

Extents of visual, auditory and bimodal receptive fields of single neurons in the feline visual associative cortex

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Extracellular microelectrode recordings were carried out on 150 neurons in the anterior ectosylvian sulcal region of halothane-anesthetized, immobilized, artificially ventilated cats. Fifty-nine neurons were visual, 60 were auditory and 31 were bimodal visual-auditory. As the extent of the receptive fields has never been exactly determined, we introduced a quasi-objective, computer-based, statistical method in order to estimate the receptive field sizes in the anterior half of the perimeter. The visual, auditory and bimodal cells had very large receptive fields, often with portions extending well into the ipsilateral hemifield. The mean extents of the visual and auditory receptive fields in the horizontal plane were 75.75° ($N=59$, $SD: \pm 28.62^\circ$, range: $15-135^\circ$), and 132.5° ($N=60$, $SD: \pm 46.72^\circ$, range: $15-165^\circ$) respectively. These data suggest that a single visual neuron can carry information from the whole visual field of the right eye and a single auditory unit can carry information of azimuths throughout the whole area of the horizontal plane studied. The mean extent of the bimodal receptive fields in the horizontal plane was 82.1° ($N=31$, $SD: \pm 24.24^\circ$, range: $30-135^\circ$). In 21 of the 31 bimodal cells we observed a facilitatory interaction between visual and auditory stimuli. The mean extent of the facilitatory interactions in these cells was 75.75° ($N=21$, $SD: \pm 24.56^\circ$, range: $45-135^\circ$).

Keywords: visual, auditory, bimodal, receptive field extent, cat, AEV

The existence of the anterior ectosylvian visual area (AEV) within the anterior ectosylvian sulcus (AES) of the feline cortex was noted in the early 1980s (11, 12). Since then, electrophysiological studies have determined particular visual receptive field properties of the neurons in this region. Most of the AEV neurons are highly direction-sensitive and elicit the most vigorous responses to fast-moving, very small

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stimuli (1, 2, 11, 14). Despite all these physiological studies, the extents of the visual receptive fields have not yet been clarified. Different attempts to draw the borders of the visual receptive fields of the AES neurons have yielded widely differing results. Olson and Graybiel (13) reported that the mean visual receptive field diameter of the AEV neurons is 15° and that the receptive fields are mostly located in the lower contralateral quadrant. Scannell et al. (14) similarly found relatively small receptive fields (mean= 18°), but their results showed that the receptive fields extended up to 10° into the ipsilateral hemifield. Benedek et al. (2) revealed that the visual neurons in the AES have extremely large receptive fields that consistently include the area centralis and cover almost the whole visual field of the eye involved. All of these receptive field mappings were the results of subjective observations where the stimuli were generated with hand-held lamps and projectors. The AEV region of the cortex, however, possesses an auditory representation, too (4, 5, 11, 16). The extents of the auditory receptive fields were examined by Middlebrooks et al. (8–10), whose subjective observations demonstrated that the auditory receptive fields are extremely large, covering 360° of azimuth of the horizontal plane. Our present study had the aims of determining the exact extents of the visual and auditory receptive fields, and of comparing the objectively determined receptive field sizes of the visual and auditory neurons situated in the AEV with earlier results (2, 13, 14). We introduced a quasi-objective, computer-based, statistical method to approach this question. Special attention was paid to bimodal cells that reacted to both modalities and showed significant cross-modal interactions, with a view to determining the extents of the bimodal interactions and the bimodal receptive fields.

Materials and methods

Animal preparation

The study was performed in 10 adult cats ranging in weight from 2.7 to 3.7 kg. The experimental protocol had been accepted by the Ethical Committee for Animal Research of the University of Szeged. The cats were initially anesthetized with ketamine hydrochloride (30 mg/kg i.m.). After cannulation of the femoral vein and the trachea, the animals were placed in a stereotaxic headholder. The wound edges and pressure points were treated generously with procaine hydrochloride (1%). The animals were immobilized with gallamine triethiodide (Flaxedil, 20 mg/kg i.v.) and the skull was fixed with dental cement. The anesthesia was maintained with halothane (1.2% during surgery and 0.6% during recording). The depth of anesthesia was monitored by repeated checks of pupil size, and electrocorticogram and electrocardiogram recordings. An infusion solution containing gallamine (8 mg/kg/h), glucose (10 mg/kg/h) and dextran (50 mg/kg/h) in Ringer's solution was infused continuously at a rate of 3 ml/h. Atropine (0.1%, 0.2 ml) was administered subcutaneously. The end-tidal CO_2 level and the rectal temperature were monitored continuously and kept constant at 3.8–4.2% and 37–38 °C, respectively. The eye contralateral to the recording was treated with

ephedrine and atropine and was equipped with a +3 diopter contact lens. The ipsilateral eye was covered during stimulation. The skull was opened to allow a vertical approach to the AES. The dura was covered with a 4% solution of 38 °C agar dissolved in saline.

