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PRINCIPLES OF AUDITORY INFORMATION-PROCESSING DERIVED FROM NEUROETHOLOGY

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Summary

For auditory imaging, a bat emits orientation sounds (pulses) and listens to echoes. The parameters characterizing a pulse–echo pair each convey particular types of biosonar information. For example, a Doppler shift (a difference in frequency between an emitted pulse and its echo) carries velocity information. For a 61-kHz sound, a 1·0-kHz Doppler shift corresponds to $2\cdot8\,\mathrm{m\,s^{-1}}$ velocity. The delay of the echo from the pulse conveys distance (range) information. A 1·0-ms echo delay corresponds to a target distance of 17 cm. The auditory system of the mustached bat, *Pteronotus parnellii*, from Central America solves the computational problems in analyzing these parameters by creating maps in the cerebral cortex.

The pulse of the mustached bat is complex. It consists of four harmonics, each of which contains a long constant-frequency (CF) component and a short frequency-modulated (FM) component. Therefore, there are eight components in the emitted pulse (CF_{1-4} and FM_{1-4}). The CF signal is particularly suited for target velocity measurement, whereas the FM signal is suited for target distance measurement. Since the eight components differ from each other in frequency, they are analyzed in parallel at different regions of the basilar membrane in the inner ear. Then, they are separately coded by primary auditory neurons and are sent up to the auditory cortex through several auditory nuclei. During the ascent of the signals through these auditory nuclei, neurons responding to the FM components process range information, while other neurons responding to the CF components process velocity information.

A comparison of the data obtained from the mustached bat with those obtained from other species illustrates both the specialized neural mechanisms specific to the bat's auditory system, and the general neural mechanisms which are probably shared with many different types of animals.

Biosonar signals

For capture of prey (flying insects) and orientation, the mustached bat (*Pteronotus parnellii*) emits orientation sounds (biosonar pulses), each of which consists of a long constant-frequency (CF) component followed by a short frequency-modulated (FM) component. Since each orientation sound contains

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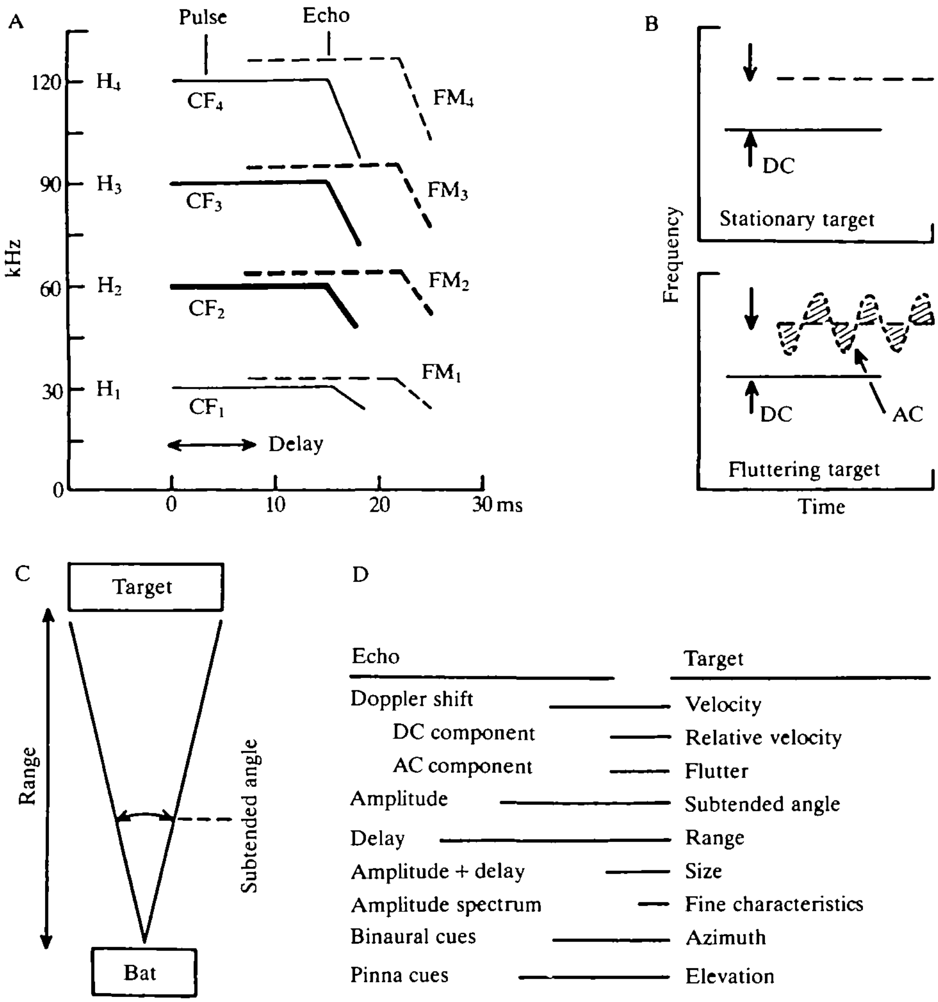
four harmonics (H_{1-4}), there are eight components that can be defined (CF_{1-4}, FM_{1-4}). In the emitted sound, the second harmonic (H_2) is always predominant and the frequency of CF_2 is about 61 kHz (Fig. 1A). The frequency of the CF component is different among subspecies and to some extent among individuals of the same subspecies. It also differs between males and females. For FM_2, the frequency sweeps down from 61 kHz to about 49 kHz. H_3 is 6–12 dB weaker than H_2, and H_1 and H_4 are 18–36 and 12–24 dB weaker than H_2, respectively.

