Areas PMLS and 21a of Cat Visual Cortex: Two Functionally Distinct Areas

We have compared the receptive field properties of neurons recorded from visuotopically corresponding regions of area 21a and the posteromedial lateral suprasylvian area (PMLS) of cat visual cortex. In both areas, the great majority of neurons were orientation-selective and binocular, and their responses to moving contours were modulated by simultaneous in-phase or anti-phase motion of large textured background stimuli ("visual noise"). However, despite the great hodological similarity between the two areas, PMLS neurons had on average significantly higher peak discharge rates, exhibited substantially greater direction selectivity indices, and preferred substantially higher stimulus velocities than area 21a neurons. Furthermore, the majority of binocular neurons in the PMLS area and in area 21a were dominated respectively by the contralateral and the ipsilateral eyes. Finally, while 48% of PMLS neurons were excited by movement of visual noise per se, only 25% of area 21a neurons could be excited by such stimuli. We argue that the PMLS area, like its presumed primate homologue the middle-temporal (MT) area, is mainly involved in motion analysis. By contrast, area 21a appears to be involved in pattern analysis rather than motion analysis. It is likely that phylogenetically area 21a derives from the PMLS area.

Introduction

The visual cortices of virtually all mammals appear to contain a number of distinct areas distinguished on a number of hodological and functional criteria (for reviews, see Kaas and Krubitzer, 1991; Sereno and Allman, 1991; Spear, 1991). In mammals with well-developed vision, such as virtually all primates and some carnivores (e.g. the domestic cat), the number of distinct visual cortical areas is quite large (15-30 areas; for reviews, see Rosenquist, 1985; Dreher, 1986; Fellerman and Van Essen, 1991; Kaas and Krubitzer, 1991; Sereno and Allman, 1991; Spear, 1991; Payne, 1993). The establishment of homologies, or even analogies, between particular cortical areas in different species of the same order or between the species of different orders could provide some crucial insights concerning the steps involved in the evolution of the mammalian visual cortex. The task is, however, very difficult (cf. Sereno and Allman, 1991; Kaas and Krubitzer, 1991; Krubitzer and Kaas, 1993; Payne, 1993), not least because the criteria for designating a particular region of the visual cortex as a distinct area are far from uniform. Thus, only some areas, such as area V1 (primary visual cortex, area 17, striate cortex) in all mammals, areas 18 and 19 in cat visual cortex, and the middle temporal area (MT) of Old World and New World monkeys, are designated as distinct areas on the basis of a whole battery of criteria such as: (i) distinct cytoarchitectonics and/or myeloarchitectonics; (ii) distinct hodology (especially in relation to the principal thalamic visual relay nucleus—the dorsal lateral geniculate nucleus—and associational and commissural cortico-cortical connections); (iii) distinct topographic (visuotopic) organization; and (iv) distinct receptive-field properties of their neurons.

By contrast, the designation of virtually all other cortical regions as distinct cortical areas, even in such widely studied orders as carnivores, primates or rodents, is based on more limited criteria. One of the examples of a region of the visual cortex being subdivided into a number of distinct areas on the basis of rather limited criteria is the lateral suprasylvian region of the cat visual cortex. One of the extreme cases in this example relates to the designation of area 21a and the posteromedial lateral suprasylvian area (PMLS—in the middle suprasylvian gyrus, in the vicinity of the middle and posterior suprasylvian sulci) as two distinct visual cortical areas on the basis of only two criteria: (i) their fairly distinct visuotopic organization and (ii) rather limited information, available at the time, concerning their hodology (Heath and Jones, 1971; Palmer et al., 1978; Tusa and Palmer, 1980; Tusa et al., 1981). Not surprisingly, the designation of area 21a and the PMLS area as two separate cortical areas has been frequently challenged. Thus, there are remarkable similarities between the two areas in the pattern of their thalamic interconnections. In particular, the principal thalamic input to each area originates in the lateral striate-recipient (or cortico-recipient) part of the lateral posterior/pulvinar complex (for reviews, see Rosenquist, 1985; Dreher, 1986; Sherk, 1986; Shipp and Grant, 1991). Furthermore, it has been pointed out that the interpretation of the visuotopic organization of the region as indicating the existence of two distinct areas is somewhat arbitrary, that the two postulated areas are cytoarchitectonically very similar, and that both areas receive their principal associational inputs from the supragranular laminae of area 17 and to a lesser extent the supragranular laminae of areas 18 and 19 (cf. Montero, 1981; Sherk, 1986; Grant and Shipp, 1991; Sherk and Mulligan, 1993). On the basis of the hodological similarities and the overall pattern of the visuotopic organization of the visual areas located around the lateral suprasylvian sulcus, a number of authors (cf. Sherk, 1986; Shipp and Grant, 1991) consider the PMLS area and at least part of the area designated as area 21a as parts of a larger single visual cortical area originally described by Marshall et al. (1943) and further delineated in 1954 by Clare and Bishop (cf. Hubel and Wiesel, 1969; Wright, 1969; Spear and Baumann, 1975; Turlejski and Michalski, 1975; Djavadian and Harutjunian-Kozak, 1983; Zumbroich et al., 1986; Grant and Shipp, 1991; Sherk and Mulligan, 1993).

The argument in favour of the idea that area 21a and the PMLS area constitute separate visual areas is strongly supported by studies reporting major differences in the receptive field properties of cells in these two areas (cf. Dreher, 1986; Mizobe et al., 1988; Speer, 1991; Dreher et al., 1993; Toyama et al., 1994). However, the analyses of the receptive field properties of area 21a neurons and those of PMLS neurons were, with only one exception (cf. Mizobe et al., 1988; Toyama et al., 1994), conducted in different laboratories. Naturally, in such a situation...
substantial functional similarities (as well as substantial additional differences) between the two areas might have been easily missed or misinterpreted. Secondly, at least some of the reported differences might be related to the fact that the comparisons between the two areas are largely based on samples of cells with receptive fields at non-corresponding retinal eccentricities. In particular, while the majority of area 21a cells analysed quantitatively had their receptive fields located within 5° of the area centralis (cf. Wimborne and Henry, 1992; Dreher et al., 1993), the majority of PMLS neurons whose responses were analysed quantitatively had receptive fields located more peripherally (Spear and Baumann, 1975; Turlejski, 1975; Camarda and Rizzolatti, 1976; Harutunian-Kozak et al., 1984; Blakemore and Zumbroich, 1987; Rauschecker et al., 1987a; Zumbroich and Blakemore, 1987; Gizzi et al., 1990a,b). Thirdly, while virtually all area 21a neurons are reported to exhibit genuine orientation selectivity, there is a substantial controversy in the literature concerning the orientation selectivity versus axis of motion selectivity of most PMLS neurons (for review, see Spear, 1991). Fourthly, although there is considerable support for the idea that the PMLS area is involved in motion rather than form analysis (Turlejski, 1975; von Grünau and Frost, 1983; Hamada, 1987; von Grünau et al., 1987), very little information is available concerning the responsiveness of area 21a neurons to the motion of two-dimensional random texture patterns (so called 2D visual noise) per se (cf. Toyama et al., 1994) and 2D visual noise/elongated contours interactions in area 21a and the PMLS area.

