activity is correlated with normal behavior. It combines the selectivity of intracellular approaches with the noninvasiveness of extracellular approaches and provides a direct link between electrophysiological procedures used to monitor and manipulate neuronal activity in intact animals and procedures used in reduced preparations. Selective stimulation and recording provide two additional methods for assessing the behavioral function of an identified neuron in an intact animal that complement recently developed techniques (*2*) for selectively destroying individual identified nerve cells (*10*).

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### References and Notes

1. I. Kupfermann and K. R. Weiss, *Behav. Brain Sci.* **1**, 3 (1978); A. I. Selverston, *ibid.* **3**, 535 (1980); W. J. Davis and M. P. Kovac, *Trends Neurosci.* **4**, 73 (1981).
2. I. Parnas and D. Bowling, *Nature (London)* **270**, 626 (1977); J. P. Miller and A. I. Selverston, *Science* **206**, 702 (1979).
3. H. M. Pinsker and L. B. Eberly, *J. Electrophysiol. Tech.* **8**, 88 (1982); H. M. Pinsker, in *Information Processing in the Nervous System*, H. M. Pinsker and W. D. Willis, Jr., Eds. (Raven, New York, 1980), pp. 285–312.
4. J. A. Hoffer and G. E. Loeb, *Ann. Biomed. Eng.* **8**, 241 (1980).
5. M. I. Phillips, in *Brain Unit Activity During Behavior*, M. I. Phillips, Ed. (Thomas, Springfield, Ill., 1973), pp. 5–40; A. B. Vallbo, K. E. Hagbarth, H. E. Torebjork, B. G. Wallin, *Physiol. Rev.* **59**, 919 (1979).
6. The wire was triple-coated Stainless Steel 304 Tri-ML (CFW 19225-TMLSR-1, California Fine Wire). Usually a shallow cut was made in the surface of the connective tissue to one side of the cell body to facilitate entry of the tip. Current passing could mark the tip location.
7. General details of surgery and recovery are described in (*3*). Cell naming follows W. T. Frazier, E. R. Kandel, I. Kupfermann, R. Waziri, and R. E. Coggeshall [*J. Neurophysiol.* **30**, 1288 (1967)]. Cell R2 has the largest darkly pigmented cell body in the right hemiganglion and is thought to be involved in mucus secretion [S. Rayport and E. R. Kandel, *Soc. Neurosci. Abstr.* **5**, 249 (1979)]. Cell R15 has a large, whitish cell body located mediocaudally in the right hemiganglion and is a neurosecretory cell believed to be involved in osmoregulation [J. Stinnakre and L. Tauc, *J. Exp. Biol.* **51**, 237 (1969); I. Kupfermann and K. R. Weiss, *J. Gen. Physiol.* **67**, 113 (1976)]. The LUQ cells have large pigmented cell bodies in the left upper quadrant of the ganglion, and their function is unknown. Under anesthesia the activity patterns are similar to those described in vitro. For example, R2 is typically silent; R15 has an endogenous "parabolic" bursting pattern; and the LUQ cells are also endogenous bursters.
8. Super Glue (or a similar commercial-grade cyanoacrylate) was applied in minute amounts (on the tip of a very fine, flame-drawn, plastic pipette tip) to the area where the wire entered the connective tissue as well as to most of the remainder of the exposed, dried ganglion surface, including the suture holding the wire to the nerve (Fig. 3). If too much glue was applied, the bond strength was reduced and adjacent structures were often glued together. For a review of cyanoacrylate chemistry and action in neurological applications, see B. E. Mickey and D. Samson [*Clin. Neurosurg.* **28**, 429 (1981)]. We observed no obvious toxic effects of Super Glue on abdominal ganglion cells over a period of 5 days, but did not examine longer periods. To date we have been unable to obtain the less toxic isobutylcyanoacrylate. Plastic rings were made by cutting thin slices from flame-drawn polyethylene pipette tips.
9. L. Goldman, *J. Cell Comp. Physiol.* **57**, 183 (1961); H. Pinsker, R. Feinstein, M. Sawada, R. Coggeshall, *J. Neurobiol.* **7**, 241 (1976).
10. We thank W. J. Davis for early discussion of fine wire recordings; J. Ayers, J. Blankenship, and R. Leonard for comments on an earlier draft of the manuscript; and J. Koppe for technical suggestions. Supported in part by a grant from the Netherlands Organization for the Advancement of Pure Science (Z.W.O.) to A. ter M., NSF grant BNS 16521 and NIH grant NS 16087 to H.M.P., and NIH grant NS 11255.

