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Contribution of area 19 to the foreground-background-interaction of the cat: an analysis based on single cell recordings and behavioural experiments

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Summary. The contribution of area 19 to pattern discrimination in the cat was studied by single cell recordings in this area and by behavioural experiments before and after bilateral lesions. In order to make quantitative comparisons between behavioural performance and that of cell systems, we introduced a new parameter that characterizes visual neurons by their signal-to-noise (S/N) thresholds. A structured visual background made up of Gaussian visual broadband noise which could be moved was superimposed on the signal (moving bars or outline patterns) and the S/N characteristics of the response were determined by varying the signal intensity. The detection performance of cats after bilateral lesion of area 19 showed no deficits. Only for slowly (11 deg/s) or quickly (110 deg/s) moving patterns, or when the background was moved relative to stationary patterns, did we find slight, but significant deficits in the low S/N range. However, when the S/N ratios were higher than 5, all cats achieved their full preoperative performances and no deficits remained. The S/N thresholds of neurons in area 19 were much higher than those found for neurons in areas 17 and 18. The lowest thresholds were found with a stationary background. Introduction of relative velocity between background and bar resulted in intermediate thresholds and the highest thresholds were observed for stimulus configurations lacking relative velocity. These effects correspond to the performance of the intact animal, in which introduction of relative motion increases the performance. The S/N thresholds did not correlate with levels of spike rate recorded at high S/N ratios, direction selectivity or speed preference, indicating that S/N threshold measurements provide a significant additional description of visual neurons. A limited number of area 19 cells recorded in area 17/18 lesioned animals showed very similar thresholds suggesting that this property may be independent of the intactness of areas 17 and 18. The residual performance by 17/18 lesioned cats in detecting small patterns corresponds well to the characteristics of the single cells of area 19. This suggests that area 19 might be able to make a considerable contribution to this task when areas 17/18 are eliminated, though by itself it seems not to be able to sustain the level of performance mediated by them. The contribution of area 19 is restricted to performances at high S/N ratios only. In contrast to what was found for areas 17 and 18, area 19 makes no essential contribution to lowering the S/N ratio at which the system is able to detect the presence of a pattern in a background of irrelevant detail.

Key words: Area 19 – Visual noise – Detection performance – Signal-to-noise thresholds – S/N profiles – Cat

Introduction

The cat neocortex contains multiple visual areas (Tusa et al. 1981) which form a highly interactive system including serial, parallel and reciprocal interconnections (Sprague et al. 1977, 1981; Rosenquist 1985). It is widely accepted that information processing is carried out essentially in parallel within cortical areas 17, 18 and 19. This parallel way of processing appears to arise in the retina, because the different channels, the X-, Y- and W-systems, represent a characteristic input for each area. While area 19 receives the major projection from W-cells (Dreher et al. 1980), area 17 receives input from X- and Y-cells and

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area 18 from Y-cells (cf. Orban 1984). Attempts to determine the individual contribution of these areas to visual pattern and shape recognition can utilize the results of electrophysiological analysis and those obtained from behavioural experiments combined with the method of cortical lesions. In order to ascertain the contributions of areas 17, 18 and 19 to pattern recognition they should be lesioned alone and in various combinations. So far the performance of cats lacking areas 17 and 18, areas 17, 18 and 19 and areas in the lateral suprasylvian sulcus has been analysed (Kiefer et al. 1989; Krüger et al. 1986, 1988). The present article tries to combine both abovementioned methods in order to ascertain the contribution of area 19 to pattern recognition and is the fourth paper in a series of experiments designed to explore pattern recognition after ablation of different visual areas. Up to now there have only been few lesion studies of this cortical area alone (Sprague et al. 1977), and the electrophysiological work on area 19 is sparse (Hubel and Wiesel 1965; Dreher et al. 1980; Kimura et al. 1980; Duysens et al. 1982ab; Dinse 1983; Dinse and Krüger 1987; Tanaka et al. 1987; Saito et al. 1988) in contrast to the enormous body of work on areas 17 and 18.

Previous failures to demonstrate clear deficits in simple pattern discrimination after lesion of areas 17 and 18 in the cat (Doty 1971; Sprague et al. 1977, 1981; Berlucchi et al. 1981; Berkley and Sprague 1979) may be attributed to the fact that the patterns presented for discrimination were not masked by visual noise. Consideration of the natural biotope of an animal makes it clear that pattern recognition always requires the extraction of significant features (signal) from a background of irrelevant detail (noise). As soon as a structured background was introduced in a pattern recognition task, significant deficits after removal of areas 17 and 18 were found (Cornwell et al. 1980; Hughes and Sprague 1986; Krüger et al. 1986; Kiefer et al. 1988). Therefore we used visual stimuli additively superimposed with Gaussian visual noise which can be interpreted as structured background – and we used them in electrophysiological as well as behavioural experiments, which are detection experiments (Fansa and von Seelen 1977; Türke 1981; Krone et al. 1983). In a visual detection experiment, an animal first learns to discriminate two visual patterns (signals) without background, and then is required to recognize the same patterns disturbed by an additively superimposed background of statistical visual noise, which can simulate the almost continuous figure-background interplay occurring in the visual field of the animal under natural conditions. This method was originally derived from signal detection theory (van Trees 1968). Therefore we tend to use the terms "detection" and "to detect" instead of "discrimination" as soon as a background is added (for detail see Krüger et al. 1986, 1988).

As to the electrophysiological experiments, we used a new approach to characterize visual neurons that was introduced by Hoffmann and von Seelen (1978). In order to compare quantitatively performance in behaviour and of single cells, the experimental paradigms used should be as similar as possible. For comparison with detection experiments as described above, conventional receptive field properties are of little use. For this reason we varied the signal-to-noise (S/N) ratio and determined S/N characteristics for single cells as well as for the performance in a behavioural paradigm from which S/N thresholds could be extracted. In both kinds of experiments the same noise process and an analogous set of stimulus configurations was used. It consisted of inphase and antiphase motion of patterns and background with or without relative velocity between them. We were able to show that the resulting S/N thresholds obtained for single cells were indeed independent from discharge rate and receptive field properties. This allows a comparison between the detection performance of single neuronal populations within an area or within different areas and the whole system "cat". This is of particular interest when the cat's performance can be determined before and after lesion of cortical areas.

Because the requirement of equivalent experimental conditions is satisfied in both the single cell recordings and in the detection experiments, we decided to present the behavioural data together with the electrophysiological findings.

Material and methods

Detection experiments

This part of the study is based on results obtained from three female adult domestic cats (Minka, Mimi, Mauz), which were tested as normals and after lesion of area 19. When the test program with these cats was finished another group of three intact male adult domestic cats (Felix, Donald, Gandhi) was tested with some additional situations.

Stimuli and testing procedure. The methodological approach has been described in detail elsewhere (Krüger et al. 1986). Briefly, the cats were trained and tested binocularly in a two alternative forced choice between two bright outline patterns, a triangle and a circle, which were equated for area. The outer base of the triangle measured 26 mm, the outer diameter of the circle measured 20 mm and the width of the outlines was 2.7 mm. The two patterns were projected onto small doors (13 × 10 cm) in the front of the testbox and additively superimposed on a Gaussian broadband noise which was projected from a second projector. The noise pattern had constant spectral power density and included spatial frequencies from 0.002 to 0.27 c/deg which covered the entire frequency range of the test patterns as determined from their Fourier transforms. The ratio of the standard deviation to the mean intensity of the noise (σ/m) was 0.314. The intensity of the test patterns was altered by neutral density filters in a range from 25 to 230 lux, while the noise was kept constant at values around 90 lux. A continuous set of signal-to-noise (S/N) ratios was thus produced by applying the formula

$$\mathrm{S/N} = \frac{\text{intensity of signal (lux)}}{\text{intensity of noise (lux)} \times 0.314}$$

The cats were food deprived for 12 hours, but with water continuously available. They were motivated by food rewards, which they only received in the test box when they had opened the door onto which the correct pattern (triangle) was projected. If they chose incorrectly they were not allowed to correct, found the door locked and received no food. Each cat was trained and tested in four daily sessions, each consisting of 36 pattern presentations, 6 days

a week. Within each session the left/right position of the triangle was changed randomly. The intertrial interval was 10–15 s. During this time a door covered the screens, the patterns were changed and the empty food dish behind the screens was replenished. Olfactory and auditory cues were controlled by filling both dishes with food and by changing the slides and moving the lock in the same sequence before each trial.

The cats could move around freely in the test box and appeared to make their choice at an average viewing distance of 4 cm from the screen. Though this distance was within the nearpoint of accommodation and convergence of the cat, it seemed improbable to us that the cats picked out a distance which made it more difficult for them to make a correct choice and get the food reward. The aim of this procedure was to measure differences rather than absolute values. Even if this close distance had an effect on the cats' detection performance, this effect would have been the same for each of the different parameters and for the preoperative performance as well as for the postoperative one.

In the dynamic conditions, patterns or noise were moved horizontally 7 cm back and forth across the doors with the aid of a galvanometric mirror system controlled by a triangular signal from a wave-generator. Depending on their velocity the direction the patterns moved in was reversed at most twice before the cats made their decision.

Minka, Mimi and Mauz were tested before and after the lesion with the following situations:

1. Both patterns and background kept stationary,
2. Patterns moved at 1.25 cm/s (11 deg/s), 2.5 cm/s (25 deg/s), 5 cm/s (55 deg/s) and 10 cm/s (110 deg/s), while the background was kept stationary,
3. Patterns kept stationary and the background moved at 5 cm/s (55 deg/s) relative to the patterns.

After the lesion the situation patterns moved at 0.35 cm/s (3.5 deg/s), background kept stationary was additionally tested. The corresponding values in degree of visual angle were calculated from an average viewing distance of 4 cm during testing. For a comparison of the electrophysiologically tested situations with behavioural ones, Felix, Donald and Gandhi were tested as normals with:

1. patterns and background both kept stationary,
2. patterns moved at 10 cm/s (110 deg/s), background kept stationary,
3. patterns kept stationary, background moved at 10 cm/s (110 deg/s),
4. patterns and background both moved at 5 cm/s (55 deg/s) antiphase to one another,
5. patterns and background both moved at 10 cm/s (110 deg/s) simultaneously inphase to one another.

