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Processing of spatial visual information along the pathway between the suprageniculate nucleus and the anterior ectosylvian cortex

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Abstract

This study describes the visual information coding ability of single neurons in the suprageniculate nucleus (Sg), and provides new data concerning the visual information flow in the suprageniculate/anterior ectosylvian pathways of the feline brain. The visual receptive fields of the Sg neurons have an internal structure rather similar to that described earlier in the anterior ectosylvian visual area (AEV). The majority of the Sg units can provide information via their discharge rate at the site of the visual stimulus within their large receptive fields. This suggests that they may serve as panoramic localizers. The sites of maximum responsivity of the Sg neurons are distributed over the whole investigated part of the visual field. There is no significant difference between the distributions of spatial location of maximum sensitivity of the AEV and the Sg neurons. The mean visual response latency of the Sg units was found to be significantly shorter than the mean latency of the AEV neurons, but there was no difference between the shortest latency values of the thalamic and the cortical single-units. This suggests that the visual information flows predominantly from the Sg to the AEV, though the cortico-thalamic route is also active. The Sg seems to represent a thalamic nucleus rather similar in function to both the first-order relays and the higher-order thalamic nuclei. These results, together with the fact that the superior colliculus provides the common ascending source of information to the suprageniculate/anterior ectosylvian pathway, suggest a unique function of the AEV and the Sg in sensorimotor integration.

Keywords: Suprageniculate nucleus; AEV; Panoramic localizers; Spatial coding; Latency; Visual

1. Introduction

The existence of the visual areas along the anterior ectosylvian sulcus (AES) of the feline brain was described in the 1980s [3,11,21,25]. Morphological studies revealed that these areas receive visual information bypassing the geniculo-striate system, through a cortical route via the lateral suprasylvian visual areas and through a tecto-thalamic route via the suprageniculate nucleus (Sg) and the lateral posterior nucleus pars medialis (LPm) of the thalamus [24,23]. The physiological properties of the LPm and its connections have been studied fairly widely [1,6,13,15,16,28,33]. The Sg, however, has attracted much less interest during the last 25 years, although the neurons in this thalamic nucleus exhibit special physiological properties. While the lateral geniculate nucleus (LGN) relays the retinal input towards the primary visual cortex without causing any fundamental modification in the size of the receptive fields, the visual receptive fields in the Sg are rather dissimilar to those of the neurons of the intermediate and deep layers of the superior colliculus (SC) from where they receive their tectal visual afferentation. The receptive fields of the Sg neurons uniformly cover the whole extent of the visual field of the stimulated eye [4,12]. These receptive field properties can appear for two reasons. The strong convergence of the collicular fibres on the Sg [14] could be responsible for the representation of the whole visual field. The Sg might mediate this information to the cortex, and thus the similarly huge receptive fields of the neurons along the AES [3,11,21] could be a consequence

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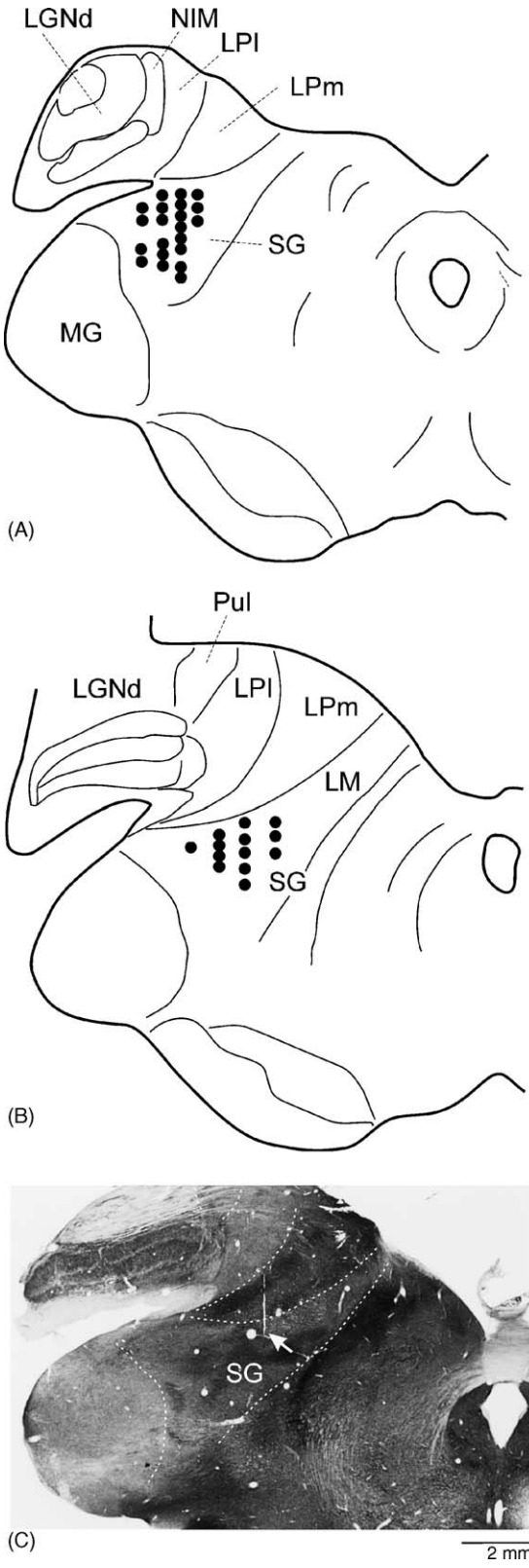
of the thalamic relaying of this convergence. On the other hand, the activity of the pathway between the visual associative cortex (AEV) and the Sg [12,33] could also result in the large receptive fields of Sg neurons. This raises at least two important questions concerning the visual information processing and flow between the AES cortex and the Sg: is the internal organization of the large receptive fields of the Sg units similar to or different from that of the AEV [2,5]? Then, as regards the direction of the information flow, are the cortico-thalamic and thalamo-cortical routes equally active during visual information processing?

