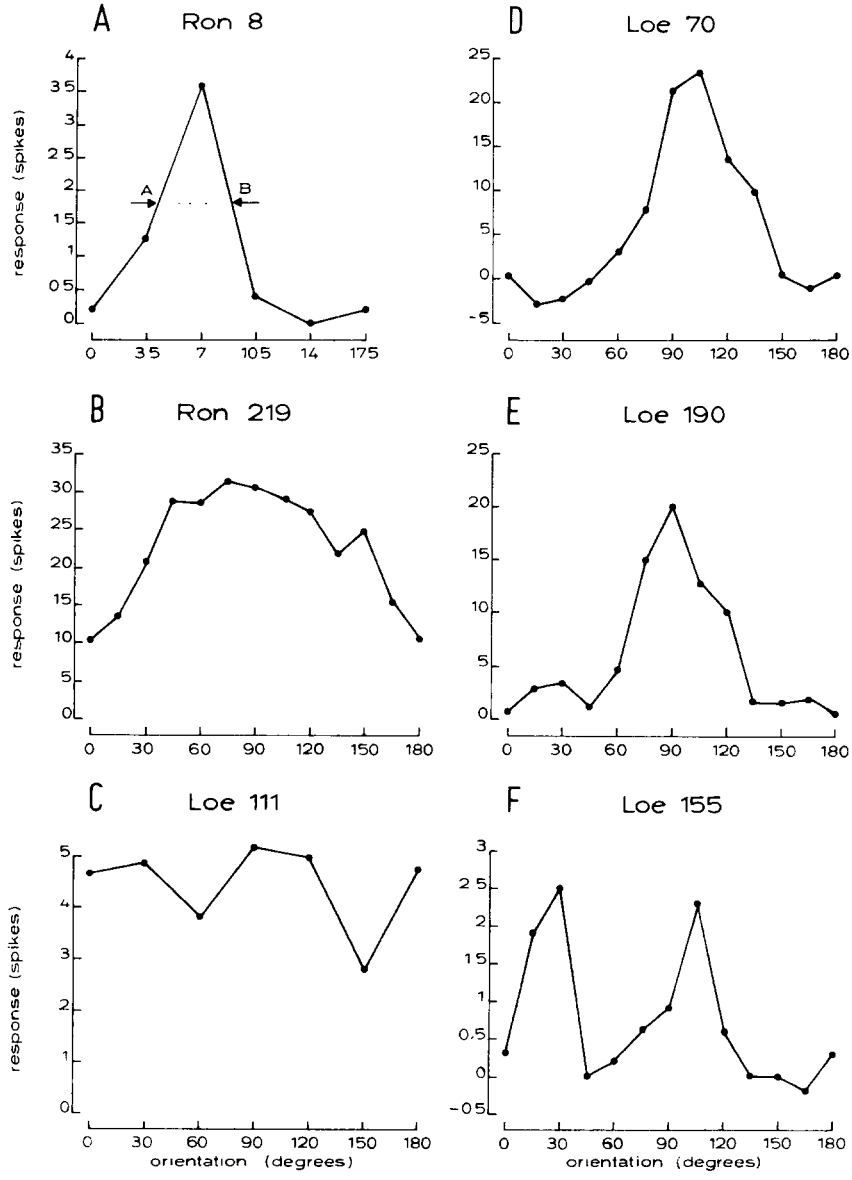


**Fig. 4A–F.** Examples of orientation tuning curves of single striate cells recorded from the behaving monkey. The net responses of the cells are plotted as a function of the orientation of the stimulus. The net response is the average number of spikes during an interval of 400 ms after grating onset, from which the average number of spikes for an interval of 400 ms before stimulus onset is subtracted. The orientation bandwidth (see Fig. 5) is defined as the width at half-height and is indicated by the line A and B in **A**