Echoes eliciting behavioral responses in the mustached bat always overlap temporarily with the emitted sound, e.g. Fig. 1A. As a result, biosonar information must be extracted from a complex sound potentially containing up to 16 components. The CF component is an ideal signal for target detection and the measurement of target velocity (relative movements and wing beats), because the reflected sound energy is highly concentrated at a particular frequency. The mustached bat uses the CF component for this purpose and performs an interesting behavior called Doppler-shift compensation (Schnitzler, 1970). The short FM component, however, is suited for ranging, localizing and characterizing a target because of the distribution of its energy over many different frequencies. Different parameters of echoes received by the bat carry different types of information about a target (Fig. 1D).

Parallel-hierarchical processing of complex biosonar signals

The eight components (CF_{1-4} and FM_{1-4}) of the orientation sound of the mustached bat all differ from each other in frequency, and are analyzed in parallel at different regions of the basilar membrane (Fig. 2, bottom). The signals are then coded and sent into the brain by peripheral neurons. In the brain, the signals are sent up to the auditory cortex through many auditory nuclei where signal-processing takes place. For simplicity, we may consider that there are eight channels for the processing of these signal elements: CF_1 channel, CF_2 channel, and so on. The CF_2 channel is very large relative to any other channel and is associated with an extraordinarily sharply tuned local resonator in the cochlea for fine frequency analysis (Fig. 2).

In the CF_1, CF_2 and CF_3 channels (Fig. 2), frequency-selectivity is increased, and amplitude-selectivity is added by inhibition to some neurons in the cochlear nucleus and also to many neurons at higher levels. In a certain region of the medial geniculate body, part of the CF_1 channel and part of the CF_2 or CF_3 channel are integrated, so that neurons in this region respond poorly to the CF_1, CF_2 or CF_3 tone when delivered alone, but respond strongly when the CF_1 tone is delivered together with the CF_2 or CF_3 tone. A deviation of the CF_2 or CF_3 frequency from the exact harmonic relationship with the CF_1 frequency, i.e. an amount of Doppler shift, is a critical parameter for their excitation (Suga, 1984). These CF/CF combination-sensitive neurons project to the CF/CF area of the auditory cortex. In the CF/CF area, two types of CF/CF neurons, CF_1/CF_2 and CF_1/CF_3, are clustered separately and form frequency-*vs*-frequency coordinates within each



Echo	Target
Doppler shift	Velocity
DC component	Relative velocity
AC component	Flutter
Amplitude	Subtended angle
Delay	Range
Amplitude + delay	Size
Amplitude spectrum	Fine characteristics
Binaural cues	Azimuth
Pinna cues	Elevation