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## Auditory Intensity Discrimination at High Frequencies in the Presence of Noise

Abstract. *Over a wide range of intensities, subjects were able to detect small differences in the intensity of a high-frequency band of noise that was presented with a relatively intense, complementary band-reject noise. This indicates that neither of two possible mechanisms for peripheral intensity coding, those based on timing and on spread of excitation, is necessary for the large dynamic range of human hearing. It is shown that the information available in the firing rate of a small number of nerve fibers can account for these data.*

A striking and fundamental property of hearing is the enormous range of intensities over which the auditory system can operate. The loudness of a pure tone increases over a 130-dB range; more important, relatively small changes in intensity, approximately 1 dB, can be perceived over at least a 110-dB range (*1*). The dynamic range demonstrable in such psychophysical situations contrasts sharply with the 30- to 50-dB dynamic range of typical fibers in the auditory nerve (*2*). Clearly, usable intensity information over at least a 110-dB range is coded in the nerve; how it is coded is not known.

One general coding scheme, that based on the firing rate of a group of fibers, has been discounted primarily because it has been thought unlikely that enough unsaturated fibers are available to signal intensity changes at high intensities (*3*). A plausible alternative scheme, that based on information available in the timing of spike discharges, is examined here. It is shown that a large psychophysical dynamic range is maintained at frequencies for which a timing code is extremely unlikely. Thus timing information, specifically temporal synchrony to waveform fine structure, is not necessary for a large dynamic range. It is also shown, using a detection theory analysis of recent physiological data, that the information available in the firing rate of a very small number of fibers is, in fact, sufficient to account for the experimental results, that is, a rate-based intensity code is at least theoretically possible.

The possibility that intensity can be coded temporally over a wide intensity range is suggested by recent data on the synchronization of the firing pattern of primary fibers to the fine structure of complex waveforms (*4*). Of particular interest is the observation that the function relating degree of synchronization to intensity, which for single components has a dynamic range comparable to that of the rate-intensity function, can be rigidly shifted to higher intensities by the addition of a second component (*5*). The effect of the second component on synchronization to the first component can be approximately described as attenuative, that is, the reduction or suppression in synchrony is similar to reducing the intensity of the first component by a constant proportion, independent of its actual intensity. This characteristic of synchrony suppression is similar to the effect of adaptation in the visual system and, as in vision, may be the mechanism that permits a large dynamic range, at least for complex stimuli.

The experiment reported here examined intensity discrimination of a band of noise that was presented with a relatively intense band-reject noise whose spectral notch corresponded to the passband of the signal. The experiment is similar to previous intensity discrimination experiments with band-reject noise (*6*), with the important difference that the frequency range over which the intensity changes occur is 6 to 14 kHz and is above that for which primary fibers preserve temporal synchrony to waveform fine structure (*7*). The use of band-reject noise minimizes the possibility that intensity changes are signaled by unsaturated fibers that are activated or "recruited" by the intensity-dependent spread of excitation along the cochlear partition. Thus, markedly elevated discrimination thresholds should be observed if either temporal synchrony or spatial spread of excitation mediates intensity coding.

