

5 minutes. On the average, it took about 2 minutes to unhook the sporangiophore from the Instron machine and prepare it for photography.

Figure 3 shows the data from four experiments. In each case, rotation predominated over elongation, compared to the results of control experiments. We often found that right after strain hardening we could measure significant rotation rates but no elongation rate (Fig. 3, b and d). This is predicted by the fibril reorientation model (the ratio of rotation to elongation increases as ϕ decreases). As shown in Fig. 3, this relative increase in rotation stems from a disproportionate decrease in elongation after strain hardening rather than an increase in the rotation rate. The net decrease in both rotation and elongation is also consistent with the reorientation model, as shown in Fig. 1b: D_t and D_s both decrease in magnitude as ϕ decreases, but D_s decreases faster. Finally, we note that the increase in the ratio of the rotational to the elongational growth rate measured after strain hardening is similar to that observed in the lower region of the growing zone (6). It is also in agreement with the concept that the right-handed spiral configuration of microfibrils is becoming less flat in the lower region of the growing zone; that is, ϕ is progressively decreasing toward the lower region of the growing zone. In conclusion, our data

are consistent with the fibril reorientation model, and to our knowledge no other proposed model predicts the change in ratios that we have measured.

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References and Notes

1. A. J. P. Oort, *Proc. K. Ned. Akad. Wet.* **34**, 564 (1931).
2. E. S. Castle, *Am. J. Bot.* **29**, 664 (1942).
3. K. Bergman *et al.*, *Bacteriol. Rev.* **33**, 99 (1969).
4. J. K. E. Ortega and R. I. Gamow, *J. Theor. Biol.* **47**, 317 (1974).
5. C. N. Ahlquist and R. I. Gamow, *Plant Physiol.* **51**, 586 (1973).
6. J. K. E. Ortega, J. F. Harris, R. I. Gamow, *ibid.* **53**, 485 (1974).
7. A. J. P. Oort and P. A. Roelofsen, *Proc. K. Ned. Akad. Wet.* **35**, 898 (1932).
8. P. A. Roelofsen, *Biochim. Biophys. Acta* **6**, 340 (1950).
9. —, *ibid.*, p. 357.
10. R. D. Preston, *The Physical Biology of Plant Cell Walls* (Chapman & Hall, London, 1974).
11. J. K. E. Ortega, R. I. Gamow, C. N. Ahlquist, *Plant Physiol.* **55**, 333 (1975).
12. Loading and unloading a sporangiophore alters the mechanical properties of the cell wall such that a sporangiophore having the same load a second time exhibits less extension. This change in extensibility decreases until it becomes negligible after a number of consecutive loadings. In the experiments reported here, each sporangiophore was loaded and unloaded ten times to a final load of 240 mg in less than 1/2 minute.
13. During elongational growth the markers in the upper region of the growing zone are slowly displaced away from the sporangium. These markers then can no longer be used to determine rotational and elongational rates of the entire growing zone since they reflect only cell wall changes that occur in the growing zone at or below their location.
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cy or repetition rate is less than 5 kHz (3). Therefore it is conceivable that almost all information-bearing elements and their combinations lower than 4 kHz are processed in the form of phase-locked discharges of many auditory neurons in the brain. This may be considered an extension of the volley theory proposed for the neural basis of frequency discrimination (4). Several papers, however, demonstrate that auditory neurons in the cerebral cortex are commonly phasic (5) and show poor phase-locked discharges to sounds above 1.0 kHz (6), and that some of them are specialized to respond best to particular sounds (2, 6–8).

Therefore an alternative hypothesis (9) is that acoustic signals are represented by neurons arranged in coordinates of frequency and amplitude. When the amplitude spectra of the acoustic signals vary with time, the spatial pattern of the neural activity in this coordinate system would vary accordingly (*the spatiotemporal pattern theory*). In still another hypothesis, acoustic signals are eventually processed by feature detectors, and the activity of the feature detectors leads to the categorization of acoustic signals in the brain (*the detector theory*). These theories are not mutually exclusive, because the auditory system appears to use all three principles in processing acoustic signals (6–9). The data supporting the detector theory are, however, very limited. The major purpose of this report is to demonstrate neurons that assemble harmonically related components in animal sounds (10) and accordingly favor the detector theory.