In the present study, in order to clarify some of these issues and establish a more solid basis for functional comparisons between the two areas, as well as the basis for comparisons with extrastriate areas of other species, we have analysed quantitatively a number of receptive field properties of area 21a and PMLS area neurons with the receptive fields located 5-20° from the area centralis. Secondly, we have examined to what extent neurons in area 21a and the PMLS area are sensitive to the background motion of 2D visual noise per se and whether the responses of area 21a neurons, like those of PMLS neurons and areas 17 and 18, which provide the principal associational inputs to area 21a and the PMLS area, are influenced by relative motion between the contoured objects and the textured background. Preliminary communications, describing some of the findings, have been published (Wang et al., 1992a,b).

Materials and Methods

Animal Preparation

The general experimental procedures were similar to those described in a series of recent papers from our laboratory (Burke et al., 1992; Dreher et al., 1992, 1993). The initial surgery, which included intravenous cannulation, tracheotomy, bilateral cervical sympathectomy and craniotomy, was carried out on cats anesthetized with 1-1.5% halothane in an N2O/O2 (67%/33%) gaseous mixture. During the recording sessions the animals were paralysed with gallamine triethiodide at the rate of 7.5 mg/kg/h and artificially ventilated. Anaesthesia was maintained in N2O/O2 (67%/33%) gaseous mixture and i.v. infusion of 1 mg/kg/h of sodium pentobarbitone in sodium lactate (Hartmann's solution) or 5% dextrose solution, the solutions being alternated every 12 h. Expired CO2 was maintained at 3.7-4.0% by adjusting the stroke volume of the pulmonary pump. Body temperature was automatically maintained at ~37.5°C. Heart rate and electroencephalogram (EEG) were monitored, and with the above regime the EEG always showed a slow wave record. Antibiotic (amoxicillin trihydrate, 125 mg; Amoxil, Beecham), dexamethasone phosphate (4 mg) and atropine sulphate (0.3 mg) were given i.m. on a daily basis.

The corneas were protected with zero-power, air-permeable plastic contact lenses. Pupils were dilated and accommodation paralysed with 1% atropine sulphate solution. The nictitating membranes were retracted with 0.128% phenylephrine hydrochloride (Isopto-Frin, Alcon). Artificial pupils (3 mm in diameter) were placed in front of the contact lenses. Slit retinoscopy was used to determine the value of correcting lenses appropriate to focus the eyes on a tangent screen located 114 cm away. The locations of the optic discs and the areae centrales were plotted at least twice daily using a back-projecting fundus camera.

Recording

Craniotomy for recording single neuron activities from areas 17 and 18 of the primary visual cortex was made at Horsley–Clarke coordinates anterior 2 to posterior 6, lateral -2 to 8 (cf. Dreher et al., 1980, 1992; Burke et al., 1993). Craniotomy for recording single neuron activities from area 21a and the PMLS area was made at Horsley–Clarke coordinates anterior 5 to posterior 7, lateral 9-17 (cf. Grant and Shipp, 1991; Dreher et al., 1993). A smaller opening in the dura was made above the appropriate region of the cortex and a perspex cylinder ~15 mm high was mounted around the opening and glued to the skull with dental acrylic to form a well around the craniotomy. A platinum/iridium glass-coated microelectrode was lowered under visual control until its tip was positioned at the cortical surface. The cylinder was then filled with 4% warm agar in physiological saline. To reduce brain pulsations the agar was covered by warm liquid bone wax, which when cooled formed a firm closure of the cylinder. The microelectrode was advanced into the cortex with a hydraulic micro manipulator. In the case of recordings from area 17 or 18 the shaft of the electrode was vertical. For recordings from area 21a the electrode shaft was angled in the coronal plane, so that the tip pointed medially -30° to the vertical. This resulted in the electrode at the level of entry into the cortex being approximately orthogonal to the cortical surface. In the case of recordings from the PMLS area the electrode shaft was angled (in the coronal plane) 30-40° to the vertical; this resulted in the electrode advancing roughly parallel to the surface of the medial bank of the lateral suprasylvian sulcus. The recordings from the PMLS area were restricted to coronal planes between anterior 3 and posterior 2. The action potentials of single neurons were recorded extracellularly and amplified conventionally; triggered standard pulses were then fed to a FDP-11 computer.

Visual Stimulation

The receptive fields of recorded units were plotted with a hand-held light slit projector. The size of the receptive fields was determined as the size of the discharge field using moving bars that were lighter or darker than the background. Consistent with previous reports in the literature, we have found that in virtually all cortical areas (cf. Dreher et al., 1993), the width of a discharge field, i.e., the dimension of the field perpendicular to the axis of preferred orientation of a neuron, could be determined more reliably than its length, i.e., the dimension of the field along the axis of the preferred orientation. Therefore, we have compared only the widths rather than the size of discharge fields. Computer-controlled light slits from a slide-projector, used for studying the properties of the receptive fields, usually had a luminance of 15 cd/m² against the background luminance of 0.9 cd/m². A number of receptive field properties, e.g., orientation tuning profile, velocity and direction selectivity, were examined quantitatively. The width of the orientation tuning curve was measured at the half-height of the profile. The direction selectivity index (DI) of a cortical cell was calculated by the following formula:

$$DI = \left[ \frac{(R_0 - R_{\ell})}{R_0} \right] \times 100\%$$

where $R_0$ and $R_{\ell}$ are the peak responses at the preferred and non-preferred direction respectively (cf. Guedes et al., 1983; Burke et al., 1992; Dreher et al., 1992, 1993).

To study the responses to 2D visual noise, one of the two texture patterns routinely used by us (cf. Hammond and MacKay, 1977, 1981; Mason 1981; von Grünau and Frost, 1983; von Grünau et al., 1987; Crook 1990a,b) was projected onto the tangent screen. One texture pattern (designated pattern 1) contained elementary rectangles of 0.28×0.35°. In the second texture pattern (designated pattern 2) elementary rectangles were much smaller (0.05-0.07°). In each case the whole pattern subtended $32^\circ \times 22^\circ$ on the screen. The responses elicited by the motion of pattern 1 and pattern 2 per se were examined separately. To study the
noise/contour interaction properties of the cortical cells, two computer-controlled slide-projectors were used, one for projecting an image of an oriented contour stimulus, usually a light slit, and the other for the contourless 2D visual noise (background stimuli).

The effect of a moving noise pattern on the response to a moving light slit was determined in two test conditions: a slit and noise pattern moving: (i) in the same direction (in-phase) and (ii) in the opposite (anti-phase) direction. The responses were compared with a control condition when a light slit moved on the background of the stationary noise pattern. Both the slit and noise pattern were superimposed at the centre of the receptive field and moved, at optimal velocity, along the axis orthogonal to the orientation optimal for the slit. The amplitudes of excursions of the stimuli were such that when the slit travelled across the receptive field, the noise pattern always covered the entire receptive field.

The net peak firing rate was used for assessment of the influence of the noise pattern on the response elicited by a moving slit. For the cells which did not respond to the noise pattern per se, net peak response was obtained by subtracting the mean spontaneous discharge rates from the peak responses. If the cell responded to the moving noise per se with either distinct peaks or an increase of mean discharge rate, the noise response locked in time with the peak responses obtained in the presence of both moving slit and noise were subtracted to get the net peak response. This was done under the assumption that the excitatory processes elicited by either the slit or noise alone were processed additively by cortical neurons. The noise effect index (NEI) was calculated using the following formula:

\[ \text{NEI} = \left( \frac{R_c - R_p}{R_p} \right) \times 100\% \]

where \( R_p \) and \( R_c \) are the net peak responses at test and control conditions respectively.

