Processing of Frequency-Modulated Sounds in the Cat’s Posterior Auditory Field

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Tian, Biao and Josef P. Rauschecker. Processing of frequency-modulated sounds in the cat’s posterior auditory field. J. Neurophysiol. 79: 2629–2642, 1998. Single-neuron activity was recorded from the posterior auditory field (PAF) in the cortex of gas-anesthetized cats. Tone bursts and broadband complex sounds were used for auditory stimulation. Responses to frequency-modulated (FM) sounds, in particular, were studied systematically. Linear FM sweeps were centered around the best frequency (BF) of a neuron and had an excursion large enough to cover its whole frequency tuning range. Rate and direction of change of the FM sweeps were varied. In the majority of PAF neurons (75%) the FM response seemed not to be linear, i.e., their best instantaneous frequency (BIF) varied by more than one octave at different FM rates (FRM). When the difference between BIF and BF at each FRM was used as a measure of linearity, it was within one-third octave at five or fewer FRM in most PAF neurons (74%). The majority of PAF neurons (70%) preferred moderate FRM rates (<200 Hz/ms). Fifty-four percent of all neurons in this area showed band-pass behavior with a clear preference in the middle range of FRM rates in at least one direction. Overall, neurons with high-pass behavior in both directions made up only a minor portion (22%) of PAF neurons. When both directions of an FM sweep (low-to-high and high-to-low frequency) were tested, 50% of the neurons were clearly selective for one direction, i.e., the response to one FM direction was at least twice as large as that to the other direction. This selectivity was not necessarily present at the preferred FRM. In general, FRM direction selectivity was equally distributed over FRM rates tested. The selectivity of PAF neurons for the rate and direction of FM sounds makes these neurons suitable for the detection and analysis of communication sounds, which often contain FM components with a moderate sweep rate in a particular direction.

INTRODUCTION

Several auditory cortical areas have been identified on the basis of their tonotopic organization and their thalamocortical connections both in cats (Imig and Reale 1980; Imig et al. 1982; Knight 1977; Merzenich et al. 1975; Morel and Imig 1987; Reale and Imig 1980) and in monkeys (Merzenich and Brugge 1973; Morel et al. 1993; Rauschecker et al. 1995, 1997). However, little progress has been made to date in terms of characterizing any functional differences between these areas. Using tone bursts, other parameters, such as sharpness of frequency tuning, response latency, level sensitivity, minimum threshold, sensitivity to different rise/fall times, and binaural interactions, have been analyzed. However, most of these studies have concentrated on primary auditory cortex (A1) (e.g., Imig and Adrian 1977; Merzenich et al. 1975; Phillips and Irvine 1981; Phillips et al. 1994; Schreiner and Cynader 1984; Schreiner and Mendelson 1990; Sutter and Schreiner 1991, 1995). Only few attempts have been made to go beyond A1, such as the anterior auditory field (AAF) (Knight 1977; Phillips and Irvine 1982) or the posterior auditory field (PAF) (Phillips and Orman 1984; Phillips et al. 1995). AAF was found to be very similar to A1, although there was some indication that neurons in AAF may be more broadly tuned than those in A1, and neurons with multiple peaks were found there (Knight 1977; Tian and Rauschecker 1994). In ferrets, the excitatory bandwidth in AAF neurons is twice as large as in A1 (Kowalski et al. 1995). Most recently, a higher proportion of nonmonotonic cells was found in PAF than in A1 (Phillips et al. 1995). Nevertheless, none of these parameters have been sufficient to clearly differentiate the various areas functionally. So far, the only known physiological parameter reliably delineating different areas in cat auditory cortex from one another remains tonotopic organization.

Whereas little is known about functional specialization in different auditory cortical areas of the cat, a great deal of knowledge about functional maps has been accumulated in the bat (for reviews see Suga 1988, 1992). These studies have demonstrated that it is not sufficient to use tone bursts to explore nonprimary auditory cortex. Rather, it appears advantageous to use complex stimuli with behavioral relevance to the species under study. Unfortunately, most work in higher mammals that has employed complex stimuli, such as species-specific calls (Newman and Symmes 1974; Ploo 1981; Symmes 1981; Wang et al. 1995; Winter and Funkenstein 1973; Wollberg and Newman 1972), or potential prey vocalizations (Sovijärvi 1975), has again concentrated on primary auditory cortex (A1).

Stimuli of intermediate complexity, such as amplitude-modulated (AM) or frequency-modulated (FM) sounds have also been used quite extensively to study A1 in cats (Eggermont 1994; Erulkar et al. 1968; Heil et al. 1992a, b; Mendelson and Cynader 1985; Mendelson et al. 1993; Mendelson and Grasse 1992; Phillips et al. 1985; Schreiner and Urbas 1986; Whitfield and Evans 1965), ferrets (Kowalski et al. 1995; Shamma et al. 1993), and squirrel monkeys (Bieser and Müller-Preuss 1996). Again, however, few attempts have been made to explore nonprimary auditory areas: AM sounds have been tested in AAF, PAF, and ventroposterior auditory field (VPAF) of the cat (Schreiner and Urbas 1986, 1988); FM sounds have only been used in AAF of cats (Tian and Rauschecker 1994) and ferrets (Kowalski et al. 1995). The latter is particularly surprising because FM...
sounds are highly relevant for two reasons: 1) they occur ubiquitously in many different kinds of communication sounds (Brown et al. 1978; Capranica 1972; Leppelsack 1983), including human speech (Liberman et al. 1967), and 2) they can be seen as analogous to moving light stimuli (Mendelson and Cynader 1985; Tian and Rauschecker 1994), which are very effective in driving neurons of extrastriate visual cortex (Hubel and Wiesel 1959).

