

## Visual acuity of neurones in the cat lateral suprasylvian cortex

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(Accepted November 20th, 1984)

*Key words:* vision — cat — PMLS — acuity — sinusoidal gratings

The spatial acuity was measured for cells of the posteromedial lateral suprasylvian area (PMLS) of the cat. Acuities were found to be 2 cycles/degree (15 mins arc) at best, and 1 cycle/degree (30 mins arc) on average. Both best acuity and average acuity remained constant with receptive field eccentricity within 20° of the area centralis, and then fell gradually with eccentricity. Acuity was good, given receptive field size, and was not correlated with receptive field size. Comparisons are drawn with other visual structures.

There is growing evidence that areas outside the striate visual cortex contribute to the processing of visual information (see for example Sprague et al.<sup>19</sup>). One large such area (of the cat) which has been implicated in several complex visual tasks<sup>2,3</sup> is the lateral suprasylvian area (LS or area of Clare–Bishop). It is a cortical structure receiving afferents from the medial non-laminated part of the lateral geniculate body (MIN), from the C laminae of the LGN, from areas 17, 18 and 19 and from the inferior and medial pulvinar. That is, it receives inputs directly from the thalamus, from the geniculo-cortical pathway and the tecto-pulvinar visual pathway<sup>7,11,21</sup>.

In this study we investigate the spatial resolution, or acuity of cells in a sub area of LS, termed the posteromedial LS (PMLS)<sup>17</sup>, and describe how acuity varies with both eccentricity and receptive field size.

Experiments were performed on 8 intact adult cats. The cats were initially anaesthetized with ketamine hydrochloride (Ketalar 10 mg/kg, intra-muscular) for incanulation of a femoral vein, and then anaesthetized with Thiopentone sodium (1–2 ml, i.v.). A small patch of skull and dura were removed for electrode insertion. Wounds and pressure points were treated with long lasting local anaesthetic (Anocaine). During recording the animal was paralyzed (Pavulon, 0.2–0.3 ml/kg/h, i.v.) and artificial-

ly ventilated with N<sub>2</sub>O/O<sub>2</sub> (70:30%). End tidal expiratory CO<sub>2</sub> was kept constant at 3.5–4%, and body temperature, EEG and ECG were constantly monitored. Soft contact lenses provided a 4 mm artificial pupil and protected the corneas, and ametropia was corrected with trial lenses. The position of the vertical meridian and area centralis of each eye was determined by the standard techniques of projection of the optic disks<sup>4,10</sup>.

Electrode penetrations were made along the medial wall of the medial suprasylvian sulcus with a micropipette (1–2 μm tip) filled with NaCl. The electrode was angled medially 25–35° from the vertical, between A6 and AP0 stereotaxic coordinates, which define the area of PMLS<sup>17</sup>. The electrical potentials from the electrode were suitably amplified, filtered and pulse shaped, and led into an auditory amplifier and a digital computer (PDP-11/10), which computed post time histograms.

On location of a cell, its receptive field (RF) was hand plotted by stimulation with light and dark spots and bars on a tangent screen, 57 cm from the cat. Dark bars moving against a light background proved to be the most useful stimuli. Properties such as ocular dominance, direction and orientation selectivity were also assessed by hand plotting techniques.

Acuity measurements were made with high con-

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trast (80%) drifting sinusoidal gratings, displayed on the face of an oscilloscope, positioned in place of the tangent screen after initial hand plotting. The oscilloscope screen (Joyce Electronics, mean luminance 50 cd/m<sup>2</sup>) subtended 30 × 30° at 57 cm. For cells of RFs greater than 30°, the central 30° of the field was stimulated. The gratings were generated by the PDP-11/10 computer and displayed with standard raster techniques.

Forty-nine neurones were analyzed quantitatively. Receptive field properties were found to be generally similar to those reported elsewhere<sup>6,9,14,17,18,22,24</sup>. Most cells had large RFs (mean 13°, range 3–45°), often extending into the ipsilateral hemifield<sup>14</sup>. They could be binocularly driven, with a preference for the contralateral eye. Virtually all neurones responded poorly to stationary stimuli and most were directionally tuned. They were also tuned for spatial and temporal frequency, which will be discussed in more detail in a forthcoming publication<sup>15</sup>.

