

## REVIEW

G. Ehret

**The auditory cortex**

Accepted: 25 July 1997

**Abstract** The division of the auditory cortex into various fields, functional aspects of these fields, and neuronal coding in the primary auditory cortical field (AI) are reviewed with stress on features that may be common to mammals. On the basis of 14 topographies and clustered distributions of neuronal response characteristics in the primary auditory cortical field, a hypothesis is developed of how a certain complex acoustic pattern may be encoded in an equivalent spatial activity pattern in AI, generated by time-coordinated firing of groups of neurons. The auditory cortex, demonstrated specifically for AI, appears to perform sound analysis by synthesis, i.e. by combining spatially distributed coincident or time-coordinated neuronal responses. The dynamics of sounds and the plasticity of cortical responses are considered as a topic for research.

**Key words** Auditory cortex · Brain mapping · Coincidence coding · Sound-pattern representation · Topographical coding

**Abbreviations** AI primary auditory cortical field · AII second auditory cortical field · AAF anterior auditory cortical field · AC auditory cortex · CF characteristic frequency · EE excitation by contralateral and ipsilateral ear · EI excitation by contralateral and inhibition by ipsilateral ear

**Introduction**

From a functional point of view, neocortical areas responding predominantly to sound may be called auditory cortex (AC). In ferrets, however, by early deprivation

of auditory input, the cortical area normally occupied by the primary AC has been shown to be taken over by the visual system and processes visual information (Pallas 1990; Pallas et al. 1990; Roe et al. 1990); conversely, the visual cortex is invaded by the auditory system in blind mole rats (Bronchti et al. 1989; Heil et al. 1991). These examples demonstrate that what we call AC is not defined on the cortical level by some independent intrinsic factors, but rather by the pattern of input connections and type of sensory inputs provided by the thalamus. In addition, the functional specificity of the various auditory cortical fields in mammals seems to be determined by their input from thalamic nuclei of the medial geniculate complex and other thalamic and extrathalamic nuclei (Winer 1992; de Ribaupierre 1997; Rouiller 1997). Hence, the auditory cortex itself and its parcellation into several fields, and functional implications from this parcellation such as responsiveness and robustness of neuronal responses to tones, clicks, and complex sounds, and orderly topographical representations of neuronal response characteristics (e.g. Woolsey 1960; Goldstein and Knight 1980; Brugge and Reale 1985; Clarey et al. 1992; Winer 1992; de Ribaupierre 1997; Rouiller 1997) can be understood only if one considers subcortical, especially thalamic, processing and the many loops of the neuronal networks between thalamus and cortex.

Today, we are not far beyond the stage of collecting anatomic evidence and investigating physiological circumstances, and are only beginning to perform physiological experiments that may elucidate the quality and quantity of contributions of more than ten thalamic and extrathalamic input sources to the neuronal activity patterns in the auditory cortical fields.

**Auditory cortical fields**

Common to all mammals studied so far is the presence of a so-called primary auditory field (AI) which is characterized by a strong reciprocal connection with the

G. Ehret  
Abteilung Vergleichende Neurobiologie,  
Universität Ulm, D-89069 Ulm, Germany,  
Fax: +49-731 5022629  
e-mail: guenter.ehret@biologie.uni-ulm.de

ventral nuclei of the medial geniculate body, robust and well-tuned responses to tone bursts, and a tonotopy that largely reflects the gradient of cochlear frequency representation (e.g. Aitkin 1990; Merzenich and Schreiner 1992; Clarey et al. 1992). In marsupials, only AI seems to exist as a well-defined auditory cortical area (Gates and Aitkin 1982; Aitkin et al. 1986). Eutherian mammals have further auditory fields besides AI, defined by their connectivity and neuronal response patterns. The number of fields increases from three or four in insectivores, to four to seven in rodents, and six to more than eight in carnivores and primates (Merzenich and Schreiner 1992; compare Fig. 5 in Stiebler et al. 1997, this volume) and, therefore, seems to depend on the relative size of the cortical surface reached at a certain evolutionary level. However, attempts to infer from the number of auditory cortical fields of a species its phylogeny or its ability to perceive, differentiate, and recognize sounds will probably fail because the acoustical ecology and the importance of sound communication may have been strong determinants for the evolution of the AC and its parcellation into fields of functional significance. Good examples are nine specialized auditory cortical fields of the echolocating mustache bat, *Pteronotus parnellii* (e.g., Suga 1988, 1994; Horikawa and Suga 1991; compare Liu and Suga 1997, this volume) compared to the three or four fields that may be suggested from mappings in the big brown bat, *Eptesicus* (Jen et al. 1989; Dear et al. 1993; compare Shen et al. 1997, this volume). The use of the number and functional specificity of auditory cortical fields as a measure of the auditory competence and specialization of a species is extremely impeded by the fact that complete maps of auditory cortices seem to exist only for nine mammalian species: the macaque monkey (Merzenich and Brugge 1973; Morel et al. 1993), owl monkey (Imig et al. 1977; Morel and Kaas 1992), cat (Merzenich et al. 1975; Reale and Imig 1980), guinea pig (Redies et al. 1989), Mongolian gerbil (Thomas et al. 1993), rat (Horikawa et al. 1988), house mouse (Stiebler 1987; Stiebler et al. 1997; this volume), mustache bat (e.g., Suga and Jen 1976; Horikawa and Suga 1991), and the FM-bat, *Carollia perspicillata* (Eiermann and Esser 1996). Determinations of auditory cortical fields in other mammals suffer from several shortcomings, such as:

1. Incomplete delimitations of the outer borders of the AC and/or of the inner borders between the cortical fields in individual animals by using a rather crude sampling technique, an inadequate set of sound stimuli, and/or averaging procedures across several individuals (the latter should not be applied because details of functional representation in the auditory cortex are individualized).
2. Use of inadequate laboratory animal strains with various, often unknown degrees of hearing loss.
3. Use of inadequate anesthesia or inadequate handling of non-anesthetized animals so that the detection of auditory cortical fields beyond AI may have been

impossible because neurons in such fields are sensitive to anesthetics and very labile in their responsiveness to sound. For example, guinea pigs were found to have two (Hellweg et al. 1977) or up to six auditory fields (Redies et al. 1989), rats were described as having two (Sally and Kelly 1988) or four fields (Horikawa et al. 1988), and house mice, depending on the strain, may have three not well-defined (Willott et al. 1993) or five clearly distinct fields (Stiebler et al. 1997, this volume).

It is important that the extension of the AC and its parcellation into functional fields is studied by high-resolution mapping techniques in many more mammals including humans (compare Langner et al. 1997, this volume) and also to re-map mammals of which data about the functional parcellation of the auditory cortex are incomplete such as the dog (Tunturi 1962), the ferret (Kelly et al. 1986; Shamma et al. 1993), the rabbit (McMullen and Glaser 1982), and horseshoe bats (Ostwald 1984; Radtke-Schuller and Schuller 1995).

In all the mammals mentioned before except marsupials, horseshoe and mustache bats, at least one other auditory field with a regular tonotopy is found besides AI. This field always lies next to AI [it is called anterior auditory field (AAF) if it lies rostral to AI], has a clear tonotopy, and often shows a frequency gradient running in opposite direction compared to AI (Winer 1992; compare Fig. 5 in Stiebler et al. 1997, this volume). These two central fields of the AC are surrounded by several fields, sometimes collectively called "secondary auditory cortex". One of these fields lying ventral of AI is named "second auditory cortical field" (AII) in a number of mammals (see Fig. 5 in Stiebler et al. 1997, this volume). At the outer borders of the fields of the secondary auditory cortex, multi-sensory association areas are located in which neurons receive visual or somatosensory in addition to auditory input (Berman 1961; Irvine and Huebner 1979; Toldi et al. 1986; Clarey and Irvine 1990; Hofstetter and Ehret 1992; Barth et al. 1993; Di et al. 1994).