**Statistics**

The sign of the effect, plus or minus, indicates the type of effect (facilitatory or inhibitory), while the absolute values give the relative strength of the effect. In most cases, non-parametric tests—the Mann-Whitney U-test, the chi-squared test, Fisher's exact probability test, the Kruskal-Wallis test and Wilcoxon's matched-pairs signed-ranks test—were used (Siegel, 1956). The parametric test was applied only for the paired data when there was no significant difference in their variance. Statistical differences were assessed at a level of \( P < 0.05 \) in all tests a two-tailed criterion was used.

**Localization of Recording Sites**

Localization of recording sites in area 21a and the PMLS area was based on: (i) their relationship to the lateral suprasylvian and lateral sulci; (ii) visuotopic maps of area 21a and the PMLS area (Palmer et al., 1978; Tusa and Palmer, 1980; Djavidian and Harutunian-Kozak, 1983; Zumbroich et al., 1986; Grant and Shipp, 1991; Sherz and Mulligan, 1993); (iii) reconstruction of electrode penetrations; and (iv) different receptive field-properties of neurons recorded in the reconstructed penetrations through the part of area 19 which abuts area 21a (e.g., smaller receptive fields, high proportion of end-stopped neurons; for reviews, see Orban, 1984; Dreher, 1986). Area 19 differs cytoarchitectonically from area 21a (cf. Sanides and Hoffmann, 1969; Heath and Jones, 1971). The reconstructions of electrode penetrations was based on small electrolytic lesions (5-7 μA for 10 s) in first and last electrode penetrations at -1.0 mm separations. At the end of the recording session (lasting usually 3-5 days) the animal was deeply anesthetized with an i.v. injection of 120 mg of sodium pentobarbitone and perfused transcardially with warm Hartmann's solution followed by a 4% solution of paraformaldehyde in 0.2 M phosphate buffer (pH 7.4). The brains were stereotaxically blocked and sectioned coronally at 50 μm on a freezing microtome, mounted on slides and counterstained with cresyl violet.

**Results**

**Receptive Field Locations and Size**

The receptive field centers of PMLS neurons were located 5-20° from the area centralis within a horizontal strip +3° to -10° from the horizontal meridian. The receptive field centers of area 21a neurons were located 5-20° from the area centralis within a horizontal strip +10° to -5° from the horizontal meridian (Fig. 1C; cf. Tusa and Palmer, 1980; Dreher et al., 1993).

For our sample of area 21a neurons the width of discharge fields varied from 1.0° to 7.2°, while for the sample of PMLS neurons it varied from 2.2° to 14.4°. Although the width of discharge fields varied considerably at all eccentricities, in both areas there was a weak positive correlation between width of discharge fields and distance of the receptive field center from the area centralis. At a given eccentricity, however, the discharge fields of PMLS neurons tended to be wider than those of area 21a neurons. Thus, while for area 21a the mean width of discharge fields of receptive fields located 5-10° from the area centralis was 3.65 ± 1.0° (n = 64), that for PMLS neurons was 5.62 ± 3.2° (n = 18). Similarly, while the mean width of discharge fields of area 21a cells with receptive fields located 10-20° from the area centralis was 4.7 ± 0.9° (n = 32), that for PMLS neurons was 7.45 ± 4.7° (n = 40). The differences are statistically significant (P < 0.05; Mann-Whitney U-test).

**Receptive Field Classes**

Almost 80% (58/74) of area 21a cells and >75% (34/45) of PMLS neurons gave detectable, often quite strong, responses to appropriately oriented stationary flashing elongated (14° × 0.6°) light slits positioned in their receptive fields. The great majorities of cells recorded in either area either gave transient responses at onset and offset of flashing stationary stimuli positioned anywhere within their discharge fields (ON/OFF discharge...
fields), and/or their discharge fields plotted with moving stimuli darker than the background overlapped completely with those revealed with moving stimuli brighter than the background. On that basis, almost 95% (70/74) of cells recorded from area 21a and >93% (42/45) of cells recorded from the PMLS area were identified as C-cells (see C-cells and A-cells of Henry, 1977; cf. complex cells of Hubel and Wiesel, 1962, 1965). The remaining few cells were identified as subtypes of S-cells since they had only the ON or only the OFF subregions in their discharge fields (see S-cells and A-cells of Henry, 1977; cf. simple cells of Hubel and Wiesel, 1962).

Orientation Selectivity

For neurons in area 21a or the PMLS area, the orientation tuning curve obtained using a stationary flashing light slit was always narrower than that obtained using moving light slit (Fig. 2A,B). Indeed, the mean orientation tuning width (at half-height) derived from the responses of 20 cells, recorded in area 21a, to a stationary elongated (10° × 0.6°) flashing light slit was 42.4 ± 17.8°, i.e., significantly narrower ($P < 0.05$; Wilcoxon's test) than that (53.6 ± 25.6°) derived from the responses of the same 20 cells to elongated moving light slits. Similarly, for 16 PMLS neurons for which we have obtained the complete orientation tuning curves using both moving and stationary flashing elongated slits, the mean width of orientation tuning curves derived from the responses to stationary flashing stimuli, was 43.4 ± 18.2° while that derived from the responses to moving stimuli was 55.5 ± 24.5°. The difference was statistically significant ($P < 0.05$; Wilcoxon's test).

Generally, consistent with previous findings (Wimborne and Henry, 1992; Dreher et al., 1993), for a given 21a cell, the width of the orientation tuning curve was very similar irrespective (within limits) of the length of elongated slits or bars used. By contrast, consistent with numerous previous reports (cf. Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; Blakemore and Zumbroich, 1987; Toyama et al., 1994), PMLS neurons were broadly tuned when stimulated with moving light spots. Indeed, the mean widths of the tuning curves derived from the responses of 13 cells to a moving light spot (2.5° in diameter) at 92.4 ± 38.1° was significantly broader ($P < 0.05$; Wilcoxon's test) than that (55.5 ± 11.9°) derived from the responses of the same cells to a moving elongated (16° × 0.6°) light slit.

Although, unlike in the case of our sample of area 21a neurons, some PMLS cells did not exhibit orientation selectivity to long (16° × 0.6°) moving light slits, and very few of them exhibited sharp orientation selectivity of <30° (Fig. 2C), the mean width, at half-height, of orientation tuning curves to moving long light slits of PMLS neurons at 57.5 ± 24.9° is not significantly different ($P = 0.35$; Mann–Whitney $U$-test) from that (54.9 ± 27.8°) for the sample of area 21a neurons.
Peak Discharge Rates

As indicated in Figure 3A in both the PMLS area and area 21a the peak discharge rates for optimally oriented stimuli moving at preferred velocities across the receptive fields varied quite considerably. The range of peak discharge rates for neurons in both areas was fairly similar (12-158 spikes/s for PMLS neurons and 6-127 spikes/s for area 21a neurons). However, the mean peak discharge rate for our sample of PMLS neurons was substantially higher than that for our sample of area 21a neurons (58.3 ± 35.1 spikes/s for the PMLS area; 34.6 ± 24.7 spikes/s for area 21a). The difference between the two areas is highly significant (P < 0.00006; Mann-Whitney U-test).

