different directions of MAE must have been established within the visual system. Only one direction was experienced at a time, as determined by the particular conditions of testing.

Taken together, our experiments show that the direction of the MAE can be synthesized from two or more components. This is a general finding independent of the specific patterns used to induce or to test the MAE. It is as if the motion-detecting cells of the brain pay no attention to the objects themselves, being concerned only with their direction of movement.

We cannot specify at this time the brain centers for the conscious and unconscious processing of motion information that our experiments have revealed. Present-day studies of single cortical cells have amply shown (*10*) that some of them are sharply tuned motion detectors. It remains, however, for electrophysiologists to identify cells or centers in which their signals are pooled to mediate new directions of motion.

On the psychophysical side, our findings are consistent with a recent report (*11*) that in the presence of a relatively strong MAE in one direction, a dot pattern of low contrast moving in another direction can seem to be deviated by as much as 10° in a direction toward that of the existing MAE.

Finally, the subjective effects that we observed are consistent with those reported in other perceptual domains. In normal color vision, for example, red and green lights can be combined to produce a yellow that appears as a new hue without any trace of its components (*12*). Similarly, a three-dimensional solid object can be made to appear in visual space by stereoscopic fusion of separately meaningless patterns presented to the left and right eyes (*13*). Our motion aftereffects may thus be added to a class of previously described instances in which the perception arises from a synthesis of unperceived components.

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8. To avoid confusion the term "deg" is used in referring to the angle subtended at the eye (visual angle) and the symbol "°" in referring to stimulus orientation and direction of movement.
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4 September 1979; revised 29 January 1980

An "Inhibitory" Influence on Brainstem Population Responses

Abstract. *Forward masking was used to obtain measurements of physiological masking and two-tone unmasking from short-latency evoked potentials and psychophysical responses in human subjects. The physiological results are in qualitative agreement with data on inhibitory phenomena in nonhuman auditory systems. The neural and behavioral data obtained thus far agree well.*

In vision, prominent edges often appear bordering regions of discontinuity in wavelength, intensity, texture, or other stimulus characteristics (*1*). Analogous "edge effects" occur in hearing at discontinuities (peaks or valleys) in the power spectra of sounds (*2*). These phenomena are apparently produced by a class of inhibitory mechanisms that effectively compare intensities in neigh-

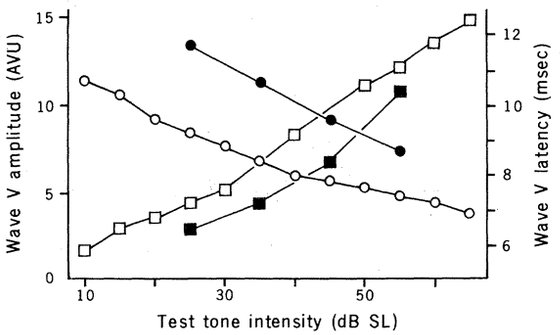

Fig. 1. Amplitudes (squares) and latencies (circles) of probe tone evoked wave V responses with and without masking. Filled symbols are for responses to masked tones. The amplitude measurements are in arbitrary voltage units; *SL*, sound level.

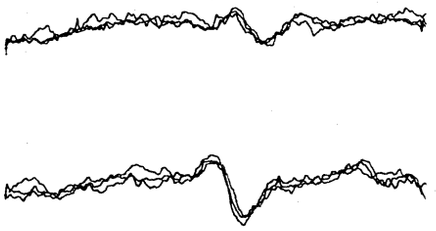

Fig. 2. Masked and unmasked probe evoked responses from one subject. Upper traces are responses to 25-dB probes in the presence of 50-dB maskers (re threshold in quiet). Lower traces show the effect of adding a 70-dB unmasker at 2.245 kHz. Positivity is upward; traces begin at probe tone onset and continue for 20 msec.

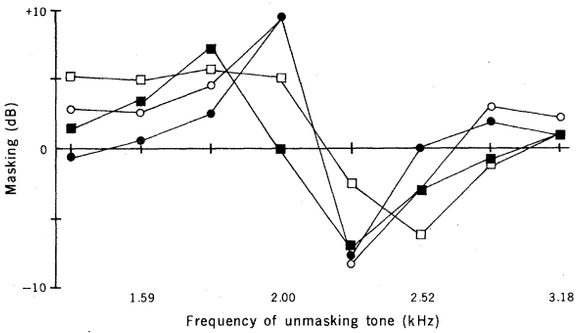

Fig. 3. Masking as a function of unmasker frequency. Open symbols are estimates based on wave V amplitudes (*13*). Filled symbols are psychophysical threshold shifts. Circles and squares denote two different subjects. Zero decibels refers to the masking produced by the masking tone alone. Unmasking is shown as negative masking.

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boring regions of the audio spectrum and enhance (exaggerate) the representation of any imbalance present (*3, 4*). Psychophysical evidence for this type of inhibition can be found in studies of auditory masking, where a pure tone's ability to interfere with the perception of subsequent stimuli (its "effective energy") can be greatly reduced in the presence of another sine wave a few semitones different in frequency [two-tone unmasking (*5*)]. A similar process is seen in single auditory neurons, whose tone-driven firing rates can be markedly reduced by adding a second tone [two-tone inhibition or lateral suppression (*6*)]. That speech formants may be more clearly defined in the perceptual representation than in the physical stimulus (*7*) suggests the biological significance of this type of sensory processing.