Intensity discrimination thresholds for 200-msec bursts of bandpass noise were measured by using a two-interval, forced-choice tracking procedure (*6*). During each trial, two noise bursts with spectrum levels of $N_0$ and $N_0 + S_0$ were presented in random order 500 msec apart. The subject's task was to indicate which burst was more intense. The value of the intensity increment ($S_0$) varied over trials, and an estimate of the value of $S_0$ necessary for 71 percent correct responses was obtained (*8*).

Thresholds were measured as a function of $N_0$ under three conditions: with no masker, with a band-reject noise masker, and with a spectrally uniform noise masker. The spectrum level of the masker was always 10 dB greater than $N_0$. The masker was gated simultaneously with the bandpass noise. Cutoff frequencies for both the band-reject noise and the bandpass signals were 6.0 and 14.0 kHz and the attenuation rates in the relevant frequency regions were in excess of 100 dB per octave (*9*). The auditory stimuli were presented binaurally and in phase through headphones that were chosen for their extended high-frequency response and their ability to produce very high levels with low distortion (*10*). Three male subjects with normal hearing were tested individually in a sound-attenuating chamber.

The average relative thresholds for the three subjects are shown in Fig. 1. The lowest curve, obtained with no masking noise, shows that as $N_0$ increased above detection threshold (arrow), there was a very slight decrease in threshold, approximately 3 dB over an 80-dB range. This deviation from constant relative threshold has been dubbed the near-miss to Weber's law and has been observed for intensity discrimination of band-limited signals at lower frequencies. When a uniform masking noise was present (upper curve), the thresholds at low $N_0$ were raised by the expected 10 dB. There was a trend for the thresholds to increase slightly with increasing $N_0$. A similar trend was observed in the band-reject condition (middle curve). The thresholds with the band-reject noise were somewhat larger, particularly at high $N_0$, than those obtained with no masker. This is attributable to a reduction produced by masking in the effective bandwidth of excitation.

The important result shown in Fig. 1 is that the thresholds in the band-reject condition were consistently lower than those with the uniform masker. This indicates that the subjects used information from the 6- to 14-kHz band in detecting intensity differences and that recruitment of unsaturated fibers by spread of excitation along the cochlear partition did not mediate intensity discrimination. Furthermore, since the frequency range over which the intensity changes were detected was above that for which temporal synchrony is preserved, intensity discrimination could not have been based on temporal synchrony.

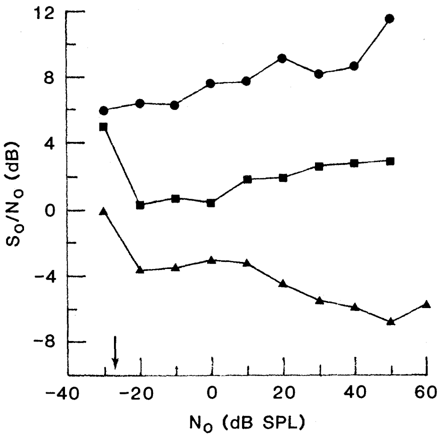

Fig. 1. Intensity discrimination thresholds for a 6- to 14-kHz bandpass noise with spectrum level $N_0$. The ordinate is equivalent to 10 log $\Delta I/I$, where $I$ is the total power in the noise band. Symbols: (●) spectrally uniform masker with spectrum level 10 dB greater than $N_0$, (■) band-reject masker with the 6- to 14-kHz region rejected and with a spectrum level in the passband 10 dB greater than $N_0$, and (▲) no masking noise. The arrow indicates absolute threshold for the noise band.

These findings indicate that neither temporal synchrony nor spread of excitation is necessary for the auditory system to maintain a large dynamic range. Although it cannot be concluded that these mechanisms are never necessary, it seems reasonable to consider schemes other than synchrony and spread of excitation as the basis for a general intensity code. Clearly, a code that can describe the data from the band-reject condition would be a likely candidate for describing intensity coding in other situations, including that of pure tones in isolation.