---

## Functional characterization of auditory cortical fields

### General considerations

It is both astonishing and confusing that more than 50 years of physiological research on the AC was not enough for a comprehensive characterization of the primary auditory field, to say nothing of all the other fields in any mammal. Beyond studies on frequency representation, there are only rather incidental contributions on sound processing in non-primary auditory cortical fields such as the anterior auditory field (Irvine and Huebner 1979; Phillips and Irvine 1982; Orman and Phillips 1984; Phillips and Orman 1984; Schreiner and Cynader 1984; Schreiner and Urbas 1986, 1988; Tian and Rauschecker 1994; Phillips et al. 1995; Rauschecker et al. 1995). A further three studies including non-pri-

mary auditory fields can be found in this volume (Horikawa et al. 1997; Hosokawa et al. 1997; Schulze et al. 1997). There is only one mammalian species, the mustache bat, in which neuronal response features and the possible functional significance of many auditory cortical fields have been elucidated, but only in the behavioral context of echolocation (reviews in Suga 1988, 1994; Horikawa and Suga 1991). These studies on the mustache bat AC will not be reviewed here because extensive reviews are available (references above). They are exemplary for several reasons:

1. A large part, if not the whole AC, is included in these studies.
2. The studies have a common theoretical framework – the physics, physiology and ecology of echolocation – which defines the demands on the processing capability of the auditory cortex.
3. Since the sound to be processed and the behavioral context belonging to it are well defined, the AC is asked the “right”, i.e., biologically significant questions.
4. The knowledge about the important questions is used as a guide in systematic tests of neuronal response behavior and coding of information-bearing sound parameters and parameter combinations.
5. Taken together, the studies lead to a number of predictions for the functioning of sound processing in auditory cortical fields of other mammals such as: (a) sound is processed in parallel in the auditory cortical fields; (b) neurons in every auditory cortical field have a preference for responding to a field-specific Gestalt aspect of the sound, e.g., they respond preferentially to a combination of certain sound parameters that together contain biologically significant information as the basis for auditory perception and response control of the species (Riquimaroux et al. 1991); (c) most auditory cortical fields contain well-ordered topographies in the responsiveness of their neurons representing certain dimensions of the sound Gestalt.

The mustache bat example suggests that sound processing in auditory cortical fields cannot be understood as a sound analysis in the sense that single sound parameters are resolved and re-encoded in certain neuronal response parameters but rather as a synthesis which combines subcortical codes of sound parameters to a new code representing parameter combinations that bear biologically significant information on an evolutionary and/or a learned basis. As a consequence of this reasoning, a statement of King (1995) can be put as a question: are we “asking the auditory cortex the right questions” when we look for neuronal response patterns in auditory cortical fields? One main problem of auditory cortical research is that for almost all mammals, and especially those like the cat that are research animals by tradition, we do not know the answer to this question (i.e. we do not know the right questions). Even for the mustache bat we do not know if social communication sounds are considered instead of echolocation calls.

Preliminary studies have begun on this species to elucidate how the auditory cortical fields, characterized as being specialized for echolocation, process communication calls (Ohlemiller et al. 1994, 1996). Since the bat has only one auditory cortex to process all kinds of sounds, it is evident that some or all auditory cortical fields must work in several behavioral contexts, not only in the highly specific case of echolocation. It will be exciting to see the AC of this bat functioning in its second mode, the processing of communication sound, which is the mode common to all mammals.

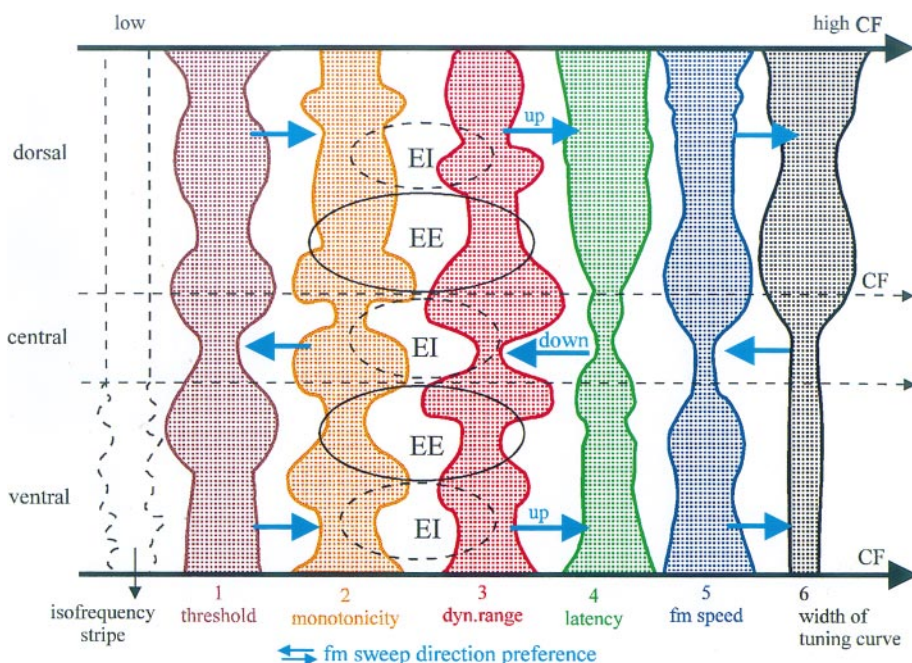
### The primary auditory cortical field

The topography of neuronal response characteristics on the cortical area occupied by the AI has been subject of many electrophysiological, high-resolution mapping studies, predominantly in the cat (e.g. Schreiner 1995). The main results for the cat are based on single-unit and multi-unit recordings and are summarized schematically in Fig. 1. In the AI of the cat, the characteristic frequency (CF) of the neurons (the frequency with the lowest response threshold at the tip of the excitatory tuning curve) increases from caudal to rostral, reflecting the cochlear tonotopy. Thus, at a given caudorostral location, there is an approximately dorsoventrally oriented stripe of neurons, all with similar CFs. This isofrequency stripe offers room for more or less systematic variations of neuronal response characteristics. Figure 1 indicates that the isofrequency stripes have basically three zones in which, on average, the neurons have certain common response characteristics or common gradients along which certain response properties vary rather systematically.

Somewhere in the center of the isofrequency stripes, i.e. in the central part of the AI, there are patches of neurons (Fig. 1) with:

1. Lowest response thresholds to tone bursts (highest sensitivity) (Schreiner et al. 1992; Heil et al. 1992, 1994; Phillips et al. 1994; Sutter and Schreiner 1995).
2. Very non-monotonic (peaked) rate-intensity functions (spike rate as a function of sound pressure level) (Schreiner and Mendelson 1990; Schreiner et al. 1992; Heil et al. 1994; Clarey et al. 1994; Phillips et al. 1994; Sutter and Schreiner 1995).
3. Smallest dynamic ranges of the rate-intensity functions (Schreiner et al. 1992; Heil et al. 1992, 1994).
4. Shortest tone-response latencies (Mendelson et al. 1997, this volume).
5. Preferences to downward frequency sweeps and slow speeds of frequency modulation (Heil et al. 1992; Mendelson et al. 1993).
6. Sharpest frequency tuning expressed by the 20-dB bandwidth (Heil et al. 1992) or 40-dB bandwidth (Schreiner and Mendelson 1990; Schreiner and Sutter 1992) of their excitatory tuning curve.