In our previous study of AAF, we found that neurons in this area prefer high FM rates (Tian and Rauschecker 1994). In addition, a prevalence of spatially tuned neurons has been reported for the anterior ectosylvian (AE) region, including AAF (Henning et al. 1995; Korte and Rauschecker 1993; Rauschecker and Korte 1993; Rauschecker et al. 1993). These findings, as well as other recent data (Middlebrooks et al. 1994), have led to the hypothesis that the AE region may be specialized for the analysis of sound location. By analogy with the visual system (Ungerleider and Mishkin 1982), one could argue further that separate streams may exist in the central auditory system for the processing of space and pattern information. Neurons involved in the processing of auditory “patterns” both in the spectral and temporal domain, especially those used in acoustic communication, might be expected to be selective for slower changes of frequency, because they occur in these sounds. A good candidate structure for such an analysis appeared to be area PAF and the surrounding areas in the posterior ectosylvian cortex. PAF has recently been found to contain a high proportion of amplitude-tuned neurons (Phillips et al. 1995), which may also be indicative of pattern-related processing. In the present study, we therefore extended the same approach that we used for AAF to the posterior auditory areas by testing neurons with FM sweeps of different rate and direction.

A brief account of this work has previously been published in abstract form (Tian and Rauschecker 1993).

METHODS

Animals and surgery

The experimental procedures were generally the same as in our previous study on the AAF (Tian and Rauschecker 1994). In brief, seven adult cats with no signs of middle ear infections were used. A total of 275 cells was collected from the posterior auditory areas.

Animals were treated with atropine sulfate (0.05 mg/kg sc) and were initially anesthetized with ketamine (10 mg/kg im). A venous catheter was placed, and the animal was intubated with a tracheal tube. The cat was then placed in a stereotaxic frame (LPC, Paris, France) and artificially respired with a ventilator (Harvard) at an intrapulmonary pressure of 500–1,000 Pa. Expiratory CO₂ content was monitored continuously (Medical Gas Analyzer LB-2, Beckman) and kept at ~3.8% by varying ventilation volume and frequency. Anesthesia was maintained with halothane (0.5–0.8%) in a mixture of 70% nitrous oxide and 30% oxygen. Occasionally, isoflurane (1–2%) was also used, but no difference was noticed. Electrocardiogram (EKG) was monitored to assure adequate anesthesia and stable physical condition of the animal. The animal’s core temperature was maintained at 38°C with a heating pad. Fluid (0.5% dextrose in 0.9% saline) was administered through the venous catheter by an infusion pump at a rate of 12–30 ml/h.

A head holder was cemented to the posterior part of the skull with stainless steel bone screws and dental cement to obviate the

![Fig. 1. Calibration curve of the sound delivery system. The sound pressure level (SPL) of standard stimuli was at ~70–80 dB. Dashed line represents the sound pressure level of the background noise. Between 0.4 and 24 kHz, the output varied by about ±6 dB. Below and about this range, there was a roll-off.](http://jn.physiology.org/)

**Acoustic stimulation**

**STIMULUS GENERATION.** Pure-tone (PT) stimuli were generated with a stimulus generator (Wavetek 148A). The tone bursts were gated by a control unit (HI-MED, HG 300G) to 50 ms duration with 5-ms rise/fall time. The amplitude was monitored on an oscilloscope.

Linear FM sweeps were generated with the program Signal (Engineering Design) on an IBM compatible AT-486 personal computer. The sampling rate was 100 kHz so that no significant quantization steps were present in the signal. The frequency range of the FM sweeps was chosen large enough to exceed the excitatory pure-tone tuning range of the neuron by one octave on either side, unless this exceeded the frequency range of the sound delivery system. While keeping the frequency range constant, the duration of the FM sweep was systematically varied from 50 to 1,600 ms in logarithmic steps, to test the responses to different FM rates (FMR). The stimuli had a rise/fall time of 5 ms to reduce the effect of transients. Stimulus amplitude, as determined by the input voltage for the loudspeaker, remained constant during each trial but was varied between trials. The interstimulus interval was ≥1 s. Each stimulus was repeated 20 times for each neuron.

All stimuli were amplified with a power amplifier (Hafler, SE 120) and played back with a high fidelity loudspeaker (Infinity 5 Kappa) in free field. The loudspeaker was positioned 1.14 m in front of the cat at the height of the ears.

Electrophysiological recording experiments were carried out in a dimly lit laboratory room (4.7 m × 7.6 m × 2.6 m), which was kept as quiet as possible. The sound pressure level (SPL in dB, re 20 μPa) of the noise in the recording room was measured with a Bruel & Kjaer (B&K) 1/4-in. condenser microphone (No. 4133, free-field) and a B&K Precision Sound Level Meter (No. 2235; A-weighting scale). The constant background noise had its peak level (35 dB) at 0.5 kHz, i.e., outside the effective range of most neurons (Fig. 1). The standard SPL for pure tones and FM sweeps was 60–85 dB, as measured at the cat’s head, which was well above the background noise level but still within the linear range of our sound delivery system.

**STIMULUS CALIBRATION AND SOUND FIELD.** The stimulus delivery system was calibrated with the same B&K equipment (Fig. 1). Between 0.4 and 24 kHz, the output varied by ±6 dB. Above and below this range a rolloff existed, partially because the signal was outside the measuring range of the microphone. The fidelity of the system in producing rapid FM sweeps was also tested, and
near free-field conditions were ensured. Details of calibration were reported in a previous paper (Tian and Rauschecker 1994).

Electrophysiological recording

For extracellular recording of neuronal spike activity, a lacquer-coated tungsten electrode (F. Haer, impedance ~1 MΩ) was advanced vertically into the brain by a hydraulic micropositioner with remote controlled stepping motor (model 650, David Kopf). The signals were band-pass filtered (0.3–20 kHz) and amplified in two stages (model 1800, A-M Systems preamplifier; AM 502, Tektronix). A “slicer” module was used to set the threshold for filtering out background noise. The output of the slicer was monitored with an audio monitor (AM 8, Grass Instruments), and a window discriminator was used to reliably separate spikes with different amplitudes and to convert the isolated spikes into transistor-transistor logic (TTL) signals. In addition, the signal at each step was monitored on an oscilloscope (5113 dual beam storage, Tektronix), so that we are quite confident that only isolated single-unit activity was recorded. The TTL signals were then registered on an IBM AT-386 PC with a data collection program (HIST, Spikes Systems), which produced peristimulus time histograms (PSTH) and raster displays with a binwidth of 1 ms for on- or off-line evaluation.