An alternative mechanism for peripheral intensity coding that at least is not inconsistent with these results involves recruitment in a restricted spatial region of unsaturated fibers with different thresholds. This "staggered-threshold" notion has had a long and uneven history in the study of audition (*11*). Recent experiments indicate, however, that among primary fibers with similar characteristic frequencies (CF's) at least two populations can be distinguished on the basis of threshold and spontaneous activity; thresholds for the population with low spontaneous firing rates (approximately 10 percent) are 20 to 80 dB higher than those with high spontaneous rates (*12*). Also, a small proportion of primary fibers, generally with low spontaneous rates, have extended dynamic ranges (*13*).

These physiological results suggest that a group of fibers with similar CF's can code intensity over a range comparable to that shown psychophysically. However, for this hypothesis to be tenable it must be shown that the number of unsaturated fibers is sufficient to account for the psychophysical thresholds observed at high intensities. On the basis of the available data, it appears that surprisingly few primary fibers are necessary for the psychophysical thresholds: one to six unsaturated fibers could account for the thresholds measured at the highest intensity in the band-reject condition (*14*). This is less than 0.1 percent of the fibers estimated to innervate the 6- to 14-kHz region of the human cochlea. For comparison, approximately 5 percent of primary fibers in the cat have dynamic ranges for CF tones in excess of 70 dB (*13*). This proportion almost certainly would provide enough fibers to account for the 75-dB range shown in the band-reject condition, even without involving variation in primary fiber thresholds. Thus, it appears that the information available in the firing rate of primary fibers with similar CF's is adequate to code intensity over a range of intensities comparable to the dynamic range of human hearing.

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### References and Notes

1. No upper intensity limit for auditory perception has been clearly demonstrated. The values given are conservative estimates based on the data of S. S. Stevens [*Psychophysics* (Wiley, New York, 1975), pp. 162–163], which indicate that the loudness of a 1-kHz tone is still increasing at 135- to 140-dB sound pressure level (SPL), and on my measurement of 1.1-dB discrimination thresholds at 120-dB SPL for 1-kHz tone pulses.
2. The dynamic range of auditory nerve fibers usually is defined as the intensity range over which increases in intensity produce increases in the average firing rate measured over a relatively long interval during stimulation. The dynamic range of the "onset response," the maximum firing rate during a small interval near stimulus onset, is much larger than that based on the steady-state firing rate [R. L. Smith and M. L. Brachman, *Brain Res.* **184**, 499 (1980)], and therefore is in better agreement with the psychophysical dynamic range. However, two psychophysical observations considerably diminish the appeal of the onset response as a general intensity code: (i) increments in the intensity of continuous waveforms are highly detectable over a wide intensity range and (ii) intensity discrimination improves with increases in duration well beyond the duration of the onset response.