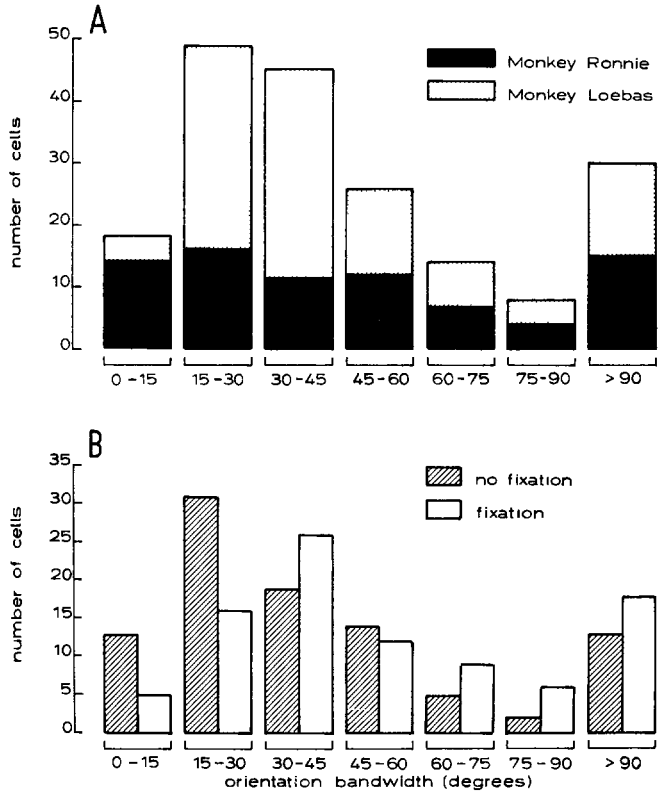


**Fig. 5A, B.** Distribution of the orientation bandwidth in the present sample. The orientation bandwidth is defined as the full width at half height of the tuning. In **A** the filled bars and stippled bars indicate the cells recorded in monkey Ronnie and Loebas, respectively. Three cells had an orientation bandwidth of 180 deg (e.g. Fig. 4C). **B** Shows the distribution of the orientation bandwidth for those cells that were activated when the monkey started fixating (right bars) and for the cells which did not exhibit a 'fixation response' (left bars). The data of both monkeys are pooled

during fixation preceding the grating onset were in most cases tuned for the orientation of the grating pattern. In figrure 5B we show the distributions of the orientation bandwidth for those cells which were activated during fixation prior to stimulus presentation (open bars) and the cells which were not activated during fixation (filled bars). These distributions differed significantly from each other (Chi Square 13.41; $p < 0.04$): cells which showed no 'fixation response' are on average more narrowly tuned than neurons which have an excitatory 'fixation response'. This effect was significant when tested in each monkey separately. Note however, that there is a considerable overlap between the distributions for cells with and without 'fixation responses'. Orientation bandwidth was not only related to the presence of fixation responses but also to the response strength. Cells with a larger orientation bandwidth tended to have a higher response strength than cells with a smaller bandwidth (Spearman rank correlation coefficient: 0.40; $p < 0.0005$). This correlation between response strength and orientation bandwidth also was statistically significant when tested separately in each monkey. We found no statistically significant anisotropy of the distribution of the preferred orientations of the cells, even not for cells with an orientation bandwidth less than 90 deg.

*Response variability and response strength*

The variance of the number of spikes collected within a 480 msec long bin starting 20 ms after grating onset was calculated for all trials of a given orientation. Only those cells (N = 183) for which we had a least 6 valid trials per condition were used. We (Vogels et al. 1989) have shown that the response variance is strongly correlated with the average response strength. In fact when Y is the response variance and X represents the mean response, then

$$Y = 1.9 * X.^{1.1}$$

This power function gives a description of the average response variance of our sample of cells. In order to quantify the response variability of a single cell one usually uses the coefficient of variation, i.e. the response standard deviation divided by the mean response strength (Schiller et al. 1976; Heggelund and Albus 1978). However, as Fig. 6A shows, the coefficient of variation strongly correlates with the mean response strength of the cell: if both variables are log transformed, the coefficient of variation decreases as the square root of the response strength (slope of regression line in Fig. 6B is −0.44; determination coefficient is 0.57). The latter follows from the power relationship of the response variance and response strength reported by Vogels et al. (1989). In order to describe the variability of single cells quantitatively by an index, the latter should be unrelated to the response strength of the cell. Otherwise, variations in this variability index may simply reflect variations in the mean response strength of the cells. Hence, the coefficient of variation is not a useful descriptor of the variability of a cell. Since the power coefficient of the power function relating the response variance and mean response strength is close to 1 (Vogels et al. 1989), the response variance divided by the mean response strength, the normalised variance, will be a better index of variability than the coefficient of variation. Indeed only 2% of the variations in the normalised variance can be accounted for by variations in response strength (Fig. 6B).