To study the neural basis of acoustic pattern recognition, it is essential to know the physical properties and biological significance of the acoustic signals used by the species and to employ these signals or their information-bearing elements as stimuli, because the auditory system has evolved to detect and process biologically significant sounds. In the mustache bat, *Pteronotus parnellii rubiginosus*, the biosonar signals (also called orientation sounds or pulses) are stereotyped, moderately complex, and essential for survival. The biological significance of individual signal elements is known (11). Furthermore, individual information-bearing elements in ultrasonic signals cannot be coded by the volley principle. The mustache bat is thus an ideal animal in which to study neural specialization to detect particular information-bearing elements or combinations of them. In this report, we describe the response properties of harmonic-sensitive neurons in the auditory cortex of

Harmonic-Sensitive Neurons in the Auditory Cortex of the Mustache Bat

Abstract. *Human speech and animal sounds contain phonemes with prominent and meaningful harmonics. The biosonar signals of the mustache bat also contain up to four harmonics, and each consists of a long constant-frequency component followed by a short frequency-modulated component. Neurons have been found in a large cluster within auditory cortex of this bat whose responses are facilitated by combinations of two or more harmonically related tones. Moreover, the best frequencies for excitation of these neurons are closely associated with the constant-frequency components of the biosonar signals. The properties of these neurons make them well suited for identifying the signals produced by other echolocating mustache bats. They also show how meaningful components of sound are assembled by neural circuits in the central nervous system and suggest a method by which sounds with important harmonics (or formants) may be detected and recognized by the brain in other species, including humans.*

In English speech sounds, there are several types of acoustic cues or information-bearing elements (1). Formants—that is, constant-frequency (CF) components, are essential for recognition of vowels. Fills—noise bursts—are important for recognition of some fricative consonants. Transitions—frequency-modulated (FM) components—and voice onset time are important for recog-

nition of plosive consonants and some fricative consonants combined with vowels. There are also FM components in other phonemes (glides). The CF, FM, and noise burst elements are found in animal sounds as well (2).

In response to sound, mammalian cochlear nerve fibers can send impulses into the brain in stimulus-locked (or phase-locked) fashion when the frequen-

the recording electrode was inserted obliquely, it was clear that neurons that assemble different elements of emitted pulses and echoes were found in separate groups located in identifiable regions of the auditory cortex. In the following, the response properties of some CF₁/CF facilitation (or specialized) neurons are explained.

To date, we have studied the response properties of 44 CF/CF facilitation neurons consisting of five types: CF₁/CF₂, CF₁/CF₃, CF₁/CF_{2,3}, CF₁/CF_{3,4}, and CF₂/CF₃ (19). Almost all of them responded to one or two individual components delivered alone at amplitudes greater than 80 dB SPL (sound pressure level). Responses were often not prominent or consistent, and the latency was usually long and fluctuating. When two or more components were combined in an appropriate frequency, amplitude, and temporal relationship, however, their responses became prominent and consistent and the response latency shorter and

more constant. Figure 1C demonstrates facilitation of responses of a CF₁/CF₂ neuron. The neuron responded very poorly to a CF₁ of 29.75 kHz and 46 dB SPL and did not respond to a CF₂ of 59.26 kHz below 76 dB SPL. When the CF₁ and CF₂ were delivered simultaneously, however, the neuron responded strongly and the latency was short, 6 to 8 msec.