We attempted to aquire data which would clarify these problems by recording single-unit responses to visual stimulation both in the AEV and in the Sg of the feline brain. The stimulation was performed by moving a randomly selected portion of a large visual white-noise pattern in front of the animal. Earlier use of the same stimulation set-up revealed that within each visual receptive field of the neurons in the AES cortex there is a "hot-spot", i.e. a region which is preferentially sensitive to visual stimulation [5]. The location of this region varies among the neurons, providing a possibility for a non-traditional spatial coding of signals in the visual field [2,5]. In the present study, we investigated the distribution of sites of maximum sensitivity within the large receptive fields of the Sg neurons and compared the organization of the receptive fields in the AEV and the Sg. We further calculated the latencies of the AEV and the Sg visual responses. Comparison of the AEV and Sg latencies could possibly shed light on the direction of information flow between the AEV and the Sg and may provide an indication as to whether the cortico-thalamic volley first reaches the thalamus, or whether the SC causes the initial excitation in the neurons of the Sg.

2. Materials and methods

2.1. Animal preparation and surgery

The experiments were performed on 19 adult cats ranging in weight from 2.4 to 4.0 kg. The experimental protocol had been accepted by the Ethical Committee for Animal Research of the University of Szeged. The anaesthesia was initiated 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 anaesthesia was continued with halothane (1.6% during surgery and 0.8% during recordings). The depth of anaesthesia was monitored by repeated checks of pupil size on the non-treated side, and checking electrocorticogram and electrocardiogram recordings. All of the parameters controlled revealed the general anaesthesia of the animals throughout the whole of the experiments. The animals were immobilized with gallamine triethiodide (Flaxedyl, 20 mg/kg i.v.). During the experiment, a 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 skull was opened with a dental drill to allow a vertical approach to the Sg and the AEV. The dura was covered with a 4% solution of agar dissolved in Ringer solution. The eye contralateral to the cortical recording was treated with phenylephrine (10%) and atropine (0.1%), and was equipped with a +2 dioptre contact lens. The ipsilateral eye was covered during stimulation. A subcutaneous injection of 0.2 ml 0.1% atropine was administered preoperatively. The retinal landmarks and major retinal blood vessels were projected routinely twice daily onto a tangent screen, using a fiberoptic light source [26]. In some cases, the area centralis could be seen directly, in others, it was plotted by reference to the optic disc 14.6° medially and 6.5° below the centre of optic disc [7].

2.2. Recording

Electrophysiological recordings were performed extracellularly with tungsten microelectrodes (AM System Inc. USA, 2–4 MΩ). Single-unit discrimination was made with a spike-separator system (SPS-8701, Australia). Vertical penetrations were performed to reach the Sg between the Horsley–Clarke coordinates anterior 4.5–6.5 and lateral 4–7 in the stereotaxic depths in the interval 10–13 mm. The AEV neurons were recorded between the co-ordinates anterior 11–14 and lateral 12–14 in the stereotaxic depths in the interval 13–19 mm. At the end of the experiments, the animals were deeply anaesthetized with pentobarbital and perfused transcardially with paraformaldehyde solution (4%). The brains were removed, cut in coronal sections of 50 μm and stained with neutral red or for acetylcholine-esterase. Electrolytic lesions marked the locations of successful electrode penetrations. All of the recorded neurons were located either in the Sg (Fig. 1) or in the AEV.

2.3. Stimulation and data evaluation

The visual responsivity of the neurons was tested subjectively by the generation of moving visual stimuli with a hand-held lamp. Whenever a single-unit was found to be sensitive to moving visual stimulation, computer-controlled visual noise patterns were used to estimate its visual response properties. For computer-controlled visual stimulation, an 18-in. computer monitor (refresh rate—60 Hz) was placed 57 cm in front of the animal. A stationary visual noise stimulus (grain size: 0.2–1.5°) was presented to the animal in an area of 24° × 32° around the area centralis. The mean luminance of the screen was 17 cd/m^2. We divided this area into 12 parts each of 8° × 8°. To avoid stationary problems, the stimuli were randomized in position over trials. The randomly selected 8° × 8° portion of the elements comprising the pattern was then moved for 2500 ms at a speed of 10°/s. We investigated the responses to eight different moving directions of the visual noise pattern along four axes (0–315° at 45° increments) to find the preferred moving direction of each single neuron. Neuronal activities were then recorded and correlated with the movement of the visual noise pattern in the preferred direction. They were stored for further analysis as peristimulus time histograms (PSTHs). The original binwidth was 62 ms, while binwidths of 1, 2, 5 and 10 ms were used to calculate the visual response latencies. The prestimulus time (during which a stationary visual noise pattern stimulus was shown) was 500 ms and the peristimulus time (while the visual noise pattern stimulus was moving) was 2500 ms. At least four trials were run in each 8° × 8° window. The interstimulus interval was 1 s.

We defined the net firing rate in each 8° × 8° window as the response when a paired *t*-test demonstrated a significant difference ($p < 0.05$) between the prestimulus and peristimulus firing rates. While the visual receptive field of the AEV and the Sg neurons are extremely large [4,22], we considered a cell to be visually responsive if it was responsive in each 8° × 8° window. The spatial selectivity of each responsive cell was investigated with one-way ANOVA. We defined a neuron as spatially selective if the net firing rate of at least one window was significantly different from the mean of the others. As maximum site, we considered the stimulus location at which the net firing rate was highest. We estimated the distance of the maximum responsive site from the area centralis and the angle of the vector connecting the maximum responsive site and the area centralis. We compared these values between the AEV and the Sg neurons. The comparison was performed either with the *t*-test, if the values exhibited normal distribution, or with the Kruskal–Wallis test, if the distribution of the values was not normal.

