9 Temporal Processing in Cat Primary Auditory Cortex: Dynamic Frequency Tuning and Spectro-Temporal Representation of Speech Sounds

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Many complex sounds, such as species-specific vocalizations and speech, consist of temporal sequences of spectrally complex acoustic segments. Typically, sensory signals have complex time-variant properties, which are manifested on a variety of time scales. In the case of speech and animal vocalizations, it is helpful to differentiate several ranges of timing-based information resolution: (a) the millisecond range for processing of different frequency components; (b) the 2- 20-ms range for processing fundamental frequencies and rapid transients; (c) the range of up to 100 ms for formant transitions and phonemes; and (d) the range of up to several hundred milliseconds for larger segments, such as syllables, words, and complete phrases or calls. This segregation is reflected in the temporal response properties of neurons by a decreasing temporal sequential resolution as the location of the neurons becomes more central. Whereas auditory nerve fibers can respond to amplitude modulation rates of more than 1 kHz, neurons in primary auditory cortex are generally limited in their following capacity to modulation frequencies of less than 30 Hz (e.g., Schreiner & Urbas, 1988). This enables cortical neurons to mark with low frequency, but high precision, the major segments in a sound stream, such as syllables or words (Dinse & Schreiner, 1996; Heil, 1997a; Phillips, 1993).

Studies of the spatial distribution of onset latency reveal that there may be systematic variations across cortex in initial response latencies (Cheung, Bedenbaugh, Nagarajan, & Schreiner, 2001; Mendelson, Schreiner, Sutter, & Grasse, 1993). There is strong evidence that the temporal fine structure of transient responses encoded by cortical neurons in the range of 10 to 30 ms reflects properties of the rising phase of the stimulus envelope (Heil, 1997a, 1997b; Heil & Neubauer, 2001; Phillips, 1988) and that the precision of the timing within the transient response can be very high, in the range of less than a few milliseconds (Heil, 1997a, 1997b; Phillips, 1993; Phillips & Hall, 1990). These response properties provide precise, but infrequent timing information distributed across auditory cor-

tex and overlying other topographic receptive field (RF) distributions. Although these observations of topographic differences for time-independent response measures are intriguing, the consequences for the spatial-temporal coding of complex sounds may depend on additional properties, such as those reflected in the dynamic behavior of receptive fields (Dinse & Jancke, 2001b; Dinse, Krüger, & Best, 1990; Ghazanfar & Nicolelis, 2001).

The overall goal of our experimental approach is to develop an understanding of the early cortical processing of complex sound features and, eventually, to identify fundamental principles that underlie the cortical representations of communication sounds such as speech. Single and multiple neuron mapping studies within the primary auditory cortical field (AI) of cats and monkeys have already revealed that, at least for simple sounds, there are spatially organized and superimposed representations of spectral properties such as signal frequency, stimulus bandwidth, sound intensity, frequency modulation direction and rate, and sound source location (Heil, Rajan, & Irvine, 1992; Mendelson et al., 1993; Schreiner & Mendelson, 1990; Schreiner, Mendelson, & Sutter, 1992). This systematic spatial segregation of specific functions in combination with specific temporal response properties of single-neuron RFs provides a framework for understanding the representation of complex sounds.

DYNAMIC TEMPORAL REPRESENTATION OF TONES IN AUDITORY CORTEX

The dynamic of transient responses was assessed by studying the response timing throughout the auditory receptive fields of single and multiple units recorded in cat AI. It is important to recall that the auditory receptive fields of cortical neurons cover a fairly broad frequency range; they respond in an intensity-dependent way to half an octave or more (e.g., Schreiner & Mendelson, 1990; Schreiner & Sutter, 1992). This study was motivated by the existence of substantial time-variant RF properties described for the cat visual cortex (DeAngelis, Ohzawa, & Freeman, 1993; Dinse, 1994; Dinse & Jancke, 2001b; Dinse et al., 1990; Dinse, Krüger, Mallot, & Best, 1991; Eckhorn, Krause, & Nelson, 1993; Ghazanfar & Nicolelis, 2001; Jones & Palmer, 1987; Shevelev, Volgushev, & Sharaev, 1992). In this analysis, RF is synonymous with frequency response area. Dynamically maintained RFs reflect the inherent neuronal temporal response properties following single tone bursts and last between approximately 10 and 30 ms after stimulus onset.

Measurements of auditory receptive fields are based on poststimulus-time-histograms (PSTHs) following tone burst stimulation with various frequencies and intensities in barbiturate-anesthetized cats. PSTH responses were used to construct tuning curves based on a stimulation matrix of 10 different frequencies at 10 different intensity levels. In light of the low firing rate of cortical neurons, each condition was presented 40 times. To visualize the dynamics of RFs, a temporal sequence of tuning curves was computed by means of a time slice technique that displays the instantaneous tuning of a cell for each narrow time window. Usually, auditory cortical responses are very transient with response durations in the range of 10 to 30 ms. We therefore used time windows of 2 to 3 ms in duration to cover the period between stimulus onset and response decay, which yielded a sequence of 10 or more individual tuning curves (the specific number of tuning curves in a sequence depended on the response duration).