Recording and stimulation

Electrophysiological recordings were performed extracellularly with tungsten microelectrodes (AM System Inc. USA, 2–4 MOhm). Vertical penetrations were made between Horsley–Clarke co-ordinates A: 10–14 and L: 12–14. At the end of the experiments, the animals were deeply anesthetized with pentobarbital and transcardially perfused with paraformaldehyde solution (4%). The brains were removed. The locations of successful electrode penetrations were denoted histologically. The brains were cut in coronal sections of 50 µm and stained with neutral red. All of the recorded neurons were within the AEV.

For auditory stimulation, we used 12 loudspeakers placed at 15° intervals on the 165° perimeter before the interaural plane that delivered white noise (40 dB). The duration of auditory stimulation was 1 s. The visual stimulus was served by the subsequent lighting of 12 light-emitting-diode (LED) pairs placed in the same way as the loudspeakers on the 165° perimeter, 30 cm from the eye, in an arc positioned according to the Horsley–Clarke horizontal zero plane. The light emission time of the first LED was 120 ms and this was followed immediately by emission for 320 ms by the second one. The computer-controlled stimuli were presented in a pseudo-random order, separately or simultaneously (bimodal). The interstimulus interval was 1 s. Neuronal activities were recorded and correlated with the visual, auditory or bimodal stimulation by a computer and stored for further analysis as peristimulus time histograms (PSTHs). The prestimulus time was 500 ms, and the peristimulus time was also 500 ms. Whenever a single unit was found that was visually or auditory-sensitive, at least 10 trials were run in each condition. Single-cell discrimination was performed with a spike-separator system (SPS-8701, Australia).

Data analysis

The net firing rate was calculated as the difference between the firing rate during the first 500 ms of stimulation and that before stimulation. The net firing rate was defined as a response when a t-test revealed a significant ($p < 0.05$) difference between the two values.

The width of the receptive field of a neuron was determined by the locations of stimuli that induced a significant response. As a maximal site we considered those stimulus localizations, at which the net firing rate was the highest. We defined laterality as a significant difference in mean net firing rate between the responses to stimuli from the ipsi- and contralateral visual fields. The area centralis was at 0° on the perimeter. When the bimodal peristimulus net firing rate was found by analysis of variance (ANOVA) to be significantly higher ($p < 0.05$) than the most effective single modality peristimulus net firing rate, a facilitatory interaction was considered to exist. The

strength of an interaction was calculated via the formula coined by Meredith and Stein (7):

$$\{(CM - SM_{\max}) / (SM_{\max})\} \times 100 = \text{interaction\%}$$

where CM is the mean number of impulses evoked by the bimodal stimulus and SM_{\max} is the mean number of impulses evoked by the most effective single-modality stimulus. The extents of the facilitatory bimodal interactions were determined by the locations of stimuli that induced significant multisensory facilitation.

Results

Altogether 150 cells were recorded that were sensitive to either visual or auditory stimulation or both. Upon comparison of the peristimulus discharge rate with the prestimulus discharge rate, visual sensitivity was found in 59 cells. Sixty cells were found to be auditory-sensitive, while 31 cells proved to be bimodal in the sense that they reacted to separate visual and separate auditory stimulation, and also to simultaneous auditory and visual stimulation to a statistically significant extent.

Receptive field sizes of the AEV single neurons

Both visual and auditory cells possess extremely large receptive fields. Since our stimulating set was confined to 165°, which was smaller than the auditory receptive field defined earlier (3, 10), we did not attempt to delineate the total extents of the auditory receptive fields. Subjective estimation of the visual receptive field indicated in all cases that it covered a major part of the contralateral hemifield and extended deep into the ipsilateral one, yielding a field that overlapped almost totally with the visual field of the right eye. No signs of retinotopy were observed within the AEV.

Objective estimation of the visual and auditory receptive fields was performed by calculating the significant responses to individual stimulation given at a distance of 15° with the help of the t-test (Fig. 1).

The mean extent of the visual receptive fields in the horizontal plane was obtained as 75.75° (N=59, SD: 28.62°, range: 15–135°, Fig. 2A). Nevertheless, only 4 visual cells revealed significant responses in the whole extent of a 135° field (visual field of the right eye) studied, in most cases since the peripheral parts of the receptive fields rarely displayed significantly increased responses. The site of maximal responsivity within the visual receptive fields varied extensively in the cells recorded. The visual field did not appear to contain any exclusive site consistently preferred by a majority of the cells. Practically all the stimulating sites produced a maximal response in some cells, while other cells had a preference for other sites. We compared the PSTHs obtained upon ipsilateral and contralateral visual stimulation. ANOVA analysis of the net firing rates yielded significant differences between these responses in 42% (25 of 59) of the visual cells.