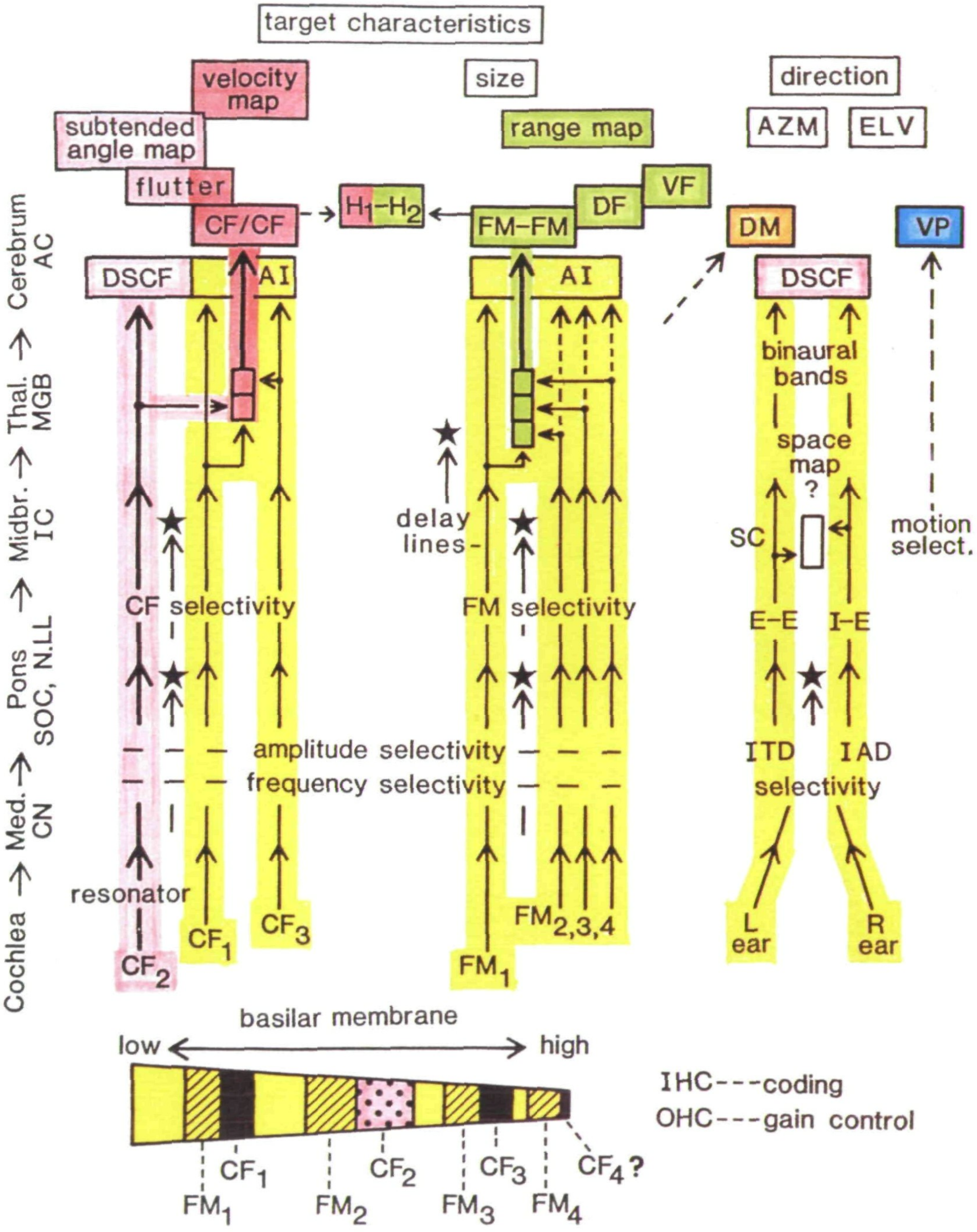
Fig. 1. Orientation sounds (biosonar pulses) of the mustached bat *Pteronotus parnellii* and the information carried by the signals. (A) Schematic sonagram of the biosonar pulse (solid lines) and the Doppler-shifted echo (dashed lines). The four harmonics (H_{1-4}) of both the pulse and the echo each contain a long CF component (CF_{1-4}) and a short FM component (FM_{1-4}). Thickness of the lines indicates the relative amplitude of each harmonic. In the pulse, H_2 is the strongest, followed by H_3, H_4 and H_1. (B) When the mustached bat flies towards or near a stationary object, the frequency of the echo becomes higher than the emitted pulse due to the Doppler effect (top graph). This steady shift is called the DC component of the Doppler shift. When the bat flies towards a flying insect the Doppler shift of the echo consists of a DC component proportional to the relative velocity and a periodic frequency modulation (FM) proportional to the speed of wing beat (lower graph). This periodic FM is called the AC component of the Doppler shift. The AC component is complicated because the insect's four wings move in complex patterns and in different phase relationships relative to the bat. The echo from the flying insect is also modulated in amplitude. (C) Target size is determined from both target range and subtended angle. (D) Relationship between echo properties and target properties (Suga *et al.* 1983).