The distribution of the normalised variance, calculated for the preferred orientation of the cells, is shown in Fig. 7. The median normalised variance was 2.49 (first quartile 1.43; third quartile 4.10). The normalised variance of the Loebas' sample, indicated by hatched bars in Fig. 7, was on average larger than the normalised variance for cells of Ronnie's sample, which are shown by the filled bars (Mann-Whitney U 3108; $p < 0.002$). In both monkeys the range of the normalised variance was quite large. There was no correlation of the normalised variance with the orientation bandwidth (Spearman rank correlation coefficient −0.085; n.s.). Also shown on Fig. 7 is the distribution of the response strength, expressed as average firing rate (binwidth used in the calculation was 480 ms). The median average firing rate was 16 spikes/s (first quartile: 8 spikes/s; third quartile: 35 spikes/s). There was no significant difffer-

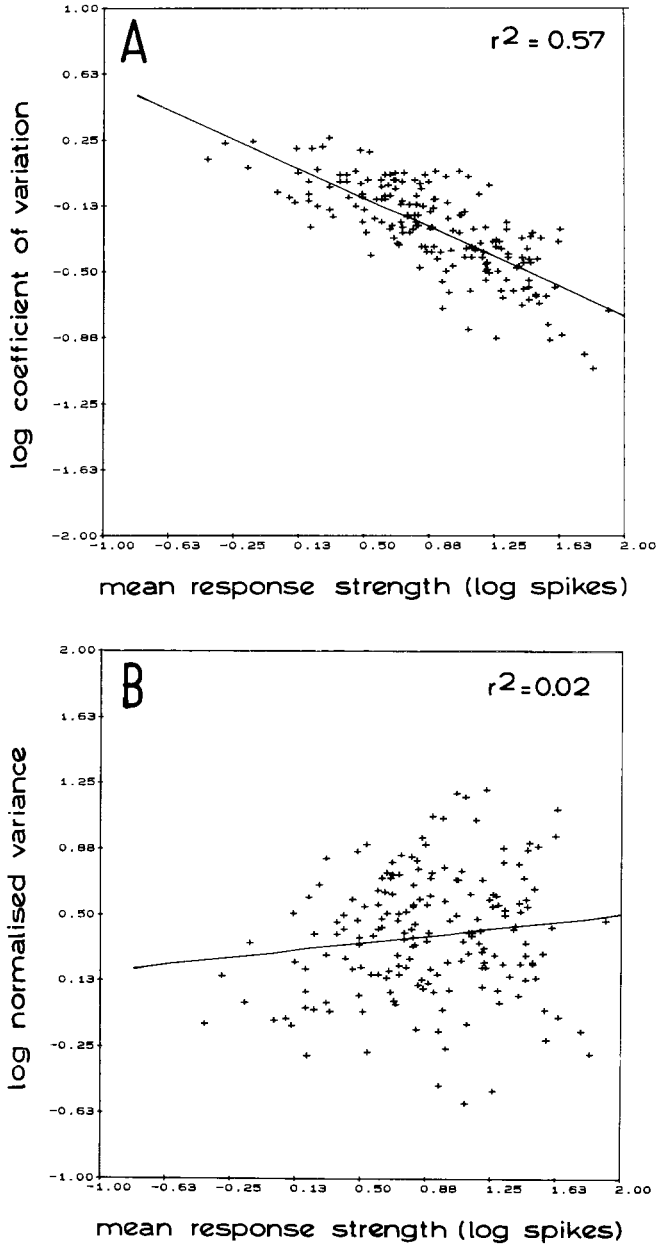


**Fig. 6A, B.** Variability indices as a function of the mean response strength. In **A** we plotted the coefficient of variation, i.e. response standard deviation divided by the mean response strength, as a function of the mean response strength. The cells of two monkeys are pooled. **B** Shows the normalised variance, i.e. the response variance divided by the mean response strength, as a function of the mean response strength for the same sample of cells as in **A**. In both graphs the regression lines are drawn

ences between the two monkeys with respect to the response strength.