To measure the latency of the responses, we used a software program developed in our laboratory. This was based on a sliding-window technique. The program slid two 350 ms windows along the frequency histogram of the responses. The first window slid through the peristimulus firing rate in 5 ms steps, and selected the 350 ms wide portion that represented the maximum frequency. Then, a second window was slid in 5 ms steps, and after each step the program calculated the significance level between the spike frequency values of the two windows with the *t*-test. The latency of the responses was calculated from the time function of these *p* values. A curve was fitted to the *p* values, and the time interval between the start of the stimulation and the inflection point provided the response latency.

Fig. 1. Histological reconstruction of the recording sites and the recorded units in the Sg. (A and B) Positions of the recorded visually responsive neurons (black dots) in the Sg. The drawings depict coronal sections of the Sg in the cat brain in A5 and A6 according to the stereotaxic atlas of Reinoso-Suarez [27]. (C) An acethylcholine–esterase stained section of the Sg within the position of the recording electrode marked by the white arrowhead. Bars in the right bottom corner provide size calibration and orientation in the dorso-ventral and medio-lateral aspect. *Abbreviations*: LGNd, lateral geniculate nucleus; LPl, lateral division of the nucleus lateralis posterior; LPm, medial division of the nucleus lateralis posterior; LM, nucleus lateralis medialis; Sg, suprageniculate nucleus; MG, medial geniculate nucleus.

3. Results

Altogether 35 visually responsive single-units were recorded extracellularly in the Sg and 32 visual responsive units in the AEV. The information processing and coding abilities of these units were analysed in detail. Fig. 1 demonstrates the histological reconstruction of the recording tracks and the positions of the analysed Sg units (A and B) a Sg section with the electrode penetration (C).

The extent of the visual receptive field was estimated subjectively by listening to the neuronal responses to movements of a light spot generated by a hand-held lamp. Similarly to earlier results, the visual receptive fields in both the extrageniculate thalamus and the visual associative cortex were extremely large (consistently larger than 6000 degree^2): they 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 [4,21]. The receptive fields consistently included the area centralis. No signs of retinotopical organization were observed within either the AEV or the Sg. The visual receptive fields of both the Sg and the AEV neurons were definitely larger than the computer monitor used for visual stimulation. Thus, we could investigate the information coding abilities of the AEV and the thalamic neurons only in a restricted, though large central part of their visual receptive fields.

3.1. Spatial selectivity of the AEV and the Sg neurons

The distributions of the preferred directions of the 35 Sg and the 32 AEV units were very similar. Only small proportions of the AEV (3/32) and the Sg neurons (4/35) exhibited optimum responsivity to movement along the horizontal axis (90° and 270° directions). The preferences for the other six directions were distributed evenly among the neurons. The data obtained for the optimum directions were used for the further analysis.