Fig. 2. Parallel-hierarchical processing of different types of biosonar information carried by complex biosonar signals. The CF_{1-4} and FM_{1-4} of the orientation sound are analyzed at different portions of the basilar membrane in the cochlea (bottom). Inner and outer hair cells (IHC and OHC) on the membrane are, respectively, related to stimulus coding and gain control. The signal elements are separately sent up to the auditory cortex (AC) through several auditory nuclei (left margin): cochlear nucleus (CN), superior olivary complex (SOC), nucleus of lateral lemniscus (N.LL), inferior colliculus (IC) and medial geniculate body (MGB). During the ascent of the signals, frequency, amplitude, CF and FM selectivities are added to some neurons (arrows with a star). Each star indicates that the addition of selectivity takes place in the auditory nuclei and cortex as well as in the nucleus where the arrow starts. The CF_2 channel is disproportionately large and projects to the DSCF (Doppler-shifted CF processing) area of the auditory cortex. In certain portions of the MGB, two channels processing different signal elements (e.g. CF_1 and CF_2 or FM_1 and FM_2 channels) are integrated to produce 'combination-sensitive' neurons. FM–FM combination-sensitive neurons utilize the delay lines created in the FM_1 channel for processing range information. CF/CF and FM–FM combination-sensitive neurons, respectively, project to the CF/CF and FM–FM areas of the auditory cortex, where relative velocity or range information is systematically represented. Because of cortico-cortical connections, DF, VF and H_1–H_2 areas also consist of combination-sensitive neurons (center top). The DSCF area has the frequency-*vs*-amplitude coordinates to represent velocity and subtended angle information of a target. The DSCF area consists of two subdivisions mainly containing I–E or E–E binaural neurons (right column). Motion-sensitive neurons appear to be in the ventroposterior (VP) area of the auditory cortex. AI, primary auditory cortex; AZM, azimuth; ELV, elevation (based upon Suga, 1988).

cluster for the representation of Doppler shifts, i.e. velocity information (Fig. 3). CF/CF neurons show sharp 'level-tolerant' frequency-tuning curves and are remarkably specialized to respond to a particular frequency relationship between the two CF tones (Suga & Tsuzuki, 1985). The signal-processing in the CF channels is thus 'parallel-hierarchical'.

In the FM_1, FM_2, FM_3 and FM_4 channels (Fig. 2), frequency-selectivity is increased and amplitude-selectivity is added to some neurons by inhibition. Interestingly, FM-selectivity is also added to some neurons by disinhibition, so that these 'FM-specialized' neurons respond to FM sounds, but not to CF tones or noise bursts. In a certain region of the medial geniculate body, part of the FM_1 channel and part of the FM_2, FM_3 or FM_4 channels are integrated, so that neurons in this region respond poorly to these FM sounds when delivered alone, but respond strongly to the FM_1 sound combined with the FM_2, FM_3 or FM_4 sound. The delay of the FM_2, FM_3 or FM_4 sound from the FM_1 sound, i.e. echo delay, is the critical parameter for their facilitative responses. These FM–FM combination-sensitive neurons act as 'delay-dependent multipliers' for processing target range information (Suga, 1989). The delay lines utilized by these neurons are created by neurons responding to the FM_1 sound in the inferior colliculus and also the medial geniculate body. The FM–FM neurons in the medial geniculate body project to the FM–FM area of the auditory cortex. In the FM–FM area, three types of FM–FM neurons, FM_1–FM_2, FM_1–FM_3 and FM_1–FM_4, are clustered separately and form

Parallel-Hierarchical Signal Processing (Tentative Scheme)