Standard sets of digitized complex sounds were used as search stimuli while the electrode was lowered. When a unit was isolated, the best frequency (BF) of the neuron and its lowest excitation threshold at the BF were determined with tone bursts. Threshold was defined as the amplitude of a BF tone at which an increase of activity above the spontaneous level was just noticeable. The excitatory frequency tuning range of the neuron was determined at a set sound pressure level 6–20 dB above threshold. PSTHs were recorded especially when multiple local maxima in response to different frequencies were apparent. The resulting “rate-frequency” or “iso-intensity” curves were analyzed as described below. FM sweeps were generated with the Signal program, as described above, and played back at the same or at a lower amplitude than the pure-tone stimuli. Responses of a neuron to different FMRs were analyzed as described below.

At the end of each penetration, electrolytic microlesions (7 μA, 7 s) were made to mark the electrode tracks and specific recording sites.

Data analysis

To quantify the response to stimulation with tone bursts and FM sweeps in the posterior areas, the same “peak firing rate” was determined from the PSTHs as described in a previous paper (Tian and Rauschecker 1994). In brief, a 10-ms window was slid at 1-ms steps across the PSTH, the number of spikes in this 10-ms interval was counted at each step until the maximum was found, and the average firing rate in the peak interval was calculated after subtracting spontaneous activity. The so obtained rate-frequency curves were smoothed with a three-point smoothing routine. Sometimes several local maxima were detected in these rate-frequency curves. A secondary or tertiary peak was defined if the firing rate between two local maxima dropped by ≥50% compared with either maximum.

FM responses were analyzed in an analogous fashion by creating rate-frequency curves from instantaneous frequency (IF). Because linear FM sweeps were used, the time axis in the PSTH can be easily converted into a frequency axis, as follows. The duration of the FM stimulus was divided into 50 equal intervals (the shortest FM stimulus was 50 ms), then peak firing rate in each interval was determined as described above. Thus, instead of looking for the peak response within the 10-ms window for the whole PSTH, the local peak response was determined in each interval. In the case of an FM duration of 1,600 ms, for example, the duration of each interval was 32 ms, but the width of the sliding window was kept at 10 ms. The obtained values were smoothed and plotted for both upward and downward FM sweeps against IF at the center of the peak interval. Best instantaneous frequency (BIF) was defined as the IF at the global maximum in the rate-frequency curve. The BIFs at different FMRs were averaged separately for each direction (upward and downward). These averaged values were compared with the BIFs determined from pure-tone stimulation. The appropriate transformation into the frequency domain required an estimation of response latency, which was obtained from the shortest onset latency in response to any of the stimuli tested. Because sometimes it was difficult to estimate the minimum latency due to relatively high spontaneous activity, the calculated rate-frequency curve was compared with the peak response for the whole FM duration. If the peak was not included in the rate-frequency curve, then the latency was reassessed until this was the case. Multiple maxima in the response to FM stimuli were defined by the 50% criterion (as for pure-tone responses) and by their occurrence at corresponding IFs for both upward and downward sweep at least for one FM.

To assess the neuron’s response to different FMR, the peak firing rates at each FMR were determined and plotted as FMR tuning curves. According to the neuron’s responses to the different FMRs, FMR tuning was categorized as high-pass (HP), low-pass (LP), band-pass (BP), all-pass (AP), or band-rejection (BR) behavior. A neuron was classified as HP or LP if the response dropped below 75% of the maximum response at lower or higher FMRs, respectively. A BP neuron had a clear optimum in the middle of the FMR tuning range, whereas the response of an AP neuron was never <75% of the maximum. A BR neuron had two optimal FMRs with <5% difference in firing rates separated by FMRs with firing rates <75% of the maximum (Tian and Rauschecker 1994). The preferred FMR (PFMR) was defined as the FMR at which the response was maximal in a given FM direction. For statistical evaluation, the PFMR in the preferred direction was used if the neuron was FM direction-selective (see below); otherwise, the PFMR at which the response was maximal was used.

To assess FM direction selectivity (DS), a quantitative index was calculated using the equation

$$DS = (RU - RD)/(RU + RD)$$

in which RU and RD are the responses to upward and downward FM sweeps at a particular FMR, respectively (Heil et al. 1992a,b; Mendelson and Cynader 1985; Phillips et al. 1985; Shamma et al. 1993; Tian and Rauschecker 1994).

Histology

At the end of an experiment, the animal was deeply anesthetized with pentobarbital sodium (Nembutal, 60 mg/kg iv) and perfused transcardially with 0.9% saline followed by 10% Formalin in 0.9% saline. The brain was removed from the skull, blocked stereotaxically, and stored in fixative at 4°C. The part of the brain containing the auditory cortex was cut in 50-μm-thick frontal sections on a freezing microtome (Jung) at −18°C. The sections were mounted on slides and stained with cresyl violet or thionin. Electrolytic microlesions were identified under a microscope (Wild) and the sections drawn with a camera lucida (Leitz). The lesion sites were compared with the stereotaxic measurements taken during the recording session to verify the location of the recording sites.

RESULTS

A total of 275 auditory cortical units from seven cats were studied with extracellular single-unit recording. Of these,
147 were located with certainty in PAF. Among the 147 PAF cells, 132 were analyzed with FM sweeps. For comparison, data recorded in AAF and A1 in a previous study (Tian and Rauschecker 1994) were also reanalyzed with the same methods.