Direction Selectivity

For all cells (whether in the PMLS area or in area 21a) exhibiting strong directional selectivities (direction-selectivity indices >70%) the preferred direction of stimulus motion along the axis orthogonal to the optimal orientation was the same whether the stimulus was brighter or darker than the background. On the other hand, most cells exhibiting strong direction selectivities at optimal velocities were less or not at all direction selective when stimuli moved at slow velocities. Quite often direction selectivity indices also decreased at velocities substantially higher than the optimal. Therefore, for each cell the DI was calculated for optimally oriented light slits moving at optimal velocities. It is apparent from Figure 3C that many PMLS cells, but few 21a cells, were strongly direction selective. Not surprisingly, the mean direction selectivity index for our sample of PMLS neurons at 72.3 ± 21.4° is much higher than that (36.7 ± 23.3°) for our sample of area 21a neurons. The difference between the two populations was highly significant (P < 0.00006; Mann-Whitney U-test).

Velocity Preferences

Neurons in area 21a and the PMLS area differ substantially in their velocity tuning profiles. Thus, applying the terminology of Orban and his colleagues (for review, see Orban, 1984), ~48.5% (35/72) of area 21a neurons were either low velocity-pass (Figs 4A and 5A) or low velocity-tuned (Figs 4B and 5A).

About 41.5% (30/72) of area 21a cells were tuned for moderate velocities (Figs 4B and 5A) and only a small proportion (9.5%; 7/72) of area 21a neurons responded more or less equally well to a wide range of stimulus velocities (broad-band cells; Figs 4C and 5A).

By contrast, relatively few PMLS neurons could be classified as low velocity-tuned (Fig. 4E) or low-pass cells (21%; 10/74; Fig. 4B). Moderate velocity-tuned (Fig. 4E) and broad-band neurons (Fig. 4F) together constituted a large majority (72.5%; 34/47; Fig. 5B) of PMLS neurons. Finally, unlike in area 21a, a distinct group of PMLS neurons (6.0%; Figs 4D and 5A) were high-pass cells which responded only at moderate and high stimulus velocities. Apart from the differences in the velocity tuning profiles, area 21a and the PMLS area differed substantially in distribution of the preferred stimulus velocities. Thus, as indicated in Figure 5B, while almost 45% (34/78) of area 21a neurons responded optimally at velocities not exceeding 5°/s, the proportion of such cells among PMLS neurons was very low (3/53). By contrast, none of area 21a neurons responded optimally at stimulus velocities exceeding 50°/s, while among PMLS neurons ~22.5% (12/53) of cells responded optimally at such velocities. The mean preferred velocity for our sample of PMLS neurons at 69.9 ± 153°/s was significantly higher (P < 0.00006; Mann-Whitney U-test) than that (12.8 ± 12.5°/s) for the present sample of area 21a neurons.

Excitatory Responses to Visual Noise Per Se

Area 21a and the PMLS area

Forty-six per cent (12/26) of neurons in the PMLS area gave excitatory responses to noise motion per se, a figure substantially higher than that (25%; 9/36) in area 21a. The difference was significant (P < 0.05; chi-squared test). However, <10% of cells in each area (3/36, 8.3% of cells in area 21a; 2/26, 7.7% of cells in area 21a). The difference between the two areas is highly significant (P < 0.00006; Mann-Whitney U-test).
the PMLS area) responded tonically to the noise motion. By tonic excitatory response we mean that the response lasted for the same time as the noise motion, although, due to the response latencies, the onset and offset of the response did not coincide with the onset and cessation of noise motion (Fig. 6A,C). This type of response to 2D noise is strongly reminiscent of the so-called 'field' responses of some collicular or striate cortex neurons (Mason, 1979; Gulyás et al., 1987). Field responses were present irrespective of the size of the pixels in the noise pattern used. Thus, if, in a given cell, pattern 1 (with its large pixels) evoked a field response, pattern 2 (with its much smaller pixels) also evoked a 'field' response (Fig. 6C).

However, in both areas, the majority of cells responding to the motion of the visual noise per se (6/9 cells in area 21a and 10/12 cells in the PMLS area) appeared to respond to distinct features in the noise pattern rather than the motion of the whole noise. In particular, the responses of these cells to noise moving through their receptive fields did not last for the whole duration of motion but consisted of one or several discharge peaks similar to those evoked by moving slits of light (Fig. 6B,D). These responses are strongly reminiscent of the so-called 'grain' responses characterizing the responses to the motion of visual noise of virtually all geniculate neurons (Mason, 1976; Gulyás et al., 1987), and those of many neurons in the superior colliculus and areas 17 and 18 (Mason, 1979; Gulyás et al., 1987). Consistent with the grain character of these responses, in some cells studied by us these responses were abolished when noise pattern 1, with its large pixels, was substituted by noise pattern 2, with its smaller pixels. The proportion of cells responding to distinct features of the noise pattern was significantly lower in the case of area 21a neurons than in the case of PMLS neurons (16.5% of the sample of area 21a neurons versus 38.5% of the sample of PMLS neurons).

Whatever the type of response to the visual noise, the peak discharge rate in the excitatory response evoked by the moving 2D noise per se was in both areas usually, but not always, lower than that in the excitatory response evoked by the moving light slit (Fig. 6). For all cells responding to the visual noise per se the preferred direction and velocity for the visual noise were similar to those for the light slits (Fig. 6). In both areas, the direction selectivity indices for the noise moving along the axis optimal for the light slits were similar to those for the light slits. In particular, for area 21a neurons, the mean direction selectivity index of the responses evoked by the motion of 2D noise at 41.3 ± 19.4% (n = 9) was not significantly different from that (47.7 ± 20.6%; n = 9) of the responses evoked in the same cells by moving light slits (P > 0.10; Wilcoxon's test). Similarly, in the PMLS area the mean direction selectivity index of responses evoked by the motion of 2D noise at 58.4 ± 28.5% (n = 12) was not significantly different from that (77.7 ± 17.5%; n = 12) of the responses evoked in the same cells by moving light slits (P > 0.10; Wilcoxon's test).

Although in area 21a all neurons giving excitatory responses to the visual noise per se had C-type receptive field organization, in the PMLS area, some neurons (all of them exhibiting a 'grain' type of response) had S-type receptive field organization.

### Areas 17 and 18

Responses to visual noise in areas 17 and 18 were examined for purposes of comparison. Consistent with previous reports (cf. Gulyás et al., 1987, 1990; Crook, 1990a), a majority of cells in the present sample of area 17 and area 18 neurons was sensitive to moving noise per se. In particular, 75% (15/20) of cells recorded from area 17 and 83.5% (15/18) of cells recorded from area 18 responded to 2D noise moving along the axis orthogonal to the optimal orientation. Of these a majority (10/15, 66.5% of area 17 cells and 12/15, 80% of area 18 cells) exhibited a 'grain' type of response. Consistent with the original reports of Hammond and Mackay (1975, 1977), all area 17 and area 18 cells which exhibited field type excitatory responses to the motion of 2D visual noise had C-type receptive field organization (cf., however, Skottun et al., 1988; Casanova et al., 1995). On the other hand, in both areas 17 and 18 a substantial proportion of cells exhibiting strong grain type responses were S-type cells (Gulyás et al., 1987, 1990; Crook, 1990a; Casanova et al., 1995).