*Temporal response properties*

In this section we will report on the way the orientation tuning and the response variance changes during the course of the response. Most of our cells (76%) had a response onset latency between 40 and 100 ms, as deter-

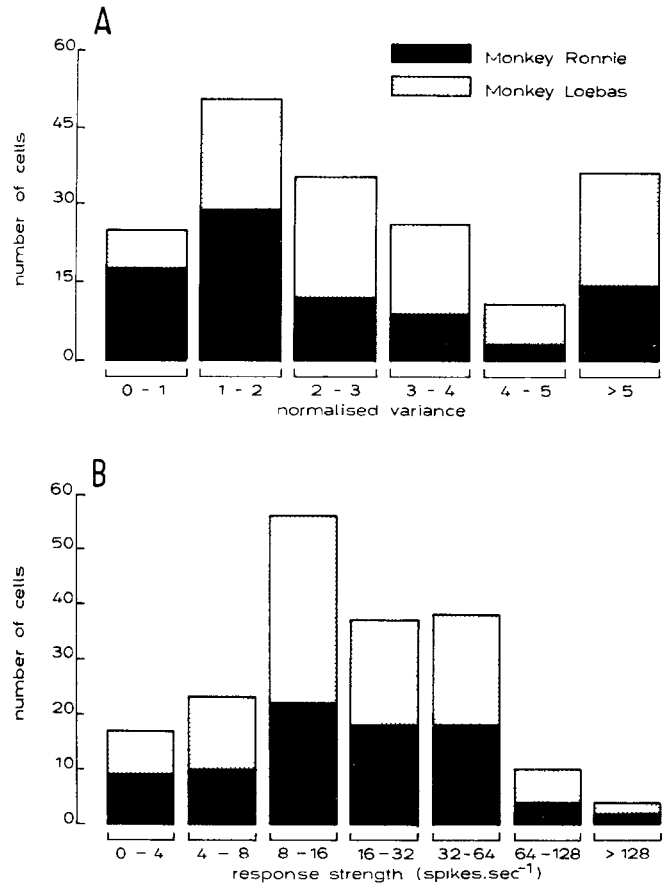


**Fig. 7. A** Distribution of the normalised variance the cells of monkey Ronnie (filled bars) and monkey Loebas (stippled bars). The normalised variance is the response variance divided by the mean response strength. **B** Distribution of the average firing rate of the cells recorded in monkey Ronnie (filled bars) and monkey loebas (stippled bars)

mined with the Cumulative Sum technique (Ellaway 1978; Vogels and Orban, in press). Using a binwidth of 20 ms, the median onset latency was between 60 and 80 ms (first quartile: 40–60 ms; third quartile: 80–100 ms). Some cells had very long latencies, up to 160 ms. There was a significant correlation between the mean response strength and the response latency of a cell (Spearman rank correlation coefficient: $r = -0.26$; $p < 0.0003$): cells with long latencies had mostly small response rates. This negative correlation between mean response strength and response latency was present in each monkey.

In order to investigate the evolution of the orientation selectivity during the stimulus presentation, we split up the responses of the cells in successive 50 ms intervals starting at grating onset, and this for each stimulus orientation. We then plotted the orientation tuning for each of these 50 ms intervals. Of all the cells examined, there were none in which there was no orientation tuning from the outset of the response. Examples are shown in Fig. 8. Each figure plots the average number of spikes for 6 successive 50 ms bins as a function of the stimulus orientation. The first 50 ms bin starts at stimulus onset, while the sixth bin ends at 300 ms after stimulus onset. Figure 9 shows the preferred orientation (9A) and orientation bandwidth (9B) as

a function of the time after grating onset for the same four cells. The preferred orientation is defined as that test orientation at which the response was maximal. If the response was similar at neighbouring test orientations the preferred orientation was set half way. Fig. 8A shows an example of a cell with a highly sustained response. The orientation tuning varies very little during the response. Note also the second peak in the orientation tuning curve, about 60 deg from the preferred orientation. Figure 8B shows an example of a typical cell whose response is more transient than that of the cell of Fig. 8A. Although the response of the cell varies in time, the orientation bandwidth of the cell, as well as the preferred orientation, remain relatively stable (Fig. 9). Only the gain of the response varies in time, and not the orientation tuning.