In the situations 2–4 the relative velocity between patterns and background was 110 deg/s, in the situations 1 and 5 a relative velocity did not occur.

Detection curves. The detection performance was described with a detection curve in which the percentage of correct decisions within a series of pattern presentations was plotted as a function of the S/N ratio. For each of the 4–8 S/N values of a curve, a minimum of 144 measurements per point was carried out in not less than four sessions (session = 36 presentations). Theoretically, we expected the detection curves to be described by error functions (Krone et al. 1983) whose slopes and positions are determined by two free parameters:

$P_D(S/N) = \mathrm{erf}((S/N - m)/\sigma)$
$P_D(m) = 0.5$
$P_D(m + \sigma) = 0.841$
σ = 1/slope = standard deviation of the curve.

The slope of the error function was estimated for each session. To determine the significance of the deficits, the samples of the pre- and postoperative slope values were subjected to a nonparametric analysis of variance using the Kruskal-Wallis test (Larsen and Marx 1986).

Different lesions lead to deficits of different degrees. As a measure for the extent of a deficit we took the shift in the position of the pre- to that of the postoperatively measured detection curve. The point of reference of each curve was the S/N value at a P_D of 84.1% of correct decisions as determined by a least square fit of the data.

Surgery. After completion of the preoperative test program, in cats Minka, Mimi and Mauz area 19 was lesioned by subpial aspiration of the grey matter by Prof. G. Berlucchi, University of Verona, with the cats under sodium pentobarbital anesthesia (35 mg/kg), using routine sterile precautions (method described by Sprague et al. 1977). Following aspiration, the defect was covered with gel-film. Since all three cats recovered rapidly and without complications, it was possible to resume behavioural testing within 11–14 days after the operation.

Histology. After a survival time of 6–12 months following the operation, the cats were given a lethal dose of sodium pentobarbital and were perfused intracardially with 4% formaldehyde. The brains were drawn, removed for histological verification of the lesions, embedded in paraffin and cut coronally at 12.5 µm. The extent of each cortical lesion was reconstructed from projection drawings of selected coronal Nissl-stained sections through the cortex and the thalamus and extrapolated using surface landmarks and cortical maps as described by Reinoso-Suarez (1961), Otsuka and Hassler (1962), Garey and Powell (1967), Niimi and Sprague (1970), Sanderson (1971), Palmer et al. (1978) and Tusa et al. (1978, 1979, 1981). Retrograde degeneration in the thalamus was studied at a magnification which allowed identification of surviving large and medium sized (but not small) cell bodies, which were plotted. For details see Sprague et al. (1977).

Neurophysiological experiments

Animal preparation and recording techniques. Experiments were carried out on 12 cats (2.5–3.4 kg). For a general account of our methods see Dinse and von Seelen (1981ab) and Best et al. (1986). Cats were anesthetized for surgery with 25 mg/kg ketamin hydrochloride (Vetalar, Parke Davies) in combination with 1.5 mg/kg Xylacin (Rompun, Bayer). A metal head-holder was cemented onto the exposed skull to allow fixation without earbars and eyeclamp. A craniotomy was performed between Horsley Clarke coordinates A1 to P7 and L1 to L10, leaving the dura intact. The opening was covered with 4% agar in physiological saline. The animal was then immobilized by injection of 15 mg/kg Flaxedil (Deutsche Abbott) and artificially ventilated with a mixture of nitrous oxide (70%) and oxygen (30%). All pressure points and wound margins were infiltrated with a local anesthetic (Xylocain). During the recording period, a weak state of anesthesia was maintained by the NO_2/O_2 mixture. The animal was then continuously infused with Flaxedil (10 mg/kg/h) together with a mixture of dextrose and fructose in a solution of various electrolytes (Sterofundin). When the experiments lasted for more than one day, small dosages (3–9 mg/h) of pentobarbital (Nembutal) were additionally delivered i.v. whenever a recording session had finished. The body temperature was kept at 37.5 to 38 degrees, ECG and endexpiratory CO_2 (Binos 1) were continuously monitored; the latter was maintained at 3,5% to 4%.

Neo-Synephrine was used to retract the nictating membrane. The eyes were covered by a liquidfilm (Allergan) and protected with contact lenses with artificial pupil (3 mm in diameter). Retinal landmarks were projected onto a tangent screen. The physiological condition of the eyes as well as the position of the optic disc were regularly checked with an ophthalmoscope.

Tungsten microelectrodes (impedance 4 to 12 MΩ) were used to record extracellularly. When a successful penetration had been completed, electrolytic lesions were made by passing high frequency current (20 A for 45 s) with a radio frequency lesion generator (Radionics). After the end of the experiments, brain sections of 40 µm were stained with cresyl violet and the recording sites were reconstructed according to Otsuka and Hassler (1962), Palmer et al. (1978) and Tusa et al. (1979).

Action potentials were conventionally amplified and converted into TTL norm pulses. Times of occurrence of spikes in relation to an additional stored trigger signal, which controlled stimulus presentation, were fed into a Hewlett-Packard 2100 S digital computer. In most cases, peristimulus time histograms were compiled as a basis for further analysis. In addition, the numbers of spikes elicited during a single stimulus presentation was used as a measure of response.

Visual stimulation. Visual stimuli were applied by projecting them via a double mirror system onto a screen 1.5 m in front of the animal. The signals used were bright bars and the same visual noise process as described in the behavioural experiments. Both the bar and the noise could be projected by separate mirror-systems so that the orientation, the velocity, the direction of movement and especially the luminance of the signals could be adjusted independently of each other.

Whenever a cell was encountered, the location of its receptive field within the visual field and its dimensions were determined by handplotting. In the subsequent quantitative testing, the neuron's sensitivity to different signal-to-noise ratios and to various speeds of the stimulus were investigated. As a rule, the dominant eye was tested quantitatively. Background luminance was kept constant at 0.2 cd/m^2; the luminance of the stimulus (bright bar) was 35 cd/m^2 and that of the background (visual noise) 5 cd/m^2.

Velocity tuning. After the optimal orientation and length of the bar had been determined, the stimulus was moved to and fro over the receptive field (RF) perpendicular to its optimal orientation at velocities ranging from 0.1 deg/s to 600 deg/s. Velocity tuning curves were compiled for each direction of movement separately.

Although most of the velocity tuning curves were rather broad thus making it somewhat arbitrary to estimate precisely the optimal velocity of the cell, we introduced a six score system of preferred velocities. We used this to characterize the speed characteristic of the cell roughly and to correlate the speed preference with the cell's S/N profile. The classes corresponded to the following ranges of velocities: 1) <5 deg/s; 2) 5–20 deg/s; 3) 21–40 deg/s; 4) 41–80 deg/s; 5) 81–160 deg/s; 6) >160 deg/s.

To determine a measure for direction sensitivity, a direction-sensitivity-index (DI) was calculated according to

$$DI = \frac{\text{response in preferred direction}}{\text{response in preferred direction}} - \frac{\text{response in non-preferred direction}}{\text{response in preferred direction}} \times 100$$

The response measure was either the maximal amplitude of the PSTH or a measure of spike count. The binwidth in the PSTH was either kept constant at 8 ms irrespectively of the speed of the stimulus or was adjusted to 0.4% of the time needed for a single stimulus presentation.

S/N profiles. The S/N ratio was calculated in the same way as described for the behavioural experiments. To establish S/N profiles, a bar in optimal orientation, length and velocity was moved to and fro over the RF superimposed with a Gaussian noise process which was either kept stationary or moved in the same or the opposite direction and with the same or a somewhat different velocity, thus producing every required degree of relative velocity between the two stimuli. The following stimulus configurations in which the the bar was always moving were used:

I: background kept stationary
II: background moved with relative velocity inphase to the bar ($v_{background} < v_{bar}$)
III: background moved with relative velocity antiphase to the bar ($v_{background} < -v_{bar}$)
IV: background moved simultaneously inphase to the bar ($v_{background} = v_{bar}$).

Then, for each of the 4 stimulus configurations, the luminance of the bar was gradually reduced by using greyfilters of different levels of transmission until a point was reached where the cell could no longer extract the bar out of the background. This point was called the S/N threshold of the cell for a given stimulus configuration and was defined as the intersection of spontaneous activity level measured at this particular S/N ratio and stimulus related activity. In this way the neuronal activity (total spike number or maximal amplitude in the PSTH) was expressed as a function of the S/N ratio, which we termed the S/N profile.

The spontaneous activity level for each experimental run was calculated either by taking the activity recorded when the bar was moving far outside the RF or by recording neuronal activity without presenting visual stimuli. In all experiments each stimulus was presented 16 to 64 times.

To study the influence of areas 17 and 18 on the performance of area 19 neurons, two additional animals with lesions of both areas (17/18) were used. For histological reconstruction of these lesions, see Krüger et al. (1986).