According to the references mentioned under items 1–6 above, the following shifts of response characteris-



**Fig. 1** Pictograph of seven topographies and clustered distributions of neuronal response characteristics in the cat primary auditory cortical field (AI) as listed in the text. The diagram shows the AI in a surface view. All through the AI, the tonotopic gradient, the best-studied and clearest topography, which is defined by the local characteristic frequency (CF) of the neurons, extends from low CFs (*left*) to high CFs (*right*). Along this frequency axis, narrow stripes can be found in which the CFs of most of the neurons are very similar (isofrequency stripes). In the ventral part of the AI, such isofrequency stripes are less well defined (the CFs of the neurons are more variable locally) compared to the central and dorsal part. This is indicated by the irregular boundaries of the ventral part of the isofrequency stripe shown. It is important to note that all the topographies shown (1-6) and the excitation by contralateral and ipsilateral ear (EE) and excitation by contralateral and inhibition by ipsilateral ear (EI) clusters are *superimposed* on every isofrequency stripe that can be considered. For better visibility, these topographies have been placed side by side. All topographies are drawn as areas of changing width along the dorsoventral extent of the AI. The necks of these areas are always in the central part of the AI. This means that, at the neck, the tone-response threshold (1) is lowest, the monotonicity (2) of the rate-intensity function is lowest (the function is very peaked), the dynamic range (3) is lowest, the tone-response latency (4) is shortest, the preferred speed of frequency modulation (5) in a sound is lowest, and the width of the excitatory tuning curve (6) is smallest. The average values of the neuronal response characteristics in the six topographies increase from the neck both towards the dorsal and ventral border of the AI as indicated by the widths of the respective areas. The irregularities of the shapes of these areas symbolize a large variability in the dorsoventral gradients seen between individual cortices and within the AI of one individual if conditions at different isofrequency stripes are compared. Superimposed on these dorsoventral gradients are clusters of neurons alternating in their binaural response between EE and EI. The direction of frequency sweeps preferred by most neurons in the dorsal, central and ventral AI is also shown. For further explanations, see text

tics occur: immediately dorsal and ventral of the central patches (Fig. 1), neurons tend to have high tone-response thresholds, monotonic rate-intensity functions, large dynamic ranges, and preferences for fast speeds of frequency modulation. At farther dorsal and ventral

locations, tone-response thresholds and dynamic ranges are variable but tend to be higher than in the center of the AI. Also, rate-intensity functions are variable there but usually less sharply peaked compared to the center of the AI. Tone-response latencies gradually increase from the center of the AI towards more dorsal and ventral locations (Fig. 1). The sharpness of tuning decreases only towards more dorsal locations. Further, neurons in the dorsal and ventral part of the AI prefer upward frequency sweeps (Fig. 1).

In addition to these average response gradients running from the center of the AI both through the dorsal and ventral, or only through the dorsal, part of the AI, there are further topographies in the AI and differences between the three parts of the AI:

1. It has long been known that the response patterns to binaural stimuli are not arbitrarily distributed along the isofrequency stripes (Fig. 1). Clusters of neurons being excited by both ears and summing up their responses (EE) alternate with clusters of neurons that are most often inhibited by the ipsilateral ear and excited by the contralateral ear (EI) (Imig and Adrián 1977; Middlebrooks et al. 1980; Reale and Kettner 1986). Neurons showing binaural summation occupy larger cortical areas than those showing binaural inhibition (Fig. 1).

2. The binaural interaction patterns mentioned above may be related to the function of sound localization. Neurons preferring tones from the central, ipsilateral or contralateral sound field have been shown to be clustered at certain positions on isofrequency stripes (Rajan et al. 1990; Clarey et al. 1994). The sizes and sequences of clusters are rather irregular and are not shown in Fig. 1.

3. In the ventral part, the scatter of CFs of neighboring neurons (Fig. 1) seems to be much larger than in the central and dorsal part (Schreiner and Sutter 1992).

4. In the dorsal part of the AI, 35% of all neurons have excitatory tuning curves with more than one peak or even two or three separate frequency-response areas. This is a significantly higher occurrence rate for multi-peaked tuning curves compared with the central and ventral AI (Sutter and Schreiner 1991).

5. Neurons in the dorsal part of the AI seem to be inappropriate to encode perceptually relevant characteristics of frequency resolution and spectral filtering (critical band measurements), while such properties are found in the central and ventral AI (Ehret and Schreiner 1997, this volume).

The above-listed 11 topographies and clustered distributions of neuronal response characteristics are all based on studies of the cat. These data are supported by contributions from other animals. The spatial distribution of tone-response latency along an isofrequency stripe in the guinea pig anterior field of the AC is very similar to that of the cat with shortest latencies represented somewhat ventral of the center and a gradient of increasing latencies towards more dorsal and ventral locations (Tanaka et al. 1994). Neurons with EE or EI binaural interaction patterns are clustered along an isofrequency stripe in the ferret (Kelly and Judge 1994), rat (Kelly and Sally 1988), and mustache bat (Liu and Suga 1997, this volume).

Finally, the following topographies have been reported for the AI of other mammals but not yet for the cat:

1. Neurons in a special area of the tonotopy of the mustache bat AI, called the Doppler-shifted, constant-frequency processing area, respond best to the main frequency component of the bat's echolocation call. This area can be regarded as an enlarged isofrequency stripe in which sound intensity is represented in a circular topography (ampliopathy) reflecting the peak positions of the neurons' rate-intensity functions (Suga 1977; Suga and Manabe 1982; see also Liu and Suga 1997, this volume).

2. Neurons responding preferentially to either short- or long-duration tones are organized in horizontal stripes in the AC of the little brown bat (Galazyuk and Feng 1997).

3. In Mongolian gerbils, responses to the periodicity of amplitude-modulated tones are represented in an orderly way in the AI according to preferred (best) modulation frequencies (Schulze and Langner 1997, this volume). Best-modulation frequencies of neurons decrease with a shift of neuronal location from dorsal to ventral on an isofrequency stripe (compare Fig. 5 in Stiebler et al. 1997, this volume). Thus, tonotopy and periodotopy, the latter being the neuronal correlate for pitch perception (e.g. Langner 1992), are organized in orthogonal orientation to each other in the primary AC. Representation of pitch as a distinct quality of perception has been shown to exist in the human (primary) AC (Winkler et al. 1995), and it is organized in a map of periodotopy orthogonal to the tonotopic gradient (Langner et al. 1997, this volume).

These 14 more or less regular topographies or clustered distributions of neuronal response characteristics on isofrequency stripes in the AI, together with the tonotopy itself, certainly express much of the sound-processing potential of the AI as a function of the loci in this auditory cortical field. Again, the evident and eminent question arises: what can we infer from this knowledge for our understanding of how the AC works, i.e., how sound is encoded at the auditory cortical level? In the following section, some evidence for a tentative answer is presented.