For the cell shown in Fig. 8C, the preferred orientation as well as the orientation bandwidth varies more over time than in the previous examples. A cell of which the orientation tuning varies even more over time is illustrated in Fig. 8D. Note that for the latter cell the maximal response is stable between 50 and 150 ms, but nonetheless the orientation bandwidth decreases strongly. For this cell the response dynamics per se differ as a function of the orientation: the cell responds more slowly at the non-preferred than at the preferred orientations. 23% of the 158 cells we examined showed stable orientation tuning properties in time, similar to the examples of Fig. 8A and B. Temporally unstable orientation tuning properties, as in Fig. 8D, were found for 37% of the cells. 40% of the cells were not classified as belonging to either category (e.g. cells as the one shown in Fig. 8C).

In one monkey (Ronnie) we performed 33 tests in which a particular S1 orientation was presented atleast 30 times. The results of these tests were used to examine possible temporal variations in the variability of the cells' reponse. In order to do this, we computed the variance and the mean of the number of spikes for two time intervals of 150 ms which started 25 and 175 ms after stimulus onset respectively. In agreement with the results of Vogels et al. (1989) the relationship between the average response strength and the response variance was well described with a power function of the form:

$$\text{response variance} = a * (\text{response strength})^b$$

in which the power b was close to 1. When the mean response strength as well as the response variance are log transformed, the power function becomes a linear function. The regression lines we obtained after log transformation of the response strength and variance for each of the two time windows used are shown in Fig. 10A. Note that while both regression lines have the same slope, the regression line for the earliest part of the response (interval 25–175 ms) has a smaller intercept than the regression line for the later time period. This indicates that, on average, the variance at a particular response strength is smaller during the first phases of the response than during the later phases. Since the power coefficients of the power functions fitted to the response strength – response variance data are