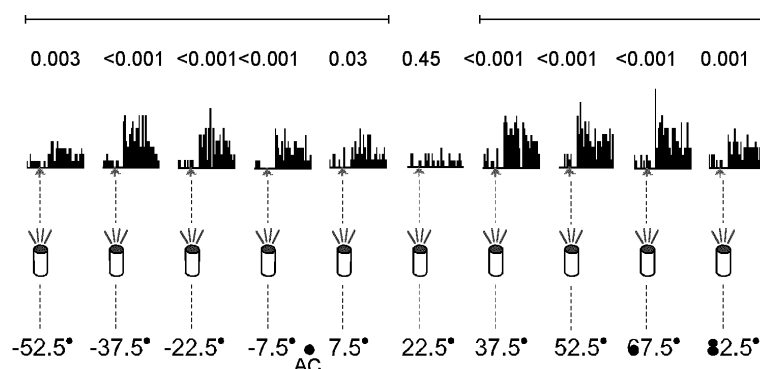


Fig. 1. Schematic drawing of the visual stimulating set-up (bottom) and PSTHs (middle) of a typical visual neuron along the AES. Schematic bulbs represent the positions of the LED diodes. Broken lines indicate the corresponding histograms and stimulus sites. The numbers in degrees denote the site of the visual stimulus related to the area centralis in the horizontal plane. The arrows below the PSTHs demonstrate the beginning of the visual stimulation (peristimulus time). The numbers above the PSTHs show the corresponding significance level of the t-test in which the prestimulus and peristimulus firing rates are compared. The lines at the top indicate the objectively estimated extent of the visual receptive field of this single neuron.

Abbreviation: AC = area centralis

The mean extent of the auditory receptive fields in the horizontal plane, as estimated statistically, was found to be 132.5° ($N=60$, $SD: \pm 46.72^\circ$, range: $15\text{--}165^\circ$, Fig. 2B) in the 165° perimeter examined. Thirty-two auditory cells displayed receptive fields extending to the 165° area studied. No signs of laterality were observed in the auditory cells. The comparison of PSTHs recorded upon ipsilateral and contralateral auditory stimulation indicated only weak, nonsignificant differences.

The mean bimodal receptive field extent of the bimodal cells in the horizontal plane was 82.1° ($N=31$, $SD: \pm 22.24^\circ$, range: $30\text{--}135^\circ$, Fig. 2C). No signs of laterality were detected upon ipsilateral and contralateral bimodal stimulation of the bimodal cells. We analysed the receptive field data for the 21 bimodal neurons that exhibited a significant facilitatory cross-modal interaction between visual and auditory stimulations. The mean extent of the facilitatory interaction in these cells was 75.75° ($N=21$, $SD: \pm 24.56^\circ$, range: $45\text{--}135^\circ$). We failed to find any site-relatedness of the cross-modal interaction within the perimeter studied. The relationship between the cross-modal facilitation calculated by the formula of Meredith and Stein (7) and the stimulation site was found by ANOVA to be statistically nonsignificant ($F(9.190) = 0.619$, $p=0.78$).