---

## Approaching the neuronal code for sound in the auditory cortex

### Static aspects

The previously mentioned orderly spatial representations of neuronal response characteristics in the AI of the cat (cf. Fig. 1) and other mammals must not be seen as spatially separated and independent of each other. Because all topographies occur in every isofrequency stripe they are all superimposed. Since the topographies are highly variable in shape, both along the frequency map of the AI and among individual animals of a species, the superposition of the topographies demonstrated in the AI creates non-arbitrary, locally specific combination patterns of neuronal response characteristics in every animal's AI. The result is that in every AI all possible combinations of neuronal response characteristics that can occur following the general rules of representations shown in Fig. 1 will be realized at a certain location or at several locations along the isofrequency stripes. The exact locations within the geometry of the AI, where neuronal response characteristics of a given combination can be found, will, however, be individualized.

One also has to consider that the various types of spatial representations of neuronal response characteristics may not be independent from each other with regard to the mechanisms of development of response types in the ascending auditory system and the AC itself. For example, the type of rate-intensity function (degree of non-monotonicity), which reflects the response strength of a neuron as a function of sound pressure level, seems to be coupled with the type of binaural interaction patterns (EE, EI) and response preference for azimuth angles (Imig et al. 1990; Semple and Kitzes 1993a, b; Clarey et al. 1994). Another case is the correlation between sharpness of frequency tuning, tone-response threshold, and the degree of non-monotonicity of rate-intensity functions (Schreiner and Mendelson 1990; Schreiner et al. 1992; Sutter and Schreiner 1995). Also, broadly tuned neurons or those with multi-peaked tuning curves in the dorsal part of the AI have longer tone-response latencies than sharply tuned neurons in the central and ventral AI (Mendelson et al. 1997, this

volume). These examples clearly indicate that the local combinations of neuronal response characteristics in the AI come about in a non-arbitrary way. They are, however, not exactly predetermined for a given spot in the AI.

If we wish to estimate the probability of response generation at a certain spot in the AI, we have to know the local status of combinations of topographies of neuronal response characteristics and the relationship among them in the AI under investigation. Provided that this knowledge were available, we would be able to predict whether a certain sound would lead to a response at the given spot. Going from one spot to the next across the whole AI, we would end up with a complete picture of the spatial distribution of spots at which responses to a certain sound are expected to occur. The instantaneous acoustical Gestalt of a given sound would be represented quite accurately by a sound-specific spatial distribution of "hot" spots in the AI. Since we do not know the topographies of the 14 or more neuronal response characteristics for any single spot on an individual AI, not to mention for several or many spots, this inductive way to the understanding of how sound is encoded in the AI by building up a complete picture from millions of pieces of experimental evidence will fail for practical reasons. The idea, however, that a given sound pattern may be encoded by an equivalent spatial pattern of hot spots in the AI (and in any other auditory cortical field) is very promising and in various ways the subject of many recent research efforts.

The first prerequisite for the search for correlations between sound patterns and spatial response representation is the complete knowledge of what aspects of sound are responsible for the generation of action potentials in auditory cortical neurons. Only very recently it was found (Heil and Irvine 1996; Heil 1997a) that the time of occurrence of the first action potential of a response in the AI and, therefore, the first-spike latency is a function of the rate of change of the peak pressure of the sound stimulus. This relationship seems to hold for most neurons in the AI and has important consequences for the coordination of action-potential timing in populations of neurons of the AI (Heil 1997b). This mechanism ensures the exact synchronization of first spikes of neurons across the AI to the onset of sounds or to rapid transients, which is necessary condition for a spatial activity code of sound-pattern representation in the AI. The timing of spikes of auditory cortical neurons in response to transients has been shown to be sufficiently precise for a temporal resolution better than 1 ms (Phillips and Hall 1990) so that a sufficient synchronization effect in populations of neurons can occur if a common trigger, such as the rate of change of peak pressure in the sound stimulus, is available.

Synchronous, or better coincident and time-coordinated firing of neurons in the AI to certain sound stimuli (click trains, noise and tone bursts, amplitude-modulated noise and tone bursts), has been demonstrated for neurons in close vicinity and up to 2 mm away from

each other (Eggermont 1994; deCharms and Merzenich 1996). The strong coordination of spike timing is present not only for transient sounds but also for the durations of longer sounds (deCharms and Merzenich 1996). These multi-electrode approaches and evaluations of spatiotemporal relationships of firing in the AC strongly support the hypothesis that a given sound pattern is encoded by an equivalent spatial pattern of hot spots in the AI, whereby the pattern of hot spots is generated and defined by the coincidentally or time-coordinated firing of the groups of neurons at the spots. In short, the AI appears to perform sound analysis by synthesis, i.e. by combining spatially distributed coincident or time-coordinated neuronal responses. Potential information carried by the acoustical patterns of sounds is transformed into effective information laid down in spatial activity patterns of the AC to be used by the brain if the effective information fits to the brain's context.

The fact that neurons in the AI can synchronize their action potentials to stimulus repetition rates or rates of amplitude modulation only for rates often far below 50 Hz (Schreiner and Urbas 1988; Eggermont 1994; Gaese and Ostwald 1995; Kowalski et al. 1996; Schulze and Langner 1997, this volume) is no longer an argument against a code based on spatially distributed time-coordinated firing of groups of neurons for sound patterns with rapid transients and modulations such as most animal calls and human speech. As Schulze and Langner (1997, this volume) propose (supported by Langner et al. 1997, this volume), synchronization to low repetition rates in sounds is the direct time-domain code for rhythm, while rapid amplitude modulations and high repetition rates in sounds – properties that are responsible for the generation of the pitch percept – are encoded by orderly spatial representations in the AI (see previous section).

The hypothesis that a given sound pattern is encoded by the equivalent spatial pattern of hot spots in the AI is based mainly on data of topographies of neuronal response characteristics of the cat and recent demonstrations of time-coordinated firing of groups of neurons at different spots in the AI. Further comparative studies in other mammals and auditory cortical fields beyond the AI are necessary to provide a broader basis and to test whether this hypothesis is applicable in general.

#### Dynamic aspects

So far, we have looked mainly on static aspects of the neuronal code for sound in the AC. We have argued that a sound pattern is encoded by equivalent spatial patterns of hot spots in the AI. This hypothesis implicates that a sound pattern can be defined as a combination of properties being static or existing as a whole (the acoustical Gestalt) over a certain period of time. We know that most sounds are dynamic for various sound properties. The question is: how can the AC encode dynamics of the sound, or how can the static model of

sound-pattern representation in the AI be extended to cover acoustical signals that vary over longer periods of time? At first view, it seems clear what we can expect to happen in the AC if it has to encode a time-varying acoustical pattern: the spatial distribution of hot spots in the AI will shift according to the shifts in the topographies of the neuronal response characteristics induced by the related shifts of the sound properties. Certain dynamics in a given sound pattern would be encoded in the equivalent dynamics of the hot-spot pattern in the AI.

Problems arise from our decision about when statics have to change to dynamics. In other words: what are the time periods over which an acoustical Gestalt can be considered as static? In terms of the neuronal code, this question deals with the integration times of cortical neurons, a topic of general relevance (compare König et al. 1996) that has only recently been addressed in various ways in experimental studies of the AC.