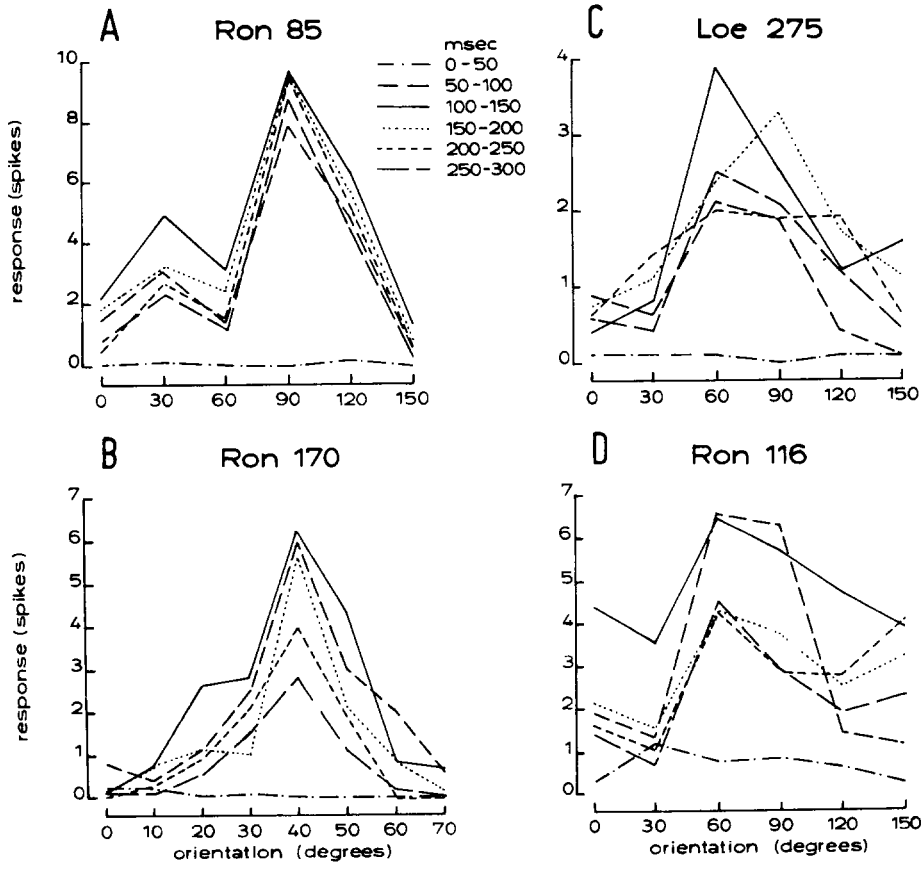


**Fig. 8A–D.** Four examples of the orientation tuning measured at successive intervals of 50 ms, starting at the stimulus onset. In each figure a single curve shows the number of spikes counted in a bin of 50 ms as a function of the orientation of the stimulus. These bins started 0, 50, 100, 150, 200 and 250 ms after stimulus onset respectively. The conventions are shown in the inset. Notice that 5 spikes per orientation in a 50 ms bin corresponds to an average firing rate of 100 spikes/s

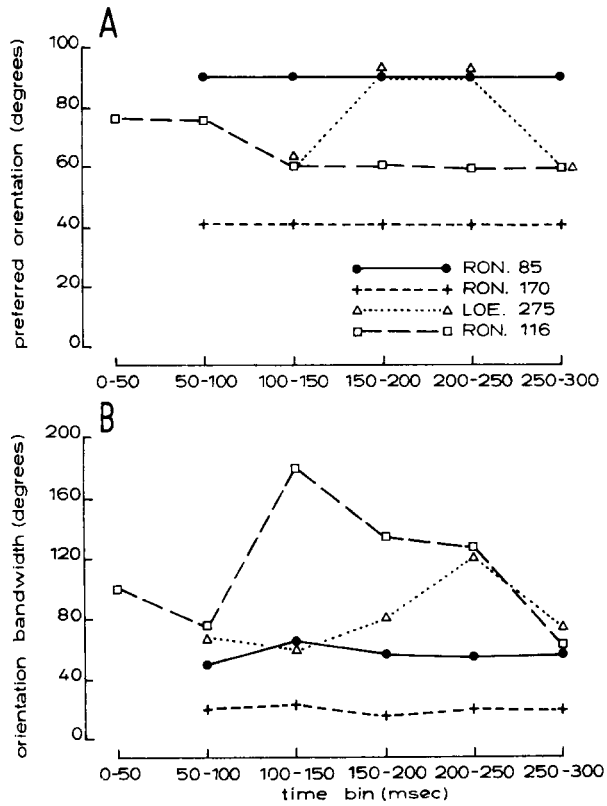


**Fig. 9A, B.** The preferred orientation (**A**) and orientation bandwidth (**B**) plotted as a function of the time after stimulus onset. The preferred orientation and the orientation bandwidth (full width at half height) of the tuning curves at successive intervals of 50 ms, starting at stimulus onset, are shown for the four cells of Fig. 8