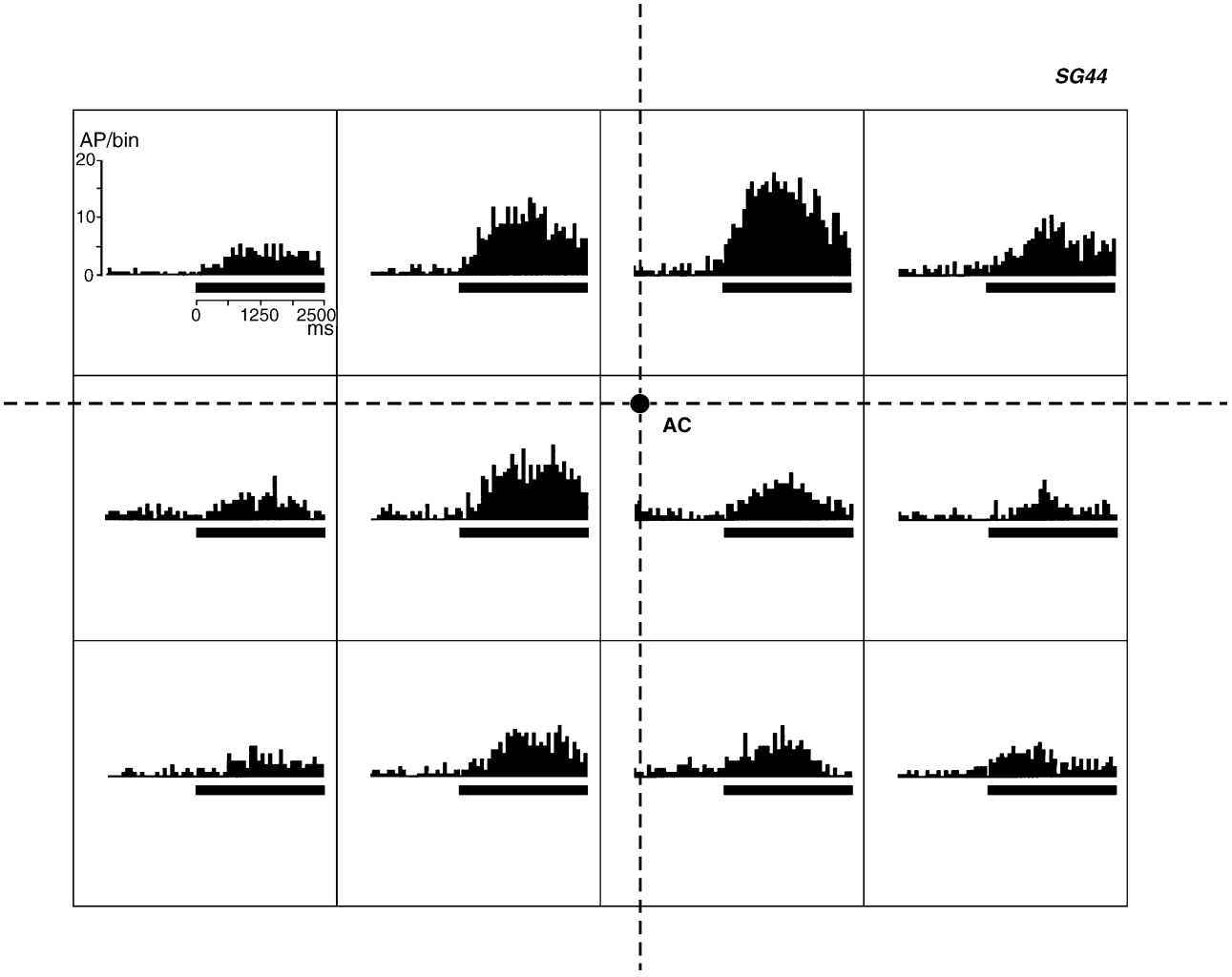


Fig. 2. Receptive field organization of a panoramic suprageniculate nucleus neuron, *SG44*. Peristimulus histograms are presented that were recorded during the motion of visual noise in the respective part of the visual field. Every window represents a 8° × 8° portion of the receptive field. In each window, the abscissa indicates time. The ordinate denotes number of action potential/binwidth values (binwidth = 62 ms). The thick black line indicates the motion of the visual noise for 2500 ms.

Spatial sensitivity towards moving stimulation within the restricted part of the receptive field was estimated by comparing the response intensities by means of one-way ANOVA. This indicated that the majority of the visually responsive neurons in both the Sg (26/35; 73.7%) and the AEV (24/32) were sensitive to the location of the moving visual stimulus (Figs. 2 and 3). Similarly to earlier results on the AEV [2,5], the site of maximum responsivity within the visual receptive fields of the Sg neurons varied extensively in the neurons recorded. For the most of the units, the visual field did not appear to contain an exclusive site. Some of the units exhibited a preference for a particular stimulus site, while other units were most responsive to other locations. Thirteen Sg units had a preference in the contralateral upper, 14 in the contralateral lower, 4 in the ipsilateral lower and 4 in the ipsilateral upper quadrant of the investigated central visual field. Our results revealed that the maximum responsive sites of the Sg neurons, similarly to those of the AEV that were described earlier [5], were distributed throughout the whole of the investigated area. Maximum responsive sites were found in each quadrant of the visual field (Fig. 4). Since recent results have demonstrated that the maximum responsive sites of the AEV neurons are distributed in the whole visual field of the right eye [2], we cannot exclude the possibility that some Sg neurons exhibit maximum responsivity to stimulation sites outside the investigated region. No inhibitory responses were recorded at all.

We estimated the distances of the maximum responsive sites from the area centralis of the AEV and the Sg neurons. The mean distance of the maximum sensitive sites of the AEV neurons from the area centralis was 7.99° ($N = 32$; range: 0–20°; S.D.: ±4.29°). The mean distance of the maximum sensitive sites of the Sg neurons from the area centralis was 8.27° ($N = 35$; range: 2–18°; S.D.: ±3.67°). Since the distribution of the distances did not satisfy the criterion of normality, we used the Kruskal–Wallis test to compare them. The test demonstrated that there was no significant difference between the distances of the maximum responsive sites from the area centralis of the cortical and that of the thalamic neurons ($p = 0.55$). Similar results were obtained as