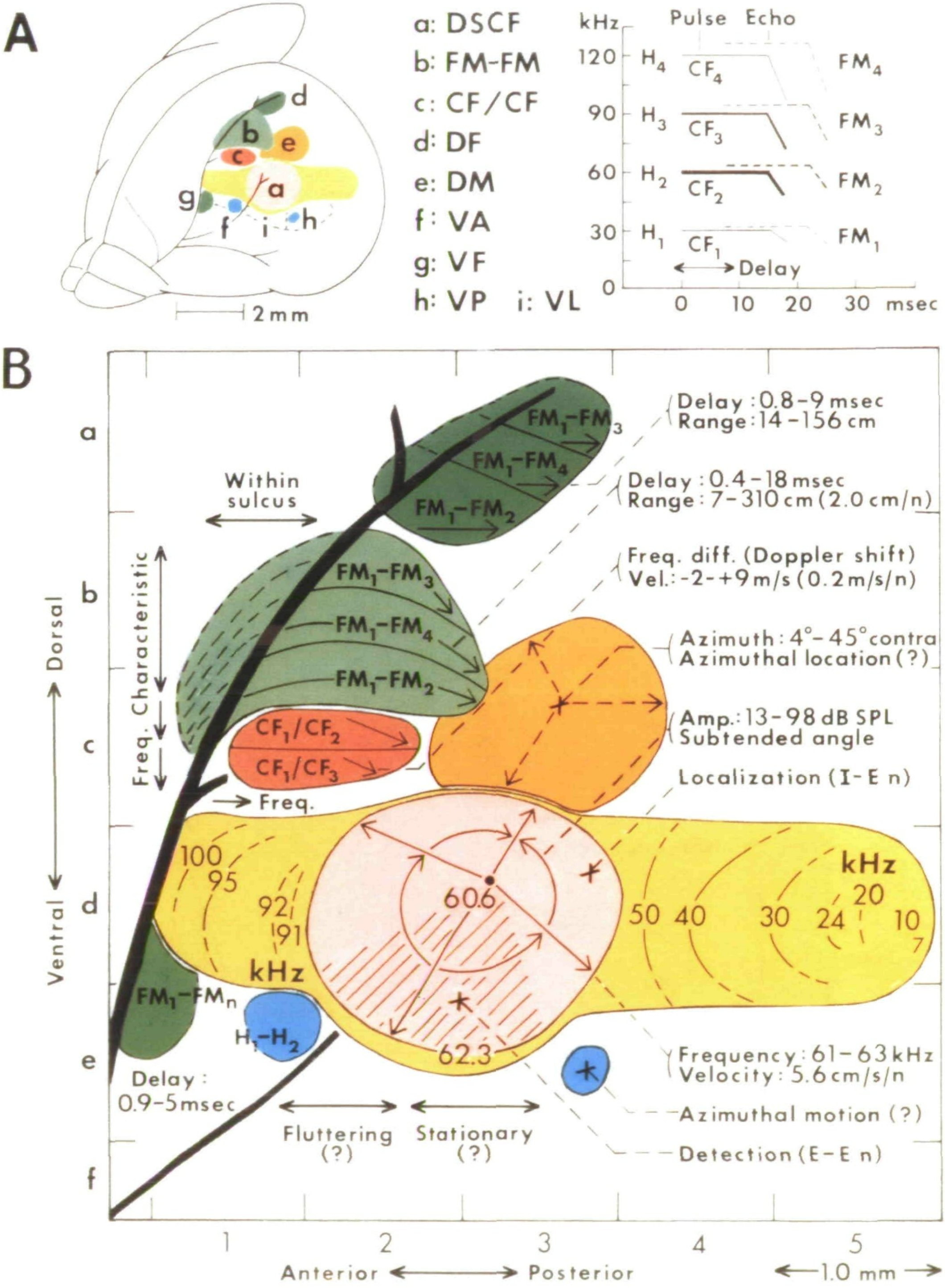

A
a: DSCF
b: FM-FM
c: CF/CF
d: DF
e: DM
f: VA
g: VF
h: VP
i: VL
2 mm
kHz
Pulse
Echo
120
90
60
30
0
H_4
H_3
H_2
H_1
CF_4
CF_3
CF_2
CF_1
FM_4
FM_3
FM_2
FM_1
Delay
0
10
20
30
msec
B
a
b
c
d
e
f
Dorsal
Ventral
Within sulcus
Freq. Characteristic
Freq.
FM_1-FM_3
FM_1-FM_4
FM_1-FM_2
CF_1/CF_2
CF_1/CF_3
Delay: 0.8-9 msec
Range: 14-156 cm
Delay: 0.4-18 msec
Range: 7-310 cm (2.0 cm/n)
Freq. diff. (Doppler shift)
Vel.: -2-+9 m/s (0.2 m/s/n)
Azimuth: 4°-45° contra
Azimuthal location (?)
Amp.: 13-98 dB SPL
Subtended angle
Localization (I-E n)
100
95
92
91
60.6
62.3
50
40
30
24
20
10
7
kHz
FM_1-FM_n
H_1-H_2
Delay: 0.9-5 msec
Fluttering (?)
Stationary (?)
Frequency: 61-63 kHz
Velocity: 5.6 cm/s/n
Azimuthal motion (?)
Detection (E-E n)
1
2
3
4
5
Anterior
Posterior
1.0 mm