Results

Reconstruction of the lesions

The location and the extent of the lesions of all three animals is reconstructed and plotted in surface views in

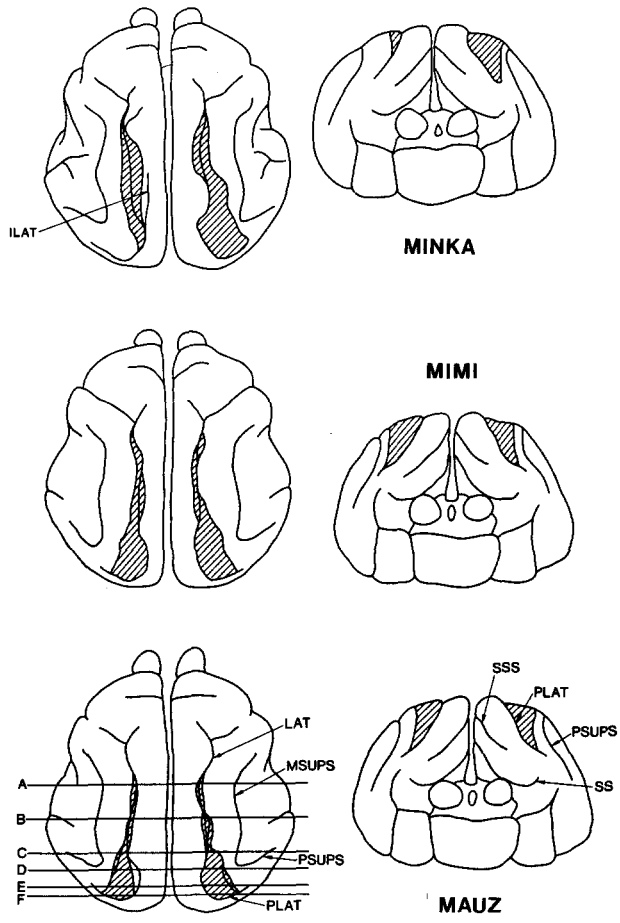

Fig. 1. Drawings of the superior (left) and the posterior (right) views of the brains of cats Minka, Mimi and Mauz, to show the extent of the lesion in area 19. A–F indicate the levels of six coronal sections drawn in Fig. 2. ILAT intralateral sulcus, LAT lateral sulcus, MSUPS middle suprasylvian sulcus, PLAT postlateral sulcus, PSUPS posterior suprasylvian sulcus, SS splenial sulcus, SSS suprasplenial sulcus

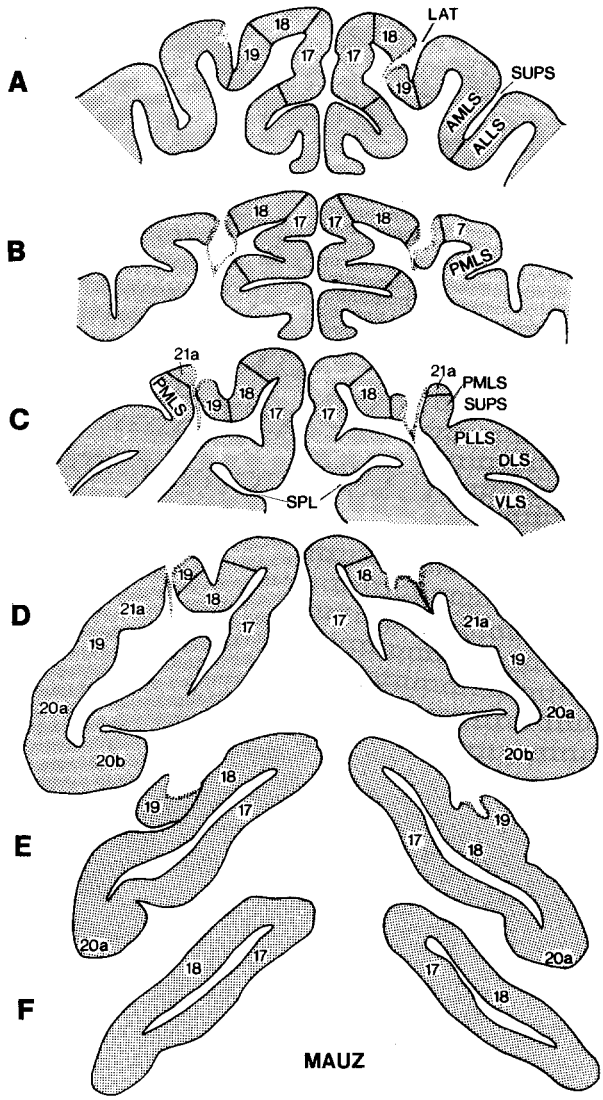

Fig. 2A–F. Projection drawings of six coronal sections, whose levels are indicated in Figure 1, to show the details of the lesion in the cortex and white matter of cat Mauz. Cyto- and myeloarchitectural areas are indicated by numerals. Straight lines indicate that layer I is intact, dotted lines indicate that it is not intact. AMLS anterior medial lateral suprasylvian area, ALLS anterior lateral lateral suprasylvian area, DLS dorsal lateral suprasylvian area, LAT lateral sulcus, PMLS posterior medial lateral suprasylvian area, PLLS posterior lateral lateral suprasylvian area, SPL splenial sulcus, SUPS suprasylvian sulcus, VLS ventral lateral suprasylvian sulcus

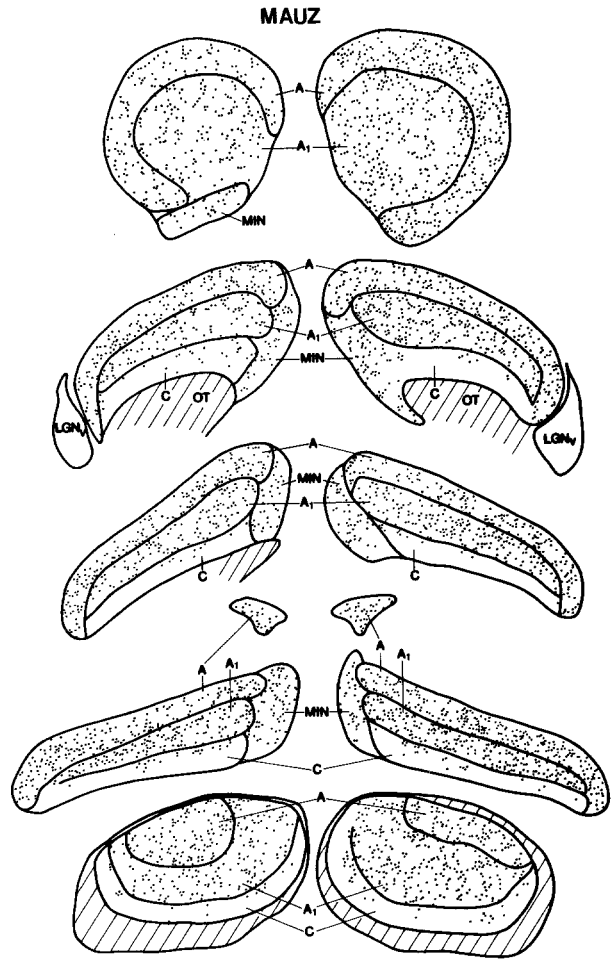

Fig. 3. Projection drawings of five selected coronal sections through the dorsal lateral geniculate complex (LGNd) of cat Mauz. The position of surviving cell bodies of medium and large cells in laminae A, A1, C and the medial interlaminar nucleus (MIN) are shown as dots. LGNv ventral lateral geniculate nucleus, OT optic tract

Fig. 1. The lesion of one animal (Mauz) is illustrated in detail. Selected coronal sections through the cortex are shown in Fig. 2 and the thalamus in Fig. 3. The estimates of the visual coordinates of the spared tissue were extrapolated from the maps prepared by Tusa et al. (1978, 1979, 1981).

In all three cats, the lesions included the central visual field representation of area 19 within an area of not less than about 5° from the representation of the area centralis, with the exception of the left hemisphere of cat Minka. Islands of various sizes in area 19 were spared in the rostral parts of both hemispheres, which represent the periphery of the lower visual field, and on the surfaces of the posterior suprasylvian gyri representing the periphery of the upper visual field.

The representation of the peripheral parts of the lower visual field (VF) was intact beginning about 15°–20° below the area centralis in the left hemispheres of cats Mauz and Mimi and beginning 10°–30° below the area centralis in their right hemispheres (Fig. 2A) whereas the representation of the horizontal meridian was intact beginning about 10° below the area centralis and the peripheral parts were intact beginning about 30° below it. In cat Minka the lower VF was spared about 25°–35° below the area centralis in both hemispheres. Small islands of area 19 were spared in the medial bank of the lateral sulcus of the left hemisphere of cat Mimi (A 0.5 to P 2) and in the range from A 3 to P 0.5 in the left and from A 2 to P 0.5 in the right hemisphere of cat Minka but the vertical meridian representation seemed to be removed in both cases, including the visual field representation of about 5° from it.

The representation of the upper visual field was removed most completely in cat Mimi. Only small islands which represent the far periphery beginning about 25°

below the horizontal meridian were spared in the right hemisphere and beginning about 15°–20° below the horizontal meridian in the left one. In both hemispheres of cat Mauz (Fig. 2D, E) and the right one of cat Minka, small part of the upper VF was intact beginning about 5° above the area centralis. Minka showed the most incomplete lesion, as the upper VF representation in its left hemisphere seemed to be completely intact, even including the representation of the area centralis.

In addition to the lesion of area 19, parts of the lateral bank and fundus of the lateral sulcus (areas 5 and 7) were lesioned in the rostral parts of both hemispheres of all cats. In cat Mauz, the left hemisphere was affected (Fig. 2B), in cat Minka they were removed over a wide range (A 14–A 0.5) and the lesion extended to the crown of the suprasylvian gyrus including areas 7 and 21a in the right hemisphere (A 4–P 4). In cat Mimi, the lateral bank of the left sulcus (A 14–A 2) together with the part of its medial bank lying below area 19 (A 14–A 12) were removed. In addition, some upper parts of the lateral bank of the right sulcus were removed in the range from A 14 to A 12.

Parts of area 21a on the surface of the suprasylvian gyrus adjacent to the representation of area centralis of area 19 were removed bilaterally in cats Mauz (Fig. 2C, D) and Mimi.

Some peripheral parts of the upper visual field representation of area 18 were removed (+30°) on the lateral bank and fundus of the postlateral sulcus in one hemisphere in each of the three cats (Fig. 2D). Otherwise, areas 17 and 18 were intact at all levels and were fully innervated.