The principle that the larger the amplitudes of combined components, the larger the facilitation, did not hold. Instead, maximum facilitation was commonly evoked when two or three components were in a particular amplitude relationship unique to the individual neurons. In Fig. 1C, for instance, maximum facilitation occurs when the CF₁ and CF₂ are 46 and 56 dB SPL, respectively. An impulse-count function, which relates stimulus amplitude to the number of impulses per stimulus, clearly demonstrates this point. In Fig. 1D, for instance, CF₂ should be 56 dB SPL and

CF₁ should be between 50 and 70 dB SPL for maximum facilitation. The difference in threshold was small, 31 dB SPL for CF₁ alone and 23 dB SPL for CF₁ with CF₂. However, the magnitude of response (number of impulses per stimulus) to CF₁ with CF₂ was much larger than to CF₁ alone at less than 80 dB SPL. At maximum facilitation, the number of impulses per stimulus was 76 percent more than the maximum number of impulses evoked by the CF₁ alone. Compared with CF₂ alone, the threshold for CF₂ with CF₁ was 53 dB SPL lower and the response magnitude was four times larger. According to our definition, facilitation always involves an increase in number of impulses, but it is not necessarily associated with a decrease in threshold (20).

Facilitation properties vary among neurons: facilitation with a dramatic decrease in threshold, facilitation without a decrease in threshold, and so on. Examples of tuning curves and facilitation-tuning curves of four single neurons are presented in Fig. 2. A CF₁/CF₂ facilitation neuron in Fig. 2A responded poorly to single tones, with minimum thresholds of 58 dB SPL at 28.91 kHz and 74 dB SPL at 60.55 kHz. However, it responded vigorously to CF₁/CF₂, with minimum thresholds of 31 dB SPL at 29.75 kHz and 37 dB SPL at 59.39 kHz. It should be noted that the thresholds for CF₁ and CF₂ were both lowered by facilitation and that the best frequencies of CF₁ and CF₂ were harmonically related. A CF₁/CF₃ facilitation neuron in Fig. 2B responded poorly to single tones, with minimum thresholds of 76 dB SPL at 29.10 kHz and 43 dB SPL at 91.53 kHz. (In spite of the low threshold for a 91.53-kHz tone, the response to it was poor and fluctuated widely.) The neuron responded strongly to CF₁/CF₃, with minimum thresholds of 38 dB SPL at 28.91 kHz and 34 dB SPL at 91.53 kHz. The decrease in threshold by facilitation was prominent for CF₁ but small for CF₃. Figure 2C represents a CF₁/CF₃ facilitation neuron whose properties were different from those in Fig. 2B. Its single-tone threshold and facilitation threshold were the same for CF₁, but different by 65 dB for CF₃. In both neurons in Fig. 2, B and C, the best frequencies for facilitation were roughly harmonically related.

A large cluster of CF₁/CF₂ facilitation neurons was found dorsal to a cluster of CF₁/CF₃ facilitation neurons. At the center of each cluster, facilitation was most prominent. Between these two clusters there were CF₁/CF_{2,3} facilitation neurons forming either an independent cluster or a transitional area between clusters. Fig-