Evidence that a neural correlate of unmasking can be observed in peripheral nerve responses from nonhumans (*8*) led us to carry out the physiological and psychophysical studies outlined here. The neural data reported are wave V brainstem responses from humans (*9*). The psychophysical data are measurements of two-tone unmasking obtained from the same subjects.

Three shaped tone bursts served as stimuli: a 17.5-msec masker, a 17.5-msec unmasker, and a 5-msec probe. Probes were presented 2 msec after stimulating with either a masking tone or the two-tone combination [masker plus unmasker (*10*)]. These stimulus complexes were presented repeatedly at a rate of 20 per second. In all conditions, masker and probe frequencies were 2.0 kHz. Unmasker frequencies were spaced at 1/6-octave intervals from 1.414 to 3.175 kHz.

Physiological masking was assessed by averaging 4096 or 8192 samples of probe-evoked electrical activity in the presence of a masker or masker-plus-unmasker (*11*). Psychophysical masking was measured by determining threshold shifts for probe tones under the same conditions.

Figure 1 shows the effect of a masking tone on wave V responses to probes. The masker (at 40 dB re threshold in quiet) reduced probe response amplitudes by approximately the same amount for each probe intensity. Probe response latencies increased in similar fashion.

Figure 2 illustrates two-tone unmasking of wave V responses. The release from physiological masking that occurs when a 2.245-kHz unmasking tone is added can be seen in the increased amplitudes and decreased latencies of responses to the probe. (Masker, unmasker, and probe are 50, 70, and 25 dB re threshold in quiet.)

Figure 3 shows how an unmasker's effectiveness depends on its frequency. Psychophysical and physiological unmasking are plotted together to show their similarity. Both functions show a 5- to 10-dB release from masking when the unmasker is placed 1/6 to 1/3 octave above the test frequency.

A substantial inhibitory effect can thus be observed in auditory population responses from the human central pathways. The inhibitory phenomenon consists of an interaction between frequencies a few semitones apart. For the range of conditions examined to date, its magnitude and form agree reasonably well with psychophysical measurements from the same subjects.

These observations do not necessarily mean that neurons in the wave V population are themselves subject to inhibition, only that inhibitory phenomena occur at some stage of the process leading to activity in the population. In fact, the extremely brief time-course of the phenomenon is consistent with [but does not necessarily imply (*12*)] inhibitory processing carried out by a preneural mechanism (*4*).

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3. Some inhibitory processing may occur in the cochlea before action potentials are generated in first-order fibers (*4*). This type of inhibition is commonly termed "suppression" in the auditory literature to distinguish it from neural inhibition, which is observed in the central auditory system [R. Galambos, *J. Neurophysiol.* **28**, 863 (1965)]. In this report, we have used "inhibition" as an inclusive term for processes of this type, regardless of mechanism (*1*). Not all authors have used the terms in exactly the same way.
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10. This is forward masking: The masking stimulus precedes the probe. Psychophysical two-tone unmasking is not observed when a probe and masker-plus-unmasker complex are presented simultaneously [T. Houtgast, in *Facts and Models in Hearing*, E. Zwicker and E. Terhardt, Eds. (Springer-Verlag, New York, 1974)]. Similarly, we have been unable to demonstrate "physiological unmasking" in the simultaneous condition.
11. The recording electrode was at vertex, the reference at right mastoid, a ground electrode at left mastoid. The electroencephalogram was filtered below 0.1 kHz and above 3.0 kHz and amplified by 10^5 through the use of cascaded preamplifiers (Grass P15 and Tektronix type 122).
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13. The effects of unmasker frequency on wave V amplitudes are converted to decibels by referring voltage measurements to the intensity function for masked tones in Fig. 1. The psychophysical threshold shifts also plotted in Fig. 3 are measured relative to the threshold of a probe tone in the presence of a masker alone.
14. We thank Bruce Masterton and David Harris for their comments on earlier versions of this report. Portions were presented at the 97th meetings of the Acoustical Society of America, Boston, 11 to 15 June 1979.

21 January 1980

Interspecific Chimeras in Mammals: Successful Production of Live Chimeras Between *Mus musculus* and *Mus caroli*

Abstract. *Live chimeras between two species of mouse,* Mus musculus *and* Mus caroli, *were produced by blastocyst injection. These chimeras were entirely similar to* M. musculus ↔ M. musculus *chimeras in their somatic tissue organization. This is the first report of completely normal development of interspecific chimeras in mammals.*

Mammalian chimeras have proved very useful for investigating early embryonic development (*1, 2*), but precise clonal analysis of cell lineages has been limited by the lack of a cell marker that is ubiquitous and that distinguishes the two parental cell types in situ (*3*). One solution to this problem is to make chimeras from embryos of two different species so that there are sufficient genetic differences for unequivocal identification of the two cell types in any tissue (*4*). This approach has been applied to mammals with various degrees of success. Although aggregation chimeras between rat and mouse (*5*) and between bank vole

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