In our sample of area 17 cells, the mean DI of the responses evoked by motion of 2D visual noise was 49.8 ± 24.0% (n = 15) and not significantly different (P > 0.10; Wilcoxon's test) from that of the responses evoked by light slits moving along the same axis (56.1 ± 33.8%; n = 15). Similarly, in our sample of area 18 cells, the mean DI of the responses evoked by motion of 2D visual noise at 51.8 ± 21.0% (n = 16) was not significantly different (P > 0.10; Wilcoxon's test) from that (52.6 ± 31.8%; n = 16) of the responses evoked by light slits moving along the same axis.

### Effect of Movement of Visual Noise on the Responses to a Moving Slit

The responses of the great majority (89%, 32/36) of area 21a cells to a moving slit were modulated by simultaneously moving 2D visual noise. Furthermore, most cells (67%, 24/36) showed a suppressive effect irrespective of the relative motion phase between the slit and the noise. Figure 7A shows an example of the responses of a typical area 21a neuron. Moving noise pattern...
Figure 6. Peristimulus-time histograms of the responses of neurons in area 21a and the PMLS area to moving light bars and moving 2D noise. The small icons show the angle of the bar and the direction of movement. On the left side of each histogram the noise or bar moves in one direction across the receptive field and on the right side moves back across the receptive field. The stimulus moves only during the time corresponding to the hatched bars beneath the abscissae. At other times the stimulus is stationary. The reverse trajectory commences at the arrowheads. Note that the response to the noise pattern can be either maintained ('field response'; A, C) or transient ('grain response'; B, D).

Figure 7. Interactions between moving bar and noise in area 21a. (A) Peristimulus histograms for four conditions. The bar moves in one direction across the receptive field in the left side of each histogram, at the arrowhead it begins to move back across the receptive field. (B) Graph of the relative effects of in-phase and anti-phase noise. Negative values on the ordinates indicate reduction of the response to the bar. The dashed line indicates an equal effect of in-phase and anti-phase noise. The solid line is the linear regression line for all points. Note that the in-phase noise has a greater inhibitory effect than the anti-phase noise.

*per se* did not produce an excitatory response. On the other hand, 2D noise moving in-phase or anti-phase with the light slit considerably reduced the response to a slit. Furthermore, for this cell the reduction during in-phase motion of the noise was greater than that during anti-phase motion.

Generally, as indicated in Figure 7B, the in-phase suppression (45.4 ± 23.6%) was substantially stronger (*P* = 0.0001; *t*-test) than the anti-phase suppression (28.4 ± 21.9%). Strong facilitatory effects of motion of 2D noise on the response to a moving contour were very rare (one cell, anti-phase motion; Figs 7B and 8A).

We found a clear correlation (*r* = 0.54, *P* < 0.02) between the strength of the in-phase and anti-phase noise/contour interactions. However, for both in-phase and anti-phase noise/contour interactions the strength of suppressive effect was similar for cells exhibiting excitatory responses to noise *per se* and those which did not (*P* > 0.2; Mann-Whitney *U*-test; cf. Fig. 7B). The strength of noise/contour interactions was not correlated (*r* < 0.32, *P* > 0.05) with other receptive field properties, such as width of the receptive field, direction selectivity index or optimal velocity.

The relative motion of noise and contour stimuli appears also...
to modulate the direction selectivity of some cells (see Fig. 7A). Indeed, the mean DI of 29.5 ± 20.5% (n = 36) when a single bar moved on a stationary noise background increased to 36.8 ± 24.2% and to 43.6 ± 26.8% respectively during in-phase movement of the background and during anti-phase movement of the background. However, the changes in direction selectivity indices were not significant (P > 0.1; Wilcoxon’s test).

For all seven PMLS neurons tested, the responses to a moving light slit were modulated by simultaneously moving 2D visual noise. All but one of them showed a suppressive effect irrespective of the relative motion phase between the slit and the noise. Unlike in area 21a, the mean suppressive effect of the in-phase motion (at 61.7 ± 26.9%) was not significantly different from that (75.4 ± 45.9%) for the anti-phase motion (P > 0.20; Mann–Whitney U-test). In one cell simultaneous motion of 2D noise and light slit substantially increased the cell’s firing rate. The facilitatory effect was restricted to the anti-phase motion, the in-phase motion of the noise and the slit resulting in a response of the same magnitude as that evoked by the slit moving against a background of stationary 2D noise.

The direction selectivity indices of PMLS neurons were not significantly affected by the noise/contour interactions. In particular, whereas the mean DI for the optimally oriented light slits moving on the background of the stationary 2D noise was 72 ± 24% (n = 7) the mean DIs for the same cells when the light slits moved in-phase or anti-phase with moving 2D noise were respectively 70.3 ± 16.9% and 69.6 ± 27.6%.

**Areas 17 and 18**

The distributions of 2D noise motion effects on the magnitude of the responses to moving elongated contours in cells recorded from areas 17 and 18 are shown in Figure 8B and C respectively. Consistent with previous reports (cf. Gulyás et al., 1987, 1990; Crook, 1990a), the major effect of noise/contour interactions in the present sample of neurons in areas 17 and 18 was the reduction of the amplitude of the responses to elongated contours. Furthermore, statistical analysis indicates that the cells in each area (21a, PMLS, 17 and 18) are subject to a similar levels (P > 0.40; Kruskal–Wallis test) of modulatory effects of 2D noise motion.

It has been shown in the past that about a third of non-direction-selective cells in area 17 became more direction-selective when the 2D noise and bar moved at the same speed, either in-phase or in anti-phase (Orban et al., 1987). In the present samples of area 17 and 18 neurons the mean DI when an optimally oriented light slit moved against a background of stationary 2D noise was 62.2 ± 8.0% (n = 20) for area 17 and 58.6 ± 25.6% (n = 17) for area 18. During in-phase movement of the background the DIs increased to 68.6 ± 23.8 and 71.3 ± 24.9% for areas 17 and 18 respectively. The differences are significant (P < 0.04 and P < 0.02 for areas 17 and 18 respectively; Wilcoxon’s test). By contrast, however, DIs during anti-phase movement of 2D noise for area 17 (59.1 ± 29.3%) and area 18 (59.1 ± 28.2%) were not significantly different from those when the light slits moved on a background of stationary noise (P > 0.10; Wilcoxon’s test).

**Discussion**

**Area 21a versus the PMLS Area: Differences and Similarities**

As mentioned in the Introduction there are strong similarities between area 21a and the PMLS area in the composition of their principal thalamic and cortical associational afferents. Consistent with this, we have found that the two areas contain almost identical proportions of C-cells and S-cells and their orientation tuning widths are not significantly different (cf. Table 1). However, in almost all other aspects of their receptive field organization, the two areas differed significantly from each other (Table 1).