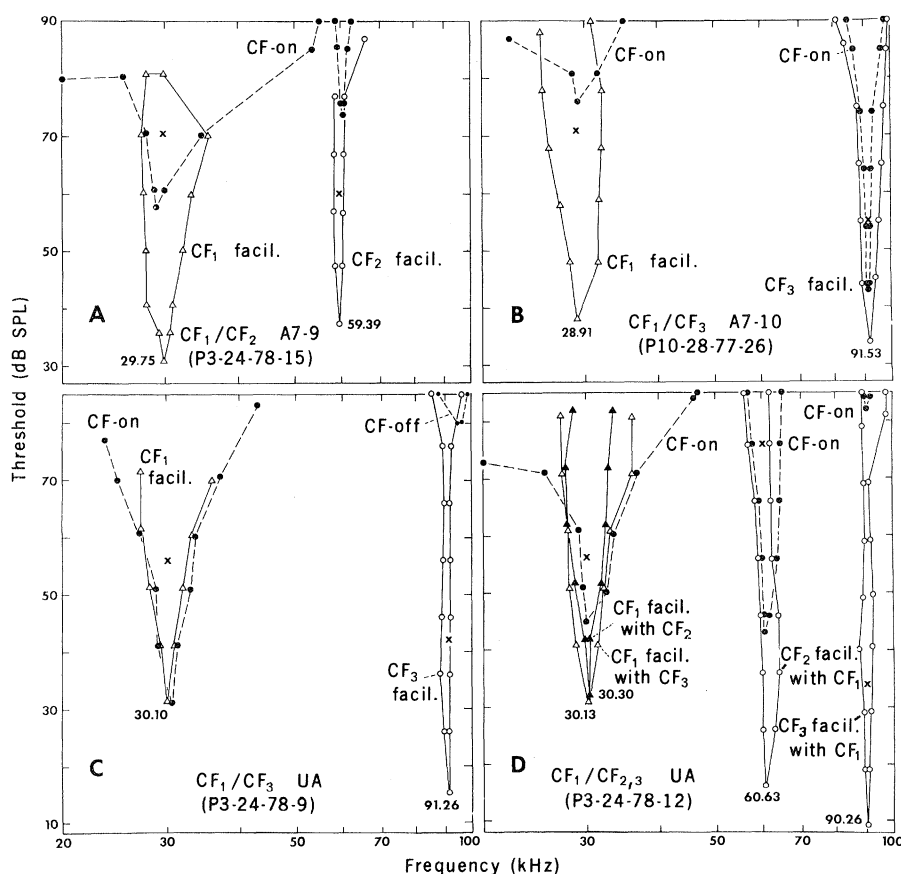


Fig. 2. Excitatory (dashed lines) and facilitation (solid lines) areas of four neurons (that is, the areas above or surrounded by tuning or facilitation-tuning curves). An excitatory area was measured by delivering a 34-msec-long CF tone, and a facilitation area was measured by delivering a 34-msec-long CF tone simultaneously with another 34-msec-long CF tone (conditioning tone) at a fixed frequency and amplitude. (A) A CF₁/CF₂ facilitation neuron recorded from an anesthetized bat 7 to 9 hours after Nembutal administration. The conditioning sound used to measure the CF₁ facilitation area was 59.39 kHz and 60 dB SPL; for the CF₂ facilitation area it was 29.75 kHz and 70 dB SPL (these are indicated by x's). (B) A CF₁/CF₃ facilitation neuron recorded 7 to 10 hours after Nembutal administration. (C) A CF₁/CF₃ facilitation neuron from an unanesthetized animal. (D) A CF₁/CF_{2,3} facilitation neuron from an unanesthetized animal. Conditioning sounds used for the data in (B), (C), and (D) are also indicated by x's.

ure 2D represents the tuning and facilitation-tuning curves of a $CF_1/CF_{2,3}$ facilitation neuron. The response of this neuron was facilitated when CF_1 was delivered together with CF_2 or CF_3 . The threshold for CF_3 decreased by 73 dB with the facilitation, and the thresholds for CF_1 and CF_2 decreased by 14 and 27 dB, respectively. CF_2/CF_3 evoked no facilitation. The response was largest when these three tone bursts were delivered simultaneously at the amplitudes indicated by the three x's in Fig. 2D. The best frequencies for facilitation, 30.13, 60.63, and 90.26 kHz, are harmonically related.

The precision of the harmonic relationship among CF best frequencies for facilitation was examined after normalizing to the mean best frequency of CF_1 , 29.66 ± 0.66 kHz ($N = 43$). The mean and standard deviation are 59.70 ± 0.98 kHz for CF_2 ($N = 33$), and 90.03 ± 2.31 kHz for CF_3 ($N = 21$). We estimate that our error in measuring the best frequency is 0.05 to 0.10 percent, less than the standard deviations. Thus the harmonic relationship among the best frequencies for facilitation is precise.