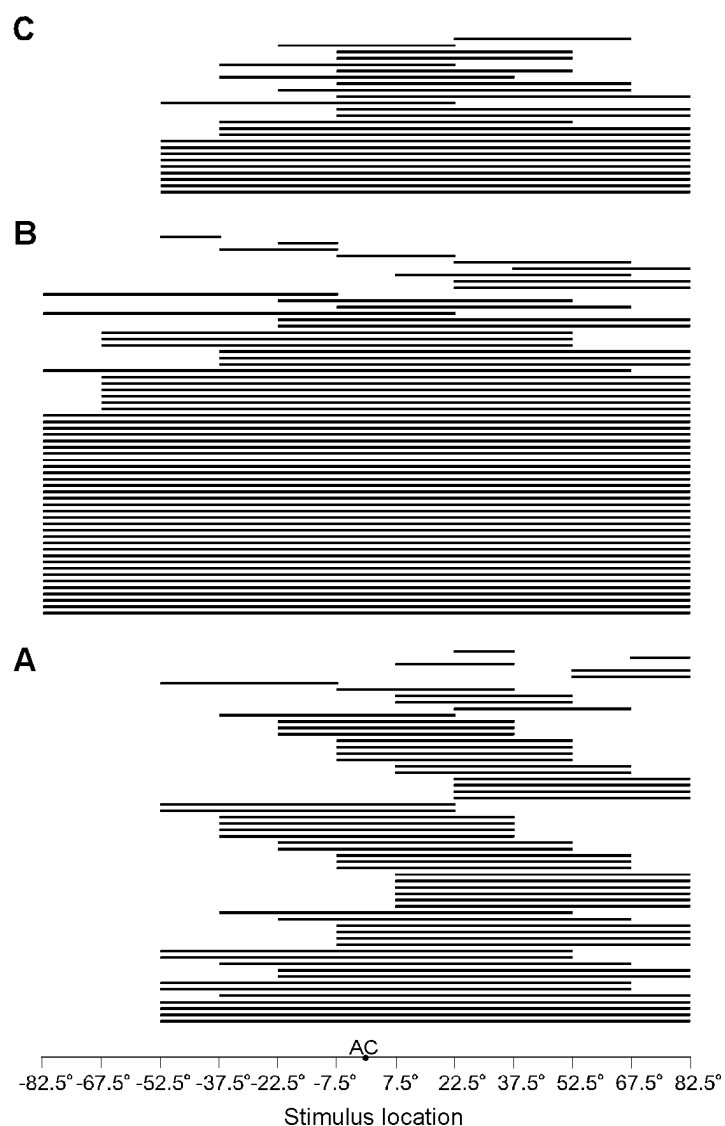


Fig. 2. The extents of 59 visual (A), 60 auditory (B) and 31 bimodal (both auditory and visual) receptive fields (C) of AES neurons estimated by our objective, statistical method. The numbers in degrees indicate the sites of the stimuli related to the area centralis in the horizontal plane. Horizontal lines reveal statistically significant increases in the firing rate as responses to stimulation in the corresponding part of the receptive field. Abbreviation: AC = area centralis

Discussion

Our results add new data to the multimodal representation of the environment in the feline cortex. The notion of the existence of a multimodal sensory area over the anterior part of the cat brain is not novel. It was first noted by Loe and Benevento (6). Detailed analyses of the visual, somatosensory and auditory properties and their cross-modal interaction were performed later (4, 15, 16). Our results on the existence of visual or auditory unimodal cells, together with bimodal cells that show a cross-modal interaction, appear to be entirely in line with these earlier results. Despite all these studies, an exact estimation of the visual receptive field extent is still missing. Even the existence of retinotopy in this area is a matter of controversy (2, 13, 14). Our subjective estimations demonstrated extremely large visual receptive fields that cover the visual field of the investigated eye. We did not observe any signs of retinotopy within the AEV. Our novel, objectively estimated, statistical approach confirmed the earlier observation by our group (2) that a large number of the AEV neurons have very large receptive fields that cover most of the whole visual field of the corresponding eye. The stimulation pattern used in our experiments was selected because some neurons were insensitive to diffuse on-off light stimulation. In line with the previous reports (4, 14), the most sensitive sites were found concentrated around the region near the area centralis of the retina. However, in some cases our objectively estimated receptive field sizes are much smaller. The reason for this may be that the stimuli were not optimal for all of the recorded neurons and our procedure obviously underestimates the actual size of the receptive field, but it yields an objective estimate that can be used in further analysis.

Similarly as in earlier reports (8–10) the auditory receptive fields were found to be extremely large. Since our stimulating set was confined to the anterior 165° of a horizontal plane, the area of which is much smaller than the auditory receptive field defined earlier (3, 8–10), we did not attempt to delineate the total extent of the auditory receptive fields. Nevertheless, in most neurons the auditory receptive field covered the whole of the area we studied.

Objective estimation of the bimodal receptive fields showed that the bimodal receptive fields are also extremely large. In most cases, the bimodal receptive fields of the bimodal neurons extended to the borders of the visual field of the right eye, although their auditory receptive fields were somewhat larger. Cross-modal interaction between auditory and visual stimuli was studied earlier (4, 16). In the experiments reported here 21 bimodal neurons displayed significant multisensory cross-modal facilitation. The extent of the bimodal facilitatory interactions was found to be similar to that of the visual receptive fields. We did not observe any relationship between the strength of the interactions calculated with the formula of Meredith and Stein (7) and the stimulation site.

In summary, our results seem to provide objective estimates for the extents of the visual, auditory and the bimodal receptive fields of AEV neurons. The results reported here suggest that the visual, auditory and bimodal receptive fields of the AEV neurons

are extremely large. Any single neuron in the AEV that receives appropriate modality sensory stimulation can carry information from stimuli within its whole physically approachable sensory field.

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