The response magnitude in the intensity-frequency domain, without exception, is not constant after stimulus onset, but highly time-variant. This is expressed by a smooth and gradual development of neural activity across the intensity-frequency space (i.e., the neuron's RF). Usually, during the first milliseconds after stimulation, neurons respond to a broad frequency range at higher stimulus intensities, exhibiting low spectral selectivity (see Figs. 9.1 and 9.3, top panels). Evoked activity after that initial response period represents frequencies closer to the characteristic frequency (CF) of a neuron and at lower intensities. Most notable is the time-dependent and late emergence of diagonal bands of activity along the low- or high-frequency border of a neuron's RF (Figs. 9.1 and 9.3, lower panels). We distinguish three differ-

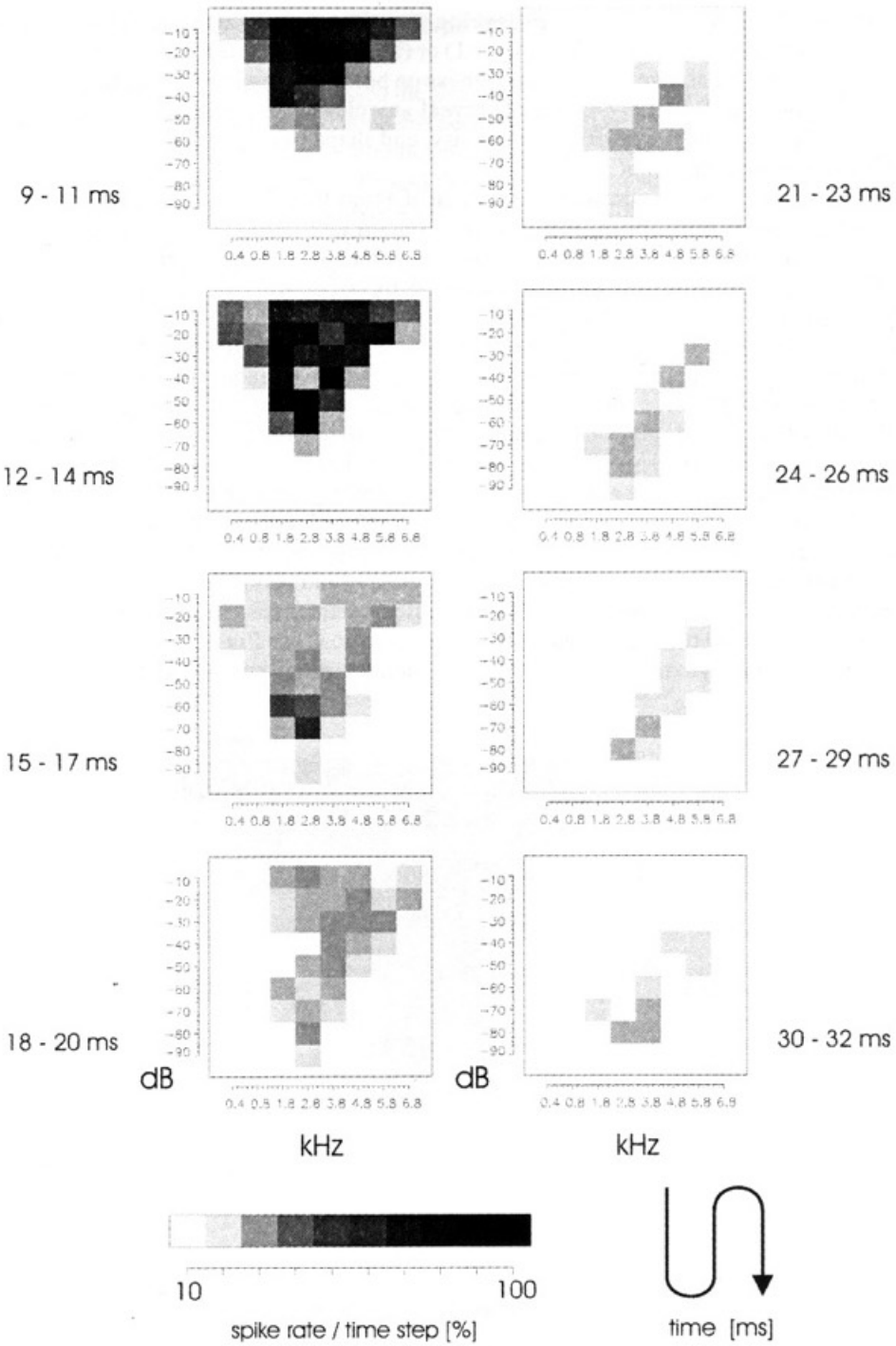

FIG. 9.1. Temporal sequence of tuning curves for a single neuron recorded in cat AI displaying a time-delayed diagonal band of activity along the high-frequency side of the tuning curve. The CF of the neuron was 2.8 kHz. Each tone was presented 40 times. Width of the time slice per panel is 3 ms. Time slices are arranged from top to bottom in each row. The temporal sequence covers 9 ms to 32 ms after stimulus onset.