CF_1/CF facilitation neurons showed poor or no facilitation to simultaneous delivery of two or three harmonically related FM sounds, and were clearly specialized for harmonically related CF tones. Their responses became poor when a delay was introduced between the two (or three) CF tones. Unlike FM_1 -FM and H_1 -FM facilitation neurons, CF_1/CF facilitation neurons were thus not suited for ranging (8, 17). However, CF_1/CF facilitation neurons might be used for the detection of conspecific bats. The CF signals produced by other mustache bats would be perceived at longer distances than FM signals because of the high concentration of sound energy at discrete frequencies.

In CF/CF facilitation neurons, CF_1 was always an essential component. In the orientation sounds of the mustache bats recorded in our laboratory, the second harmonic is always predominant and the amplitudes of the first and third harmonics are about 12 and 6 dB lower, respectively. As recently found in the long-eared bat (*Plecotus phyllotis*) (21), the mustache bat may enhance the first harmonic of the orientation sound while flying in the open, but may emphasize the higher harmonics in a confined environment such as our laboratory. Also, there is less atmospheric attenuation for lower frequencies. The first harmonic may thus be detected at amplitudes appropriate for facilitation.

As demonstrated in Figs. 1D and 2,

CF_1/CF facilitation neurons are tuned to particular combinations of CF sounds. The best frequencies and best amplitudes of sounds for facilitation are different from neuron to neuron. Such variation is probably important for the detection of conspecific bats, which emit orientation sounds differing in amplitude spectrum. During echolocation, the mustache bat produces sounds at repetition rates between 5 and 100 per second. All CF_1/CF facilitation neurons studied responded to orientation sounds delivered at a rate of 5 to 40 per second, mimicking the search and approach phases of echolocation. Some of them responded to sounds delivered at a rate of 100 per second, corresponding to the terminal phase. Thus these neurons can function in all phases of echolocation (22).

During echolocation, sounds of other bats may be masked by self-vocalized sounds. As shown in Fig. 2 and in (23), neurons with best frequencies near the CF components (in particular CF_2) of the orientation sound are very sharply tuned, so that the masking effect of vocal self-stimulation would be greatly reduced by any difference in amplitude spectrum at the two ears between self-vocalized biosonar signals and signals emitted by other bats. Muscular (24) or neural (25) mechanisms for attenuation of vocal self-stimulation would also play a role in reducing the masking effect.

In conclusion, the bat's auditory system contains neural circuits that integrate signal components in different combinations at different identifiable places in the brain. We believe that our results demonstrate one of the most important neural mechanisms for processing biologically significant sounds. Human speech and animal sounds share several acoustic elements. Among different species and human groups, however, the acoustic parameters of the individual elements and the combinations of these elements are different and may carry different information. This implies that the functional organization of the auditory system should differ according to the type of signal processing. This speculation has some support from recent discoveries about functional organization which go beyond tonotopy (8, 9, 16, 17, 26). In humans, the neural mechanisms that process verbal sounds might appear to be unique, but they are derived from those that process nonverbal sounds. Therefore, some of the mechanisms in humans can be explored indirectly by comparative auditory neurophysiology. The auditory system of echolocating bats is specialized for processing biosonar signals. It may show us

the advanced state to which the system can be specialized for processing certain types of information and give us insight into the neural mechanisms for processing other types of information. Accordingly, this research will contribute to understanding the auditory mechanisms in other animals and humans. If, as in the mustache bat, neural processing of complex sounds in other animals is performed by neurons assembling their information-bearing elements, combination-sensitive neurons may suggest the possibility that vowels, vowel-like sounds, certain consonants, and their combinations in speech are processed by analogous neurons assembling formants or transitions, or both (27).