Fig. 3. Functional organization of the auditory cortex of the mustached bat. (A) Dorsolateral view of the left cerebral hemisphere. The auditory cortex consists of several areas (a–i). The DSCF, FM–FM, CF/CF, DF, VF and DM areas (a, b, c, d, g and e, respectively) are specialized for the systematic representation of biosonar information. The branches of the middle cerebral artery are shown by the branching lines. The longest branch is on the sulcus. (B) Graphic summary of the functional organization of the auditory cortex. The tonotopic representation of the primary auditory cortex and the functional organization of the DSCF, FM–FM, CF/CF, DF and DM areas are indicated by lines and arrows. The DSCF area has axes representing either velocity (echo frequency: 60·6–62·3 kHz) or subtended target angle (echo amplitude: 13–98 dB SPL) and is divided into two subdivisions suitable for either target detection (hatched) or target localization (unhatched). These subdivisions are occupied mainly by excitatory–excitatory (E–E) or inhibitory–excitatory (I–E) binaural neurons, respectively. The FM–FM area consists of three major types of FM–FM combination-sensitive neurons (FM_1–FM_2, FM_1–FM_3 and FM_1–FM_4), which form separate clusters. Each cluster has an axis representing target ranges from 7 to 310 cm (echo delay: 0·4–18 ms). The dorsoventral axis of the FM–FM area probably represents fine target characteristics. The CF/CF area consists of two major types of CF/CF combination-sensitive neurons (CF_1/CF_2 and CF_1/CF_3), which cluster independently. Each cluster has two frequency axes and represents relative velocities from -2 to $+9\,\mathrm{m\,s^{-1}}$ (echo Doppler shift: $-0{\cdot}7$ to $+3{\cdot}2$ kHz for CF_2 and $-1{\cdot}1$ to $+4{\cdot}8$ kHz for CF_3). The FM–FM area projects to the DF area and a posterior part of the VA area. The DF area projects to the VF area. The DF and VF areas each consist of the three types of FM–FM neurons, whereas the VA area contains only H_1–H_2 combination-sensitive neurons. The DM area appears to have an azimuthal axis representing the azimuthal location of a target. In the VP area, motion-sensitive neurons have been found. n, neuron (after Suga, 1988).

an echo-delay axis in each cluster for the representation of target range information (Fig. 3; Suga, 1984). Therefore, the signal-processing in the FM channels is also parallel-hierarchical.

As described above, part of one channel is integrated with part of the other channel in the medial geniculate body. The remaining parts of these channels project to the auditory cortex, which is not described above. For instance, part of the CF_2 channel projects to the DSCF (Doppler-shifted CF processing) area of the auditory cortex which has frequency-*vs*-amplitude coordinates to represent target velocity information and subtended target angle information. The DSCF area overrepresents frequencies between the CF_2 resting frequency (about 61 kHz) of the bat's own sound and 1·0 kHz above it. The DSCF area has two subdivisions which predominantly contain either I–E or E–E binaural neurons (Figs 2, 3). Fig. 2 is only to illustrate the parallel-hierarchical processing of biosonar information which has thus far been explored.

Almost all frequencies found in the biosonar signals are represented not only in the areas which appear to be important for echolocation, but also in the other areas which do not appear to be important for echolocation. These other areas are probably important for processing communication sounds. Except for the CF_2 channel, which is specialized for processing biosonar information, from the periphery to the auditory cortex, a clear separation of biosonar signal processing from non-biosonar signal processing first appears in the medial geniculate body.