ent patterns of RF dynamics. Two types develop over time with obliquely shaped RFs, either on (a) the high-frequency side of the RF (Fig. 9.1) or (b) the low-frequency side (Fig. 9.3). A third type is symmetric and shows late responsiveness on both high- and low-frequency borders (not shown). Although initial analysis did not reveal any clear relationship between the dynamic properties of tuning and the position, symmetry, and shape of inhibitory side bands, such a relationship cannot be ruled out.

The RF dynamics in AI neurons cover a range of about 10 to 30 ms following stimulus onset. As the stimuli were pure tones, they did not contain any dynamics, except different onset slopes associated with the wide range of stimulus intensities. The neural dynamics described can thus be regarded as reflecting inherent properties of neural processing in addition to peripheral trigger mechanisms (Heil, 1997a, 1997b) that may determine the local latencies observed at different locations within RFs. In general, the dynamics are due to the fact that response latency and response duration are independent variables. Early in the response, high-intensity stimuli have short-latency responses and short response durations. Consequently, after that period, neurons are not responsive to high-intensity stimuli; this results in systematic and substantial shifts of response areas with time. In other words, the informational content distributed across the activity of many neurons differs, depending on the position and extent of the time window during which activity is analyzed. The asymmetries of RFs observed in the frequency-intensity plots are equally expressed in spectro-temporal RFs; that is, cross-sections of the RF that display stimulus frequency and response timing for a given intensity. Finally, it should be mentioned that the temporal sequences of tuning curves can be converted to conventional tuning curves by simple integration (see Fig. 9.2). As a rule, all aspects of the described RF dynamics are contained in such temporally integrated tuning curves.

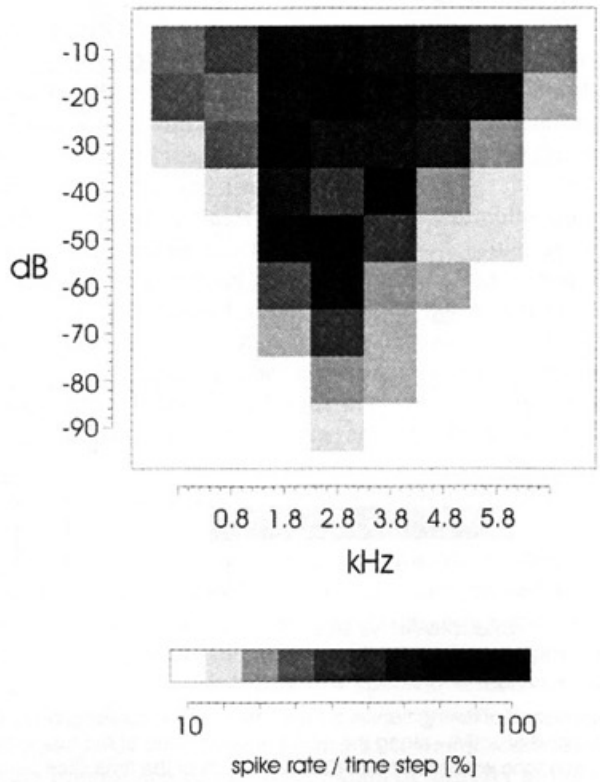

FIG. 9.2. A temporally integrated tuning curve for the neuron shown in Fig. 9.1.

Relation to Previous Studies and Functional Interpretation

Several studies in auditory cortex addressed the issues of response latency as a function of intensity and stimulus rise time. The main observation had been that onset latency and duration of the transient response decreases with an increase in stimulus intensity (e.g., Mendelson et al., 1993; Raggio & Schreiner, 1994; Sutter & Schreiner, 1995) and that onset latency and duration of the transient response depend on the slope of the stimulus onset (Heil, 1997a, 1997b; Phillips, 1988; Phillips & Hall, 1990; Phillips, Hall, & Hollett, 1989; Phillips & Sark, 1991). These experiments were usually performed for tones near the best frequency (BF) of a neuron or with broadband stimuli. Fundamental aspects of this behavior can be related to peripheral mechanisms sensitive to the rate of change in stimulus intensity (Heil, 1997a, 1997b; Heil & Neubauer, 2001). The findings reported here confirm most of those previous observations and extend them in an interesting way. The lengthening of the onset latency and the duration of the transient response near threshold can be observed for all stimulus frequencies throughout the excitatory receptive field. However, the range of latencies and response durations is not necessarily the same at the BF and stimulus frequencies above and below BF.