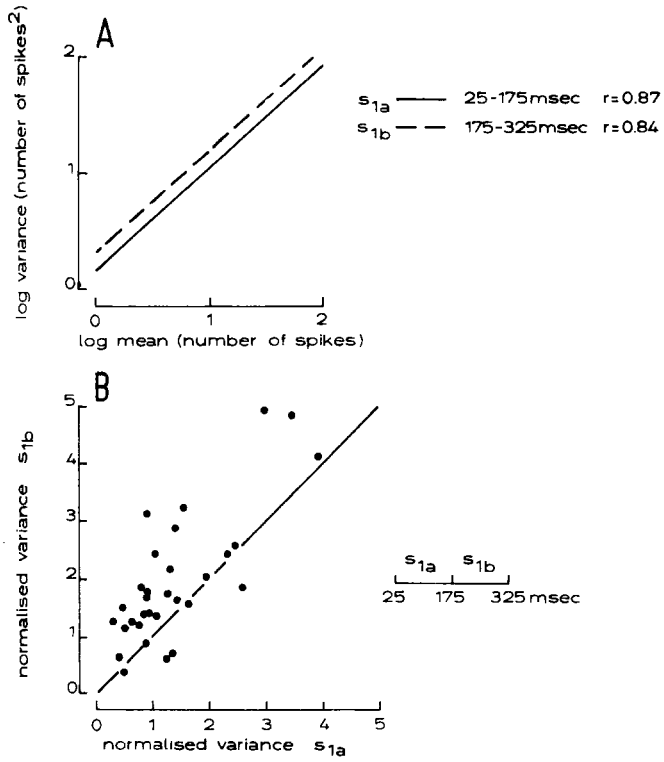


**Fig. 10A, B.** Temporal dependence of the response variance of single cells. **A** Regression lines describing the relationship of the response mean and response variance at two successive time intervals. The first time interval (S1a) started 25 ms after stimulus onset and ended 175 msec after stimulus onset. The second time interval started at 175 (S1b) and ended at 325 ms after stimulus onset. The conventions, as well as the correlation coefficient belonging to each regression line, are shown in the inset. **B** The normalised response variance measured during the second time interval, S1b, plotted as a function of the normalised response variance measured during the first time interval, S1a. The time intervals are defined in the inset, and correspond to those of **A**

close to one, we also calculated normalised variances (see above for definition) for each test and time period. For each of the cells, the normalised variance calulated for the second time window is plotted as a function of the normalised variance of the first time window in Fig. 10B. 82% of the data points lie above the diagonal indicating that the normalised response variance is significantly lower in the initial phase of the response, i.e. following stimulus onset, than during the later response phase (Chi Square 13.36; $p<0.0003$).

*Functional organisation*

We have not reconstructed histologically the electrode penetrations and therefore any classification of the cells according to their cortical layer is tentative. We classified 166 of our total sample as belonging either to the infra- or supragranular layers based upon the following criteria: (1) their position under or below the typical band of strong activity which corresponds to layer IV (Poggio et al. 1977), (2) their occurrence at the start of the penetration or just before entering the white matter, and (3) the microdrive depth readings with respect to the first cortical activity or entrance of the white matter. For most neurons that were encountered at the middle of a penetration we were unable to identify the cortical layer to which they belonged. Fifty three cells (32%) were identified as belonging to the infragranular layers and 68% of the cells of our sample were supragranular cells. Cells which responded before grating onset when the monkey fixated the LED were encountered in infra- as well as supragranular layers. Narrowly orientation tuned neurons were generally encountered in the supragranular layers: 95% of the neurons with an orientation bandwidth less than 15 deg ($N=21$) were located in the supragranular layers. More broadly tuned neurons were as often encountered in the infragranular layers as in the supragranular layers. In some penetrations we found very responsive neurons some 100–200 microns before entering the white matter. They usually were well tuned for orientation, responded in a sustained manner, and also showed a 'fixation response'. In the supragranular layers cells were usually less responsive.

## Discussion

For the first time, we measured the orientation tuning, response variance, and the time dependence of the latter parameters, in monkeys, while they were engaged in an

orientation discrimination task. This ensures that the monkey really needs to analyse the grating orientation in order to perform well behaviorally. We found a large variation in the type of response to the grating stimulus, in the orientation bandwidth, and the response variability of the cells. An important result was that all orientation selective cells were orientation selective from the start of the response.

Since the purpose of the present experiments was not to study the receptive field properties of V1 cells but to examine the response characteristics of neurons to a stimulus in an orientation discrimination task, we did not adapt the stimulus to the cell's RF properties (except RF position). Hence it is likely that in several instances the cells were not stimulated optimally by our relatively large square wave grating. This may partly explain why 13% of our cells did not respond in our paradigm. However, it is worth noting that Creutzfeldt et al. (1987), in the most extensive study to date of receptive field properties of V1 cells in the alert monkey, were unable to drive 11% of their cells, despite stimulus optimisation.

*Response properties: orientation tuning*

Our results concerning the orientation bandwidth of striate neurons recorded during orientation discrimination agree well with the results of other quantitative studies in paralysed and anaesthetised monkeys (Schiller et al. 1976; De Valois et al. 1982; Parker and Hawken 1988) and the fixating alert monkey (Poggio et al. 1977). All studies reported a similar wide range in the orientation tuning bandwidth of visual cortical neurons, going from narrowly tuned cells to non oriented ones.

We observed some neurons in which there also was a response for orientations orthogonal to the preferred orientation. Similar tuning curves with two peaks have been reported by De Valois et al. (1982). De Valois' et al. (1982) data and our own suggest that there is a continuous gradation in the strength of the secondary peak. Furthermore, in some neurons we saw an inhibition at the non preferred orientation, indicating that inhibitory mechanisms are involved in the generation of orientation selectivity. Precisely which mechanisms are involved in the generation of orientation selectivity may well differ from neuron to neuron.