3. E. F. Evans, in *Neuronal Mechanisms of Hearing*, J. Syka and L. Aitkin, Eds. (Plenum, New York, 1981), p. 69; M. B. Sachs and E. D. Young, *J. Acoust. Soc. Am.* **66**, 470 (1979).
4. J. E. Rose, J. E. Hind, D. J. Anderson, J. F. Brugge, *J. Neurophysiol.* **34**, 685 (1974); D. H. Johnson, thesis, Massachusetts Institute of Technology (1974); M. B. Sachs and E. D. Young, *J. Acoust. Soc. Am.* **68**, 858 (1980).
5. E. Javel, *J. Acoust. Soc. Am.* **69**, 1735 (1981).
6. N. F. Viemeister, *ibid.* **56**, 1594 (1974); B. C. J. Moore and D. H. Raab, *ibid.* **57**, 400 (1975).
7. D. H. Johnson, *Biophys. J.* **22**, 413 (1978).
8. The final threshold for each subject was based on the average of at least five separate threshold estimates. The standard deviation of these estimates was typically less than 2 dB and ranged from 0.7 to 3.8 dB.
9. The cutoff frequencies were chosen such that at the highest level of the band-reject masker, the bandpass noise was approximately 10 dB above its masked threshold for all subjects. The noises were produced by multiplying a lowpass and a bandpass noise by a 10-kHz sinusoid and adding a 20-kHz highpass noise.
10. Audio Technica ATH-7 Electret headphones were used. Since no high-frequency calibration standard exists for these or any headphones, the spectrum levels reported are the 1-kHz equivalents measured with a flat plate coupler. The overall level is approximately 43 dB greater than the reported spectrum level; the highest levels used in this experiment were in excess of 100-dB SPL overall.
11. M. H. Lurie, *J. Acoust. Soc. Am.* **11**, 420 (1940); Y. Katsuki, N. Suga, Y. Kanno, *ibid.* **34**, 1396 (1962); N. Y.-S. Kiang, *Ann. Otol. Rhinol. Laryngol.* **77**, 656 (1968).
12. M. C. Liberman, *J. Acoust. Soc. Am.* **63**, 442 (1978); *Science* **216**, 1239 (1982).
13. A. R. Palmer and E. F. Evans, *Exp. Brain Res. Suppl. II* (1979), p. 19; *Hear. Res.* **7**, 305 (1982).
14. This is the number of independent, optimally combined Poisson channels that would yield a threshold equal to that observed in the band-reject condition. For a single channel the performance measure, $d'_i$, is approximately $\Delta I_{dB} r'(I)[T/r(I)]^{1/2}$, where $T$ is the interval over which events (spikes) are counted, $r(I)$ is the mean firing rate at intensity $I$, $r'(I)$ is the slope of the rate-intensity function at $I$, and $\Delta I_{dB}$ is the decibel difference between the two stimuli. For $n$ independent, optimally combined channels with equal $d'_i$, the resulting overall performance is $d' = n^{1/2} d'_i$. Thus, $n = [d'/\Delta I_{dB} r'(I)]^2 r(I)/T$. [See J. P. Egan, *Signal Detection Theory and ROC Analysis* (Academic Press, New York, 1975), pp. 162–217, for an excellent treatment of Poisson observers.] At $N_0 = 50$ dB in the band-reject condition, $\Delta I_{dB} = 4.8$ for $d' = 0.77$. Assuming a fixed counting interval of 100 msec and a mean firing rate of 100 spikes per second at $N_0 = 50$ dB, then for slopes of five or two spikes per second per decibel, $n$ is 1.03 or 6.4 fibers, respectively. These slopes are reasonable for rate-intensity functions obtained with broadband noise at lower spectrum levels [T. B. Schalk and M. B. Sachs, *J. Acoust. Soc. Am.* **67**, 903 (1980)]. The assumption of optimum combination requires, in effect, that saturated channels, those with $d'_i = 0$, be ignored. Whether the auditory system actually achieves or approximates optimum combination is not directly relevant to the question of whether, at the level of primary fibers, a rate code is even possible.
15. I thank D. A. Burkhardt, W. D. Ward, M. Ruggero, and G. Wakefield for their comments on the manuscript. I also thank H. S. Colburn and W. M. Rabinowitz for stimulating discussions on this topic. This work was supported by grant NS12125 from the National Institute of Neurological and Communicative Disorders and Stroke.

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# Autonomic Nervous System Activity Distinguishes Among Emotions

Abstract. *Emotion-specific activity in the autonomic nervous system was generated by constructing facial prototypes of emotion muscle by muscle and by reliving past emotional experiences. The autonomic activity produced distinguished not only between positive and negative emotions, but also among negative emotions. This finding challenges emotion theories that have proposed autonomic activity to be undifferentiated or that have failed to address the implications of autonomic differentiation in emotion.*