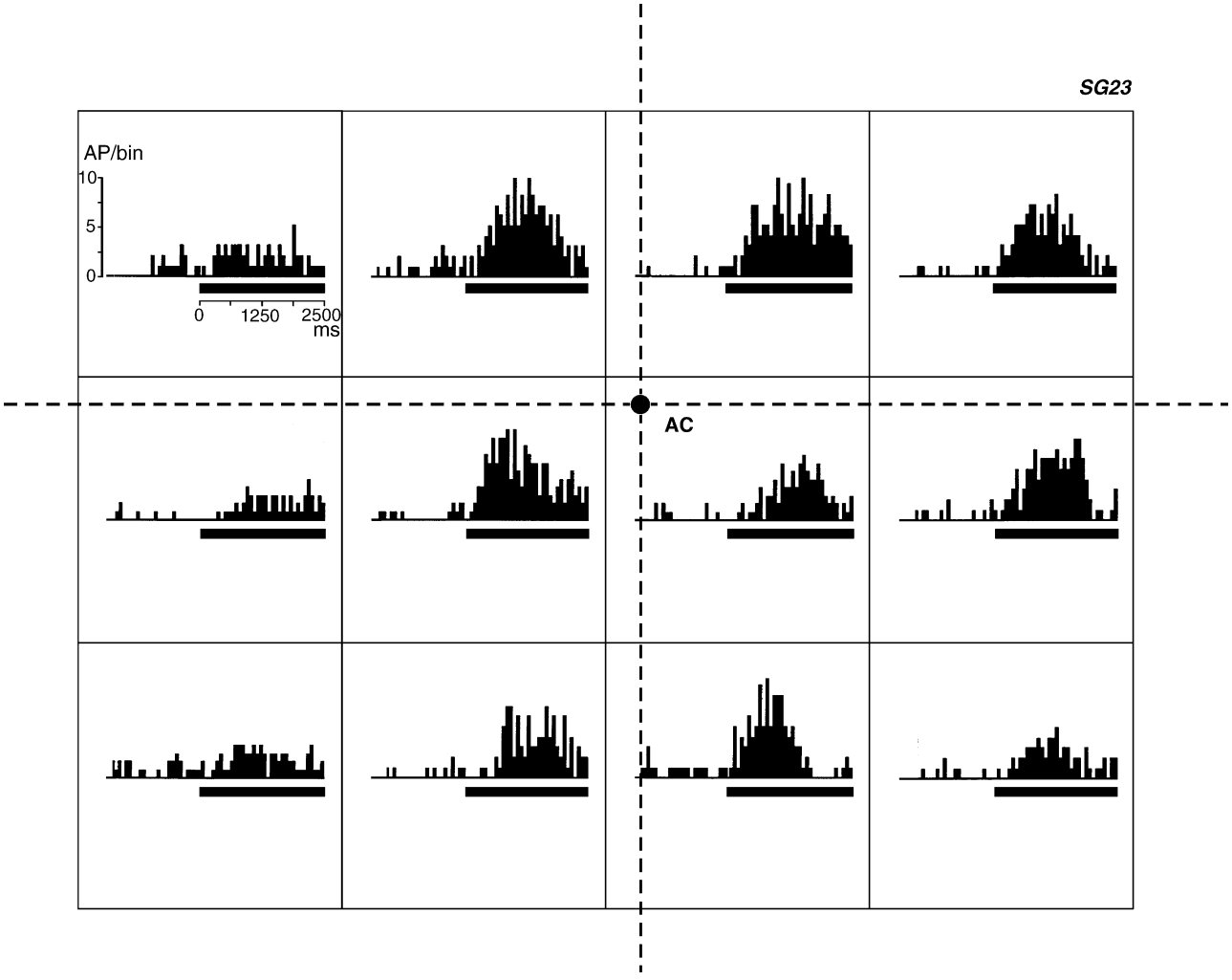


Fig. 3. Receptive field organization of another panoramic suprageniculate nucleus neuron, *SG23,* recorded in another cat. The arrangement here is the same as that in Fig. 2.

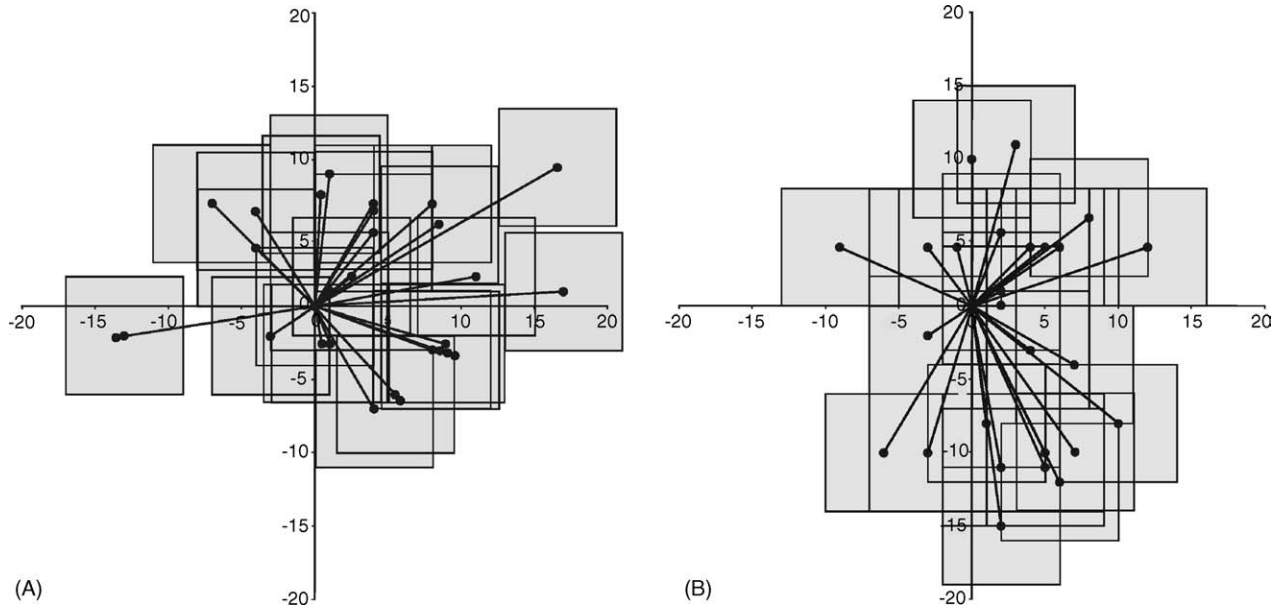


Fig. 4. Position of the site of maximum responsivity in the receptive fields of 32 AEV single-units (A) and 35 Sg single-units (B) determined by the highest firing rate in the respective window. Every single-unit is represented by an 8° × 8° grey window representing the motion of the visual noise and a vector line between the area centralis and the centre of the "window" from where the highest activity was elicited. Vertical and horizontal meridians are presented as thick lines, with scaling given in degrees.

concerns the direction of the line connecting the maximum responsive sites to the area centralis relative to the horizontal meridian. The distributions of the directions for the AEV neurons (mean = 136.5°; $N = 32$; range: 0–345°; S.D.: ±118.0°) and that for the Sg neurons (mean = 146.7°; $N = 35$; range: 0–350°; S.D.: ±114.9°) were very similar. Both displayed a normal distribution. The *t*-test showed no difference between the directions of the sites of maximum sensitivity from the area centralis of the AEV and the Sg neurons ($p = 0.87$). These results indicate that the maximum responsive sites of the AEV and the Sg neurons are distributed similarly in the investigated central part of the visual field.