The lesion of area 19 and the intactness of areas 17 and 18 were reflected in the intactness of laminae A and A1 in the lateral geniculate body and in a medium to light degeneration in laminae C and MIN which left a number of cells intact (Fig. 3).

Detection performance

Figure 4 shows the detection curves of one normal cat (Felix) for three situations with relative velocity between patterns and background (2–4) and two situations without relative velocity (1, 5). The detection curves for the situations with relative velocity are shifted in the lower signal-to-noise range, i.e. it is easier for the cat to detect the patterns out of the background as soon as a relative velocity occurs between both, whereby it does not matter if the patterns are moved or the background is moved or both. In tendency this was found for all cats tested, but not always as strongly marked as for Felix, a cat which made its decisions very carefully and seemed very keen to make no mistakes. The more inattentive a cat was, the smaller were the differences between the detection curves in the different test situations.

Figure 5 shows the pre- (continuous lines) and postoperatively tested (dashed lines) detection curves of the cats Minka, Mimi and Mauz for all situations tested. The significance level between the pre- and the postoperative set of data is given for each pair of curves. Additionally,

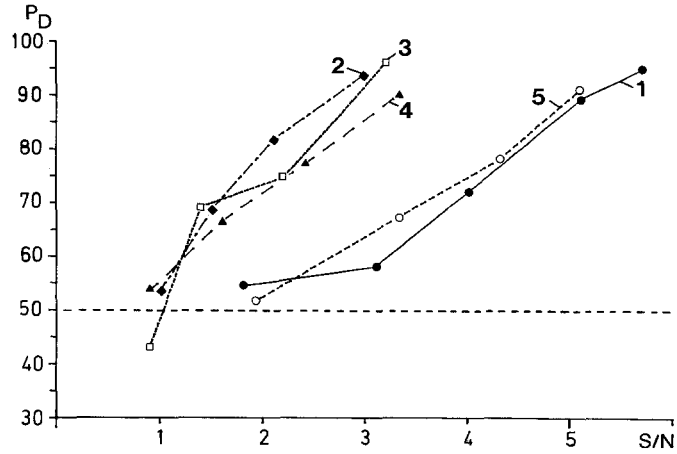

Fig. 4. Detection curves of an intact cat. (1) patterns and background both kept stationary, (2) patterns moved at 10 cm/s (110 deg/s), background kept stationary, (3) patterns kept stationary, background moved at 10 cm/s (110 deg/s), (4) patterns and background both moved at 5 cm/s (55 deg/s) antiphase to one another, (5) patterns and background both moved at 10 cm/s (110 deg/s) simultaneously inphase to one another. In the situations 2–4 the relative velocity between patterns and background is 110 deg/s, in the situations 1 and 5 a relative velocity is missing

the S/N values at a P_D of 50% and of 84.1%, the shifts between pre- and postoperative curves and the levels of significance of the deficits are listed for all detection curves in Table 1.

We found slight, but significant deficits in the low signal-to-noise range only for slowly (11 deg/s) or quickly (110 deg/s) moving patterns (Fig. 5B, E), or when the background was moved relatively to stationary patterns (Fig. 5F, cats Minka and Mimi). With S/N ratios higher than 5, however, all lesioned cats performed no less proficiently than intact cats and were able to regain their preoperative performances. For stationary patterns (Fig. 5A), for patterns moving at 25 deg/s (Fig. 5C) or 55 deg/s (Fig. 5D) with the background kept stationary even in the low signal-to-noise range we found no deficits, though in this last case (D) the relative velocity between patterns and noise was the same as in situation F.

Cat Minka was always the one with the lowest shift values corresponding to the most incomplete lesion of its area 19.

In an additional postoperative test – for which we have no preoperatively tested reference curves – the velocity of the patterns was reduced to 3.5 deg/s. For this test, the highest S/N values at a P_D of 84.1% were determined for all three cats (Table 1). This could be an indication that it is more difficult for cats with lesions of area 19 to detect moving patterns the slower they are moved.

Figure 6 shows that all the deficits we found for the cats with subtotal lesions of area 19 were slight compared to the substantial deficits we found for cats with lesions of areas 17 and 18 (Krüger et al. 1986). In the 19-lesioned cats, the shifts in the positions of the pre- to those of the postoperative curves lay between 0 and 1.7. By contrast, in the 17/18 lesioned cats the shifts came to 5.4–12.7 for the same parameters (Krüger et al. 1986). A second

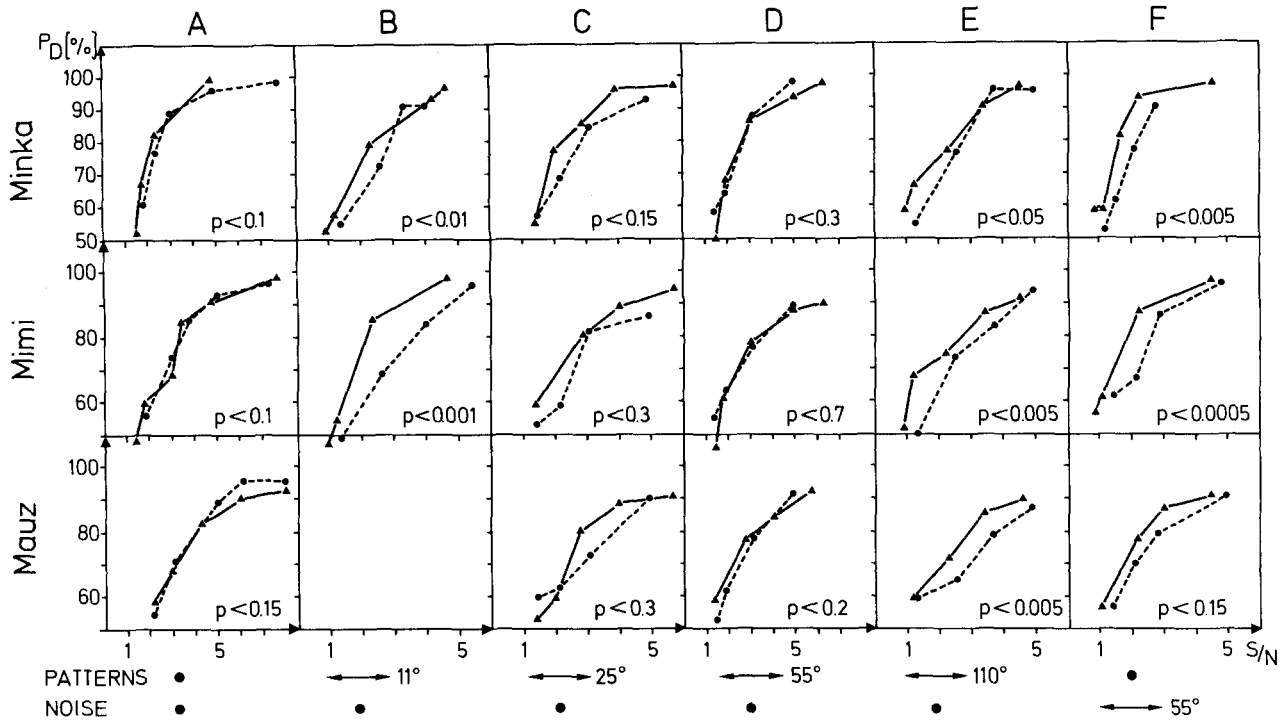

Fig. 5A–F. Detection performances of cats Minka, Mimi and Mauz before (continuous lines) and after (dashed lines) lesion of area 19. They were tested with small patterns superimposed on broadband noise. Patterns and noise were kept stationary (**A**), the patterns were moved relatively to the noise at 11 deg/s (**B**), 25 deg/s (**C**), 55 deg/s (**D**) and 110 deg/s (**E**) while the noise was kept stationary, and the noise was moved relatively to the patterns at 55 deg/s (**F**) while the patterns were kept stationary

Table 1. Test series performed with intact and area 19 lesioned cats. The numbers correspond to the S/N values at a P_D of 50% and 84.1% of correct decisions determined by a least square fit of the corresponding detection curves, to the shift in the position of the pre- to that of the postoperative detection curves and to the level of significance of the deficits ($p < x$)

Test	Cat	S/N at 50%		S/N at 84.1%		Shift	$p<$
		Intact	Lesioned	Intact	Lesioned		
Patterns + noise stationary	Minka	1.3	1.5	2.6	2.8	0.2	0.0833
	Mimi	1.4	1.5	3.8	3.8	0	0.0833
	Mauz	1.5	1.8	4.7	4.3	−0.4	0.1573
Patterns moved at 3.5 deg/s	Minka	–	1.2	–	3.6	–	–
	Mimi	–	0.5	–	4.6	–	–
	Mauz	–	1.4	–	6.1	–	–
Patterns moved at 11 deg/s	Minka	0.8	1.2	2.8	3.2	0.4	0.0065
	Mimi	1.1	1.5	2.2	3.9	1.7	0.0005
	Mauz	–	–	–	–	–	–
Patterns moved at 25 deg/s	Minka	1.1	1.1	2.6	3.2	0.6	0.1380
	Mimi	0.7	1.3	3.4	4.1	0.7	0.3173
	Mauz	1.3	0.8	3.3	4.3	1.0	0.2207
Patterns moved at 55 deg/s	Minka	1.4	1.2	2.7	2.9	0.2	0.3173
	Mimi	1.5	1.0	3.8	4.0	0.2	0.6547
	Mauz	0.6	1.2	4.0	3.8	−0.2	0.1923
Patterns moved at 110 deg/s	Minka	0.4	1.1	2.7	2.9	0.2	0.0320
	Mimi	0.4	1.2	3.1	3.6	0.5	0.0047
	Mauz	0.5	0.5	3.5	4.6	1.1	0.0455
Noise moved at 55 deg/s	Minka	0.8	1.1	1.8	2.3	0.5	0.0038
	Mimi	0.7	0.9	2.0	3.0	1.0	0.0003
	Mauz	0.7	0.8	2.9	3.5	0.6	0.1213