If the neurons in the AI of the cat can synchronize their action potentials to stimulus repetition rates or amplitude modulation rates of up to about 50 Hz (Schreiner and Urbas 1988), the integration times roughly calculated as  $1/\text{rate}$  would be 20 ms minimum. Since most AI neurons in the cat and other mammals synchronize best of rates around 10 Hz (Schreiner and Urbas 1988; Eggermont 1991; Gaese and Ostwald 1995; Kowalski et al. 1996; Schulze and Langner 1997, this volume), the usual integration times in the AI are around 100 ms. An integration time greater than 100 ms has been demonstrated in another experiment in which a linear frequency sweep had a gap of 100 ms (Sugita 1997). A number of cat AI neurons did not respond if the sweep had this gap and they did not respond to a noise of the gap duration, but they responded well to the sweep and the noise filling the gap. Thus, these neurons demonstrate temporal integration over a stimulus duration of more than 100 ms. Integration times of AI neurons in the order of 100 ms could be the result of intrinsic oscillations of the AC which have periods of nearly 100 ms in the cat (Eggermont 1992) and between 25 ms and 100 ms in the guinea pig (Fukunichi and Murai 1995).

It is interesting to note that the integration time does not simply indicate the duration between bursts of action potentials of the given neuron but rather reflects a rhythm between excitation and inhibition in the AC. A spatial distribution pattern of excitation in the AI, for example generated by binaural or two-tone stimuli, is followed by a spatial pattern of inhibition whereby the strength of inhibition is highest at the spot of the previously highest excitation (Horikawa et al. 1997, this volume; Hosokawa et al. 1997, this volume). It seems that a certain period after the excitation maximum at a given spot in the AI, the spot is cleared from excitation so that the following excitation can emerge as a distinct peak of activity at the same spot. The "reset" of auditory cortical activity will be time coordinated at all hot spots in the AI that are activated coincidentally or time coordinated by a certain combination of sound proper-

ties over the whole duration of the sound pattern. This mechanism of periodical reset of neuronal activity, the effectiveness of the reset depending on the strength of the previous excitation, may provide the timing for the sampling of one spatial pattern of hot spots after the other and thus for the encoding of the dynamics of sound patterns in the AI. Further research efforts will have to focus on the temporal dynamics of coding in the AC in order to clarify the concept of a periodic sampling of spatial activity patterns in the AI and probably other auditory cortical fields.

#### Aspects of plasticity

Plasticity of behavioral responses to sounds can be observed when the behavioral state of an animal changes (e.g. from sleep to waking, from non-attentive to attentive) or when learning changes the significance of a certain sound pattern. With regard to the hypothesis of sound-pattern representation in the AI put forward in the previous paragraphs, one can ask how behavioral states and learning influence the topographies of neuronal response characteristics, the coincidental and time-coordinated firing of groups of neurons at certain spots in the AI, the spatial pattern of hot spots associated with listening to a certain acoustical pattern, and the dynamics of sampling over the hot-spot patterns.

The responsiveness of neurons in the AI of the rat to tones at their specific characteristic frequency can be increased by electrical stimulation in the basal forebrain a short period (30–50 ms) before the tone presentation. This facilitation effect by the time-coordinated coupling of the two stimuli is mediated by cholinergic projections to the AC (Hars et al. 1993; Edeline et al. 1994a, b). Cholinergic influence on neurons in the cat AI also leads to plasticity of frequency-response areas and sharpness of frequency tuning (Ashe et al. 1989; McKenna et al. 1989). These studies indicate that topographies of neuronal response characteristics in AI such as the widths of tuning curves, degrees of monotonicity, and dynamic ranges can change by the action of the brain cholinergic system. Since this and other neurotransmitter systems such as the dopaminergic and serotonergic systems are associated with functions of regulation of attention, learning and memory (e.g. Levin et al. 1992; McCormick 1992; Marrocco et al. 1994; Aigner 1995; Buhot 1997; Schultz 1997), learning-induced plasticity in the AC can be expected and has actually been demonstrated. Tone-response habituation and classical and operant conditioning change the response thresholds of neurons, the shapes of the frequency response areas and sharpness of tuning of neurons in the AC (e.g. Condon and Weinberger 1991; Recanzone et al. 1993; Weinberger 1995; Bakin et al. 1996; Ohl and Scheich 1996, 1997). Also, the size of isofrequency stripes in the AI (Recanzone et al. 1993), the response strength to certain frequencies, and the timing of the response maximum can change owing to learning (Ohl and Scheich 1996, 1997). Finally, the

strength of the time-coordinated coupling of action potentials between groups of neurons in the AI can be increased in a behavioral auditory task mainly during the time while the task is performed (Ahissar et al. 1992).

The above-mentioned findings, many of them summarized by Ahissar and Ahissar (1994), clearly indicate the potentially profound influence of behavioral states and of acoustical learning on many topographies of neuronal response characteristics and the time-coordinated firing of groups of neurons, and thus on the generation of the spatial patterns of hot spots in the AI. That is, the neuronal code for a given sound pattern in the AI can be expected to change as a function of the animal's attention to and experience with a certain sound. Whether such expected changes of activity patterns directly reflect related changes in the perception of the sound, as the case of sound processing in the auditory cortical fields of the echolocating mustache bat suggests, must remain open. Studies, in which small local lesions are introduced in areas of learning-based response patterns and response-pattern changes, are necessary to estimate the significance of the spatial hot-spot pattern in the AI for the differential perception of a learned sound pattern.

Most studies on auditory plasticity used only pure tones as stimuli, so that the effects of changes in neuronal response patterns found may be much too large and non-representative for complex sounds which are expected to generate a spatially diverse activity pattern in the AI, not a single focal activity on the isofrequency stripe related to the tone frequency. This calls for studies in which complex sounds of biological relevance are used to investigate the plasticity of auditory cortical topographies and distributions of neuronal activity. The first approaches are in progress (Braun and Scheich 1997, this volume).

**Acknowledgements** Thanks to my colleagues in our Human Frontier Science Program project on the auditory cortex for stimulating discussions and excellent cooperation, colleagues in the SFB 527 in Ulm for insights in brain function, U. Seifert for expert secretarial work and E. Wacker for producing the figure.