Recording sites

Vertical or near-vertical electrode penetrations were made through the posterior ectosylvian gyrus (PEG). Figure 2 shows examples of recording tracks through one cat brain in frontal sections (9C978, left hemisphere). Penetrations were made at 1-mm distances along the anteroposterior axis (Fig. 2A). Sometimes, more than one penetration was made in the same frontal plane (Fig. 2B). Lateral distances between two parallel penetrations were 0.5–1 mm.

To ensure that the recording sites were within PAF, both topographic and physiological criteria were used. The posterior border lies on the caudal bank of the posterior ectosylvian sulcus (PES) and generally extends onto the rostral bank of PES and PEG (Reale and Imig 1980). Anteriorly, PAF shares a common low-frequency border with A1. Because a reversal of the frequency representations occurs along this border, neurons with a higher BF than those in the next posterior penetration were counted as A1 neurons. Ventral to PAF, the VPAF shares common iso-frequency lines in the middle and high-frequency range (>6 kHz) with PAF, whereas the lowest BFs in VPAF are situated near the ventral end of PES (Reale and Imig 1980). Dorsal and posterior to A1, an area was found with BFs that were not consistent with the tonotopic organization of A1. This field had been termed previously as dorsoposterior auditory field (DPAF) (Reale and Imig 1980).

Responses to pure tones and tonotopic organization in the PAF

PAF units generally responded to tone bursts. The BF and the frequency tuning range could be determined for the majority (112/135 = 83%) of the neurons with BFs represented in every part of the spectrum. However, 23 of 135 units (17%) tested with tone bursts could not be driven at any amplitude level tested (up to 95 dB SPL). Therefore their BF and tuning range remained undefined. Among these units, only three did not show responses to FM stimuli. Inhibitory responses were not explored in any of the neurons.

When the penetrations moved from anterior to posterior, the BF of the neurons first decreased, then increased (Fig. 2B). In the same frontal plane, the BF of the neurons also changed as the electrode was moved to more lateral positions. In most of these cases, when the tracks ran oblique to the cortical surface, BF also decreased with depth at more medial locations, but increased at more lateral locations. In summary, iso-frequency lines in PAF run in a general medio-caudal-to-lateral-rostro direction, which turns into a more dorsoventral direction (Fig. 2B) (Reale and Imig 1980).

For most neurons (120/135) in PAF, responses to tone bursts were assessed audiovisually, i.e., by listening to the response on the audiometer and assessing the mean number of spikes on a storage oscilloscope. BF at threshold and tuning range at one to several levels above threshold were determined in this way. In 15 cases, when there seemed to be an indication of a secondary peak or the audiovisual assessment of BF was unsatisfactory, PSTHs at one or several suprathreshold amplitudes were recorded (Fig. 3). The resulting rate-frequency or iso-intensity curves mostly had a well-defined maximum at the same BF as determined at threshold: in 9 of 15 neurons a peak was found within 1/6 of an octave from the BF at threshold. Among the examples displayed in Fig. 3, one unit had a BF at 1.8 kHz and a maximum in the rate-frequency curve at 2 (75 dB) or 1.7 kHz (55 dB; Fig. 3A). Two units had their BFs at 6.5 and 11 kHz, respectively, and rate-frequency maxima at precisely the same frequencies (Fig. 3, B and C). Hence the BFs derived from rate-frequency curves were similar to those derived audiovisually.

No units with secondary peaks were found in the 15 units recorded with PSTH.

Minimum latency

The minimum latency was estimated for each neuron in PAF. The distribution of minimum latency is shown in Fig. 4A. For comparison, data from AAF and A1 (unpublished observations) are also shown here (Fig. 4, B and C, respectively). The minimum latency of PAF neurons varied from 10 to 141 ms. From 10 to 50 ms, the distribution was almost even. The mean and SD for PAF neurons was 42 ± 29 ms. In contrast, neurons in AAF (19 ± 11 ms) and A1 (23 ± 12 ms) had much shorter latencies than those in PAF (Mann-Whitney U-test, P < 0.001). Only a few of AAF and A1 neurons exceeded 50 ms in latency.

Response to FM sounds

GENERAL PROPERTIES. When stimulated with linear FM sweeps, 125 of 132 PAF neurons (95%) responded in at least one FM direction (Fig. 5). Only in seven units (5%) a response was not detectable at any tested FMR in either direction. The PSTHs in response to FM were transformed into rate-frequency curves of IF by substituting frequency for time, and the locations of local and global maxima in these curves were determined. Both procedures are described in detail in METHODS.

Some PAF neurons responded linearly to FM stimuli, i.e., the BIF was about the same at different FMRs (Fig. 6A). However, for the majority of the neurons, the response to FM stimuli did not appear to be linear, i.e., BIF was not always the same at different FMRs. The example shown in Fig. 5 had a BF at 5 kHz when tested with PT, but the BIF varied from 21.7 to 1.3 kHz at FMRs from 600 to 18.75 Hz/ms for upward FM sweeps. Corresponding peaks were not found in the downward sweeps at the same FMRs. A second peak that was occasionally seen at higher FMRs disappeared at lower FMRs. When plotted against FMR, the BIF could be relatively constant for one FM direction, but could vary in the other direction (Fig. 6B). In other cases, BIF varied both in the upward and downward direction (Fig. 6, C and D), and the nature of the variation often seemed unrelated in the two directions (Fig. 6D). In the 125 PAF neurons tested with FM, BIF varied at different FMRs by >1 octave in 75% and by >2 octaves in 60% of the neurons.
FIG. 2. Location of posterior, ventroposterior, and dorsoposterior auditory fields (PAF, VPAF, and DPAF, respectively) and position of recording tracks (1–7) in left cerebral hemisphere. A: lateral view of a cat brain and location of auditory cortical areas (after Imig et al. 1982). The PAFs are darkly shaded, whereas all other auditory areas are lightly shaded. A1, primary auditory field; A2, “secondary” auditory field; AAF, anterior auditory field; VAF, ventral auditory field; aes, anterior ectosylvian sulcus; pes, posterior ectosylvian sulcus; sss, suprasylvian sulcus. B: reconstruction of electrode tracks through the posterior ectosylvian gyrus, shown in a series of anterior to posterior frontal sections separated by ~1 mm (1–7). Numbers next to each recording site indicate the best frequency (BF) in kHz found with pure-tone stimuli.