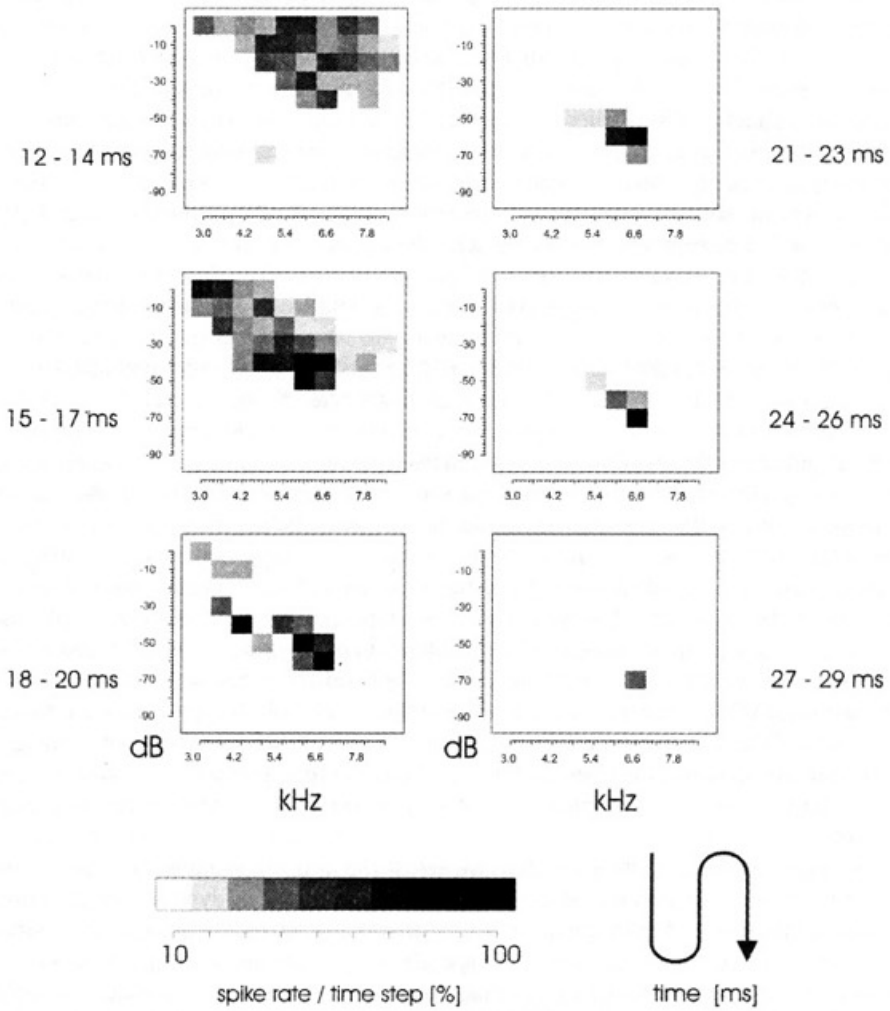

FIG. 9.3. Temporal sequence of tuning curves for a neuron recorded in cat AI displaying a time-delayed diagonal band of activity along the low-frequency side of the tuning curve. The CF of the neuron was 6.8 kHz. Sequence covers 9 ms to 26 ms post-stimulus onset.

In fact, we show that there can be systematic differences between the latency behavior for the high- and low-frequency borders of the RF. This latency behavior of a given cortical neuron is most likely not exclusively determined by peripheral mechanisms, such as slope of the envelope (Heil, 1997a, 1997b; Heil & Neubauer, 2001) but is also shaped by multifactorial excitatory and inhibitory influences along the auditory pathway (Mendelson et al., 1993; Tan et al., 2004; for visual cortex see Dinse, 1994). As a consequence, predictions of the spectro-temporal response behavior to complex stimuli from pure-tone tuning curves is difficult without detailed knowledge of the temporal development or dynamics of cortical RF.

The data indicate that on the behaviorally relevant time scale of 10 to 30 ms, single cells recorded in the primary auditory field are characterized by coherent temporal dynamic response properties. These temporally structured responses give rise to a complex, time-variant evolution of a cell's RF. In more detail, different frequency-intensity combinations evoke neural responses that differ in their response latency, duration, and firing rate. Accordingly, activity within subregions of an RF is only expressed for certain time periods that depend on the particular type of stimulation. As a result, activity develops smoothly and gradually throughout the RF.