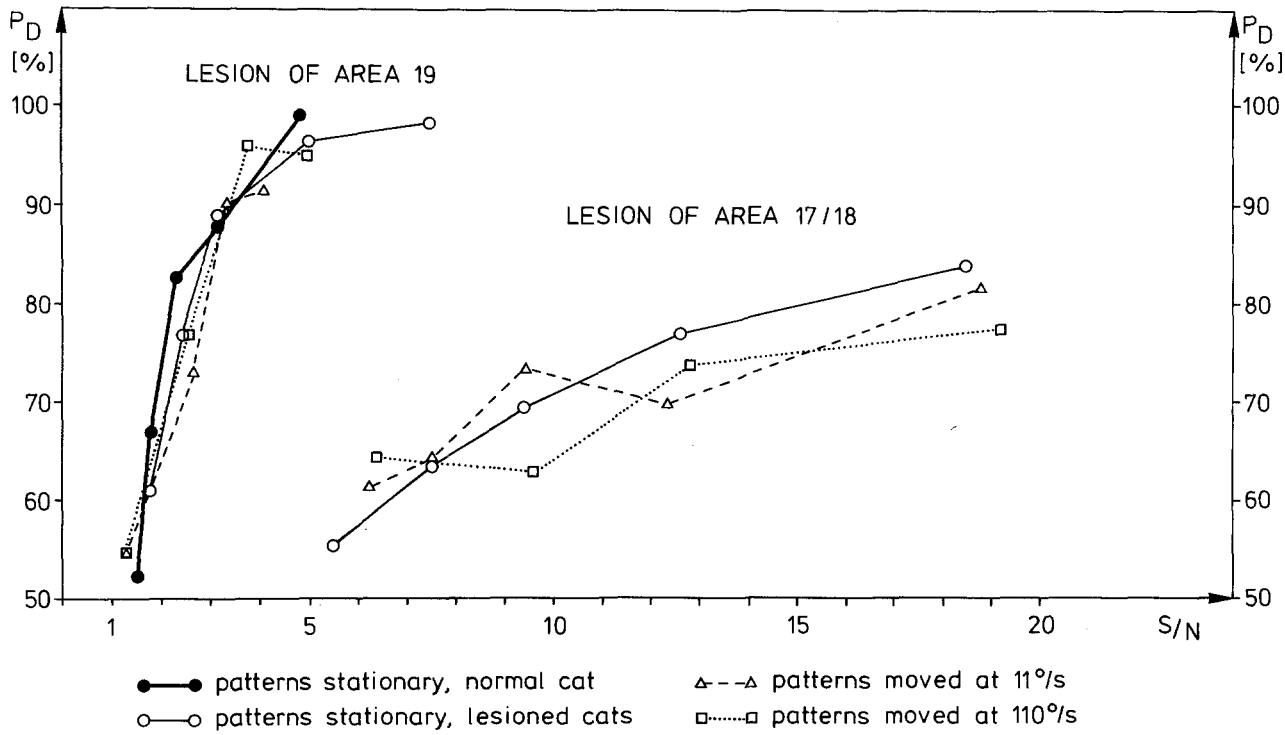

Fig. 6. Detection curves of one area 19 (Minka) and one area 17/18 lesioned cat (Nero) tested with stationary small patterns and ones moved relatively to the broadband background at different rates. Background is kept stationary

Table 2. Comparison between intact, area 19 and area 17/18 lesioned cats. The numbers correspond to the mean S/N values at a P_D of 50% and 84.1% of correct decisions determined by a least square fit of the corresponding detection curves

Test	Intact		17/18-lesioned		19-lesioned	
	50%	84%	50%	84%	50%	84%
Small patterns + broadband noise Kept stationary	1.4 ($n=14$)	3.5	3.2 ($n=6$)	15.7	1.6 ($n=3$)	3.6
Small patterns moved at 55 deg/s, Broadband noise kept stationary	1.0 ($n=12$)	3.2	4.2 ($n=3$)	20.9	1.1 ($n=3$)	3.6

substantial difference between both groups of lesioned cats was that cats with lesions of areas 17 and 18 were still able to discriminate the small patterns, but their performances were significantly ($p=0.01$) worse than those of intact cats at all S/N ratios, even at very high S/N values (> 15). By contrast, cats with lesions of area 19 were able to regain the 90% level of their preoperative performances at S/N values higher than 5. Table 2 shows a comparison of the mean S/N values at a P_D of 50% and 84.1% of correct decisions between intact, area 19 and areas 17/18 lesioned cats.

Electrophysiological findings

From a total number of 109 neurons, 50 cells were quantitatively tested for their sensitivity to changes of the S/N ratio and 77 for their velocity tuning. In addition, a limited sample of 14 cells was recorded in the area 17/18 lesioned animals.

In a first series of experiments, cells were recorded within the anterior portion of area 19 along an anteroposterior extent of about 4 mm between Horsley-Clarke coordinates A 0 and A 4 (Reinoso-Suarez 1961). In a second series, recording sites were in the posterior portion of area 19 between P 3 and P 7. We identified area 19 neurons using two criteria. During the experiment we were guided by the characteristic temporal-nasal displacement of receptive field locations when successive electrode penetratons were placed along the medial lateral extension of the sulcus lateralis. After the experiment we used the electrolytic landmarks to identify area 19 borders according to cytoarchitectonic characteristics described by Otsuka and Hassler (1962). The actual penetrations were intended to collect cells lying within 10 degree of the visual field.

S/N profiles. A typical recording sequence illustrating the effect of decreasing S/N ratios is shown in Fig. 7 for stimulus configuration I with the background kept stationary. Based on these responses we compiled S/N profiles which characterize the cell's sensitivity to different S/N levels as well as the absolute threshold beyond

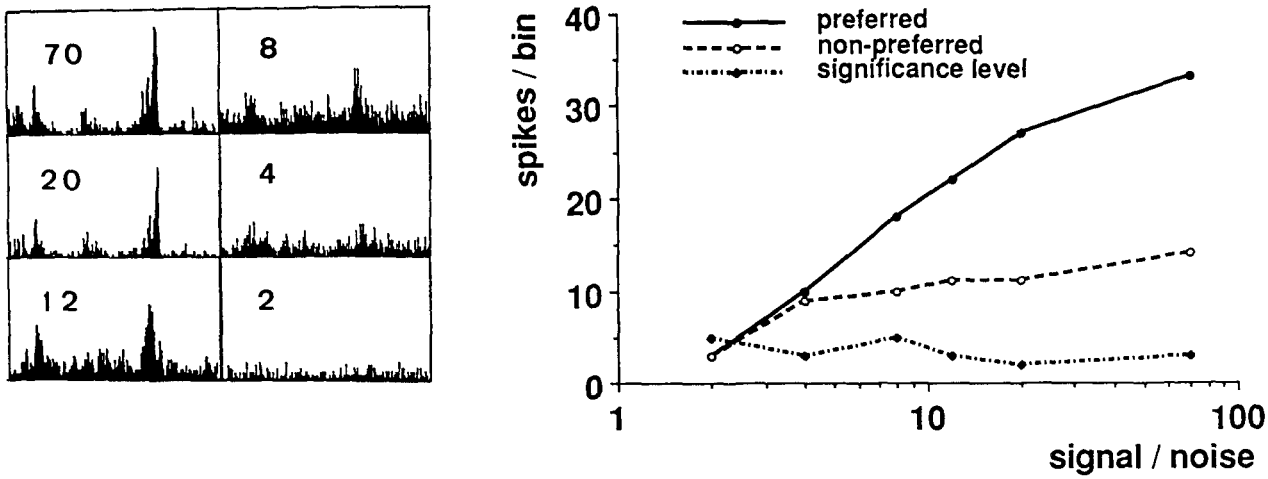

Fig. 7. Sequence of PSTH responses of an area 19 neuron to stimulation with a moving bar with stationary background recorded at different S/N ratios. The actual S/N ratios are given as numbers. The threshold of this neuron is at a S/N ratio of about 4 (left). S/N profile as obtained from the response sequence is shown on the right side. The significance level is indicated and was 2 σ of the spontaneous activity (right). The ordinate is 40 spikes/bin. Note that the direction selectivity of the cell seen at high S/N ratios is maintained during the decrease of S/N ratios, but lost at very low S/N ratios, resulting in the same threshold for both directions

Table 3. Comparison of the mean S/N thresholds of the individual cells and the S/N ratios at 84.1% above threshold as read from the probability functions shown in Fig. 8 and 10 obtained for different stimulus configurations for area 19 neurons, area 19 neurons recorded in area 17/18 lesioned cats, area 17 neurons (Hoffmann and von Seelen 1984) and area 18 neurons (Dinse and von Seelen 1981b; Dinse unpublished)

Stimulus	Area 19 neurones		Area 19 neurones of area 17/18 lesioned cats		Area 17 neurones		Area 18 neurones	
	Mean S/N threshold	S/N at 84%	Mean S/N threshold	S/N at 84%	Mean S/N threshold	S/N at 84%	Mean S/N threshold	S/N at 84%
Noise kept stationary	8.1	10.7	9.2	11.5	0.8	0.7	6.8	6.7
Noise moved relatively inphase to the bar	8.7	10.3	–	–	–	–	9.9	10.3
Noise moved relatively antiphase to the bar	11.2	18.5	–	–	–	–	–	–
Noise moved simultaneously inphase to the bar	15.4	22.0	16.9	19.0	1.6	3.5	14.3	18.2

which the cell cannot extract the stimulus out of the background. An example of such a profile is shown in Fig. 7. It shows the threshold, the working range over which changes in the S/N ratio evoke different responses and a point of saturation, at which an increase of the S/N ratio has no further effect on the cell's discharge rate. We obtained such S/N profiles for all four stimulus configurations (I–IV) described above.

The threshold was determined as the intersection between stimulus related activity and 2 σ of the spontaneous activity level. Spontaneous activity was always measured for each particular S/N ratio. As can be seen from Fig. 7, spontaneous activity increases slightly as the S/N ratio decreases. The means of the S/N thresholds of the 50 cells tested for each stimulus configuration are summarized in Table 3.

