

Acoustic Sensitivity and Bimodal Properties of Cells in the Anterior Suprasylvian Gyrus of the Cat

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Summary. The properties of acoustically responsive neurons were studied in the anterior part of the gyrus suprasylvius (A_{SG}) of the cat. The most important features of the responses given to pure tones of different frequencies were: short latency, sharp tuning curves with well definable best frequency (BF). In these respects the cells showed a close resemblance to those of primary acoustic area (AI), and at the same time they proved to be true bimodal cells (responding to somatosensory stimuli, too) like those of the associative areas.

Key words: Anterior suprasylvian gyrus – Polysensory cortex – Acoustic responsiveness

The acoustic sensitivity and polysensory properties of the units in the anterior suprasylvian gyrus (A_{SG}) of the cat were studied. The experiments were carried out on sixteen animals anaesthetized either with Nembutal (40 mg/kg i.p.) or with α -chloralose-urethan (chloralose 60 mg/kg, urethan 0.42 g/kg i.p.).

The middle part of the suprasylvian gyrus (MSG) of the cat is known as a polysensory area characterized by polysensory responses with long latencies (Albe-Fessard and Fessard 1963; Thompson et al. 1963).

Units in the MSG have a far less specificity than those of the primary receptive fields (Dow and Dubner 1969, 1971). The acoustically responsive units exhibit tuning curves with high thresholds and without definite best frequency (Irvine and Huebner 1979; Wester et al. 1974).

On the contrary, the neurons of the primary acoustic area (AI) which respond with short latency, have very sharp tuning curves with definitive best frequency (BF) (Phillips and Irvine 1981). According to the literature the A_{SG} can be considered as a polysensory area but it shows short latency evoked responses resembling those of the primary sensory cortices (Poliakova 1972; Toldi et al. 1981).

Experimen

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The aim of the present experiments was to obtain evidence about the frequency specificity of the acoustically sensitive neurons in the A_{SG} and to compare them with cells in the primary auditory area and association fields. For most of the acoustically sensitive units, the somato-sensory responses were also examined.

In the course of the experimental preparation we exposed the anterior part of the suprasylvian gyrus and opened the cisterna magna to reduce cortical pulsation. During the experiments the cats were positioned in a modified stereotaxic frame without using ear bars. Single unit responses were recorded extracellularly making use of Corning glass micropipettes filled with 3 M potassium-acetate. Electrode impedances ranged from 8 to 20 M Ω . The electric signals were amplified and filtered with a two channel recording system (DISA Electromyograph), stored on magnetic tape and photographed from the screen of a Tektronix storage oscilloscope. From several units post-stimulus time histograms were also constructed with the aid of a Motorola MC-6800 computer.

Click responsive units were further tested with spectrally pure tone pulses which were produced by gating the output of a sine wave generator (A.F. Power Generator typ.: TR.-P-I-F. III Medicor). The pulses were shaped by an electronic switch to give trapezoidal pulses of 100 ms duration and 10 ms rise and fall times. The tone pulses were presented binaurally by matched MOTOROLA-piezo-transducers 2 cm apart from the external meatus. The transducers were calibrated using a Bruel and Kjaer sound level meter. The sound pressure levels (SPL)

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Table 1. Summarized data of acoustically responsive cells in A_{SG} . Thirty-eight cells were analysed. Twenty-seven cells were recorded under barbiturate, 11 under chloralose anaesthesia. Minimum latencies have been obtained from 38 cells. The response latency to the acoustical signal was measured from the beginning of the rising phase

Cell Number	Anaesthe Barbiturate	tized with Chloralose	Averaged k Ac	atency (ms) Ss ²	Frequency narrow	band [≜] wide
38	27	11	15,07±2,8	11,8±1,7	25(78,1%)	7(21,9%)
	△84,2% of examined cells answered to forepaw shock					
			tuning curves of 6 cells have not been established			

were measured in experimental circumstances and expressed in decibels (dB). In order to detect the bimodal inputs of the A_{SG} cells electric stimuli were delivered to the contralateral forepaw with 4–12 V intensity and 0.3 ms duration.