Using time slice and reverse-correlation techniques, RF dynamics have been studied for many years in the auditory system of the frog and cat, and in the visual and the somatosensory system (DeAngelis et al., 1993; Dinse, 1994; Dinse & Jancke, 2001b; Dinse et al., 1990; Dinse et al., 1991; Eckhorn et al., 1993; Eggermont, Aertsen, Hermes, & Johannesma, 1981; Ghazanfar & Nicolelis, 2001; Jones & Palmer, 1987; McLean & Palmer, 1989; Miller et al., 2002; Nicolelis, Lin, Woodward, & Chapin, 1993). From these investigations there is general agreement that cortical neurons have time-variant RFs. However, the absolute timing of these dynamics is significantly varied. In the visual system, RF dynamics are in the range of 50 to 100 (or more) ms, whereas somatosensory cortical neurons exhibit a range of 10 to 20 ms. Although the first finding supports the notion that RF dynamics might represent a general feature of cortical processing, the latter indicates that the dynamics almost certainly reflect the constraints of cortical wiring and network properties, but might also reflect an adaptation to the nature of the dynamics of the sensory signals in each modality. Whereas traditionally the temporal and spectral properties of cortical RFs were obtained under the assumption of mutual independence, the data presented here reflect essential and nonseparable spectro-temporal properties (cf. Dinse et al., 1990; Dinse et al., 1991). At a level of neural population representations, a complex, but coherent and gradual temporal evolution of activity was observed, indicating that the RF dynamics seen in single cells are reflected in a systematic global dynamic when viewed from the point of larger cell assemblies (Jancke et al., 1999). However, compared to single-cell RF dynamics, the time scale of population RFs was much shorter and activity was more uniform across the population RFs, as indicated by a remarkable spatial coherence of activity (Dinse & Jancke, 2001b). Accordingly, the temporal structure of single-cell RF dynamics that is characterized by highly complicated distributions of activity in space and time transforms into a much simpler spatio-temporal activity pattern when the dynamics of large numbers of neurons are taken into account. A comparable compression in overall dynamics has also been observed for somatosensory cortical populations (Dinse & Jancke, 2001a). It remains to be seen if similar effects hold for the auditory system.

Independent of the way dynamic RFs are generated in terms of subcortical or cortical contributions, they seem to constitute an essential feature of cortical functions and represent an adaptational step toward the processing of complex sounds, such as vocalization and speech, in that particular time domain.

The emergence of diagonal bands of activity across the frequency-intensity space, as well as the frequency-time space, suggests that stimuli characterized by static or dynamic spectral profiles that change both in intensity and in frequency can lead to a synchronized neural response with constant latency. This provides a transformation of the specific static and time-varying features of a complex sound into single and simple neural events that allows synchronization with near-zero delay across neurons. When a dynamically organized RF is stimulated with a frequency transition, as is typical of speech formants, the temporal dispersion in the stimulus is transformed into a brief and temporally precise neuronal event (Wang et al., 1995). This is because a dynamic RF provides spectro-temporal

activity windows of only a few milliseconds in duration. The main effect therefore can be described as a temporal normalization. This normalization can lead to an overall synchronized and temporally coherent neuronal discharge. This effect might not only be acting on the single-cell level, but may also hold for populations of neurons, thereby producing time-locked and synchronized discharges across large numbers of neurons.

From a computational point of view, the predicted and experimentally reported (see later) temporal normalization is due to the nonseparability of spectral and temporal properties. The implications of separability may be illustrated by an example. Suppose a set of spectral stimuli is presented with different temporal modulations. The use of complex sounds implies differential temporal dependencies. In a separable system, temporal behavior can be factored out. Therefore, the spectral characteristics of the system would be the same for all temporal modulations of the stimulus. In a piecewise, separable system, the temporal characteristics of the RFs together with the temporal modulation of the stimulus impose a weight on each spectral processing subfield. The set of weights will be different for each temporal modulation and the overall spectral filter will thus be modified by the temporal modulation of the stimulus. In the extreme case, the system is entirely nonseparable. Under these conditions the complete time-dependence of the spectral filter is established (cf. Dinse et al., 1990; Dinse et al., 1991). Combined, the described nonseparability of auditory cortical RFs leads to a considerable deviation from the responses compared to narrowband stimulation applied in temporal isolation.

Experimental evidence for a temporal normalization process comes from studies of the cortical representation of species-specific vocalizations in the common marmoset (Nagarajan et al., 2002; Wang, Merzenich, Beitel, & Schreiner, 1995) and the study of speech sounds in AI described later. Both studies observed time-locking of the discharge to discrete stimulus events but not to rapid sequential details of their rapidly changing spectral contents. As a consequence, a reduction of temporal complexity and an increase in cross-population response synchronization was found. Both findings are compatible with the predictions previously outlined that were derived by considering only the implications of a dynamically maintained RF organization.