One could argue that since our comparisons of functional properties of neurons in the two areas were restricted to cells with receptive fields located 5–20° from the area centralis, our conclusions are valid only in relation to those eccentricities. However, several lines of evidence suggest to us that our conclusions about the significant differences in the receptive field properties between area 21a and the PMLS area are also valid for cells with centrally located receptive fields. In particular, the receptive field properties of area 21a neurons with receptive fields located within 5° of the area centralis are in all aspects of receptive field organization (except receptive field size and sharpness of the orientation tuning) indistinguishable from those with receptive fields located more peripherally (cf. Dreher et al., 1993). Furthermore, although to our knowledge no systematic quantitative comparison is available, most PMLS cells with centrally located receptive fields like those with peripherally located fields are binocular, dominated by the...
The great majority of PMLS neurons is indeed orientation selective rather than exhibiting axial motion selectivity (cf. Henry et al., 1987; Hamada, 1987; Gizzi et al., 1990). When moving elongated light bars were used, area 21a and the PMLS area are used, combined with the previous findings (Blakemore and Zumbroich, 1987; Blakemore and Henry, 1987a, 1992; Dreher et al., 1992; cf. Sherk, 1989). In the striate- (or cortico-) recipient zone of the lateral posterior-pulvinar complex (LPI) which receives its principal input from areas 17 and 18 and provides the principal thalamic input to area 21a and the PMLS area, 75-90% of neurons are binocular (Rauschecker et al., 1987b; Casanova et al., 1989; Chalupa and Abramson, 1989; Casanova and Savard, 1995). As in the PMLS area, but unlike in area 21a, only a small proportion of binocular neurons in the cortico-receptive zone of LPI is dominated by the ipsilateral eye and the majority of monocular neurons could be activated via the contralateral eye (Rauschecker et al., 1987b; Casanova et al., 1989; Chalupa and Abramson, 1989; Casanova and Savard, 1995).

The effect of inactivation of areas 17 and 18 on ocular dominance of area 21a neurons is not known. However, chronic or acute, irreversible bilateral or unilateral (ipsilateral) removals of areas 17 and 18 result in a dramatic reduction in the proportion of PMLS neurons that can be activated via the ipsilateral eye—the large majority of neurons become monocular and can be activated only via the contralateral eye (Spear and Baumann, 1979; cf., however, Guedes et al., 1983).

Receptive-Field Classes.

The high proportions of C-type and low proportions of S-type cells in the present sample of area 21a neurons are in good agreement with our own data in the previous sample of area 21a neurons (Dreher et al., 1993; cf. Dreher, 1986) as well as with the data of Wimborne and Henry (1992). Although the great majority of PMLS cells responding to stationary flashing stimuli give transient ON/OFF responses and would therefore correspond to our C-cells, a proportion of PMLS cells could be classified as subtypes of S-cells since they contained either only OFF or only ON discharge regions in their receptive fields (Turlejski, 1975; Harutunian-Kozak et al., 1984; Blakemore and Zumbroich, 1987; for review, see Spear, 1991). The predominance of C-type cells in the PMLS area in good agreement with previous reports (Hubel and Wiesel, 1969; Wright, 1969; Morrone et al., 1986; Blakemore and Zumbroich, 1987; Zumbroich and Blakemore, 1987; Gizzi et al., 1990b).

Orientation Selectivity.

When moving elongated light bars were used, area 21a and the PMLS area do not differ significantly with regard to the widths of orientation tuning curves of their respective neurons. However, while cells in area 21a give similar orientation tuning curves, regardless of the length of the bar used (Wimborne and Henry, 1992; Dreher et al., 1993), cells in the PMLS area were considered to exhibit axial motion selectivity rather than orientation selectivity since they are very broadly tuned for orientation when the short bars or spots are used (Spear and Baumann, 1979; cf., however, Guedes et al., 1983). The mean direction selectivity indices for the present samples of area 17 and area 18 neurons (cf. Burke et al., 1992; cf. Dreher et al., 1992). Despite the strong direction selectivity indices of PMLS neurons, removal of the PMLS area (and the PLLS area) does not produce a detectable deficit in the animal's ability to discriminate directions of moving gratings (Pasternak et al., 1989). Thus, it appears that the direction discrimination is based on signals coming from visual areas outside the lateral suprasylvian cortex. Chronic or acute, bilateral or unilateral (ipsilateral) removal of areas 17 and 18 results in a dramatic reduction in the proportion of direction-selective PMLS neurons (Spear and Baumann, 1979; cf., however, Guedes et al., 1983), but tends to increase the direction selectivity of area 21a neurons (Michalski et al., 1993). However,
since such ablations strongly reduce the responsiveness of both sets of neurons to photic stimuli (cf. Spear and Baumann, 1979; Michalski et al., 1993, 1994) this result is difficult to interpret.

The contribution of neurons in LP1 (which constitute the principal thalamic input to both area 21a and the PMLS area) to the direction selectivities of area 21a and PMLS neurons is not known. However, direction selectivity indices of LP1 neurons appear to be much greater than those of area 21a neurons but comparable to those of areas 17 and 18 or even to those of PMLS neurons (Rauschecker et al., 1987b; Casanova et al., 1989; Chalupa and Abramson, 1989; Casanova and Savard, 1995; see also Mason, 1981).

**Velocity Preferences**

As in the case of our previous sample of area 21a neurons (Dreher et al., 1993), preferred velocities of the present samples of area 21a were not significantly different from those of area 17 neurons (Burke et al., 1992; for review, see Orban, 1984). Furthermore, as in the case of area 17 neurons (for review, see Orban, 1984), almost all area 21a neurons in the present sample were either velocity low-pass or velocity-tuned with a very small proportion of broad-band cells. By contrast, preferred velocities of area 21a neurons in the present sample were significantly lower than those in our sample of area 18 neurons (Dreher et al., 1992; for a review, see Orban, 1984).

In the present sample of PMLS neurons, the distribution of preferred velocities and the range of velocities to which individual neurons respond is very similar to those in several earlier samples of PMLS neurons (Rauschecker et al., 1987a; von Grünau et al., 1987; Zumbroich and Blakemore, 1987; cf. Turlejski, 1975; Spear and Baumann, 1975; Camarda and Rizzolatti, 1976). The preferred velocities of the present sample of PMLS neurons are significantly higher than those of area 21a neurons and those of area 17 neurons. By contrast, the mean preferred velocity of our sample of PMLS neurons is substantially lower than that of area 18 neurons (Dreher et al., 1992).

Both areas 21a and PMLS receive >50% of their associational input from laminae 2 and 3 of area 17 (Dreher, 1986; cf. Rosenquist, 1985). Furthermore, both areas receive 15-20% of their associational input from supragranular layers of area 18 and ~10% of their associational afferents originate in the supragranular layers of area 19 (Dreher, 1986; cf. Rosenquist, 1985). Despite these striking similarities in the associational inputs, the velocity profiles of the neurons in the two areas are quite different. The velocity profile of area 21a neurons is very similar to that of area 17 neurons, while the velocity profile of PMLS neurons appears to reflect the properties of its associational inputs from both area 17 and 18 neurons (cf. Burke et al., 1992; Dreher et al., 1992).

There are, however, significant—albeit numerically small—differences in the composition of afferents to the PMLS area and area 21a which are likely to underlie the differences in the velocity preferences of cells in the two areas. Y-type input to the PMLS area presumably underlies the preference of >20% of PMLS neurons in our sample for stimulus velocities >50°/s (cf. Dreher et al., 1980). Indeed, almost all PMLS neurons receive excitatory Y-type input (Berson, 1985; Rauschecker et al., 1987b). Both area 21a and the PMLS area receive direct input from the pretecto-recipient zone of the lateral posterior-pulvinar complex (cf. Symonds et al., 1981; Raczkowski and Rosenquist, 1983; for reviews, see Rosenquist, 1985; Dreher, 1986). In turn, many pretectal neurons that project to the LP-pulvinar complex receive a Y-input and respond optimally to rapid motion (>1000°/s; Sudkamp and Schmidt, 1995; cf. Schoppmann and Hoffmann, 1979). These cells presumably project to the PMLS area but not to area 21a. In addition, some of the Y-type input to the PMLS area probably originates directly in the retino-recipient parts of the thalamus (especially the medial interlaminar nucleus) and/or is relayed to the PMLS area via area 18 (Berson, 1985; Dreher, 1986; Lee et al., 1986).