The results of these experiments are summarized in Figs. 1 and 3 and in Table 1.

Thirty-eight tone sensitive units were examined. The threshold criterion was a consistent increase of discharge rate over spontaneous activity.

Sharpness of tuning was quantified by use of the Q_{10} measurement. Q_{10} values of 31 cells have been calculated. The data show that the Q_{10} is BF dependent, the most sharply tuned cells being those of high BFs (Fig. 2).

The majority of the neurons (78.1%) had a narrow tuning curve ($Q_{10} > 4$) with well defined best frequency between 2 and 40 kHz (Fig. 1).

21.9% of the recorded neurons had broad tuning curves $(Q_{10} < 4)$ with relatively high threshold intensities.

The relationship between threshold and BF is illustrated in Fig. 3. Although the thresholds are widely distributed it is clear that the most sensitive neurons are those with BFs in the range from 4 to 8 kHz.

"On" type responses were shown by 36 neurons. Short latency "onset" responses of two cells were followed by transient excitatory responses with 70–80 ms latency. "Sustained" responses to tone pulses were not encountered.

Forepaw shocks evoked responses in 84.2% of the examined neurons (Table 1).

The width of the tuning curves was not influenced by the choice of the anaesthetic (Fig. 2). In addition, no differences occurred in thresholds and latencies of acoustic responses obtained under chloralose and barbiturate anaesthesia, respectively. There was,



Fig. 1. Tuning curves for typical cells in A_{SG} . Ordinate: threshold intensity in dB. SPL: sound pressure level. Abscissa: frequency of tone pulses in kHz. The insert illustrates the site of the electrode penetrations



Fig. 2. Q_{10} measurements plotted as a function of BF. Triangles represent Q_{10} dB values obtained under chloralose-urethan anaesthesia. Q_{10} values of 31 neurons have been calculated



Fig. 3. Distribution of thresholds to BF stimuli as a function of BF

however, a marked difference in their effect on the spontaneous activity of the neurons. In chloraloseurethan anaesthesia very low, if any, background activity was observed. The detection of evoked firing was easier under such circumstances.

Though we did not examine all details of the auditory characteristics of these cells (spatial distribution of BF, dependence of BF on cortical depth) we can conclude that the acoustic sensitivity of the neurons in the A_{SG} shows remarkable similarities to those of area AI: short latency, sharp tuning curve with well defined BF (Fig. 1 and Table 1).

Acoustically responsive neurons were found in cortical depths between 500 and 1,500 µm. Although the neurons were not grouped according to their localisation in the cortical depth it turned out that the average minimum latency (15.07 ± 2.8) was 2.2 ms longer compared to the minimum latency of AI area neurons recorded at comparable depths by Phillips and Irvine (1981); however, they were shorter than the latencies of MSA neurons reported by Wester et al. (1974).

Two kinds of anaesthesia were used but we could not find any differences either in latencies and thresholds or in the sharpness of the tuning curves. Sharp tuning of cells has been found in area AI under chloralose or nembutal anaesthesia (Phillips and Irvine 1981; Reale and Imig 1980). By contrast, the tuning curves of AI area obtained in unanaesthetized animals were broader (Abeles and Goldstein 1970; Goldstein et al. 1970).

The tuning properties of the A_{SG} cells resembled not only those of AI area neurons, but also those of the anterior auditory fields (AAF) as described by Woolsey et al. (Woolsey 1961; Merzenich et al. 1975; Reale and Imig 1980).

Although nothing is known about the extension of the AAF to the anterior suprasylvian gyrus, the close spatial relationship between the A_{SG} and AAF is obvious. AAF extends upon the ventral bank of the suprasylvian sulcus and upon the banks of the anterior ectosylvian sulcus. The tuning properties and BF values obtained in AAF along the suprasylvian sulcus (Merzenich 1975; Reale and Imig 1980) are in good accordance with the properties of the neurons in the A_{SG} .

The recorded responses had short latency not only to acoustic stimuli but to contralateral forepaw shocks as well (Table 1). 84.2% of the examined cells responded with short latency to contralateral forepaw shock.