*Response properties: response variability*

Vogels et al. (1989) reported that the response variance of visual cortical neurons recorded in an orientation discrimination task is on average two times the response strength. In the present paper we introduced a novel index of the response variability of a neuron: the variance normalised by the mean response strength of the cell. This normalised variance has the advantage of being independent of the response strength, which is not the case for the commonly used coefficient of variation. The range of the normalised variance we observed agrees well with those very recently reported for the alert fixating monkey by Trotter et al. (1989). Part of the response variability we observed may have been due to small positional errors in fixation, especiallly for the phase- sensitive simple cells. However, it should be noted that the same fixational errors are also present during orientation discrimination, and hence should be taken into account when relating single cell responses and behavioural discrimination accuracy.

*Time course of response properties*

In some neurons, the orientation tuning properties remain invariant throughout the response of the cell. For others, the orientation tuning properties change during the response. For these neurons, the response dynamics differ as a function of the stimulus orientation. Dinse et al. (1988) in a study of the cat visual cortex also reported changes in the orientation tuning properties during the response. However, in contrast to Dinse et al. (1988) but in agreement with Trotter et al. (1989) we saw no neurons for which the orientation tuning was not already present at the start of the response. The latter observation, that the orientation specificity is present at the start of the cellular response, is not unexpected from a functional point of view: it decreases the time necessary to encode reliably the stimulus orientation. The relatively lower response variability during the initial compared to the later response phases is also in line with this view: it assures a fast reliable behavioural response. Indeed monkeys respond in the orientation discrimination task with a 200–300 ms reaction time.

*Link of cellular responses to discrimination accuracy*

The main purpose of this study was to obtain quantitative measures of the orientation bandwidth and response variance of single striate cells during orientation discrimination. These data can then be used in models of orientation coding, linking single cell responses to the orientation discrimination accuracy as measured behaviorally (jnds in orientation) (see Orban et al. in press; Vogels in press).

It has been suggested that small differences in the response strength of a cell underlie fine visual discriminations (Bradley et al. 1987; Parker and Hawken 1985; Swindale and Cynader 1986). Indeed we (Vogels and Orban, in press) showed that the 'best' V1 cells can discriminate differences in orientation which are comparable to the jnd in orientation measured behaviorally in the same monkeys. These cells are only able to discriminate these fine differences at restricted parts of their tuning functions.

Nonetheless, there is a fundamental theoretical reason why one single V1 cell is insufficient for reliable orientation coding. It has been shown that just noticeable differences in orientation are immune to random changes of other stimulus parameters such as spatial frequency (Burbeck and Regan 1983), contrast (Regan and Beverley 1985) and position (Paradiso et al. 1989). On the other hand, V1 cells are sensitive to changes in any one of these parameters: the information delivered by a single V1 cell is ambiguous, in the sense that a change in its activity can be

due to a change in any one of several stimulus features. This ambiguity problem can only be solved by using the reponses of more than one cell, i.e. some kind of ensemble coding of the stimulus orientation.

One possible scheme is the population coding model as used by Georgopoulos et al. (1986) and others (Lee et al. 1988). In this model (Vogels in press) each neuron 'votes' for its preferred orientation. The weight of its vote is determined by its response magnitude for a particular stimulus. The accuracy by which a single cell can discriminate small differences in a particular feature will partly determine how many cells are needed in order to get a fine discrimination. And this accuracy depends on the orientation bandwidth, response variance, response strength and temporal response properties of the neuron (Vogels and Orban in press), the neuronal properties which have been studied in the present experiment.

*Acknowledgements.* This research was supported by grant GOA 8488-62 of the Belgian Ministry of Sciences to G.A.O., and R.V. was supported as "Aangesteld Navorser" from the National Research Council of Belgium. We thank G. Vanparrijs for drawing the figures, and P. Kayenbergh and G. Meulemans for technical assistance. W. Spileers helped with the eye coil operation and participated in some of the recording sessions. We thank S. Raiguel for critical reading of an earlier draft of this paper.

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