For assessment of acuity, only the dominant eye was stimulated, and grating orientation, temporal

frequency and drift direction were adjusted for maximum cell response. Acuity was determined in two ways: by increasing spatial frequency until the cell produced a clear but just discernible audible response (which was typically, but not always, an unmodulated increase in discharge rate<sup>15</sup>); and by extrapolation of spatial frequency response curves, obtained from post-stimulus time histograms to stimulation of spatial frequencies near acuity. Both methods yielded similar results.

Figs. 1 and 2 report all measured cell acuities and describe how they vary with RF eccentricity and size. Acuities ranged from 0.13 to 2 cycles per degree (c/deg) (4°–15' arc resolution), with an average of 0.96 c/deg (31' arc). Fig. 1 shows the relationship between acuity and RF eccentricity. Up to about 20° from the area centralis average acuity does not vary at all with eccentricity (correlation coefficient  $r = -0.02$ ), and the best acuity varies very little. More peripherally, acuity begins to drop with eccentricity, at a rate of about 0.2 log units per 10° ( $r = -0.5$ ). Fig. 2 shows the relationship between acuity

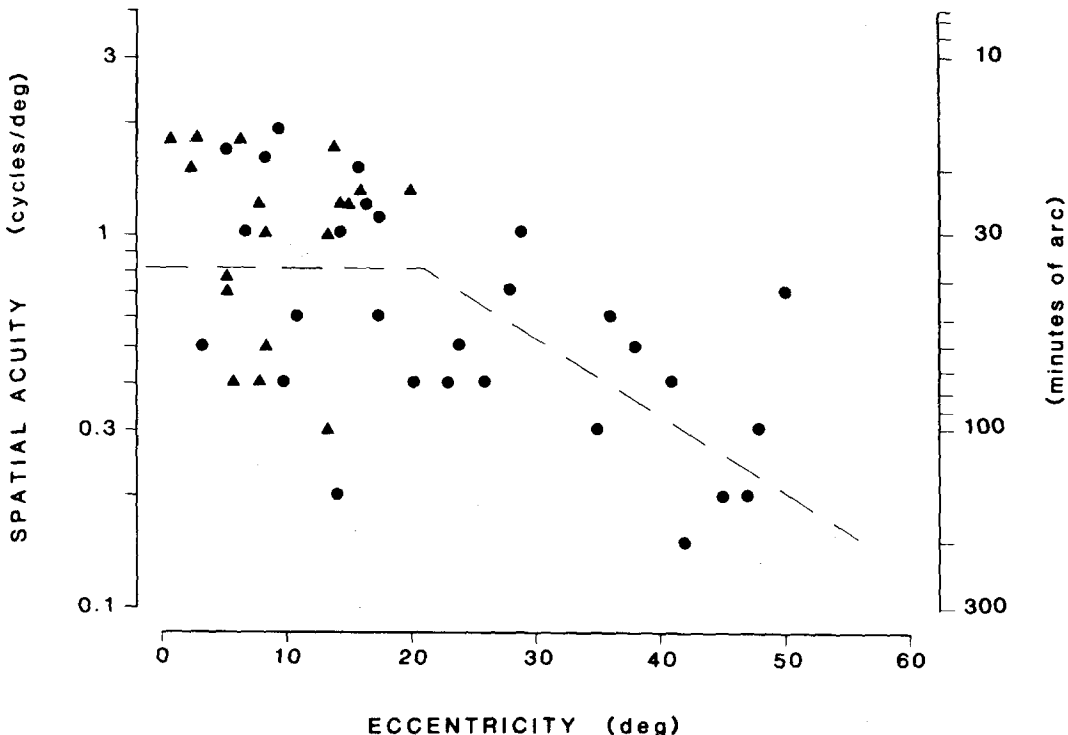


Fig. 1. Acuity of 49 cells, plotted against eccentricity of receptive field centres. Acuity is expressed as spatial frequency on the left, and bar width  $1/2$  (spatial frequency)<sup>-1</sup> on the right. The triangular symbols refer to cells whose fields had ipsilateral extensions. The broken lines are the least squares best fit, calculated separately for RFs within 20° of area centralis and for those more peripheral. The correlational coefficients for log acuity against eccentricity were  $-0.02$  and  $-0.5$ , respectively.