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References and Notes

1. F. S. Cooper, P. C. Delattre, A. M. Liberman, J. M. Borst, L. J. Gerstman, *J. Acoust. Soc. Am.* **24**, 597 (1952); A. M. Liberman, *ibid.* **29**, 117 (1957); P. B. Denes and E. N. Pinson, *The Speech Chain* (Williams & Wilkins, Baltimore, 1963); L. Lisker and A. S. Abramson, *Word* **20**, 384 (1964).
2. N. Suga, *Audiology (Basel)* **11**, 58 (1972); in *Basic Mechanisms in Hearing*, A. R. Møller, Ed. (Academic Press, New York, 1973), pp. 675-742.
3. In the little brown bat, *Myotis lucifugus*, N_1 responses clearly follow up to 2200 stimuli per second [A. D. Grinnell, *J. Physiol. (London)* **167**, 67 (1963)] and cochlear nerve fibers and neurons in the cochlear nucleus fully recover within 1 to 3 msec [N. Suga, *ibid.* **175**, 50 (1964)]. Primary auditory neurons in other mammals also follow acoustic events at high rates—up to 5000 sec⁻¹ in squirrel monkeys [J. E. Rose, J. F. Brugge, D. J. Anderson, J. E. Hind, *J. Neurophysiol.* **30**, 769 (1967)], up to 3000 sec⁻¹ in guinea pigs [I. Tasaki, *ibid.* **17**, 97 (1954)], and up to 3000 sec⁻¹ in domestic cats [W. T. Peake, M. H. Goldstein, N. Y.-S. Kiang, *J. Acoust. Soc. Am.* **34**, 562 (1962)]. The upper limit of stimulus-locked responses becomes higher when the responses are averaged by computer.
4. E. G. Wever, *Theory of Hearing* (Wiley, New York, 1949).
5. Y. Katsuki, in *Sensory Communication*, W. A. Rosenblith, Ed. (MIT Press, Cambridge, 1961), pp. 561-583.
6. M. Goldstein, J. Hall, B. Butterfield, *J. Acoust. Soc. Am.* **43**, 444 (1968); E. F. Evans and I. C. Whitfield, *J. Physiol. (London)* **171**, 476 (1964).
7. N. Suga, *J. Physiol. (London)* **181**, 671 (1965).
8. —, W. E. O'Neill, T. Manabe, *Science* **200**, 778 (1978).
9. N. Suga, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **37**, 2342 (1978).
10. This does not mean that the neurons themselves assemble the components, but that there are underlying neural circuits which respond to the individual elements and that the neurons express the output of groups of such neural circuits. The particular response properties of single neurons are the result of the particular neural circuits that are directly and indirectly connected with them.
11. J. A. Simmons, D. J. Howell, N. Suga, *Am. Sci.* **63**, 204 (1975); G. Sales and D. Pye, *Ultrasonic*