No systematic change of BIF was found in relation to FM duration. Neurons with multiple maxima in their IF tuning curves were not found in the posterior areas, using the criteria described in METHODS.

COMPARISON BETWEEN FM AND PURE-TONE RESPONSE. In 102 of 125 PAF neurons, it was possible to determine the BF with tone bursts, and thus a direct comparison between BF and BIF could be performed. In the examples shown in
FIG. 3. Frequency tuning in PAF neurons after pure-tone stimulation. Three examples of neurons are shown, whose unit numbers are given on top. A–C: threshold tuning curves: the sensitivity of the neuron for different frequencies is measured by determining the threshold amplitude at which a neuronal response can be elicited by a tone burst. D–F: "rate-frequency" or "iso-intensity" curves corresponding to A–C, respectively: the peak firing rate of the neuron at each frequency was measured from peristimulus time histograms (PSTHs). Dashed line depicts baseline activity of each neuron. Sound pressure level was 55 dB (○) or 75 dB (●). Good correspondence was found for all 3 neurons between BFs and tuning widths determined with either procedure.

Fig. 6, BIFs were close to BF at some FMRs (Fig. 6A, both in upward and downward direction; B, in upward direction; and C, in downward direction), but not at others. When the difference between BIF and BF at each FMR was used as a measure for response linearity, it was within $\frac{1}{3}$ octave only in 1 of 102 neurons (1%) at all 12 different FMRs for both upward and downward sweeps (Fig. 7A). In most neurons (75/102 = 74%) it was the case only at five or fewer FMRs. Furthermore, it was not within $\frac{1}{3}$ octave in 19 neurons (19%) at any of the FMRs.

In contrast to PAF, the difference between BIF and BF was within $\frac{1}{3}$ octave in 35 of 205 (17%) AAF neurons at all 12 FMRs. Only in a minority of neurons (77/205 = 38%), it was within $\frac{1}{3}$ octave at 5 or fewer FMRs, and in a small portion of AAF neurons (14/205 = 7%), it was not the case at any of the 12 FMRs (Fig. 7A). The difference between AAF and PAF was highly significant ($\chi^2$ test, df = 11, $P < 0.0001$).

When the upper border is compared, the difference is even more dramatic (Fig. 7B). Only in 9 PAF neurons (9%) the BIF did not differ by $>1$ octave of BF at any FMR, whereas this number for AAF neurons was 128 (62%; Fig. 7B). Although BIF did not differ from BF by $>2$ octaves at any FMR in one-third of PAF neurons (34/102), the number for AAF neurons was much higher (176/205 = 86%).

When the mean difference between BIF and BF was averaged over the six different FMRs for each direction, the result was more than one-third of an octave in 68% (69/102) and 76% (78/102) of PAF neurons for upward and downward sweeps, respectively (Fig. 7, C and E). The distribution for upward and downward sweeps was almost identical. By contrast, these proportions were only 40% (81/205) and 35% (71/205) in AAF neurons, respectively. The distribution for AAF neurons was asymmetric for upward and downward sweeps, i.e., the mode was lower than the BF for upward sweeps and higher than the BF for downward sweeps. More than 84% of PAF neurons had a SD larger than one-third octave, whereas this was the case only in <38% of AAF neurons (Fig. 7, D and F). This indicates that the BIF varied much more in PAF neurons. Again, these data suggest that the response to FM in PAF neurons is not linear.

TUNING TO FM RATE. Neurons in the posterior areas showed great sensitivity to changes in the rate (or speed) of FM. Four different examples of FM tuning curves are
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ple, show HP behavior for FM sweeps in one direction, but AP in the other. Figure 10 shows the percentages of neurons with different combinations in a three-dimensional display. In PAF, the HP-HP and BP-BP neurons formed two almost equally large proportions (28/125 = 22% and 27/125 = 22%, respectively), followed by the LP-LP neurons (13/125 = 10%) (Fig. 10A). AP or BR behavior only appeared in combination with others, such as HP, LP, or BP. More than one-half of all neurons (68/125 = 54%) showed BP, and 10 units (8%) showed BR behavior in at least one FM direction. For comparison, data of AAF neurons are also shown here (Fig. 10B). BR behavior was not encountered in AAF neurons.

Figure 11 shows the distributions of PFMRs for both directions. Seventy percent of all PAF neurons prefer lower FMRs (\(\leq 200 \text{ Hz/ms} \)). This corresponds largely to the high percentage of BP and LP neurons. Stippled bars in Fig. 11 show the distribution of PFMRs in BP neurons, which covers the middle range of FMRs tested. The median of the PFMRs was 75 and 150 Hz/ms for upward and downward sweeps, respectively. In general, the PFMR for upward sweeps was lower than the PFMR for downward sweeps (paired sign test, \(P < 0.01 \)). However, there was no difference for PFMR in neurons showing BP behavior (Mann-Whitney U-test, \(P > 0.05 \)) (Fig. 11, stippled bars). Preferred FMR and BF of each neuron were weakly positively correlated (Fig. 12A: for upward sweeps, \(r = 0.27, n = 115, t\text{-test, } P = 0.0086; \) Fig. 12B: for BP neurons only, \(r = 0.20, n = 69, t\text{-test, } P = 0.096 \)) . However, even among units with lower BF (\(\leq 2 \text{ kHz} \)), 10 units (8.0%) preferred higher FMRs (\(\geq 100 \text{ Hz/ms} \)). The BR neurons were not included in the evaluation, because they had more than one PFMR.