By contrast, excitatory Y-type input to area 21a, although present, appears to be rather minor (Dreher et al., 1993). Our retrograde double-labelling experiments indicate that topographically corresponding parts of area 21a and the PMLS area receive their thalamic and associational inputs from almost completely non-overlapping populations of neurons (Turlejski et al., 1992; Dreher et al., 1996). Thus, it is possible that Y-type neurons, which are quite numerous in the medial interlaminar nucleus (for review, see Garey et al., 1991), project to the PMLS area but not to area 21a.

Similarly, it is likely that most area 18 neurons which project to area 21a prefer low stimulus velocities. By contrast, projection from area 18 to the PMLS area is likely to include a substantial proportion of neurons which respond optimally or exclusively at stimulus velocities >50°/s (broad-band and high-pass cells). Furthermore, input from area 18 to area 21a (but not that to the PMLS area) might actively suppress the responses of area 21a neurons to high-velocity stimuli. Such a possibility is suggested by the fact that in ~40% of cells located in layer 5 of area 17, reversible inactivation of area 18 reveals responses to high-velocity stimuli to which the cells were previously hardly responsive (Alonso et al., 1993). Finally, it is important to point out that many cells in the LPI, which provides the principal thalamic input to area 21a and the PMLS area, are broad-band cells that respond over a wide range of stimulus velocities, with >75% of cells responding reliably at stimulus velocities >200°/s (Chalupa and Abramson, 1989; cf. Rauschecker et al., 1987a,b). Again it appears that populations of neurons projecting from the LPI to area 21a and those projecting to the PMLS area virtually do not overlap (Turlejski et al., 1992; Dreher et al., 1996). It is likely that the LPI neurons preferring fast velocities do not project to area 21a. Reversible bilateral inactivation of areas 17 and 18 reduces the response of some area 21a neurons to slowly moving stimuli (<10°/s), while in others the reduction of the responses to faster-moving stimuli (15-20°/s) is apparent (Michalski et al., 1993).

**Excitatory Responses to Visual Noise Per Se**

While in area 21a only 25% of cells exhibited excitatory responses to the motion of visual noise per se, in the PMLS area the proportion of such cells was significantly larger (46%; Table 1). Less than 10% of cells in each area responded tonically to the noise motion ('field' responses). In both areas, the majority of cells responding to the motion of the visual noise per se responded to distinct features of the noise pattern rather than the motion of the whole noise ('grain' responses).

The proportions of area 17 and 18 neurons responding to the motion of 2D visual noise were significantly higher than those of area 21a and PMLS area neurons (75% of our sample of area 17 cells and 83.5% of our sample of area 18 cells). Again, as in the case of area 21a and the PMLS area, only minorities of those cells (25% in area 17 and 16.5% in area 18) exhibited a field type of response. Furthermore, in our samples, the proportions of neurons in areas 17 and 18 which exhibited the field type and the grain type of response were very similar to those in the
earlier samples of cells recorded from those areas (Gulyás et al., 1987, 1990; Crook, 1990a).

Although it has been reported that some cells in areas 17 and 18 of the cat exhibit dissimilar preferred directions for noise and for elongated contour stimuli (Hammond and MacKay, 1977; Hammond, 1978; Crook, 1990a), several lines of evidence suggest that the low proportions of cells responding to the motion of 2D visual noise in our samples of area 21a and PMLS neurons do not represent a serious underestimate due to the restriction of our testing procedure to the axis of movement optimal for the moving slit. Thus, none of four area 21a cells and none of three PMLS cells which did not respond to the noise motion per se at the velocities and axis of movement optimal for the moving slit showed a response when the noise was presented at various orientations and velocities. Secondly, as mentioned above, the proportions of area 17 and 18 neurons responding to the motion of 2D noise per se were much higher than those in area 21a and the PMLS area and very similar to the proportions of such neurons in the samples of area 17 and area 18 neurons in which the testing procedures were not restricted to the motions of the noise along the axis optimal for the moving slits and/or bars (Gulyás et al., 1987, 1990; Crook, 1990a). Thirdly, layers 2 and 3 of area 17—the principal source of associational input to area 21a and the PMLS area (cf. Rosenquist, 1985; Dreher, 1986)—contain very few cells that are strongly sensitive to the motion of 2D visual noise (Edelstyn and Hammond, 1988; Casanova et al., 1995). Such cells are located mainly in layer 5 (Hammond and MacKay, 1975, 1977; Edelstyn and Hammond, 1988), which contributes very little to the associational projections to area 21a and the PMLS area (cf. for reviews Rosenquist, 1985; Dreher, 1986).

The low proportion of area 21a and PMLS area cells exhibiting a field type of response to motion of 2D visual noise contrasts with a high proportion (almost 40%) of such cells in the striate-(cortico-)recipient zone of the lateral pulvinar complex (Casanova and Savard, 1995; cf. Mason, 1981). It is likely, therefore, that area 21a and the PMLS area receive their principal thalamic input from subpopulations of cells in the cortico-recipient zone which respond poorly to the motion of 2D visual noise.

Noise/Contour Interactions

It has been demonstrated in the present study that the responses of a majority (86%) of cells in area 21a to moving contour stimuli are modulated by the background motion of 2D noise. With one exception, the effect of motion of 2D noise on responses evoked by the moving contour stimuli was inhibitory. The proportion of area 21a neurons whose responses to the moving contours are affected by motion of 2D noise is fairly similar to the proportions of such cells in the present samples of area 17 (70%) and area 18 (89%) neurons (cf. also earlier studies of areas 17 and 18 by Hammond and MacKay, 1981; Gulyás et al., 1987, 1990).

In all cortical areas studied here the suppression was equally strong in cells not responding to noise motion per se and those responding to it (cf. Gulyás et al., 1987, for area 17). In area 21a, in-phase suppression was significantly stronger than anti-phase suppression, but in areas 17, 18 and the PMLS area there was no significant difference. In the present study a moving noise background did not affect significantly the direction selectivity of neurons in areas 21a, PMLS, 17 or 18 (for similar results for neurons in areas 17 and 18, see Orban et al., 1987; Gulyás et al., 1990).

The suppressive effect of moving background is already present in the geniculate neurons and the suppression observed in cortical areas 17, 18 and 21a, based on the simplest assumption of linear additivity, appears to be similar to the effects observed in their geniculate afferents (Gulyás et al., 1987, 1990; the present study). Similarity of modulatory effects of moving noise on neurons in areas 17, 18 and 21a suggests that neurons in area 21a reflect, to a large extent, the properties of their associational afferents from areas 17 and 18. On the other hand, the responses of some direction-selective cells in the lateral suprasylvian areas (LSSAs), including the PMLS area, tend to be suppressed during in-phase background motion and much less suppressed or even strongly facilitated during anti-phase background motion (von Grünau and Frost, 1983). Indeed, both the excitatory receptive fields and suppressive surroundings of some direction-selective cells in LSSAs are direction selective but have opposite preferred directions (von Grünau and Frost, 1983). This may suggest that receptive field properties of directionally specific cells in LSSAs (including the PMLS area), unlike those of area 21a, rather than simply reflecting the properties of their afferents, are largely elaborated by the local circuitry.