Probability functions of S/N thresholds. The behavioural data which represent the performance of the animal are presented in this paper in form of so-called detection curves with the S/N ratios on the abscissa and the probability of correct decisions on the ordinate. In order to establish a comparable measure for the single cell data that allows a direct comparison with the behavioural ones, we compiled the distribution of S/N thresholds for all cells and replotted them as a probability function. In this way we obtained graphs that give the percentage of neurons above threshold on the ordinate as a function of the S/N ratio. These probability functions were prepared for each stimulus configuration (Fig. 8). The basic idea behind this was that the number of neurons above threshold is the decisive factor determining the performance of the cat in the detection experiment. A corresponding approach was used by Hoffmann and von Seelen (1984) in the analysis of neurons of area 17. The advantage of this method is that one obtains a quantitative measure which allows comparison of the performance of either different cell systems from one or more neuronal substrates with one another or with behavioural data. Additionally, when one assumes that, due to the Gaussian distribution of the input signal (i.e. background stimulus), the distribution observed for the cells probability above threshold is also Gaussian, then one can characterize the obtained probability function by

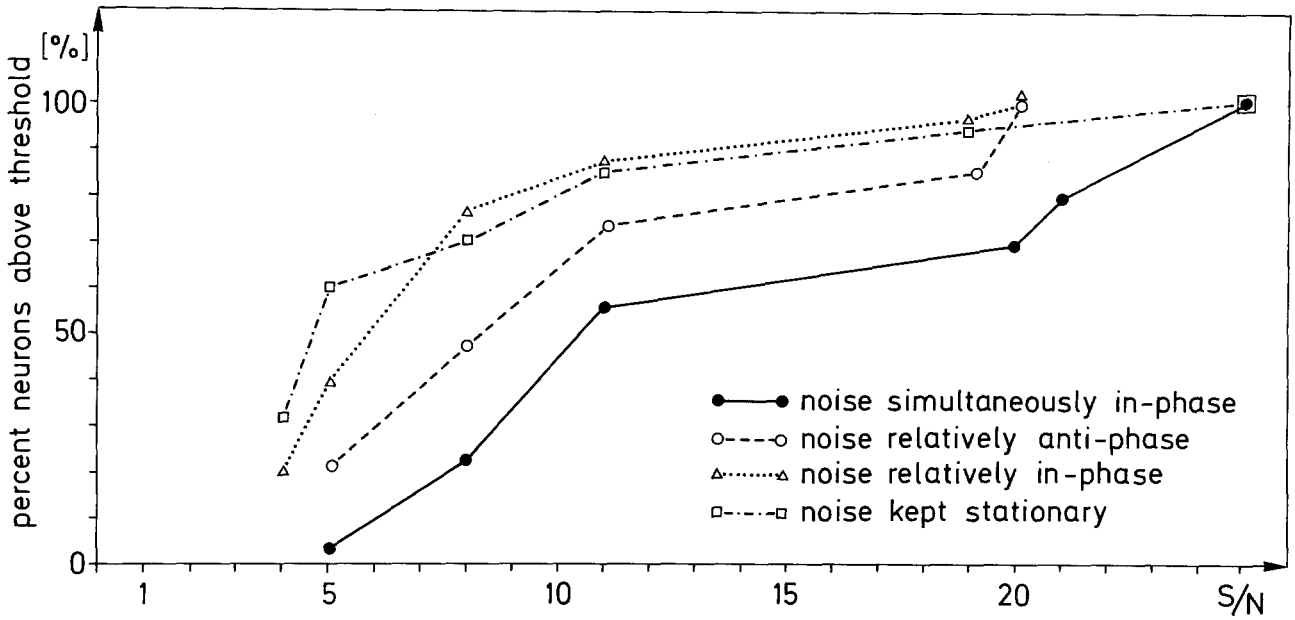

Fig. 8. Probability functions as obtained from the distribution of S/N thresholds for single neurons of area 19. Abscissa: S/N ratio; ordinate: % neurons above threshold. Assuming a Gaussian distribution of the function due to the Gaussian distribution of the input signal, these functions can be completely described by the S/N ratio at 84.1%. As could be already seen from the mean S/N thresholds, stationary background indicates the best performance, while inphase moved background without relative velocity reveals worst characteristics. Introduction of relative velocity is intermediate

a single value, the S/N ratio at 84.1%. These values are summarized in Table 3 for each stimulus configuration.

Influence of background motion. We observed a very uniform response pattern of the S/N profiles and the probability functions of the S/N thresholds measured with the different stimulus configurations (Fig. 8, Table 3). The situation with the background kept stationary revealed the lowest thresholds and thus the best performance of the cells. Introduction of relative motion inphase to the bar (configuration II) lead to a slight increase in thresholds. This shift of thresholds towards higher values was more pronounced when the background was moved relative antiphase to the bar (configuration III). The highest thresholds, and thus the worst performances, were observed for the situation IV, background simultaneously moved inphase to the bar without relative motion.

Correlation of S/N thresholds with receptive field properties. If the S/N threshold of a cell is to be regarded as an additional characteristic parameter which is suited for further identification or description of visually driven neurons, one has to prove independence from other parameters such as discharge rate and one has to establish possible associations with other receptive field properties such as direction selectivity or velocity preference.

Discharge rate. As to discharge rate, one has to rule out that the threshold is merely a function of maximal spike rate that is recorded for a cell at high S/N ratios. The thresholds of all cells tested in area 19 with stimulus configuration I, background stationary, were correlated with the maximal response rate obtained at the highest S/N ratio tested (expressed in spikes/s). According to the correlation coefficient of $r=0.04$, there is no association between the two parameters. Similar correlation coefficients were obtained for the other stimulus configurations tested (type II $r=0.12$; type III $r=-0.09$; type IV $r=0.18$). This overall lack of correlation between maximal spike rate and threshold indicates that the threshold as defined in these experiments signals a true property of the cells and cannot be explained by their discharge properties.

Direction selectivity. The independence of the S/N threshold from the discharge rate of a cell could already be seen for the neuron shown in Fig. 7, in which the response for the preferred direction exhibits the same threshold as the response for the non-preferred direction, which at high S/N ratios shows about half the spike rate of the preferred response. This led us to a more detailed investigation of the influence of changing S/N ratios on the direction selectivity of a cell.

According to the index of direction selectivity measured at high S/N ratios, we subdivided our sample of neurons into three groups: group I with a DI of 0 to 25, group II with a DI of 26 to 50 and group III with a DI > 50. We used linear regression analysis to correlate the S/N threshold of a cell with its degree of direction selectivity according to group I, II or III. The correlation coefficient of $r=0.21$ for the stimulus configuration I, stationary background, indicates a lack of association between threshold and direction selectivity. The correlation coefficients for the stimulus configurations II to IV were $r=0.088$, 0.15 and 0.22, respectively.

As a next step, for each group we determined the percentage of cells that did not change their degree of direction selectivity at the threshold condition. The per-

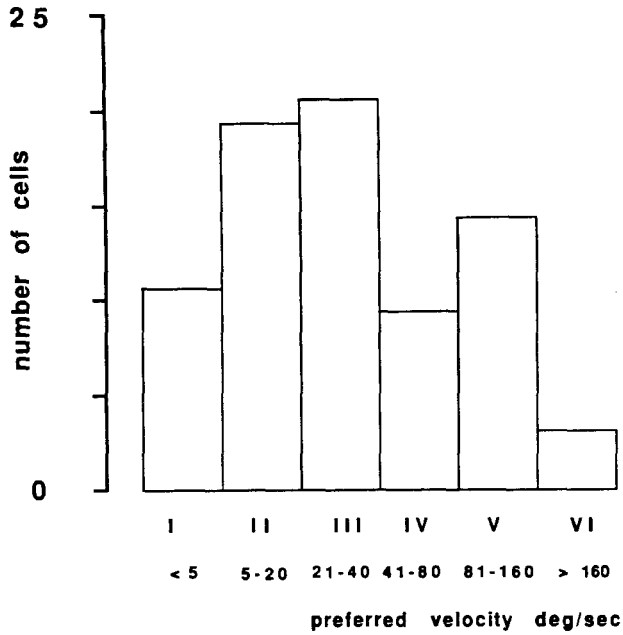

Fig. 9. Distribution of optimal velocities ($n=77$) according to a six score rating. There is a weak bimodal trend for neurons preferring velocities <40 deg/s or >80 deg/s

centage of so-called direction permanent cells, i.e. cells that exhibit the same index of direction selectivity at high and low S/N ratios, was different in each group. The overwhelming majority of non-direction selective cells was permanent, while the contrary was true for cells of group II and III. This leads to the phenomenon that cells that are non-direction selective at high S/N ratios maintain this property at low S/N ratios. In contrast, cells that are direction sensitive at high S/N ratios lose this property at low S/N ratios and exhibit the same thresholds for both directions of movement. An example of such behaviour is demonstrated by the cell shown in Fig. 7. A quarter of group II neurons and an even lower percentage of group III neurons are permanent with the result that the response of these neurons to the preferred and non-preferred direction reveals different S/N thresholds. However, due to the low percentage of cells belonging to group II and III, different thresholds for the preferred and the non-preferred direction are only found in a small portion of area 19 cells.

Velocity preference. All cells for which a S/N profile could be compiled were tested for the preferred velocity of stimulus. Most cells exhibited broad tuning indicating that they were sensitive over a wide range of velocities. This made it difficult to assess their optimal preferred velocity precisely. However, we estimated optimal preferred velocities on the bases of the peak in the velocity tuning curve and used a 6 point scale to classify cells according to the following ranges of velocities: <5 deg/s; 5–20 deg/s; 21–40 deg/s; 41–80 deg/s; 81–160 deg/s and >160 deg/s. The resulting distribution is shown in Fig. 9. On the basis of these data we correlated the velocity sensitivity of a cell with its S/N threshold. The correlation coefficient of $r=-0.204$ indicates that the S/N threshold seems to be independent of the preferred velocity of a cell.