- Communication by Animals* (Wiley, New York, 1974), pp. 230-233.
12. H.-U. Schnitzler, Z. *Vgl. Physiol.* **68**, 25 (1970); W. E. O'Neill, D. B. Kuriloff, H. G. Berry, N. Suga, in preparation. *Pteronotus parnellii rubiginosus* was previously called *Chilonycteris rubiginosa*. Mustache bats from different Central American populations may have slightly different resting frequencies in their biosonar signals.
 13. N. Suga and P. H.-S. Jen, *Science* **194**, 542 (1976).
 14. N. Suga, J. A. Simmons, T. Shimoza, *J. Exp. Biol.* **61**, 379 (1974).
 15. D. R. Griffin and A. Novick, *J. Exp. Zool.* **130**, 251 (1955); A. Novick and J. R. Vaisnys, *Biol. Bull. (Woods Hole, Mass.)* **127**, 478 (1964); A. Novick, in *Biology of Bats*, W. A. Wimsatt, Ed. (Academic Press, New York, 1978), vol. 3, p. 74.
 16. N. Suga, *Science* **196**, 64 (1977).
 17. W. E. O'Neill and N. Suga, *ibid.* **203**, 69 (1979). Ranging in bats is performed by measurement of the time delay between the bat's emitted sound and the subsequent echo [J. A. Simmons, *Ann. N.Y. Acad. Sci.* **188**, 161 (1971)].
 18. The bats were anesthetized only for initial surgery, and recording of single-unit activity was made 3 to 15 hours after the injection of 30 mg of sodium pentobarbital per kilogram of body weight. If an electrode was placed at nearly the same place in the auditory cortex of the same animal a few days or a few weeks later, using no general anesthesia, the data obtained were nearly the same as those obtained from the lightly anesthetized bat. We thus pooled the data obtained from anesthetized and unanesthetized bats. In the experiments with anesthetized animals the effect of sodium pentobarbital on neural activity was apparently minimal, because we recorded 3 to 15 hours after the injection from bats that showed many different reflexes, voluntary movements, and occasional sound emissions. By unanesthetized animals we mean those that do not receive any general anesthetic for at least 48 hours prior to and during the experiments and that can eat, drink, and fly voluntarily. When unanesthetized or very lightly anesthetized bats were used for the experiments, a local anesthetic (lido-caine) was applied to their surgical wounds.
 19. The dash and slash mean, respectively, successive and simultaneous deliveries of two sounds for maximum excitation of combination-sensitive neurons. For instance, H_1 -FM₂ means that FM₂ should be delivered after H_1 for best facilitation, and CF₁/CF₂ means that CF₁ and CF₂ should be delivered simultaneously. A multiple suffix such as CF_{2,3} in CF₁/CF_{2,3} means that either CF₂ or CF₃ delivered together with CF₁ effects similar facilitation. The CF₁/CF₂ facilitation neurons are those whose response (or subthreshold response) to CF is facilitated by CF₁, so this category includes CF₁/CF₂, CF₁/CF₃, CF₁/CF_{2,3}, CF₁/CF_{2,4}, and CF₁/CF_{3,4}. The H_1 -FM facilitation neurons are those whose response (or subthreshold response) to FM is facilitated by H_1 or its components CF₁ and FM₁, so this category includes all H_1 -FM₂, H_1 -FM₃, H_1 -FM₄, H_1 -FM_{2,3}, H_1 -FM_{2,4}, H_1 -FM_{3,4}, and H_1 -FM₂₋₄. The FM₁-FM facilitation neurons are those whose response (or subthreshold response) to FM is facilitated by the FM₁ component of H_1 , but not CF₁, so this category includes FM₁-FM₂, FM₁-FM₃, and FM₁-FM_{2,3}. In a previous report (8), we said that all these neurons were in the FM processing area. However, the response properties of CF₁/CF₂ facilitation neurons are clearly different from those of H_1 -FM and FM₁-FM facilitation neurons in time domain and are apparently located in a different cluster. Therefore we now introduce a new term, the CF/CF processing area. The FM processing area thus consists of H_1 -FM and FM₁-FM facilitation neurons.
 20. Threshold (or facilitation threshold) is defined as the smallest amplitude of the stimulus that evokes just-noticeable response (or facilitation). The criterion of just-noticeable response is 0.1 impulse per stimulus when neurons are not spontaneously active or are discharging at low rates.
 21. J. A. Simmons and M. J. O'Farrell, *J. Comp. Physiol.* **122**, 201 (1977).
 22. The orientation and nonorientation sounds of the mustache bat are discrete, so our speculation concerning a possible role of CF/CF neurons is probably reasonable. However, an additional role may become evident when the communication sounds are more thoroughly studied in the future.
 23. N. Suga, J. A. Simmons, P. H.-S. Jen, *J. Exp.*

- Biol.* **63**, 161 (1975); N. Suga and P. H.-S. Jen, *ibid.* **69**, 207 (1977).
24. O. W. Henson, Jr., *J. Physiol. (London)* **180**, 871 (1965); N. Suga and P. H.-S. Jen, *J. Exp. Biol.* **62**, 277 (1975).
25. N. Suga and P. Schlegel, *Science* **177**, 82 (1972); N. Suga and T. Shimoza, *ibid.* **183**, 1211 (1974).
26. T. Manabe, N. Suga, J. Ostwald, *ibid.* **200**, 339 (1978); E. I. Knudsen and M. Konishi, *ibid.*, p. 795.
27. K. M. Mudry and R. R. Capranica [Abstr. 8th Annu. Meet. Soc. Neurosci. **4**, 101 (1978)] found that, in the dorsal thalamus of the bullfrog *Rana catesbeiana*, responses of neurons were facilitated by simultaneous presentation of two major signal elements of its call. This is particularly interesting for us because this strengthens our

view that biologically significant complex sounds may generally be processed by neurons sensitive to combinations of information-bearing elements, even though peripheral neurons show phase-locked discharges to low-frequency acoustic waves.