## References

- Ahissar E, Ahissar M (1994) Plasticity in auditory cortical circuitry. *Curr Opin Neurobiol* 4: 580–587
- Ahissar E, Vaadia E, Ahissar M, Bergman H, Arieli A, Abeles M (1992) Dependence of cortical plasticity on correlated activity of single neurons and on behavioral context. *Science* 257: 1412–1415
- Aigner TG (1995) Pharmacology of memory: cholinergic-glutamatergic interactions. *Curr Opin Neurobiol* 5: 155–160
- Aitkin LM (1990) The auditory cortex. Chapman and Hall, London
- Aitkin LM, Irvine DRF, Nelson JE, Merzenich MM, Clarey JC (1986) Frequency representation in the auditory midbrain and forebrain of a marsupial, the northern native cat (*Dasyurus hallucatus*). *Brain Behav Evol* 29: 17–28
- Ashe JH, McKenna TM, Weinberger NM (1989) Cholinergic modulation of frequency receptive fields in auditory cortex: II. Frequency-specific effect of anticholinesterases provide evidence for a modulatory action of endogenous ACh. *Synapse* 4: 44–54
- Bakin JS, South DA, Weinberger NM (1996) Induction of receptive field plasticity in the auditory cortex of the guinea pig during instrumental avoidance conditioning. *Behav Neurosci* 110: 905–913
- Barth DS, Kithas J, Di S (1993) Anatomic organization of evoked potentials in rat parietotemporal cortex: somatosensory and auditory responses. *J Neurophysiol* 69: 1837–1849
- Berman AL (1961) Overlap of somatic and auditory cortical response fields in anterior ectosylvian gyrus of cat. *J Neurophysiol* 24: 595–607
- Braun S, Scheich H (1997) Influence of experience on the representation of the “mothering call” in auditory and other cortices of pups of the rodent *Octodon degus*: a FDG mapping study. *J Comp Physiol A* 181: 697–709
- Bronchti G, Heil P, Scheich H, Wollberg Z (1989) Auditory pathway and auditory activation of primary visual targets in the blind mole rat (*Spalax ehrenbergi*): I. 2-deoxyglucose study of subcortical centers. *J Comp Neurol* 284: 253–274
- Brugge JF, Reale RA (1985) Auditory cortex. In: Peters A, Jones EG (eds) *Cerebral cortex*, vol 4. Association and auditory cortices. Plenum Press, New York, pp 229–271
- Buhot MC (1997) Serotonin receptors in cognitive behaviors. *Curr Opin Neurobiol* 7: 243–254
- Clarey JC, Irvine DRF (1990) The anterior ectosylvian sulcal auditory field in the cat: I. An electrophysiological study of its relationship to surrounding auditory cortical fields. *J Comp Neurol* 301: 289–303
- Clarey JC, Barone P, Imig TJ (1992) Physiology of thalamus and cortex. In: Popper AN, Fay RR (eds) *The mammalian auditory pathway: neurophysiology*. Springer, Berlin Heidelberg New York, pp 232–334
- Clarey JC, Barone P, Imig TJ (1994) Functional organization of sound direction and sound pressure level in primary auditory cortex of the cat. *J Neurophysiol* 72: 2383–2405
- Condon CD, Weinberger NM (1991) Habituation produces frequency-specific plasticity of receptive fields in the auditory cortex. *Behav Neurosci* 105: 416–430
- Dear SP, Fritz J, Haresign T, Ferragamo M, Simmons JA (1993) Tonotopic and functional organization in the auditory cortex of the big brown bat, *Eptesicus fuscus*. *J Neurophysiol* 70: 1988–2009
- deCharms RC, Merzenich MM (1996) Primary cortical representation of sounds by the coordination of action-potential timing. *Nature* 381: 610–613
- Di S, Brett B, Barth DS (1994) Polysensory evoked potentials in rat parietotemporal cortex: combined auditory and somatosensory responses. *Brain Res* 642: 267–280
- Edeline JM, Hars B, Maho C, Hennevin E (1994a) Transient and prolonged facilitation of tone-evoked responses induced by basal forebrain stimulations in the rat auditory cortex. *Exp Brain Res* 97: 373–386
- Edeline JM, Maho C, Hars B, Hennevin E (1994b) Non-awaking basal forebrain stimulation enhances auditory cortex responsiveness during slow-wave sleep. *Brain Res* 636: 333–337
- Eggermont JJ (1991) Rate and synchronization measures of periodicity coding in cat primary auditory cortex. *Hear Res* 56: 153–167
- Eggermont JJ (1992) Stimulus induced and spontaneous rhythmic firing in single units in cat primary auditory cortex. *Hear Res* 61: 1–11
- Eggermont JJ (1994) Neural interaction in cat primary auditory cortex II. Effects of sound stimulation. *J Neurophysiol* 71: 246–270
- Ehret G, Schreiner CE (1997) Frequency resolution and spectral integration (critical band analysis) in single units of the cat primary auditory cortex. *J Comp Physiol A* 181: 635–650
- Eiermann A, Esser KH (1996) Tonotopic organization and parcellation of auditory cortex in the FM-bat *Carollia perspicillata*. In: Elsner N, Schnitzler HU (eds) *Brain and evolution*, vol II. Thieme, Stuttgart, p 237