S/N thresholds in cats with lesion of area 17 and 18. Since we compare the S/N thresholds of neurons from intact animals with behavioural data from lesioned ones we have to consider the possibility that the damage to one

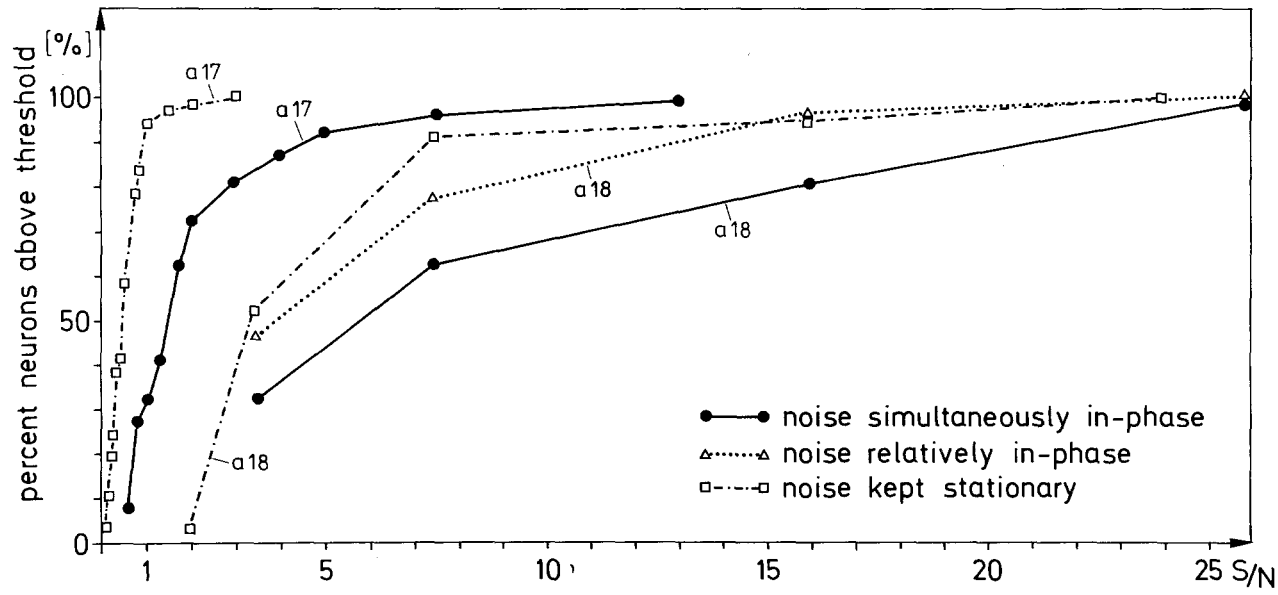

Fig. 10. Probability functions as obtained from the distribution of S/N thresholds for single neurons of area 17 (Hoffmann and von Seelen 1984) and area 18 (Dinse and von Seelen 1981b; Dinse unpublished). For the area 17 population stimulus configurations I and IV and for the area 18 population stimulus configurations I, III and IV were available. While these characteristics show basically the same dependencies on background motion, they differ considerably in threshold and 84.1% value. Area 17 neurons show by far the best performance, while area 18 cells are shifted towards much higher S/N ratios, but still slightly better than those obtained for area 19 cells

visual area changes the S/N characteristics in the remaining areas. We therefore recorded single cells in area 19 of 2 cats with a lesion of areas 17 and 18.

These measurements were restricted to assessing S/N profiles and obtaining S/N thresholds. The results of this limited sample ($n = 14$) are summarized in Table 3. Although only two out of the four stimulus configurations were tested (I, IV) the results suggest that the performance of area 19 neurons seems not to be impaired when areas 17 and 18 are lesioned. In both conditions there is a slight shift towards higher mean thresholds, a decrease in performance that might be associated with the limited sample of neurons. However, we observed no dramatic shift in the S/N thresholds. Extrapolating from this limited number of cells would indicate that the performance of area 19 in the tasks tested does not depend on the intactness of areas 17 and 18.

Comparison with neurons of areas 17 and 18. To provide a comparison between thresholds for area 19 neurons and those of neurons of areas 17 and 18, we made use of the data of Hoffmann and von Seelen (1984) concerning area 17 (96 cells) and of Dinse and von Seelen (1981b) and Dinse (unpublished) concerning area 18 (84 cells). These neurons were tested under equivalent conditions i.e. the same stimuli (Gaussian noise process), the same stimulus configurations, the same eccentricity range and the same way of data processing. The probability functions are shown in Fig. 10 and the mean thresholds as well as the S/N ratios at 84.1% are listed in Table 3.

The effects of the different stimulus configurations are the same in all areas tested so far: lack of relative motion between bar and background revealed the worst performance, while introduction of relative motion led to a better performance as was reflected by decreasing S/N thresholds. The best values in all three areas tested were found for the situation with the background stationary.

However, as to the absolute values of S/N thresholds and thus the absolute level of neuronal performance, there were considerable differences between the three areas. Area 17 has by far the lowest thresholds obtained for each of the stimulus configurations in the visual system. Area 18 cells are somewhat intermediate, while area 19 cells are characterized by the highest thresholds, i.e. they show the worst performance of all areas tested.

Discussion

S/N thresholds of single cells in area 19

To avoid confusion we use the term S/N threshold measurement for the investigation of single cells, while the term detection performance relates to the behavioural experiments. We measured the input-output characteristics of area 19 neurons, which provide information on threshold, working range and saturation of a cell (cf. von Seelen and Hoffmann 1976; Hoffmann and von Seelen 1978). We used this procedure in order to obtain a quantitative measure that allows direct comparison with the detection performance in behavioural experiments. In order to show that the S/N threshold of a cell is a genuine additional measure for description of visual neurons, we determined its independence from other parameters such as discharge rate and receptive field properties. A very simple explanation for different S/N thresholds could be that high S/N thresholds are due to low spike activity and that low S/N thresholds are due to high discharge rates. However, the correlation coefficients between S/N threshold and spike rate recorded at high S/N ratios in the range of $r = 0.1$ rule out such a possibility. Similarly, we found no correlation between S/N threshold and receptive field properties such as direction selectivity or velocity preference. Although we did not investigate the whole spectrum of possible receptive field properties, this total lack of association observed for direction selectivity and velocity preference indicates that the S/N thresholds may be regarded as independent from conventional receptive field properties. We were, however, able to demonstrate significant differences in threshold when cells were stimulated with different stimulus configurations consisting of different types of background motion. Stationary background (stimulus configuration I) revealed lowest thresholds. In contrast, moving the background in the same direction as the bar without relative velocity between both stimuli (IV) led to the highest thresholds. Introduction of relative velocity (II and III) led to an increase in performance compared to the situation without relative velocity with the inphase motion resulting in somewhat lower thresholds than the antiphase motion. The situation I, stationary background, is difficult to interpret. The fact that this situation led to lowest thresholds may be due to the presence of relative motion, although the background is not moved by itself, a view advanced by Hoffmann and von Seelen (1978, 1984).

S/N thresholds of single cells in areas 17 and 18

The comparison with the S/N thresholds in areas 17 and 18 was made on the basis of a population of area 17 cells according to the data of Hoffmann and von Seelen (1984) and a population of area 18 cells (Dinse and von Seelen 1981b; Dinse unpublished). It is important to mention that all cells were recorded and stimulated under the same conditions. However, not all of the stimulus configurations described in the present paper were available (cf. Fig. 10, Table 3).

While the overall effects of moving background used were shared by neurons of areas 17 and 18 (i.e. stationary background gives lowest thresholds, simultaneously inphase moving background without relative velocity results in highest thresholds), neurons of the three areas differ considerably in the absolute level of thresholds. As area 17 and 18 neurons were tested under the same conditions as area 19 neurons, it seems rather unlikely that different experimental settings are responsible for these effects.

Neurons of area 17 have the lowest thresholds, not only for the three areas tested, but for six visual systems so far investigated under identical conditions, including Superior Colliculus (Frömel 1980), PMLS and area 7

(Krüger unpublished; Kiefer et al. 1988). The thresholds of area 18 neurons are already shifted to higher values by a factor of about 8. Finally, thresholds of area 19 neurons are even higher than those of area 18, exhibiting on the whole the worst performance seen so far.

Because we wanted to compare S/N characteristics obtained from single neurons in intact animals with those obtained in behavioural experiments with area 17/18 lesioned animals we had to prove that this lesion has no influence on the neuronal S/N characteristics in the remaining areas. Recently, Kimura et al. (1980) reported no differences in the responsiveness to photic stimulation after inactivation of areas 17 and 18. Indeed, in the cats with lesions of areas 17 and 18 we found no differences in the threshold of area 19 neurons as compared with intact animals. Although this finding is based on a limited sample of cells ($n=14$), this suggests that the performance of neurons in area 19 may not deteriorate after ablation of areas 17 and 18. This, in turn, is an important presupposition for comparing the performances of area 17/18 lesioned cats with the performance of the neuronal population of area 19 in the intact animal.