SPECTRO-TEMPORAL REPRESENTATION OF SPEECH SOUNDS IN PRIMARY AUDITORY CORTEX

One possible strategy of encoding complex sounds in the cortex (Creutzfeldt, Hellweg, & Schreiner, 1980; Pelleg-Toiba & Wollberg, 1991) is by the temporal-spatial discharge pattern of distributed neuronal populations across the cortical field. There has been increasing evidence that distributed coding schemes operate in other sensory or motor cortical regions (e.g., Georgopoulos, Crutcher, & Schwartz, 1989; Gochin, Colombo, Dorfman, Gerstein, & Gross, 1994; Merzenich, Grajski, Jenkins, Recanzone, & Peterson, 1991). A recent study of the representation of species-specific vocalizations in the AI of the marmoset provides strong evidence that behaviorally relevant vocalizations are indeed represented by spatially distributed neuronal discharges, and that behaviorally distinguishable sounds of the same "linguistic" category are represented by clearly distinct, only partially overlapping populations of neurons (Wang et al., 1995). Studies of the cortical encoding of speech signals with clearly defined phonetic features in AI of primates have provided evidence that some of the major phonetic distinctions are reflected in the activity of cortical neurons (see Fig. 9.3; Eggermont, 1995; Steinschneider, Arezzo, & Vaughan, 1982, 1990; Steinschneider, Schroeder, Arezzo, & Vaughan, 1993). These findings indicate that phonetically important distinctions can be preserved in the activity distribution of AI.

To evaluate the temporal and spectral or spatial aspects of the coding of speech sounds across a large population of neurons, cortical representation of synthesized consonant–vowels phonemes (CVs) ([bɛ] and [pɛ]) were obtained by mapping the multiple-unit responses from locations in the low-frequency region of cat AI. Animals were anesthetized with Ketamine. For each recording location we determined the pure-tone frequency-response area and the responses to the syllables at different sound intensities and under different background noise conditions.

Figure 9.4 illustrates the population PSTHs for two CV syllables and the spectrogram of the sounds. In general, the combined evoked activity to the syllables for all neurons is characterized by brief transient responses at the beginning of the consonants and at the beginning of voicing. For the CV [bɛ] this results in a single strong transient response at the beginning of the stimulus because the voicing onset and the beginning of consonantal formant transitions coincide. By contrast, two distinct phasic responses can be discerned for the CV [pɛ]: one marking the consonant onset and the second one at the beginning of voicing after a voice-onset time (VOT) of 60 ms.

In addition to the response characteristics already seen in the population histograms, neurograms reveal frequency-specific response attributes (Fig. 9.5) by plotting the number of spikes (in response to 20 stimulus presentations) as a function of time and CF for each recording location. The firing rate in each bin is normalized to the maximum firing rate for a given neuron or neuronal cluster response to a tone presented at the cell's CF. As a result, one can see one or two prominent bands of enhanced firing probability in response to CV stimulation. The first response corresponds to the beginning of the voiced and unvoiced CVs, and the second response corresponds to the delayed onset of voicing after the unvoiced consonant. The first formant response (F_1 = 500–800 Hz) is absent in the initial response for [pɛ] but is present in both the voicing response in [pɛ] and the initial response to [bɛ] (Fig. 9.5). Both effects are to be expected given the spectrograms of the two sounds.

In this animal, two response latency patterns can be seen. The first phasic responses to [bɛ] and [pɛ] show a fairly clear latency dependence of the response as a function of CF. Although the third