3.2. Response latencies of the AEV and the Sg neurons

We calculated and compared the visual response latencies of the 35 investigated Sg and 32 AEV units to assess whether the cortico-thalamic or the thalamo-cortical information processing route has a temporal priority between the Sg and the AEV (Fig. 5). The shortest latency in both the Sg and the AEV was 35 ms. Generally, however, the latencies of the responses measured for the AEV units were longer than those for the Sg units. The mean latency of the response of the Sg neurons (calculated at their maximum responsive sites) was 59.4 ms ($N = 35$; range: 35–130 ms; S.D.: ± 26.28 ms). The mean latency of the AEV units was 81.7 ms ($N = 32$; range: 35–185 ms; S.D.: ±42.48 ms). The distribution of the latencies did not reveal normal distribution, presumably reflecting the fact that there is no homogeneous population of units producing this response. Comparison of the cortical and thalamic latencies by means of the Kruskal–Wallis test revealed that the visual response latencies of the investigated Sg neurons were significantly shorter than the visual response latencies of the AEV neurons ($p = 0.011$).

4. Discussion

Our results demonstrated that the visual receptive fields of the Sg neurons have an internal structure which resembles that described earlier in the AEV [2,5]. We found that the visual receptive fields of the neurons in both structures are similar; they consistently cover the whole visual field of the stimulated eye [4,22]. The size of the receptive fields found in the AEV by Olson and Graybiel [25] and later by Scannel et al. [29] was considerably smaller than that described by us. This discrepancy could originate from the different types of anaesthesia used or in the obvious difficulties in drawing these huge receptive fields. Both Olson and Graybiel [25] and Scannell et al. [29] concentrated on finding the locations of the most intense areas, while we attempted to find the border between the responsive and absolutely non-responsive areas and sought the locations of the regions of maximum sensitivity. The majority of the Sg and the AEV units in our experiments proved selective to the stimulus location; they exhibited significantly different responses to stimuli from different spatial locations. These indicate that as it has been described earlier for the AES units [2], the Sg units have similar abilities to serve as panoramic localizers [18,19]. The regions of maximal sensitivity within the investigated central part of the visual field are widely distributed for both the AEV [2] and the Sg neurons. This is in agreement with the report

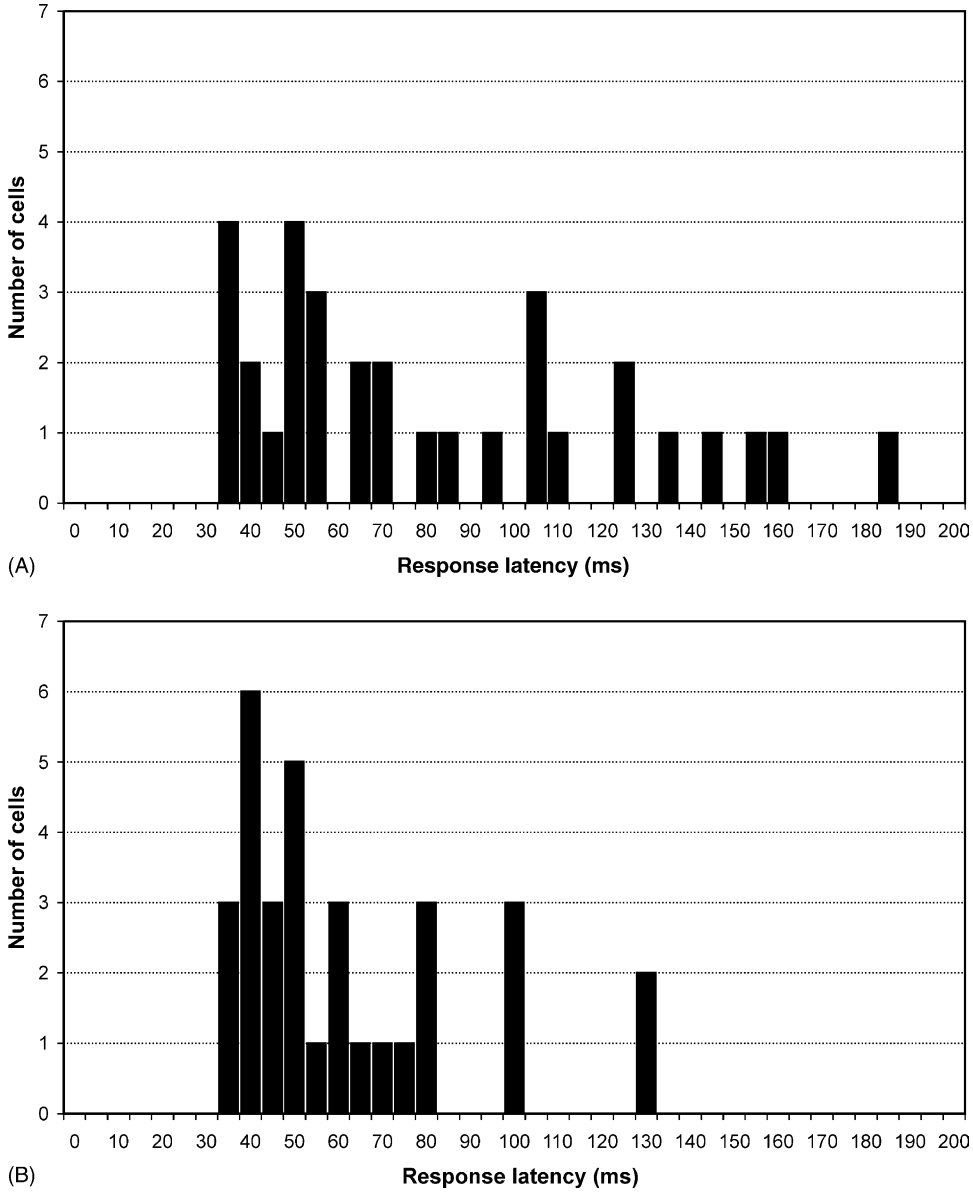


Fig. 5. Frequency distributions of AEV (A) and Sg (B) cells according to their response latency to a visual noise moving in their receptive fields. The abscissa shows the latency of the single-unit activity response in milliseconds. The ordinate indicates the numbers of units with the respective latency values.