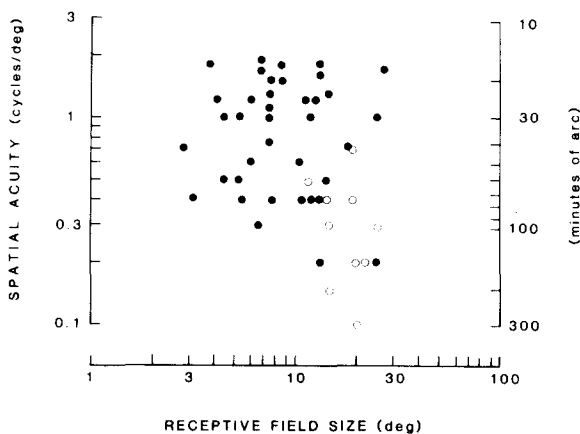


Fig. 2. Acuity of 49 cells, plotted against receptive field size (calculated as the square root of the area). The open circles report data from cells whose receptive field centers were more peripheral than  $30^\circ$ . The correlation coefficients for log acuity against size are  $-0.24$ , or  $-0.03$  if cells with RFs of more than  $30^\circ$  eccentricity are excluded.

and RF size. Acuity is unexpectedly high, given the large fields, and is not correlated with RF size ( $r = -0.24$  for all cells, and  $-0.03$  if cells with RFs more peripheral than  $30^\circ$  are excluded).

To view the present results in context, it is interesting to compare PMLS acuities and the distribution of acuities with those of other visual areas. Average acuity for area 17 is 2 c/deg, and the maximum about 5 c/deg<sup>12,13,16</sup>. In area 18, acuities are lower, more like those of PMLS: average about 0.8 c/deg and maximum less than 2 c/deg<sup>1,16</sup>. Superior colliculus acuities are also comparable with PMLS, averaging 1 c/deg and peaking at 1.7 c/deg<sup>5</sup>. Thus, PMLS resolution is lower than area 17 by a factor of 2 or 3, but comparable with resolution of the other visual areas where acuity has been measured.

In area 17, acuity falls off rapidly with eccentricity, by a factor of 3 (0.5 log units) in the first  $10^\circ$  from the area centralis<sup>16</sup>. Acuities for area 18, on the other hand, are relatively constant over this region, more like those of PMLS (Fig. 1)<sup>16</sup>. In area 17, acuity is correlated with receptive field size<sup>13</sup> ( $r = -0.94$ ): the smaller the receptive fields, the higher the acuity. In

general receptive fields are about 6 times the size of the smallest resolvable bar. In PMLS, however, there is virtually no correlation between receptive field size and acuity, and the ratios between the two are much higher: 19 on average, and 91 in the extreme.

It is interesting that PMLS cells have acuities and a distribution of acuities similar to those of area 18 and superior colliculus (both of which project to PMLS), but are lower in acuity by a factor of 2 or 3 than cells of area 17, and have quite different distributions. It would seem that the high resolution cells of area 17 cells do not contribute to PMLS acuity. This suggestion is supported by evidence that it is only the complex cells from laminae 2 and 3, and possibly lamina 5, that project to PMLS from area 17<sup>8</sup>, and that cells of these laminae have low acuity<sup>1</sup>.

The large PMLS receptive fields with reasonable acuity may reflect the properties of the afferent structures. There is some evidence that W-cells have very large fields combined with reasonable acuity<sup>20,23</sup>. Another plausible explanation could be that PMLS cells combine the input from many afferents whose receptive fields do not correspond exactly in space. This would give PMLS cells extensive receptive fields, without necessarily a loss of acuity. The two possibilities will be considered further in a forthcoming publication<sup>15</sup>.

Our results do not address the issue of what visual tasks PMLS may be performing. They do, however, indicate that PMLS neurones have sufficient resolution to be at least capable of specialized visual processing, such as pattern recognition and form analysis, suggested by others<sup>2,3,19</sup>.

M.D. was on leave from the Istituto di Fisiologia Umana, and M.C.M. from the Scuola Normale Superiore, Pisa. The research was partly supported by the Australian NH and MRC, and we thank Hydrion Australia Pty Ltd for providing the contact lenses. We also thank Peter Meyer and Tony Gibbs for expert technical assistance.

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