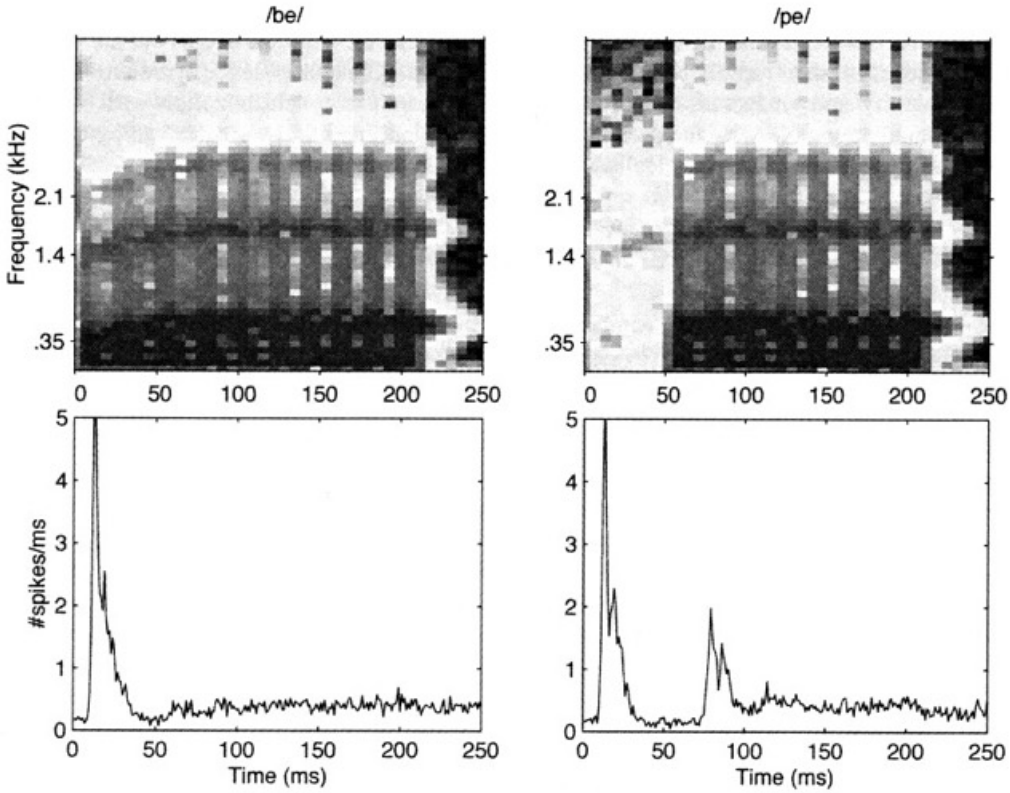

FIG. 9.4. Spectrograms of the CV stimuli [bɛ] and [pɛ] with the corresponding spike response accumulated across all the units recorded within the low-frequency region of AI. The responses were recorded in the middle layers of AI in a Ketamine-anesthetized cat at 80 locations across a CF range of 0.7 to 6 kHz. Sound delivery was binaural.

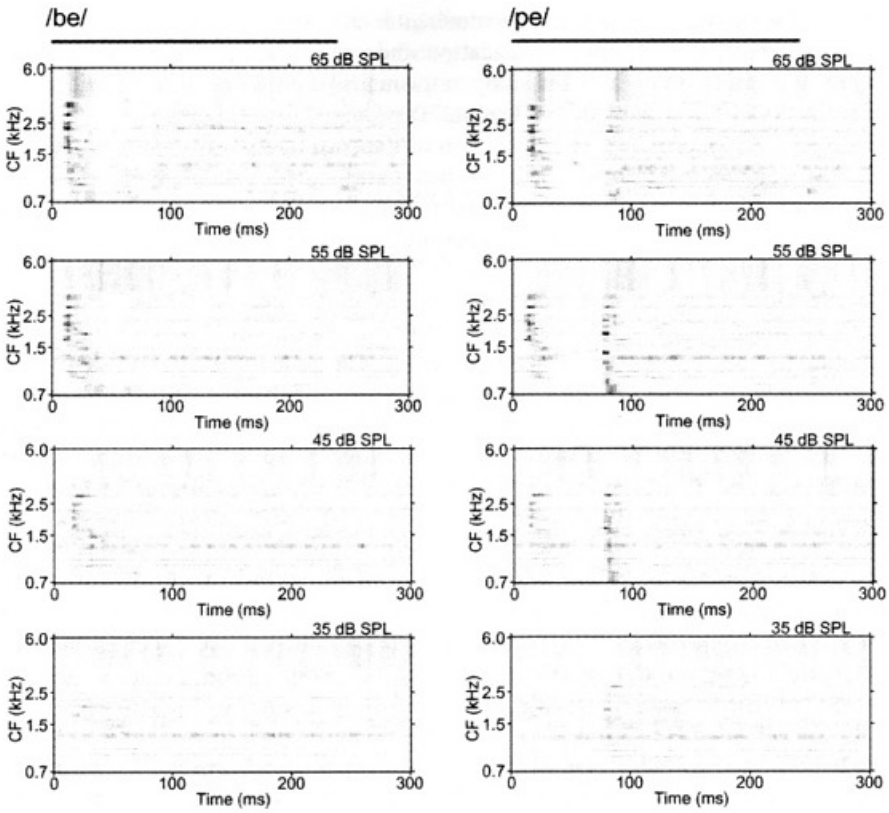

FIG. 9.5. Neurograms of AI for two CVs as a function of sound intensity. Spike count for each cortical location was normalized by the response to a CF tone at the transition point of the rate/level function (Schreiner et al., 1992). The grayscale bar shows the normalized response magnitude. Each CF is plotted at its proper location along the logarithmic frequency axis along the ordinate. The width of each trace is inversely proportional to the relative sampling density at a given CF. Stimulus onset is at time zero ms. The duration of [bɛ] was 200 ms, and 260 ms for [pɛ]. Voice-onset time for [pɛ] was 60 ms.

formant frequency (2.5 kHz) is the least intense of the three formants, neurons near this frequency respond with the shortest latencies, whereas neurons near the second formant (1.7 kHz) and the first formant (0.6 kHz) respond with increasingly longer latencies. This may reflect a mechanism enhancing minor latency differences already present in more peripheral stations (Greenberg, Poeppel, & Roberts, 1997). By contrast, the second phasic response for the unvoiced stop-consonant shows a quite uniform onset latency at the beginning of voicing across all neurons. There are only small effects on absolute timing and response duration, due directly either to CF or to sound intensity, at least between 45 to 65 dB SPL (sound pressure level). Below 45 dB SPL, the initial response disappears for both voiced and unvoiced CVs.