from the AEV of Scannell et al. [29], who found the sites of the most intense responses within the same areas of the receptive fields. These observations point to the possibility of a distributed population code of visual information in the Sg, similarly as in the AEV [2], based on panoramic localizer cells [18–20]. The very high similarity of the receptive fields of the Sg and the AES cortex points to the existence of a very intense exchange of information between the two stages of visual processing.

The results of our latency studies provide interesting data on the sequence of volleys of excitation between the cortex and the thalamus. Latency studies are not widely used in the investigation of thalamo-cortical relations, most probably because of the technical limitations in calculating spike latency values amidst considerable spontaneous activity. We found that there was no difference between the shortest latency values of the thalamic and the cortical single-units. Both structures responded to visual motion with a minimum latency of 35 ms. The mean response latency of the Sg units, however, is significantly shorter than the mean latency of the AEV neurons. These results might suggest that both the thalamo-cortical and the cortico-thalamic route are active between the extrageniculate visual thalamus and the visual associative cortex. The generally shorter latencies in the thalamus might indicate that the visual information flows predominantly from the thalamic nucleus to the AEV. The fact that there is a temporal priority of the thalamus over the cortex, however, does not prove the superiority of the thalamo-cortical volleys over the cortico-thalamic ones. We cannot exclude the possibility either that the information

concerning the receptive field properties reaches the Sg (albeit with a delay) through a cortico-thalamic route.

The function of the thalamus in the mammalian brain is based on the existence of two types of relays [30,31]. Thalamic first-order relays receive their driving afferents from ascending pathways and transmit messages to the cortex that the cortex has not received before. Higher-order relays bring driver messages to the thalamus from the cortex for transmission from one cortical area to another. This ambiguity stresses the importance of the cortico-thalamic and the thalamo-cortical pathways. The distinction between the two types of relays, however, is not always equivocal. There are thalamic nuclei that receive driving from both the cortex and lower centres. The best-known such nuclei are the pulvinar and the lateralis posterior nuclei, which receive driving afferents from the visual cortex, and there is an additional tectal input to them [8,17]. Similarly, Sommer and Wurtz [32] described that the medial dorsal nucleus of the thalamus that innervates the frontal eye field receives drive from both the cortex and the intermediate and deep layers of the SC, but its main drive arrives from the tectal region. These thalamic nuclei process messages that have already reached the cortex and been processed in at least one cortical area, and at the same time they serve the role of first-order relays receiving signals from the ascending pathways. A similar ambiguity seems to characterize the role of the Sg of the thalamus and its connections with the cortex along the AES. The Sg receives heavy afferentation both from the intermediate and deep layers of the SC [14] and from the visual associative cortex along the AES [12]. Thus, it could serve either as a higher-order relay nucleus or as a simple first-order relay of tectal information. Since our data suggest that visual information flows bidirectionally between the Sg and the AES cortex, further investigations are necessary to elucidate whether the thalamo-cortical and cortico-thalamic axons are drivers or modulators, and to determine the direction of information flow between the Sg and the AES cortex. Antidromic microstimulation of the AES cortex or the Sg can help reveal direct connections between the responses of the neurons in each area, and neuronal lesions of the Sg or the AES cortex can demonstrate any interdependence of the investigated AES cortex or Sg neuronal activities.

To summarize, our data suggest that the Sg takes part in visual information processing through complex cortico-thalamo-cortical loops. It seems, therefore, that it represents a thalamic nucleus rather similar in function to the pulvinar or lateral posterior nuclei, structures that have been described as higher-order thalamic nuclei [8,17]. Because of the paucity of morphological data available, it is difficult to support this conclusion with histological evidence concerning the same arrangement of cortico-thalamic synapses in the Sg as that described for both the pulvinar and the lateral posterior nuclei [9,10]. The similarities of the physiological responses of all three structures, however, together with the fact that the SC provides their common ascending source of information, suggest a common function for them in the process of sensorimotor integration.