The auditory cortex of the mustached bat shows multiple cochleotopic (tonotopic) representation, which is directly related to representation of different types of biosonar information. Fig. 3 shows several functional areas that have been explored electrophysiologically. In these areas, certain response properties of single neurons arranged orthogonally to the cortical surface are identical. (For example, each column in the CF/CF area is characterized by a particular combination of two frequencies.) In this sense, there is a columnar organization. Along the cortical surface, however, the response properties vary systematically and form axes for representation of particular types of biosonar information, as shown in Fig. 3. Among the various functional areas, the CF/CF, FM–FM, DF, VF and VA areas consist of combination-sensitive neurons, so that these areas are particularly interesting in terms of neural mechanisms for processing complex sounds. [For further information of the auditory cortex of the mustached bat, see Suga (1984, 1988).]

The FM–FM area, representing target ranges of up to 310 cm, projects to the DF and VA areas of the cerebrum as well as other regions of the brain (Fig. 3). The DF area consists of three clusters of FM–FM neurons. In each cluster, target ranges of up to 140 cm are systematically represented. The DF area projects to the VF area, as well as other areas in the brain to which the FM–FM area does not project. The VF area also consists of three clusters of FM–FM neurons and represents target ranges of up to 80 cm. We do not yet know the functional significance of these multiple-range (delay) axes. One may hypothesize that these three different areas are related to echolocation behavior at different distances to targets. The H_1–H_2 area, part of the VA area, contains combination-sensitive neurons that are different from FM–FM and CF/CF neurons. They show facilitative responses to the CF_2 and/or FM_2 of an echo when these are combined with the CF_1 and/or FM_1 of the biosonar pulse.

Auditory information is sent not only to the association cortex from the auditory cortex, but also to the motor system. Both the FM–FM and CF/CF areas project to the pontine motor nuclei which, in turn, project to the cerebellum. In the cerebellar vermis, there are tiny clusters of FM–FM and CF/CF neurons. Biosonar information is also sent to the vocal system. Some neurons in the periaqueductal gray and midbrain reticular formation, for instance, become active prior to vocalization and respond to acoustic stimuli delivered from a loudspeaker.

The projections of the CF/CF area thus far studied do not overlap with those of the FM–FM area. All the data indicate that complex acoustic signals are processed in a parallel-hierarchical way in the ascending auditory system and beyond the auditory cortex.

Principles for the processing of information-bearing parameters

A comparison of the data obtained from the mustached bat with those obtained from other species illustrates the specialization of the bat's auditory system for echolocation and also general neural mechanisms that are probably shared by many different species. These mechanisms are listed below. The data indicating the existence of each mechanism were obtained mainly from the animals listed in parentheses. The data obtained from the owl are related to sound localization, and those obtained from the other species are related to sound reception, frequency analysis and/or processing of complex sounds important to a species.

(1) The peripheral auditory system has evolved not only for the reception of biologically important sounds, but also for frequency analysis of these sounds that fulfil species-specific requirements. The sharpness of a frequency-tuning curve, sensitivity and/or population can be higher for peripheral neurons tuned to frequencies of sounds that are most important to the species [bats (Suga, 1984; Neuweiler *et al.* 1980), mice (Brown, 1973*a*,*b*) and frogs (Narins & Capranica, 1976)]. A population is larger for neurons with sharper frequency tuning [bats (Suga, 1984; Neuweiler *et al.* 1980)].

(2) The frequency tuning of some central neurons is sharpened by lateral inhibition, which eliminates the 'skirt' of a frequency-tuning curve [bats (Suga, 1973, 1988, 1989), cats (Katsuki *et al.* 1958; Evans & Nelson, 1973; Young & Brownell, 1976), mice (Ehret & Moffat, 1985) and frogs (Fuzessery & Feng, 1982)]. The more important the frequency analysis of particular components of sounds, the more pronounced is the neural sharpening for neurons tuned to these components [bats (Suga & Tsuzuki, 1985)].

(3) The frequency tuning of some other central neurons is broadened by 'excitatory' convergence. Broadly tuned neurons are clustered separately from sharply tuned neurons in different portions of the auditory system [bats (Suga, 1973) and cats (Aitkin, 1973; Aitkin *et al.* 1975; Schreiner & Cynader, 1984)].

(4) A phase-locked or stimulus-locked response is commonly strong and observed up to 3 kHz at the periphery, but it is weak and rarely observed to stimuli higher than 0·3 kHz in the auditory cortex. The population of 'phase-locking' neurons is smaller and the degree of phase-locking is progressively lower at higher levels of the auditory system [cats (de Ribaupierre *et al.* 1972; Rouiller *et al.* 1979)]. Thus, a temporal code at the periphery can be changed into a place code at higher levels of the auditory system [bats (Suga, 1984, 1989), owls (Konishi *et al.* 1988) and frogs (Rose & Capranica, 1984)].