SELECTIVITY FOR FM DIRECTION. Another distinct property of PAF neurons in response to FM stimuli is their selectivity to the direction of an FM sweep. The four examples in Fig.
FIG. 7. Distribution of deviations of BIF from BF in PAF neurons (■). For comparison, data from AAF are also shown here (□). A: percentage of neurons whose BIF deviates from BF at different FMR in ω/3 octave. B: percentage of neurons whose BIF differs from BF at different FMR in ω > 1 octave. C and D: distribution of averaged difference between BIF and BF and its SD for upward sweeps. E and F: distribution for downward sweeps. Vertical dashed lines indicate the border at ω/3 octave.

8, besides demonstrating FM rate selectivity, also show FM direction selectivity.

To characterize this response property quantitatively, a DS index was calculated at each FMR, as described in METHODS. A neuron was considered direction selective when the response in one FM direction for one or more FMR was at least twice as large as that in the other direction (Mendelson and Cynader 1985). This corresponds to an absolute value of the DS index of 0.33. Of 125 units, 71 units fulfilled the criterion and were classified as direction selective (Fig. 13). Among them, in eight units (6.4% of all 125 cells) direction preference depended on FMR, i.e., these cells preferred one direction at one FMR but the opposite direction at another. Of the remaining 63 neurons, 42 (33% of all 125 cells in the sample) preferred upward and 21 (17%) downward sweeps. Thus a majority of the cells with a clearly defined direction preference (42/63 = 67%) preferred upward motion. The remaining 54 units (43%) did not meet the criterion and responded about equally to upward and downward direction at all FMRs. No significant differences were found between animals.

The selectivity for FM direction did not only occur at the PFMR. The neuron in Fig. 8, B and F, for example, preferred relatively high FMRs (160 Hz/ms for upward and 320 Hz/ms for downward sweep), but showed direction selectivity all at rates of 160 Hz/ms and below. FM direction selectivity in PAF was equally distributed over the whole range of FMRs tested (Fig. 14).

DISCUSSION

Tonotopic organization and extent of PAF

When stimulated with tone bursts, the BF of neurons in the posterior ectosylvian region first decreased, then increased along a rostrocaudal axis. In the same penetration, BF decreased in the dorsal part of the PEG. In the posterior bank of PES, BF first increased, then decreased, when the
FIG. 8. Neuronal activity as a function of FMR and FM direction selectivity in PAF neurons. Firing rate (top panels) and direction selectivity (DS) index (bottom panels) at different FMRs are plotted for 4 neurons (A and E to D and H). In the top panel, open circles symbolize the responses to upward FM sweeps, filled circles to downward sweeps. In the bottom panel, dashed lines at a DS index of ±0.33 indicate the criterion for DS applied to an FM sweep (cf. Mendelson and Cynader 1985). Values beyond these limits indicate that the response to one FM direction is <50% of that in the other direction. Thus the neuron is direction selective at this particular FMR. Positive and negative values refer to upward and downward preference, respectively. A and E: neuron with high preferred FMR [PFMR; high-pass (HP) neuron] but no DS. B and F: neuron with a preference for moderate FMR [band-pass (BP) neuron] and direction preference for upward sweep at lower FMRs. C and G: neuron with low PFMRs [low-pass (LP) neuron] and direction preference for downward FM sweep at moderate FMRs. D and H: neuron with a preference for lower FMRs (LP neuron) and direction preference for upward FM sweep at lower FMRs.

FIG. 9. Examples of FMR tuning curves in 5 different categories. A: HP neurons. B: BP neurons. C: LP neurons. D: all-pass (AP) neurons. E: band-rejection (BR) neurons. Each diagram depicts several examples for each of the 4 categories. Responses are normalized to the maximum response (100%) for each neuron. Dashed line marks 75% of the maximal response, which was used as the criterion to categorize the neurons. Note that the FMR tuning curves cover the whole range of FMRs tested.

Unlike in AAF neurons, multiple peaks were not found in the frequency tuning curves of neurons in the posterior areas, as assessed on the basis of suprathreshold responses.

Responses to FM sweeps

In a previous report, we had studied responses of AAF neurons to FM stimuli (Tian and Rauschecker 1994). In the present study, we have applied the same approach to neurons in PAF. We will try to compare the response in PAF with those in AAF.

RATE SELECTIVITY. When stimulated with linear FM sweeps, the vast majority of PAF neurons showed some selectivity for the rate (or speed) of the frequency change. Unlike AAF neurons that comprised a high proportion of HP neurons (Tian and Rauschecker 1994), neurons with
FIG. 10. Distribution of cells in PAF in FMR tuning categories. Cells in AAF are displayed for comparison. All the possible combinations of responses in 2 FM directions are shown here. Up, upward sweep; Down, downward sweeps; HP, high-pass behavior; BP, band-pass behavior; LP, low-pass behavior; AP, all-pass behavior; BR, band-rejection behavior. N refers to number of animals, n to number of neurons.

HP-HP tuning only made up 22% of the PAF neurons that responded to FM stimuli. By contrast, the proportions of BP-BP (22%) and LP-LP neurons (10%) were higher in PAF than in AAF. This is also reflected in the PFMR. In general, the PFMR of PAF neurons was significantly lower than that of AAF neurons (Mann-Whitney U-test, \( P < 0.02 \)). This indicates that PAF neurons have a preference for slower temporal changes.

Another novel finding was the group of neurons with BR properties, which was not found in AAF neurons. Band rejection is complementary to band-pass. However, the function of BR neurons may be quite similar to BP neurons in that they filter out FM sounds with particular rates. Thus, although the proportion of BR neurons in PAF is small, their existence adds to the above evidence that PAF may be more suitable for processing of auditory patterns. Different call types with specific FM rates have been characterized in cats (Brown et al. 1978; Härtel 1975). The FM rate ranges from below 1 Hz/ms in a standard 'meow' up to around 100 Hz/ms in communication calls of young kittens or mothers (Table 1). As for potential prey, FM components with a large range of FM rates are also found in mouse squeaks (20–100 Hz/ms) and bird songs (see Table 2 in Tian and Rauschecker 1994).