- Fukunishi K, Murai N (1995) Temporal coding in the guinea-pig auditory cortex as revealed by optical imaging and its pattern-time-series analysis. *Biol Cybern* 72: 463–473
- Gaese BH, Ostwald J (1995) Temporal coding of amplitude and frequency modulation in the rat auditory cortex. *Eur J Neurosci* 7: 438–450
- Galazyuk AV, Feng AS (1997) Encoding of sound duration by neurons in the auditory cortex of the little brown bat, *Myotis lucifugus*. *J Comp Physiol A* 180: 301–311
- Gates GR, Aitkin LM (1982) Auditory cortex in the marsupial possum, *Trichosurus vulpecula*. *Hear Res* 7: 1–11
- Goldstein MH, Knight PL (1980) Comparative organization of mammalian auditory cortex. In: Popper AN, Fay RR (eds) *Comparative studies of hearing in vertebrates*. Springer, Berlin Heidelberg New York, pp 375–398
- Hars B, Maho C, Edeline JM, Hennevin E (1993) Basal forebrain stimulation facilitates tone-evoked responses in the auditory cortex of awake rat. *Neuroscience* 56: 61–74
- Heil P (1997a) Auditory cortical onset responses revisited: I. First-spike timing. *J Neurophysiol* 77: 2616–2641
- Heil P (1997b) Auditory cortical onset responses revisited: II. Response strength. *J Neurophysiol* 77: 2642–2660
- Heil P, Irvine DRF (1996) On determinants of first-spike latency in auditory cortex. *Neuroreport* 7: 3073–3076
- Heil P, Bronchti G, Wollberg Z, Scheich H (1991) Invasion of visual cortex by the auditory system in the naturally blind mole rat. *Neuroreport* 2: 735–738
- Heil P, Rajan R, Irvine DRF (1992) Sensitivity of neurons in cat primary auditory cortex to tones and frequency-modulated stimuli. II: Organization of response properties along the 'isofrequency' dimension. *Hear Res* 63: 135–156
- Heil P, Rajan R, Irvine DRF (1994) Topographic representation of tone intensity along the isofrequency axis of cat primary auditory cortex. *Hear Res* 76: 188–202
- Hellweg FC, Koch R, Vollrath M (1977) Representation of the cochlea in the neocortex of guinea pigs. *Exp Brain Res* 29: 467–474
- Hofstetter KM, Ehret G (1992) The auditory cortex of the mouse: connections of the ultrasonic field. *J Comp Neurol* 323: 370–386
- Horikawa J, Suga N (1991) Neuroethology of auditory cortex. *Jpn J Physiol* 41: 671–691
- Horikawa J, Ito S, Hosokawa Y, Homma T, Murata K (1988) Tonotopic representation in the rat auditory cortex. *Proc Jpn Acad Ser B* 64: 260–263
- Horikawa J, Hosokawa Y, Nasu M, Taniguchi I (1997) Optical study of spatiotemporal inhibition evoked by two-tone stimuli in the guinea pig auditory cortex. *J Comp Physiol A* 181: 677–684
- Hosokawa Y, Horikawa J, Nasu M, Taniguchi I (1997) Real-time imaging of neural activity during binaural interaction in the guinea pig auditory cortex. *J Comp Physiol A* 181: 607–614
- Imig TJ, Adrián HO (1977) Binaural columns in the primary field (AI) of cat auditory cortex. *Brain Res* 138: 241–257
- Imig TJ, Ruggero MA, Kitzes LM, Javel E, Brugge JF (1977) Organization of auditory cortex in the owl monkey (*Aotus trivirgatus*). *J Comp Neurol* 171: 111–128
- Imig TJ, Irons WA, Samson FR (1990) Single-unit selectivity of azimuthal direction and sound pressure level of noise bursts in cat high-frequency primary auditory cortex. *J Neurophysiol* 63: 1448–1466
- Irvine DRF, Huebner H (1979) Acoustic response characteristics of neurons in nonspecific areas of cat cerebral cortex. *J Neurophysiol* 42: 107–122
- Jen PHS, Sun XD, Lin PJJ (1989) Frequency and space representation in the primary auditory cortex of the frequency modulating bat *Eptesicus fuscus*. *J Comp Physiol* 165: 1–14
- Kelly JB, Judge PW (1994) Binaural organization of primary auditory cortex in the ferret (*Mustela putorius*). *J Neurophysiol* 71: 904–913
- Kelly JB, Sally SL (1988) Organization of auditory cortex in the albino rat: binaural response properties. *J Neurophysiol* 59: 1756–1769
- Kelly JB, Judge PW, Phillips DP (1986) Representation of the cochlea in primary auditory cortex of the ferret (*Mustela putorius*). *Hear Res* 24: 111–115
- King AJ (1995) Asking the auditory cortex the right questions. *Curr Biol* 5: 1110–1113
- König P, Engel AK, Singer W (1996) Integrator or coincidence detector? The role of the cortical neuron revisited. *Trends Neurosci* 19: 130–137
- Kowalski N, Depireux DA, Shamma SA (1996) Analysis of dynamic spectra in ferret primary auditory cortex. I. Characteristics of single-unit responses to moving ripple spectra. *J Neurophysiol* 76: 3503–3523
- Langner G (1992) Periodicity coding in the auditory system. *Hear Res* 60: 115–142
- Langner G, Sams M, Heil P, Schulze H (1997) Tonotopy and periodotopy in the human auditory cortex: a magnetoencephalographic study. *J Comp Physiol A* (in press)
- Levin ED, Decker MW, Butcher LL (eds) (1992) *Neurotransmitter interactions and cognitive function*. Birkhäuser, Boston
- Liu W, Suga N (1997) Binaural and callosal organization of the primary auditory cortex of the mustached bat. *J Comp Physiol A* 181: 599–605
- Marrocco RT, Witte EA, Davidson MC (1994) Arousal systems. *Curr Opin Neurobiol* 4: 166–170
- McCormick DA (1992) Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamocortical activity. *Prog Neurobiol* 39: 337–388
- McKenna TM, Ashe JH, Weinberger NM (1989) Cholinergic modulation of frequency receptive fields in auditory cortex: I. Frequency-specific effects of muscarinic agonists. *Synapse* 4: 30–43
- McMullen NT, Glaser EM (1982) Tonotopic organization of rabbit auditory cortex. *Exp Neurol* 75: 208–220
- Mendelson JR, Schreiner CE, Sutter ML, Grasse KL (1993) Functional topography of cat primary auditory cortex: responses to frequency-modulated sweeps. *Exp Brain Res* 94: 65–87
- Mendelson JR, Schreiner CE, Sutter ML (1997) Functional topography of the primary auditory cortex: response latencies. *J Comp Physiol A* 181: 615–633
- Merzenich MM, Brugge JF (1973) Representation of the cochlear partition on the superior temporal plane of the macaque monkey. *Brain Res* 50: 275–296
- Merzenich MM, Schreiner CE (1992) Mammalian auditory cortex – some comparative observations. In: Webster DB, Fay RR, Popper AN (eds) *The evolutionary biology of hearing*. Springer, Berlin Heidelberg New York, pp 673–689
- Merzenich MM, Knight PL, Roth GL (1975) Representation of cochlea within primary auditory cortex in the cat. *J Neurophysiol* 38: 231–249
- Middlebrooks JC, Dykes RW, Merzenich MM (1980) Binaural response-specific bands in primary auditory cortex (AI) of the cat: topographical organization orthogonal to isofrequency contours. *Brain Res* 181: 31–48
- Morel A, Kaas JH (1992) Subdivisions and connections of auditory cortex in owl monkeys. *J Comp Neurol* 318: 27–63
- Morel A, Garraghty PE, Kaas JH (1993) Tonotopic organization, architectonic fields, and connections of auditory cortex in macaque monkeys. *J Comp Neurol* 335: 437–459
- Ohl FW, Scheich H (1996) Differential frequency conditioning enhances spectral contrast sensitivity of units in auditory cortex (field AI) of the alert Mongolian gerbil. *Eur J Neurosci* 8: 1001–1017
- Ohl FW, Scheich H (1997) Learning-induced dynamic receptive field changes in primary auditory cortex (AI) of the unanesthetized Mongolian gerbil. *J Comp Physiol A* 181: 685–696
- Ohlemiller KK, Kanwal JS, Butman JA, Suga N (1994) Stimulus design for auditory neuroethology: synthesis and manipulation of complex communication sounds. *Audit Neurosci* 1: 19–37
- Ohlemiller KK, Kanwal JS, Suga N (1996) Facilitative responses to species-specific calls in cortical FM-FM neurons of the mustached bat. *Neuroreport* 7: 1749–1755