Physiologically it means that these cells have inputs from the somatosensory system, too. This is in good accordance with the data of Mickle and Ades (1952) and Dykes et al. (1977). Short latency acoustic and somatosensory responses in A_{SG} are well known (Lombroso and Merlis 1957; Poliakova 1972; Petrek 1977; Toldi et al. 1981). The question has been raised where projections to the A_{SG} come from. The short latencies and properties of responses suggest rather "direct" sensory projections from the thalamic relay nuclei but as far as we know this suggestion has not been confirmed by anatomical studies (Heath and Jones 1971; Graybiel 1974). Because of its polysensory character and the short latency evoked responses, the A_{SG} has been considered as a polysensory primary projection area (Mickle and Ades 1952).

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References

- Abeles M, Goldstein MH (1970) Functional architectures in cat primary auditory cortex: columnar organization and organization according to depth. J Neurophysiol 33: 172–187
- Albe-Fessard D, Fessard A (1963) Thalamic integrations and their consequences at the telencephalic level. Prog Brain Res 1: 115-148
- Dow BM, Dubner R (1969) Visual receptive fields and responses to movement in an association area of cat cerebral cortex. J Neurophysiol 32: 773–784
- Dow BM, Dubner R (1971) Single unit responses to moving visual stimuli in middle suprasylvian gyrus of the cat. J Neurophysiol 34: 47-55
- Dykes RW, Publicover HG, Tanji DG, Dudar JD (1977) Multiple loci of evoked potentials in somatosensory cortex. Brain Res 124: 162–167
- Goldstein MH, Abeles M, McIntosh RL (1970) Functional architecture in cat primary auditory cortex: Tonotopic organization. J Neurophysiol 33: 188–197
- Graybiel AM (1974) Studies on the anatomical organization of posterior association cortex. In: Schmitt FO, Worden FG (eds) The neurosciences third study program. The MIT Press, Cambridge, pp 205–214
- Heath CI, Jones EG (1971) The anatomical organization of the suprasylvian gyrus of the cat. Ergebn Anat Entwickl-Gesch 45: 1–64
- Irvine ORF, Huebner H (1979) Acoustic response characteristics of neurons in nonspecific areas of cat cerebral cortex. J Neurophysiol 42: 107–122
- Lombroso CT, Merlis JK (1957) Suprasylvian auditory responses in the cat. Electroencephalogr Clin Neurophysiol 9: 301–308
- Merzenich MM, Knight PL, Roth GL (1975) Representation of cochlea within primary auditory cortex in the cat. J Neurophysiol 38: 231–249
- Mickle WA, Ades HW (1952) A composite sensory projection area in the cerebral cortex of the cat. Am J Physiol 170: 682-689
- Petrek J (1977) Some basic characteristics of suprasylvian shortlatency acoustic responses and primary responses in cats with implanted electrodes. Sechenov Physiol USSR 63: 47–57

- Phillips DP, Irvine DRF (1981) Responses of single neurons of physiologically defined primary auditory cortex (AI) of the cat: Frequency tuning and responses to intensity. J Neurophysiol 45: 48-58
- Poliakova AG (1982) Origin of the early component of the evoked response in the association cortex of the cat. Electroencephalogr Clin Neurophysiol 32: 129–138
- Reale RA, Imig TJ (1980) Tonotopic organization in auditory cortex of the cat. J Comp Neurol 192: 265-291
- Thompson RF, Johnson RH, Hoopes JJ (1963) Organization of auditory, somatic sensory and visual projection to association fields of cerebral cortex in the cat. J Neurophysiol 26: 343–364

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systems in the suprasylvian gyrus of the cat. An electrophysiological and autoradiographic study. Neuroscience 6: 2539–2545

- Wester KG, Irvine DRF, Thompson RF (1974) Acoustic tuning of single cells in the middle suprasylvian cortex of cat. Brain Res 76: 493-502
- Woolsey CN (1961) Organization of cortical auditory system. In: Rosenblith WA (ed) Sensory communication. The MIT Press, Cambridge, pp 235–257

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