FM DIRECTION SELECTIVITY. PAF neurons also showed selectivity for FM direction, but the proportion of such neurons was actually somewhat smaller than in AAF (Fig. 13). In PAF, one-half of the neurons showed selectivity for one particular direction, whereas in AAF this proportion was about two-thirds. Like in AAF, we found that a majority of FM direction-selective neurons preferred upward sweeps. One reason could be the presence of low-frequency masking noise in the recording room. However, when neurons with higher BF (\( \approx 3 \) kHz) were examined, which were unlikely affected by the low-frequency background noise, the same biased ratio toward upward sweeps persisted. It would be interesting to see whether there is a genuine difference between PAF and A1, since two-thirds of A1 neurons prefer downward sweeps (Heil et al. 1992a; Mendelson and Cy- nader 1985). In contrast to neurons in AAF, which show FM direction selectivity only for low FMRs and lose it at high FMRs (Tian and Rauschecker 1994), the selectivity of PAF neurons for FM direction was almost equally distributed over the whole FMR range tested (Fig. 14). This indicates

FIG. 11. Distribution of PFMRs for all cells (open bars) and BP cells only (stippled bars) in PAF. Top panel: data for upward sweeps. Bottom panel: downward sweeps. Preference for FMR was distributed over the whole range tested. For BP cells, the PFMRs were in the midrange. Binwidth of the graphs is \( \frac{1}{2} \) octave, i.e., \( 2^{0.5}(k = 1, 2, \ldots, 18) \) in Hz/ms.
FIG. 12. Preferred FMRs as a function of BF for each PAF unit in one FM direction. Preferred FMR and BF of the neurons showed a weak positive correlation (top graph: total, \( r = 0.27, n = 115 \); bottom graph: BP only \( r = 0.20, n = 69 \)). Inset histogram at the bottom of each graph displays the distribution of BFs in the sample. Binwidth of the graphs is \( 1/2 \) octave, i.e., \( 2^n/k \) (\( k = 1, 2, 3, \ldots, 10 \)) in kHz.

FIG. 13. Distribution of PAF neurons with different types of FM direction selectivity (top panel). Units from all animals are combined; error bar indicates SD in each category. For comparison, AAF data are replotted from Tian and Rauschecker (1994) (bottom panel). Up, Down: neurons that responded better to an upward or downward FM sweep, respectively, at all FMRs. Up/down: neurons that responded better to one FM direction at some FMRs, but better to the other direction at other FMRs. None: no difference between both FM directions at any FMR.

Multiple maxima, also have relatively large bandwidths, but they still have their BIF close to the BF. The bimodal distribution of mean BIF-BF in PAF neurons indicates that BIF cannot be related to FM direction, whereas BIF clearly depends on FM direction in AAF neurons (Fig. 7). This indicates that, in contrast to AAF and A1, a linear model (Heil multiple maxima, also have relatively large bandwidths, but they still have their BIF close to the BF. The bimodal distribution of mean BIF-BF in PAF neurons indicates that BIF cannot be related to FM direction, whereas BIF clearly depends on FM direction in AAF neurons (Fig. 7). This indicates that, in contrast to AAF and A1, a linear model (Heil
Conversely, if the inherent latency was assessed too long, cat, AAF with its preference for easily localizable transient ing FM duration for upward FM sweeps, but increase for could give rise to dual pathways specialized for the pro-

would deviate from the correct values. Because we kept the monkey ( Rauschecker et al. 1997 ). Paradoxically, monkey and the FMR. If, however, the inherent latency is assessed mation ( Tian and Rauschecker 1994 ) , in much the same 

( Tian and Rauschecker 1994 ) . In this case, the time at which In a previous paper, we have proposed that A1 and AAF 

to the BF of the neuron. Both is indeed the case for A1 stage because they can process FM direction over the whole 

of an FM sweep enters the excitatory response area of the over the whole FMR range tested can be seen in the same 

attributed to the inaccurate estimation of minimum latency. ear behavior than neurons in AAF or A1. The fact that FM 

of spike latency in PAF neurons is large ( Phillips et al. tested with FM sweeps, PAF neurons clearly display more 

Rouiller et al. 1991 ) and the longer minimum latency in the area is still at a fairly low level in the hierarchy. On the 

temporal interactions between combinations of frequencies, Laminar analysis of corticocortical connections in the cat 

nonlinear effects, such as facilitation or suppression from 

versus the BF of the neuron. Both minimal (FMR min ) and maximal (FMR max ) 

varies in different call types. For each FM portion in the spectrogram, its starting and ending frequencies and the time interval were measured, and the FMR was calculated. Both minimal (FMR min ) and maximal (FMR max ) 

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grams published in a study on cat vocalizations (Hartel 1975). Call type classification in the original paper is used. A call typically has an “arch” pattern consisting of a rising FM, a steady frequency midportion, and a falling FM component. However, calls with just single or multiple components were also found. The duration and frequency range of each component varies in different call types. For each FM portion in the spectrogram, its starting and ending frequencies and the time interval were measured, and the FMR was calculated. Both minimal (FMR min ) and maximal (FMR max ) 

While these data suggest that the neuron in Fig. 6c maintained its characteristic behavior across a range of stimulus conditions, our data. 

The frequency-modulation rates (FMRs) are estimated from the spectrograms published in a study on cat vocalizations (Hartel 1975). Call type classification in the original paper is used. A call typically has an “arch” pattern consisting of a rising FM, a steady frequency midportion, and a falling FM component. However, calls with just single or multiple components were also found. The duration and frequency range of each component varies in different call types. For each FM portion in the spectrogram, its starting and ending frequencies and the time interval were measured, and the FMR was calculated. Both minimal (FMR min ) and maximal (FMR max ) 

If the neuron is linear, it will start responding once the IF 

Temporal interactions between combinations of frequencies, may be responsible for this effect (Suga 1988, 1992). This kind of processing requires convergent inputs from lower stages. Thus PAF can be considered as a higher-order stage in FM processing, which is consistent with neuroanatomic findings on the connectional hierarchy within auditory cortex (Rouiller et al. 1991) and the longer minimum latency in our data. 