- Orman SS, Phillips DP (1984) Binaural interactions of single neurons in posterior field of cat auditory cortex. *J Neurophysiol* 51: 1028–1039
- Ostwald J (1984) Tonotopical organization and pure tone response characteristics of single units in the auditory cortex of the greater horseshoe bat. *J Comp Physiol A* 155: 821–834
- Pallas SL (1990) Cross-modal plasticity in sensory cortex. In: Finlay BL (ed) *The neocortex*. Plenum Press, New York, pp 205–218
- Pallas SL, Roe AW, Sur M (1990) Visual projections induced into the auditory pathway of ferrets. I. Novel inputs to primary auditory cortex (AI) from the LP/pulvinar complex and the topography of the MGN-AI projection. *J Comp Neurol* 298: 50–68
- Phillips DP, Hall SE (1990) Response timing constraints on the cortical representation of sound time structure. *J Acoust Soc Am* 88: 1403–1411
- Phillips DP, Irvine DRF (1982) Properties of single neurons in the anterior auditory field (AAF) of cat cerebral cortex. *Brain Res* 248: 237–244
- Phillips DP, Orman SS (1984) Responses of single neurons in posterior field of cat auditory cortex to tonal stimulation. *J Neurophysiol* 51: 147–163
- Phillips DP, Semple MN, Calford MB, Kitzes LM (1994) Level-dependent representation of stimulus frequency in the cat primary auditory cortex. *Exp Brain Res* 102: 210–226
- Phillips DP, Semple MN, Kitzes LM (1995) Factors shaping the tone level sensitivity of single neurons in posterior field of cat auditory cortex. *J Neurophysiol* 73: 674–686
- Radtke-Schuller S, Schuller G (1995) Auditory cortex of the rufous horseshoe bat: 1. Physiological response properties to acoustic stimuli and vocalizations and the topographical distribution of neurons. *Eur J Neurosci* 7: 570–591
- Rajan R, Aitkin LM, Irvine DRF (1990) Azimuthal sensitivity of neurons in primary auditory cortex of cats. II. Organization along frequency-band strips. *J Neurophysiol* 64: 888–902
- Rauschecker JP, Tian B, Hauser M (1995) Processing of complex sound in the macaque nonprimary auditory cortex. *Science* 268: 111–114
- Reale RA, Imig TJ (1980) Tonotopic organization in auditory cortex of the cat. *J Comp Neurol* 192: 265–291
- Reale RA, Kettner RE (1986) Topography of binaural organization in primary auditory cortex of the cat: effects of changing interaural intensity. *J Neurophysiol* 56: 663–682
- Recanzone GH, Schreiner CE, Merzenich MM (1993) Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *J Neurosci* 13: 87–103
- Redies H, Sieben U, Creutzfeldt OD (1989) Functional subdivisions in the auditory cortex of the guinea pig. *J Comp Neurol* 282: 473–488
- Ribaupierre F de (1997) Acoustic information processing in the auditory thalamus and cerebral cortex. In: Ehret G, Romand R (eds) *The central auditory system*. Oxford University Press, New York, pp 317–397
- Riquimaroux H, Gaioni SJ, Suga N (1991) Cortical computational maps control auditory perception. *Science* 251: 565–568
- Roe AW, Pallas SL, Hahn JO, Sur M (1990) A map of visual space induced in primary auditory cortex. *Science* 250: 818–820
- Rouiller EM (1997) Functional organization of the auditory pathways. In: Ehret G, Romand R (eds) *The central auditory system*. Oxford University Press, New York, pp 3–96
- Sally SL, Kelly JB (1988) Organization of auditory cortex in the albino rat: sound frequency. *J Neurophysiol* 59: 1627–1638
- Schreiner CE (1995) Order and disorder in auditory cortical maps. *Curr Opin Neurobiol* 5: 489–496
- Schreiner CE, Cynader MS (1984) Basic functional organization of second auditory cortical field (All) of the cat. *J Neurophysiol* 51: 1284–1305
- Schreiner CE, Mendelson JR (1990) Functional topography of cat primary auditory cortex: distribution of integrated excitation. *J Neurophysiol* 64: 1442–1459
- Schreiner CE, Sutter ML (1992) Topography of excitatory bandwidth in cat primary auditory cortex: single-neuron versus multiple-neuron recordings. *J Neurophysiol* 68: 1487–1502
- Schreiner CE, Urbas JV (1986) Representation of amplitude modulation in the auditory cortex of the cat. I. The anterior auditory field (AAF). *Hear Res* 21: 227–241
- Schreiner CE, Urbas JV (1988) Representation of amplitude modulation in the auditory cortex of the cat. II. Comparison between cortical fields. *Hear Res* 32: 49–64
- Schreiner CE, Mendelson JR, Sutter ML (1992) Functional topography of cat primary auditory cortex: representation of tone intensity. *Exp Brain Res* 92: 105–122
- Schultz W (1997) Dopamine neurons and their role in reward mechanisms. *Curr Opin Neurobiol* 7: 191–197
- Schulze H, Langner G (1997) Periodicity coding in the primary auditory cortex of the Mongolian gerbil (*Meriones unguiculatus*): two different coding strategies for pitch and rhythm? *J Comp Physiol A* 181: 651–663
- Schulze H, Ohl FW, Heil P, Scheich H (1997) Field-specific responses in the auditory cortex of the unanesthetized Mongolian gerbil to tones and slow frequency modulations. *J Comp Physiol A* 181: 573–589
- Semple MN, Kitzes LM (1993a) Focal selectivity for binaural sound pressure level in cat primary auditory cortex: two-way intensity network tuning. *J Neurophysiol* 69: 462–473
- Semple MN, Kitzes LM (1993b) Binaural processing of sound pressure level in cat primary auditory cortex: evidence for a representation based on absolute levels rather than interaural level differences. *J Neurophysiol* 69: 449–461
- Shamma SA, Fleshman JW, Wiser PR, Versnel H (1993) Organization of response areas in ferret primary auditory cortex. *J Neurophysiol* 69: 367–383
- Shen JX, Chen QC, Jen PHS (1997) Binaural and frequency representation in the primary auditory cortex of the big brown bat, *Eptesicus fuscus*. *J Comp Physiol A* 181: 591–597
- Stiebler I (1987) A distinct ultrasound-processing area in the auditory cortex of the mouse. *Naturwissenschaften* 74: 96–97
- Stiebler I, Neulist R, Fichtel I, Ehret G (1997) The auditory cortex of the house mouse: left-right differences, tonotopic organization and quantitative analysis of frequency representation. *J Comp Physiol A* 181: 559–571
- Suga N (1977) Amplitude-spectrum representation in the Doppler-shifted CF-processing area of the auditory cortex of the mustache bat. *Science* 196: 64–67
- Suga N (1988) Auditory neuroethology and speech processing: complex sound processing by combination-sensitive neurons. In: Edelman GM, Gall WE, Cowan WM (eds) *Auditory function. Neurobiological bases of hearing*. Wiley, New York, pp 679–720
- Suga N (1994) Multi-function theory for cortical processing of auditory information: implications of single-unit and lesion data for future research. *J Comp Physiol A* 175: 135–144
- Suga N, Jen PHS (1976) Disproportionate tonotopic representation for processing species-specific CF-FM sonar signals in the mustache bat auditory cortex. *Science* 194: 542–544
- Suga N, Manabe T (1982) Neural bases of amplitude-spectrum representation in auditory cortex of the mustached bat. *J Neurophysiol* 47: 225–255
- Sugita Y (1997) Neuronal correlates of auditory induction in the cat cortex. *Neuroreport* 8: 1155–1159
- Sutter ML, Schreiner CE (1991) Physiology and topography of neurons with multi-peaked tuning curves in cat primary auditory cortex. *J Neurophysiol* 65: 1207–1226
- Sutter ML, Schreiner CE (1995) Topography of intensity tuning in cat primary auditory cortex: single-neuron versus multiple-neuron recordings. *J Neurophysiol* 73: 190–204
- Tanaka H, Komatuzaki A, Taniguchi I (1994) Spatial distribution of response latency in the anterior fields of the auditory cortex of the guinea pig. *Audiol Jpn* 37: 222–228
- Thomas H, Tillein J, Heil P, Scheich H (1993) Functional organization of auditory cortex in the Mongolian gerbil (*Meriones unguiculatus*). I. Electrophysiological mapping of frequency

- representation and distinction of fields. *Eur J Neurosci* 5: 882–897
- Tian B, Rauschecker JP (1994) Processing of frequency-modulated sounds in the cat's anterior auditory field. *J Neurophysiol* 71: 1959–1975
- Toldi J, Fehér O, Wolfe JR (1986) Sensory interactive zones in the rat cerebral cortex. *Neuroscience* 18: 461–465
- Tunturi AR (1962) Frequency arrangement in anterior ectosylvian auditory cortex of dog. *Am J Physiol* 203: 185–193
- Weinberger NM (1995) Dynamic regulation of receptive fields and maps in the adult sensory cortex. *Annu Rev Neurosci* 18: 129–158
- Willott JF, Aitkin LM, McFadden SL (1993) Plasticity of auditory cortex associated with sensorineural hearing loss in adult C57BL/6J mice. *J Comp Neurol* 329: 402–411
- Winer JA (1992) The functional architecture of the medial geniculate body and the primary auditory cortex. In: Webster DB, Popper AN, Fay RR (eds) *The mammalian auditory pathways: neuroanatomy*. Springer, Berlin Heidelberg New York, pp 222–409
- Winkler I, Tervaniemi M, Huotilainen M, Ilmoniemi R, Ahonen A, Salonen O, Standertskjöld-Nordenstam CG, Näätänen R (1995) From objective to subjective: pitch representation in the human auditory cortex. *Neuroreport* 6: 2317–2320
- Woolsey CN (1960) Organization of cortical auditory system: a review and a synthesis. In: Rasmussen GL, Windle WF (eds) *Neural mechanisms of the auditory and vestibular systems*. Thomas, Springfield, pp 165–180