Receptive field properties in area 19 vs. S/N thresholds

S/N threshold measurements revealed considerable differences between areas 17, 18 and 19. These differences are much less striking, when these areas are compared on the basis of their receptive field properties. In contrast to the original work of Hubel and Wiesel (1965), who reported dramatic differences of receptive field properties for neurons in areas 18 and 19 in comparison to area 17, which led them to suggest a serial way of processing within areas 17, 18 and 19, these areas seem to work rather in parallel according to recent studies and most authors stress similarities rather than dissimilarities of receptive field properties of areas 17, 18 and 19 (Duysens et al. 1982ab; Tanaka 1987). For example, as regards orientation selectivity, area 19 neurons are much more broadly tuned and their direction selectivity is poor in contrast to area 17 neurons (Duysens et al. 1982a). According to this, differences in receptive field properties are best characterized in terms of percentages of occurrence which reflects quantitative rather than qualitative differences. Tanaka et al. (1987) reported that the peaks of distribution of spatial frequency in area 19 lie between those of areas 17 and 18. However, the distributions are so wide that they cover those of areas 17 and 18 except for very high frequencies. Recently, a new type of receptive field (dot responsive cells) has been described (Saito et al. 1988). Although this type seems to be more specific for area 19, it is not restricted to this area where it is found twice as frequently as in area 17, which again indicates differences in incidence only. Given that area 17 contains the largest proportion of narrow-tuned orientation specific cells of the whole visual system, then it is very surprising to find that lesions of area 17 reveals no deficit in orientation discrimination tasks when tested with high contrast stimuli (Orban et al. 1988). This might indicate that extrapolation from conventional receptive field properties of single cells to behaviour and to the contribution of areas possibly involved in this task must be done with caution.

In this view, S/N threshold measurements seem to provide a more general description of one aspect (working range characteristics) of visual neurons. The lack of correlation with receptive field properties we observed supports this assumption. More important support is provided by the fact that stimulus dependent S/N thresholds reveal the same pattern as observed in the detection experiments (Fig. 4) and that overall area-specific thresholds are compatible with changes in the detection performance after cortical lesions, which will be discussed in more detail in the following sections.

Effects of lesion of area 19 on the detection performance

Given the clear deficits found after lesion of areas 17/18 (Krüger et al. 1986) and the devastating effect of a combined lesion of areas 17, 18 and 19 (Krüger et al. 1988) it was a surprising finding that the cats with lesions of area 19 alone showed no deficits in the discrimination of stationary small patterns.

The only significant deficits after lesion of area 19 were found for slowly and quickly moving patterns. However, these deficits were marginal in comparison with those found after lesion of area 17 and 18 (Krüger et al. 1986). Interestingly, these small deficits observed upon stimulating with low and fast velocities are not due to motion alone because we found no deficits when stimulating with medium velocities (cf. Fig. 4 and Table 1). It should be noted that the restriction of deficits at slow and fast velocities and the lack of deficits in the medium velocity range (cf. Table 1) corresponds to the bimodal distribution of preferred velocities found for our sample of area 19 neurons. Generally, all the deficits found were restricted to the performance at low S/N ratios and disappeared at high S/N ratios.

Behaviour vs. single cell performance

Drawing conclusions on the performance of the whole animal from the properties of a limited sample of single neurons must be done with caution. The comparison between the data of single cell recordings and those of the behavioural measurements presented in this paper is made on the assumption that the proportion of cells above threshold is the important parameter for the performance in the detection task (Hoffmann and von Seelen 1984). However, it must be clear that the single cells can be tested only in their detection performance (i.e. extraction of stimuli out of a noise process), and not in their ability to recognize a pattern.

Single neurons in areas 17, 18 and 19 showed their highest thresholds for the situation with the background moved simultaneously inphase to the bar without relative velocity (IV), but a much better performance when relative velocity between bar and background was introduced (Fig. 8, 10, Table 3). In the behavioural experi-

ments, we found a very similar response pattern. The best performances were found when there was a relative velocity between pattern and background (Fig. 4), no matter the relative velocity was produced by inphase or antiphase motion and which one of the two stimuli was stationary or moved. On the other hand, a lack of relative velocity led to a decrease in performance. In this case we observed no differences, no matter whether both stimuli were stationary or both moved at the same velocity. This finding led us to conclude that stimulus configuration IV in the single cell recordings (background inphase without relative velocity) corresponds best to the behavioural situation when both patterns and background are stationary.

The situation using antiphase movement of the background relative to the bar (III) in the single cell recordings seems to correspond best to the situation in the behavioural experiment when the patterns were moved and the background was kept stationary. We assume that, in this situation, the cat tries to follow the moving patterns, at least at low velocities of the pattern. Consequently, during this eye pursuit the background would move with the same velocity but in the opposite direction on the retina.

Comparison with other lesions

To draw further conclusions concerning the function of area 19 from the behavioural experiments the results of the following lesions have to be compared with the electrophysiological findings:

1. the lesion of area 19, leaving intact areas 17/18 and the rest of the visual system, especially the extrageniculocortical pathway and the lateral suprasylvian visual areas (subject of this paper),

2. the lesion of areas 17/18, leaving intact area 19 as well as the other above mentioned parts of the visual system (Krüger et al. 1986),

3. the lesion of areas 17, 18 and 19, interrupting completely the geniculo-cortical system, but leaving the extrageniculo-cortical pathway and the lateral suprasylvian visual areas intact (Krüger et al. 1988).

The 17/18 *lesioned cats* showed small deficits for the detection of stationary large patterns but much more substantial deficits for the detection of small ones. This means that recognition of large patterns can be performed successfully by cats lacking areas 17 and 18. One promising candidate for this performance could be area 19 with its massive W-projection (Dreher et al. 1980; Kimura et al. 1980). This assumption would be consistent with the data of Duysens et al. (1982a), which supported the hypothesis that area 19 is involved in coarse form discrimination during fixation as well as during slow visual movement (up to 4 deg/s), and with the finding that the addition of an area 19 lesion to that of areas 17 and 18 made the cats completely unable to discriminate stationary large or small patterns (Krüger et al. 1988). However, the characteristics of area 19 neurons and their extremely high S/N thresholds makes the participation of this area in the low S/N range rather unlikely. The characteristics suggest a contribution of area 19 only in the much higher S/N range. This means that at least in the low S/N range the recognition of large patterns must involve areas outside area 19, a conclusion that required the combination of behavioural and electrophysiological experiments. The more substantial deficits for detection of *small patterns* after *lesion of area 17 and 18* (Fig. 6) can be related to the X-type input in these areas. The inability of area 19 to compensate this lack of visual acuity corresponds to its total lack of X-type input. It is clear that the residual performance of the 17/18 lesioned cats corresponds well to the characteristics of the single cells of area 19 (Fig. 8). This would suggest that area 19 might be able to make a considerable contribution to the detection of small patterns in the higher S/N range even when areas 17/18 are eliminated, though it is not able to compensate the performance mediated by them in the low S/N range. On the other hand, due to the much lower thresholds found for area 17 and 18 neurons, these areas seem to be able to compensate the loss of area 19 neurons easily so that there are no or only minor deficits after lesion of area 19. However, the most important conclusion was that areas 17 and 18 make an essential contribution to pattern recognition by lowering the S/N ratio at which the system is able to detect the presence of a pattern in a background of statistical visual noise (Krüger et al. 1986; Aglioti et al. 1988). Again, area 19 seems unable to compensate for this performance. A straightforward explanation for this is provided by the much higher thresholds of area 19 neurons.

The notion of lowering the S/N ratio at which a system is able to detect the presence of a pattern in a background of statistical visual noise (Krüger et al. 1986) offers a quite novel and interesting interpretation on studies of brain function. In most of the detection experiments in combination with cortical lesions available so far the deficits were restricted to low S/N ratios (except for the lesion of areas 17, 18, 19; Krüger et al. 1988), i.e. the cats performed well under high S/N ratios. More generally, the difficulty of any task can be modified simply by changing the S/N ratio. A similar conclusion was drawn by Orban et al. (1988), who observed no deficits in orientation discrimination tested at high contrasts after area 17 ablation, but were able to find deficits at low contrasts. In this view the contribution of area 17 neurons is not so much providing the substrate for orientation discrimination, but rather discriminating orientation at low S/N ratios.

In contrast with a 17/18 removal, the extensive disruption of the geniculo-cortical system, as effected by *bilateral ablation of area 17/18/19* is followed by an immediate loss of pattern discrimination ability (Krüger et al. 1988). This means that area 19 seems to be very essential for the residual performance of pattern recognition found after a lesion of areas 17 and 18 in the high S/N range. However, the animals with 17/18/19 lesions could regain some discrimination ability by virtue of a prolonged remedial training and detection was partially regained for stationary patterns, but permanently lost for moving patterns. This last finding possibly implicates area 19 in the visual perception of object motion, a

function which is strongly interfered with by lesions in the suprasylvian visual areas (Kiefer et al. 1989).

The possible contribution of the rest of the extrageniculate pathway to these tasks and so the reason why it cannot compensate the loss of areas 17/18 must be determined by further experiments. Preliminary results indicate that neurons of the so-called extrageniculate pathway are characterized by S/N thresholds that are only slightly higher than those found for area 17 (Frömel 1980; Krüger unpublished; Kiefer et al. 1988). From these findings it is not clear why neurons in these areas do not compensate for the loss of areas 17 and 18 or for the loss of areas 17, 18 and 19, although S/N thresholds in the Superior Colliculus and PMLS are much lower than the thresholds in the behavioural detection curves after these lesions (Krüger et al. 1986, 1988). Accordingly, neurons of these areas either do not functionally participate in these tasks or, in contrast to area 19, their full performance depends on the integrity of areas 17 and 18, i.e. the S/N thresholds are changed following ablation of areas 17 and 18 or areas 17, 18 and 19.

Because of its massive W-input, area 19 in the cat is widely believed to represent a phylogenetically older part of the cortex (Kimura et al. 1980; Duysens et al. 1982b; Diamond and Hall 1969). According to Diamond and Hall (1969) relatively simple sensory functions can still be performed by phylogenetically older parts of the neocortex while those developed during the evolutionary expansion of the sensory cortex are involved in abstraction of figures embedded in larger patterns. This assumption fits well with our results that area 19 is able to perform simple form discriminations in the high S/N range, as long as no extraction of the pattern against a structured background is required. At low S/N ratios however, area 19 is not able to perform as well, both for the behavioural situation and for single neurons. In contrast, area 17 and 18 are able to perform well even at very low S/N ratios, leading us to suggest that these areas are especially well suited for the extraction of relevant details against a structured background.

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