Because the linear relationship between BF and BIF no longer existed in PAF, BIF was not as closely tied to BF as in AAF neurons. Because the estimate of BIF depends on an estimate of minimum latency, and the intertrial variance of spike latency in PAF neurons is large (Phillips et al. 1985), the variation of BIFs at different FMRs could be attributed to the inaccurate estimation of minimum latency. If the neuron is linear, it will start responding once the IF of an FM sweep enters the excitatory response area of the neuron; the response will reach its peak when the IF is close 

then the BIF would increase for upward sweeps, but decrease for downward sweeps, when the FM duration increased. However, this kind of behavior was only observed in four neurons, but also with some reservations. For example, the neuron in Fig. 6c showed this behavior, with an exception at an FMR of 100 Hz/ms for downward sweep. At this point, the BIF was 0.2 kHz. Because the frequency range of the FM sweeps was 0.1–10.1 kHz, this means that the peak response occurred almost at the end of the downward FM sweep. On the other hand, the BIFs at higher FMRs for upward sweeps were also very low, i.e., the peak responses occurred at the very beginning of the upward sweeps. Therefore the latency had to be compromised to cover both the peaks for upward and downward sweeps. In other neurons, the BIFs were rather scattered over a large range (Fig. 6D).

Multiple maxima were not found in the rate-IF curves of PAF neurons, whereas one-third of AAF neurons showed such multiple maxima (Tian and Rauschecker 1994). Multiple maxima were also found in A1 neurons (Heil et al. 1992a). This suggests that some of the A1 and AAF neurons might act as logical ‘‘or’’-gates, because input in each of the several channels alone can elicit a response from these neurons. By contrast, neurons in PAF act as ‘‘and’’-gates, because input in more than one channel is needed to excite the neuron (Suga 1988, 1992). In other words, PAF neurons have higher thresholds, or more input is needed to elicit a response from them.

Parallel processing in the auditory cortex?

Laminar analysis of corticocortical connections in the cat has demonstrated that AAF and A1 are on the same processing level, whereas the posterior auditory areas are hierarchically ‘‘higher’’ than A1 (Rouiller et al. 1991). The tonotopic organization of PAF, as revealed with pure-tone stimuli (Imig and Reale 1980; Reale and Imig 1980), suggests that the area is still at a fairly low level in the hierarchy. On the other hand, use of AM sounds has shown that the posterior areas have a lower temporal resolution than AAF (Schreiner and Urbas 1988), which could be due to temporal integration. Our present observations are consistent with the view of PAF being at a more advanced stage of processing. When tested with FM sweeps, PAF neurons clearly display more complex response properties and a greater degree of nonlinear behavior than neurons in AAF or A1. The fact that FM direction selectivity in PAF neurons is equally distributed over the whole FMR range tested can be seen in the same light, namely, that PAF neurons are at a higher processing stage because they can process FM direction over the whole range.

In a previous paper, we have proposed that A1 and AAF function as parallel processors of ascending auditory information (Tian and Rauschecker 1994), in much the same way as areas A1 and R are wired in parallel in the rhesus monkey (Rauschecker et al. 1997). Paradoxically, monkey area R shares its low-frequency border with A1, whereas AAF borders A1 at its high-frequency end. Nevertheless, we have speculated in either case that the parallel scheme could give rise to dual pathways specialized for the processing of auditory space and pattern information. In the cat, AAF with its preference for easily localizable transient

### Table 1. Range of FMRs in cat communication calls

<table>
<thead>
<tr>
<th>Call Type</th>
<th>FM Pattern</th>
<th>FMR&lt;sub&gt;min&lt;/sub&gt;</th>
<th>FMR&lt;sub&gt;max&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>Arch</td>
<td>9.3</td>
<td>14.3</td>
</tr>
<tr>
<td>1d</td>
<td>Arch</td>
<td>1.2</td>
<td>8.9</td>
</tr>
<tr>
<td>1n</td>
<td>Arch</td>
<td>3.6</td>
<td>40</td>
</tr>
<tr>
<td>1i</td>
<td>Raising</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>1k</td>
<td>Falling-rise-falling</td>
<td>8</td>
<td>30</td>
</tr>
<tr>
<td>1l</td>
<td>Falling</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>1m</td>
<td>Falling-falling</td>
<td>8</td>
<td>30</td>
</tr>
<tr>
<td>5a, c, d, e</td>
<td>Undulating</td>
<td>20</td>
<td>80</td>
</tr>
</tbody>
</table>

The frequency-modulation rates (FMRs) are estimated from the spectrograms published in a study on cat vocalizations (Hartel 1975). Call type classification in the original paper is used. A call typically has an “arch” pattern consisting of a rising FM, a steady frequency midportion, and a falling FM component. However, calls with just single or multiple components were also found. The duration and frequency range of each component varies in different call types. For each FM portion in the spectrogram, its starting and ending frequencies and the time interval were measured, and the FMR was calculated. Both minimal (FMR<sub>min</sub>) and maximal (FMR<sub>max</sub>) rates are listed. Most calls have multiple harmonics. FMRs are estimated at the one with maximal intensity, which is normally the first harmonic. FMRs at higher harmonics are hence the multiples of the rates listed. Besides monotonically rising or falling FM components, undulating FM sounds were also found both in mother and young kittens called. With a modulation depth at 0.1–0.4 kHz and a modulation frequency at 50 Hz, the FMR can be calculated as a linear approximation at 20–80 Hz/ms.

et al. 1992a,b; Kowalski et al. 1995, 1996a,b; Shamma and Versnel 1995; Shamma et al. 1995; Suga 1968; Tian and Rauschecker 1994) can no longer predict the response in PAF neurons to FM (or other complex sounds). Instead, nonlinear effects, such as facilitation or suppression from
FM PROCESSING IN CAT PAF