28. We thank P. Wasserbach for the design and construction of the harmonic generators used in these experiments, and J. Jaeger for his assistance in our laboratory. Supported by NSF grant BMS 75-17077 and BNS78-12987 to N.S. and NINDS (PHS) training grant 1-T32-NS07057-01 to W.E.O.

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Psychophysical Evidence for a Monocular Visual Cortex in Stereoblind Humans

Abstract. Human observers who lack stereopsis reliably make eye-of-origin discriminations for grating patterns under conditions that render the performance of normal observers unreliable. This lends support to the view that stereoblind individuals possess proportions of monocular and binocular cortical cells similar to those of cats and monkeys deprived of early binocular visual experience.

The visual cortex of normally raised cats and monkeys contains a high proportion of binocularly innervated cells (1). In contrast, the visual cortex of animals deprived of early binocular visual experience shows a high proportion of monocularly driven cells (2). Compared to normal animals, cats with a paucity of binocular cortical neurons perform poorly on behavioral tasks requiring binocular depth discrimination (3). Some humans, too, perform poorly on such tasks. These so-called stereoblind individuals

also display little, if any, interocular transfer of visual aftereffects (4) and show no binocular summation on visual threshold tasks (5). Stereopsis, interocular transfer, and binocular summation are believed to depend on binocularly driven cells, and their combined absence in stereoblind humans suggests that these individuals have fewer than usual binocular cells. Presumably, they also have more than the usual number of monocular cells, but neither stereopsis, interocular transfer, nor binocular summa-

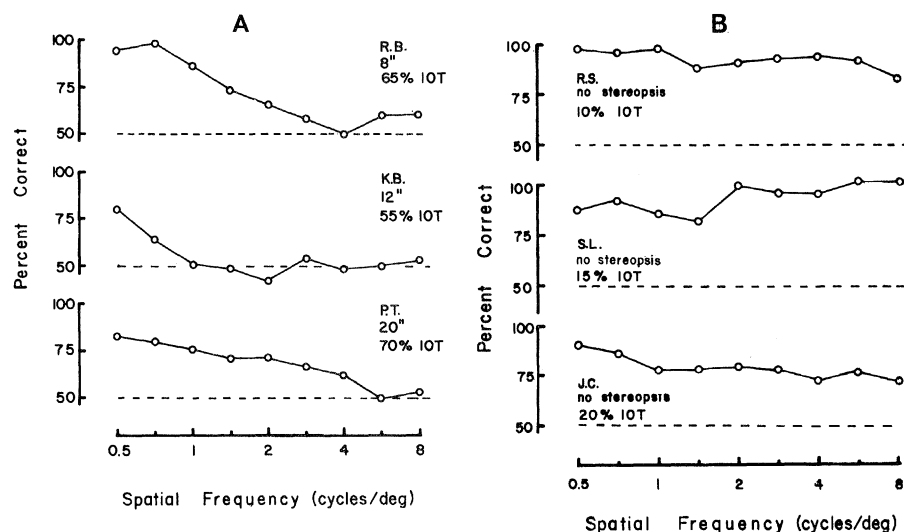


Fig. 1. Percent correct on a two-alternative, forced-choice task on which observers reported which one of the two eyes received a briefly presented, vertical grating pattern. Each point is based on at least 100 trials, and the dotted line denotes the level of performance expected purely on the basis of chance. (A) Representative results for three observers with good stereoacuity. The values under each observer's initials refer to stereoacuity in seconds of arc and the percentage of interocular transfer (IOT) on a conventional threshold-elevation aftereffect. Subject P.T. was the best performer of the seven normal subjects tested; K.B. was the worst. (B) Results from three stereoblind observers on the same task.