Relation to Previous Studies and Functional Interpretation

To ultimately understand the neuronal basis of human speech perception and the transformations of acoustic to phonetic and, eventually, linguistic information, a number of parallel approaches need to be considered including the study of the songbird system, behavioral mammalian speech-perception models, neurophysiological mammalian models of peripheral and central mechanisms of speech coding, and imaging techniques in the human brain. Although there is currently some, albeit limited, experimental evidence on the mechanisms by which the central auditory system creates or arrays

representations of vocalizations and speech features, it is still not clear which representational principles contribute to the discrimination, classification, and perceptual grouping of complex signals.

These results, in combination with the study of the neural representation of species-specific vocalizations of cats (Gehr, Komiya, & Eggermont, 2000) and marmoset monkeys (Nagarajan et al., 2002; Wang et al., 1995), provides an impression of the cortical activation pattern for a complex signal across the frequency axis in AI. These studies reveal that the spectro-temporal pattern in the acoustics of vocalizations is reflected in the spectro-temporal firing pattern of individual neurons and distributed neuronal populations in AI. Neuronal responses to any complex sound signal are distributed very widely across AI. At the same time, the response evoked by a vocalization scattered in discrete cortical patches are synchronized to stimulus events and to each other. As a result, at any major transition during the course of the signal, a temporally coherent activation of specific neuronal subpopulations of the cortical field is present. The cells that respond to a given stimulus share membership in some but not all neuronal assemblies involved in coding that sound. Major phonetic distinctions, such as VOT, formant locations, formant transitions, and presence or absence of the first formant, can be reflected in the spatial-temporal activity patterns. These results suggest that AI represents species-specific vocalizations and complex signals such as CV sounds by temporally integrated, spectrally distributed, spatially dispersed, and synchronized cortical cell assemblies that represent each individual vocalization in a specific way (see Nagarajan et al., 2002; Wang et al., 1995; Wong & Schreiner, 2003). The formation of such representational structures within AI neuronal populations reflects the anatomical and functional organization of dynamic RF properties in AI that is also reflected in the spatial organizations seen for responses to more simple stimuli. The establishment of the relationship between the responses to complex sounds and the functional organizations seen with simple sounds is key to a better understanding of the coding principles for speech sounds in auditory cortex.

Combined, these findings underscore the fact that temporal processing properties are significant for sensory cortical processes as evidenced by the global and local distribution of neurons with different onset latencies. This has direct consequences for the form of the cortical representation of complex signal sequences such as animal vocalizations, speech, and music. Onset latencies in auditory cortical layers IIIb and IV have subregional differences and, as in other modalities, onset latencies can differ significantly between cortical layers (e.g., Ferster & Lindström, 1985; Welker, Rao, Dorfl, Melzer, & Van der Loos, 1992). Thus, the temporal grain of the signal representation in areal and laminar dimensions can differ substantially. Together with subregional differences in bandwidth, intensity, and binaural coding, the potential of AI emerges for creating or maintaining segregated processing streams in which several stimulus representations are interleaved across the framework imposed by tonotopic organization. Certain features thus resemble those found in visual and somatic sensory cortex. In each of these two modalities, there is subregional segregation of certain properties across a topographic map in some cases (e.g., chromatic and submodality representation, respectively), whereas other features have a non-isotropic representation (e.g., certain patchy intrinsic connections in area 17, and irregularities in the commissural projections of areas 1, 2, and 3). The distributed nature of spectral and temporal response properties results in a complex and distinct pattern of spatial-temporal activation of primary auditory cortex for every distinct auditory stimulus.

CONCLUSIONS

Auditory receptive fields recorded in cat auditory cortex are time-variant within 10 to 30 ms after stimulation with tone-burst stimuli that do not contain any specifically time-variant properties besides the level-dependent slope of the stimulus envelope. The fact that time-variant RFs show various asymmetries that are likely not based on peripheral trigger mechanisms is a strong indication of the nonseparable nature of spectro-temporal processing properties. It is argued that dynamically maintained RFs are a specific adaptation to the processing of complex speech-like sounds. They are hypothesized to act as a temporal normalization of the rapidly

changing spectral contents, thereby aligning the occurrence of neural events leading to a globally or locally synchronized and coherent firing of single cells or populations of cells. This activity marks and characterizes the occurrence of relatively infrequent but perceptually defining segments in natural vocalization, as demonstrated in the spectral-temporal representation of CV syllables in auditory cortex.

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