(5) The cochlea, or part of it, projects in parallel to different subdivisions of a nucleus or nuclear complex at each level of the ascending auditory system [bats (Suga, 1984, 1988), cats (Woolsey, 1961), monkeys (Merzenich & Brugge, 1973), owls (Konishi *et al.* 1988) and frogs (Hall & Feng, 1987)]. These multiple cochleotopic or tonotopic representations result from the divergence of axons. This divergence is usually associated with a convergence of axons for sorting out different types of auditory information. This combined divergence–convergence occurs repeatedly in the central auditory system and is the anatomical basis of parallel-hierarchical processing of information for both acoustic pattern recognition and sound localization. By this divergence–convergence, neural filters are

created which are tuned to various information-bearing parameters (IBPs) other than frequency [bats (Suga, 1984, 1988), owls (Konishi *et al.* 1988) and frogs (Hall & Feng, 1987)]. These IBP-tuned neurons (hereafter, IBP neurons or filters) act as cross-correlators which correlate incoming signals with their filter properties, i.e. with neurally stored information. It should be noted that 'biologically important' complex sounds are processed by combination-sensitive neurons, i.e. IBP filters tuned to different combinations of signal elements [bats (Suga, 1984, 1988), song birds (Margoliash, 1983) and frogs (Mudry *et al.* 1977; Fuzessery & Feng, 1983)].

(6) IBP filters can be sharpened by lateral inhibition [bats (Suga, 1988, 1989; Suga & Tsuzuki, 1985), owls (Konishi *et al.* 1988) and frogs (Rose & Capranica, 1984)].

(7) Different types of IBP filters are clustered separately at particular locations of the central auditory system. In other words, the system contains functional subdivisions or areas specialized for processing particular types of auditory information important to a species [bats (Suga, 1984, 1988), owls (Konishi *et al.* 1988) and frogs (Hall & Feng, 1987)].

(8) In each subdivision or area, IBP filters are systematically arranged so that they form an axis or axes representing the IBP or IBPs [bats (Suga, 1984, 1988) and owls (Konishi *et al.* 1988)]. If small differences in IBP values are not biologically important, the IBP axis may not be formed within the subdivision [frogs (Hall & Feng, 1987)]. It should be noted that, with the exception of frequency, there is no peripheral anatomical basis for IBP axes: they are created centrally from neural interactions. That is, they are computational axes or maps.

(9) The axis and/or population of neurons representing an IBP is apportioned according to the species-specific importance of the IBP [bats (Suga, 1984, 1988) and owls (Konishi *et al.* 1988)].

(10) The bandwidth of IBP filters is not so narrow as to express a particular value of an IBP by the excitation of only a few neurons located at a single location along the IBP axis. Even after the sharpening of the tuning of IBP filters by lateral inhibition, it is expressed by a spatiotemporal pattern of excitation of many neurons distributed along the IBP axis [bats (Suga, 1984, 1988) and owls (Konishi *et al.* 1988)].

(11) The functional organization of the auditory system can be different among different species, reflecting differences in species-specific auditory behavior and/or the properties of the acoustic signals used by them. The organization can also be different among individuals or between sexes within the same species when the properties of their biologically important acoustic signals are different among conspecifics or sexes [bats (Suga *et al.* 1987) and frogs (Narins & Capranica, 1976)].

(12) The auditory cortex consists of specialized areas excited only by biologically important sounds and an unspecialized area (primary auditory cortex) excited by less important and unfamiliar sounds as well as by the biologically important sounds [bats (Suga, 1984)]. The primary auditory cortex is tonotopically organized and contains neurons somewhat similar to peripheral neurons, probably for maintaining 'raw data'.

(13) For protection of information-processing during and immediately after vocalization, vocal self-stimulation is reduced not only by the middle ear muscles, but also by inhibition occurring in the central auditory system [bats (Suga & Shimozawa, 1974), monkeys (Müller-Preuss, 1980) and song birds (McCasland & Konishi, 1981)].

(14) Cortical representation of certain types of auditory information by combination-sensitive neurons is protected from masking by their unique response properties [bats (Suga, 1984)].

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