'Division and Sharing of Labor' by the PMLS Area and Area 21a

The PMLS area, with its responsiveness over a wide range of velocities, high direction selectivity indices and broad orientation selectivity for short contours, appears to be part of a motion-processing stream; area 21a, with its preference for low velocities, low direction selectivity indices and sharp orientation selectivity to both long and short contours, appears to be part of a pattern-processing stream. Not surprisingly, the selective ablations of the lateral suprasylvian cortex (including the PMLS area, but not area 21a) do not seem to affect significantly discriminations of stationary patterns (Sprague et al., 1977; Spear et al., 1983). By contrast, chronic removals of the PMLS area (as well as the PMLS area) without involvement of area 21a result in permanent deficits in a cat's ability to discriminate differences in speed of moving (especially low-contrast) stimuli (Pasternak et al., 1989).

PMLS neurons appear to be clearly involved in discrimination of object-induced and self-induced motion (Rauschecker et al., 1987a; von Grünau et al., 1987). Indeed, Krüger et al. (1993b) reported that the bilateral removal of the lateral suprasylvian areas (including the PMLS area) results in a specific deficit in the animal's ability to discriminate the patterns moving in anti-phase (or even in-phase as long as there is a relative movement between patterns and background) with the background. Although the effect of ablations of area 21a on the cat's ability to discriminate patterns moving relatively to the background is not known, we believe that the strong involvement of this area in discrimination of object-induced and self-induced motion is unlikely. In particular, in area 21a, unlike in the PMLS area, there is a paucity of neurons that are influenced by the 'efference copy signals' of eye movements (corollary oculomotor signals: Kennedy and Magnin, 1977; Vanni-Mercier and Magnin, 1982; Komatsu et al., 1983; Yin and Greenwood, 1992b).

Despite the fact that the great majority of cells in areas 21a and the PMLS area could be activated through either eye, and both areas appear to play a role in depth perception, each area seems to play a different role in this process. Area 21a appears to be involved in processing static binocular positional disparity (Wang and Dreher, 1996), while the PMLS area appears to be involved mainly in dynamic or movement-in-depth binocular
perception (cf. Turlejski, 1975; Toyama et al., 1985; Krüger et al., 1993a).

The idea of the ‘division of labor’ between the PMLS area and area 21a is also supported by distinct patterns of efferent projections from the two areas. Thus, while the projection of area 21a to the ipsilateral superior colliculus (SC) terminates exclusively in the superficial layers, PMLS projections terminate in both the superficial SC layers and in the dorsal part of the intermediate gray layer (for reviews, see Dreher, 1986; Harting et al., 1992). Indeed, like the deep collicular laminae, the corticocortical projection from the lateral suprasylvian cortex (including the PMLS area) is clearly implicated in visually guided behavior and plays an important role in determining direction and velocity selectivities as well as the binocularity and spatial organization of receptive field of the collicular neurons located in the deep laminae (for review, see Stein and Meredith, 1991).

Secondly, the PMLS area, but not area 21a, is strongly interconnected with the antero medial lateral suprasylvian area (AMLS), the ventral lateral suprasylvian area (VLS) and, albeit to a lesser extent, the ectosylvian visual area (EVA), i.e., the areas which appear to constitute some of the ‘higher order’ areas in the motion processing stream (cf. Tusa et al., 1981; Mucke et al., 1982; Rosenquist, 1985; Dreher, 1986; Olson and Graybiel, 1987; Spear, 1991). By contrast, area 21a, unlike the PMLS area, is directly interconnected with area 20b, which together with area 20a has been implicated in the learning of discrimination of stationary patterns (Sprague et al., 1977).

On the other hand, there is a clear correspondence of some visual tasks by area 21a and the PMLS area. For example, both areas, unlike areas 17, 18 and 19, appear to make a significant contribution to the interhemispheric transfer of visual learning (cf. Marzi et al., 1982; Pito and Lepore, 1985).

Furthermore, both areas project directly to the accessory optic tract nuclei (Berson and Graybiel, 1980; Marcotte and Updyke, 1982) which play a major role in horizontal optokinetic nystagmus (for reviews, see Hoffmann, 1986; Grasse and Cynader, 1991). Indeed, both area 21a and the PMLS area might play some role in the control of horizontal optokinetic nystagmus since in both areas there is a significant increase in glucose utilization when animals are viewing vertically oriented stripes moving horizontally (optokinetic nystagmus drum) as compared to viewing the stationary nystagmus drum (Herdman et al., 1989).

Finally, both areas appear to contribute to foreground/background interactions. Thus, in both areas the motion of 2D visual noise has a clear effect on the responses to moving contour stimuli (for area 21a, see the present study; for the PMLS area, see von Grünau and Frost 1983; von Grünau et al., 1987; the present study).

One Area, Two Areas or Spatially Segregated Distinct Functional Modules?

There is very strong evidence (a review of which is beyond the scope of the present paper) indicating that the PMLS area is homologous with the middle temporal (MT or V 5) 'motion area' area of Old World and New World monkeys (cf. Zeki, 1974; Payne, 1993; cf., however, Gizzi et al., 1991a). The extensive hodological similarities between area 21a and the PMLS area, combined with the fact that the PMLS area contains mainly the representation of the lower visual field and the horizontal meridian (cf. Hubel and Wiesel, 1969; Turlejski, 1975; Palmer et al., 1978; Djavadian and Harutjunian-Kozak, 1983; Zumbroich et al., 1986; Grant and Shipp, 1991; Sherk and Mulligan, 1993) while area 21a contains mainly the representation of the central part of the horizontal streak (±5° on either side of the horizontal meridian) plus a small representation of the central part of the upper visual field (cf. Tusa and Palmer, 1980; Dreher et al., 1993), are consistent with the suggestion that area 21a and the PMLS area constitute distinct parts of a single cortical area (Clare-Bishop or LS; Sherk, 1986; Grant and Shipp, 1991). One can try to accommodate the existence of clear functional differences between the two regions (affirmed, or revealed for the first time, in the present study) in the concept of a single area by regarding the PMLS area and area 21a as distinct modules comparable to hodologically and functionally distinct modules described in areas V1 and V2 of primate visual cortex (see for reviews Livingstone and Hubel, 1988; Zeki and Shipp, 1988, Kaas and Krubitzer, 1991; Casagrande and Kaas, 1994).

However, the distinct modules in areas V1 and V2 of primate visual cortex, unlike the PMLS area and area 21a, are intermingled and neighbouring modules contain the representation of the same parts of the visual field. It has been postulated that the initial segregation of a given cortical field and eventual segregation of distinct modules into distinct new areas might be related to slight differences in composition of thalamic and/or cortical afferents to different regions of a given area (Krubitzer, 1995). The small differences in composition of thalamic and cortical afferents (for reviews, see Rosenquist, 1985; Dreher, 1986; Turlejski et al., 1992; Dreher et al., 1996) might indeed have played an important role in the spatial segregation of the PMLS area and area 21a.

Notes

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References


Chalupa LM, Abramson BP (1989) Visual receptive fields in the striate-