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References

[1] B.P. Abramson, L.M. Chalupa, Multiple pathways from the superior colliculus to the extrageniculate visual thalamus of the cat, J. Comp. Neurol. 271 (1988) 397–418.
[2] G. Benedek, G. Eordegh, Z. Chadaide, A. Nagy, Distributed population coding of multisensory spatial information in the associative cortex, Eur. J. Neurosci. 20 (2004) 525–529.
[3] G. Benedek, L. Mucke, M. Norita, B. Albowitz, O.D. Creutzfeldt, Anterior ectosylvian visual area (AEV) of the cat: physiological properties, Prog. Brain Res. 75 (1988) 245–255.
[4] G. Benedek, J. Perenyi, G. Kovacs, L. Fischer-Szatmari, Y.Y. Katoh, Visual, somatosensory, auditory and nociceptive modality properties in the feline suprageniculate nucleus, Neuroscience 78 (1997) 179–189.
[5] G. Benedek, L. Sztriha, G. Kovács, Coding of spatial co-ordinates on neurones of the feline visual association cortex, Neuroreport 11 (2000) 1–4.
[6] D.M. Berson, A.M. Graybiel, Organization of the striate-recipient zone of the cats lateralis posterior-pulvinar complex and its relations with the geniculostriate system, Neuroscience 9 (1983) 337–372.
[7] P.O. Bishop, W. Kozak, G.J. Vakkur, Some quantitative aspects of the cat's eye: axis and plane of reference, visual field coordinates and optics, J. Physiol. (Lond.) 163 (1962) 466–502.
[8] C. Casanova, L. Merabet, A. Desautels, K. Minville K., Higher-order motion processing in the pulvinar, Prog. Brain Res. 134 (2001) 71–82.
[9] R.W. Guillery, S.L. Feig, D.P. Van Lieshout, Connections of higher order visual relays in the thalamus: a study of corticothalamic pathways in cats, J. Comp. Neurol. 438 (2001) 66–85.
[10] R.W. Guillery, S.M. Sherman, Thalamic relay functions and their role in corticocortical communication: generalizations from the visual system, Neuron 33 (2002) 163–175.
[11] T.P. Hicks, G. Benedek, G.A. Thurlow, Organization and properties of neurons in a visual area within the insular cortex of the cat, J. Neurophysiol. 60 (1988) 397–421.
[12] T.P. Hicks, C.A. Stark, W.A. Fletcher, Origins of afferents to visual suprageniculate nucleus of the cat, J. Comp. Neurol. 246 (1986) 544–554.
[13] B. Hutchins, B.V. Updyke, Retinotopic organization within the lateral posterior complex of the cat, J. Comp. Neurol. 285 (1989) 350–398.
[14] Y.Y. Katoh, G. Benedek, Organization of the colliculo-suprageniculate pathway in the cat: a wheat germ agglutinin-horseradish peroxidase study, J. Comp. Neurol. 352 (1995) 381–397.
[15] R. Mason, Differential responsiveness of cells in the visual zones of the cat's LP-pulvinar complex to visual stimuli, Exp. Brain Res. 43 (1981) 25–33.
[16] R. Mason, G.A. Groos, Cortico-recipient and tecto-recipient visual zones in the rat's lateral posterior (pulvinar) nucleus: an anatomical study, Neurosci. Lett. 25 (1981) 107–112.

[17] L. Merabet, A. Desautels, K. Minville, C. Casanova, Motion integration in a thalamic visual nucleus, Nature 396 (1998) 265–268.
[18] J.C. Middlebrooks, A.E. Clock, L. Xu, D.M. Green, A panoramic code for sound location by cortical neurones, Science 264 (1994) 842–844.
[19] J.C. Middlebrooks, L. Xu, A.C. Eddins, D.M. Green, Codes for sound-source location in nontonotopic auditory cortex, J. Neurophysiol. 80 (1998) 863–882.
[20] J.C. Middlebrooks, L. Xu, S. Furukawa, E.A. Macpherson, Cortical neurones that localize sounds, Neuroscientist 8 (2002) 73–83.
[21] L. Mucke, M. Norita, G. Benedek, O.D. Creutzfeldt, Physiologic and anatomic investigation of a visual cortical area situated in the ventral bank of the anterior ectosylvian sulcus of the cat, Exp. Brain Res. 46 (1982) 1–11.
[22] A. Nagy, G. Eordegh, G. Benedek, Extents of visual, auditory and bimodal receptive fields of single neurons in the feline visual associative cortex, Acta Physiol. Hung. 90 (2003) 305–312.
[23] M. Norita, T.P. Hicks, G. Benedek, Y. Katoh, Organization of cortical and subcortical projections to the feline insular visual area, IVA, J. Hirnforsch. 32 (1991) 119–134.
[24] M. Norita, L. Mucke, G. Benedek, B. Albowitz, Y. Katoh, O.D. Creutzfeldt, Connections of the anterior ectosylvian visual area (AEV), Exp. Brain Res. 62 (1986) 225–240.
[25] C.R. Olson, A.M. Graybiel, Ectosylvian visual area of the cat: location, retinotopic organization, and connections, J. Comp. Neurol. 261 (1987) 277–294.
[26] J.D. Pettigrew, M.L. Cooper, G.G. Blasdel, Improved use of tapetal reflection for eye-position monitoring, Invest. Ophthalmol. Vis. Sci. 18 (1979) 490–495.
[27] F. Reinoso-Suarez, Topographischer Hirnatlas der Katze für experimental-physiologische Untersuchungen, Meck AG, Darmstadt, 1961.
[28] M.L. Rodrigo-Angulo, F. Reinoso-Suarez, Topographical organization of the brainstem afferents to the lateral posterior-pulvinar thalamic complex in the cat, Neuroscience 7 (1982) 1495–1508.
[29] J.W. Scannell, F. Sengpiel, M.J. Tovee, P.J. Benson, C. Blakemore, M.P. Young, Visual motion processing in the anterior ectosylvian sulcus of the cat, J. Neurophysiol. 76 (1996) 895–907.
[30] S.M. Sherman, R.W. Guillery, On the actions that one nerve cell can have on another: distinguishing “drivers” from “modulators”, Proc. Natl. Acad. Sci. U.S.A. 95 (1998) 7121–7126.
[31] S.M. Sherman, R.W. Guillery, The role of the thalamus in the flow of information to the cortex, Philos. Trans. R. Soc. Lond. B. Biol. Sci. 357 (2002) 1695–1708.
[32] M.A. Sommer, R.H. Wurtz, What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus, J. Neurophysiol. 91 (2004) 1381–1402.
[33] B.V. Updyke, Projections from visual areas of the middle suprasylvian sulcus onto the lateral posterior complex and adjacent thalamic nuclei in cat, J. Comp. Neurol. 201 (1981) 477–506.