For almost a century scientists have argued about whether or not activity in the autonomic nervous system (ANS) is emotion-specific. Some of the most influential cognitive theories of emotion (*1*, *2*) presume undifferentiated autonomic arousal despite a number of reports of emotion-specific autonomic activity (*3*–*5*). We now report evidence of such specificity in an experiment designed to remedy methodological problems that have lessened the impact of previous studies: (i) A broad sample of six emotions was studied, rather than the two or three that are typical. (ii) Verification procedures were instituted to maximize the likelihood that each sample contained only the single target emotion and no other. (iii) A sufficiently broad sample of autonomic measures was obtained to enable differentiation of multiple emotions, with appropriate statistical protection against spurious findings due to multiple dependent measures. (iv) Autonomic measures were taken from the onset of emotion production continuously until it was terminated. More typical measures taken before and after production of an emotion may completely miss short-lived target emotions. (v) Multiple eliciting tasks were used with the same subjects. (vi) Professional actors ($N = 12$) and scientists who study the face ($N = 4$) served as subjects to minimize contamination of emotion samples by extraneous affect associated with frustration or embarrassment.

We studied six target emotions (surprise, disgust, sadness, anger, fear, and happiness) elicited by two tasks (directed facial action and relived emotion), with emotion ordering counterbalanced within tasks. During both tasks, facial behavior was recorded on videotape, and second-by-second averages were obtained for five physiological measures: (i) heart rate—measured with bipolar chest leads with Redux paste; (ii) left- and (iii) right-hand temperatures—measured with thermistors taped to the palmar surface of the first phalanges of the middle finger of each hand; (iv) skin resistance—measured with Ag-AgCl electrodes with Beckman paste attached to the palmar surface of the middle phalanges of the first and third fingers of the nondominant hand; and (v) forearm flexor muscle tension—measured with Ag-

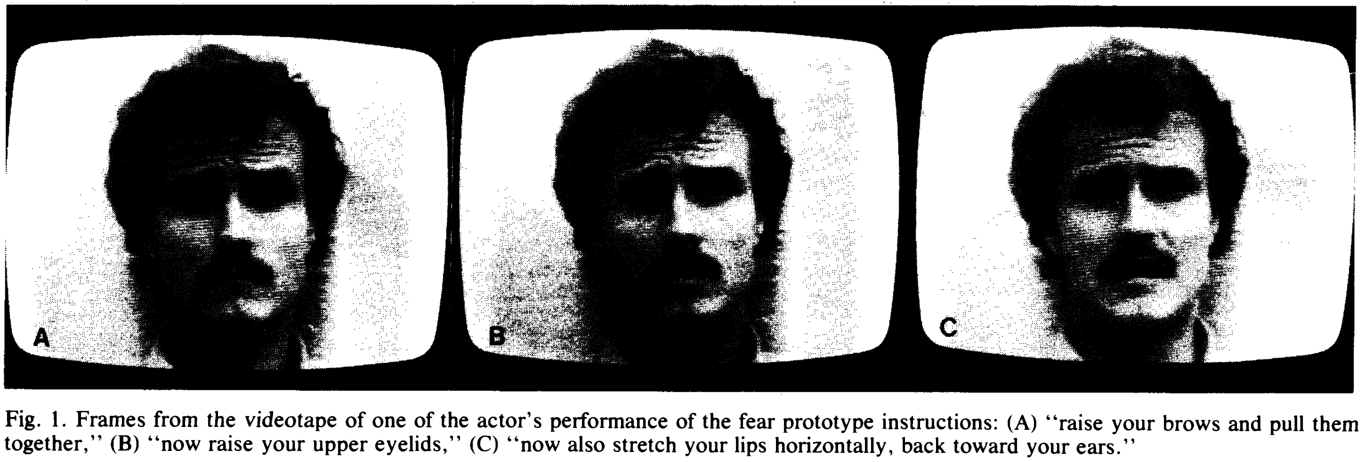

Fig. 1. Frames from the videotape of one of the actor's performance of the fear prototype instructions: (A) "raise your brows and pull them together," (B) "now raise your upper eyelids," (C) "now also stretch your lips horizontally, back toward your ears."