

the Set II band is always correlated with the position of the band in the Set I region. Plants with the fastest migrating Set I isozyme (ADH^C) also show the fastest migrating Set II band. The same is true for the slow (ADH^S) and intermediate (ADH^F) migrating Set I and Set II isozymes. This correlation is complete and no exceptions have been found in thousands of samples analyzed to date. In heterozygotes, a hybrid isozyme appears in the Set I region but not in Set II although the Set I and Set II enzymes do not differ significantly in size.

We have explained (1) the ADH zymogram patterns by postulating the existence of two *Adh* genes. The *Adh*₁ gene is polymorphic, and dimers composed of two ADH_1 subunits appear as bands in the Set I region. The *Adh*₂ gene is considered to be represented by only a single allele, and it specifies an enzymatically inactive, but more negatively charged, polypeptide. It was hypothesized that Set II isozymes are heterodimers composed of an active ADH_1 and an inactive ADH_2 subunit. This hypothesis readily explains the correlation between the Set I and Set II isozyme band positions and the absence of a hybrid Set II isozyme in heterozygotes. In heterozygotes, such as Adh_1^S/Adh_1^F , only the $ADH_1^S \cdot ADH_2$ and $ADH_1^F \cdot ADH_2$ Set II bands can be formed.

Scandalios (2) proposed an alternative explanation. He considers that the two sets of isozyme bands are independently controlled by two closely linked *Adh* genes. According to his nomenclature, *Adh*₂ specifies the major slow migrating isozyme (our Set I), and *Adh*₁ specifies the weak, more anodal migrating set of isozymes (our Set II). He suggests that the ADH_2 isozymes are dimers, but that the ADH_1 isozymes either exist as monomers or are dimers with polymerization restricted to identical subunits.

This explanation was previously considered but we held it to be unlikely because of (i) the complete correlation in the migration rates of the Set I and Set II isozymes in Adh_1^S , Adh_1^F , and $Adh_1^{C(t)}$ genotypes; (ii) the occurrence of a fourth allele, $Adh_1^{C(m)}$, which specifies isozymes at the same Set I and Set II positions as $Adh_1^{C(t)}$ but with much reduced activity in both regions; and (iii) the fact that in homozygotes the duplicate gene Adh_1^{FO} produces isozymes in the F and C positions in both the Set I and Set II regions.

If the two sets of ADH isozymes are

under the independent control of two linked genes as proposed by Scandalios, induced mutations that alter the migration rate of one isozyme should not affect the position of the second ADH band. However, according to the hypothesis proposed by this author, mutations at the *Adh*₁ locus which change the charge of the *Adh*₁ subunit should alter the migration rates of both the Set I and Set II bands since both are composed entirely or partially of ADH_1 subunits.

The Adh_1^S homozygous kernels were treated with ethyl methanesulfonate (EMS) according to the procedure of Briggs *et al.* (3), planted in the field and the plants were pollinated by homozygous Adh_1^F plants. The F_1 kernels were screened electrophoretically for mutants of the Adh_1^S allele.

Results indicated that the Set I and Set II isozymes have subunits in common. Four mutations at the *Adh*₁^S locus were found which produced an isozyme with an altered migration rate in the Set I region. In every case there was a concomitant and correlated change in

the position of the Set II band (Fig. 1). If the two ADH isozymes were independently controlled by different genes, these results would require simultaneous, correlated mutations in both genes—a highly unlikely condition. Numerous mutations were recovered which resulted in the elimination of the ADH^S band in both the Set I and Set II regions but these are not critical to the argument since they could represent aberrations which deleted closely linked loci. The *Adh*₂ mutations which should alter the migration rate of only the Set II isozyme were not found in this study.

DREW SCHWARTZ

Department of Botany,
Indiana University,
Bloomington 47401

References and Notes

1. D. Schwartz, *Proc. Nat. Acad. Sci. U.S.* **56**, 1431 (1966).
2. J. G. Scandalios, *Biochem. Genet.* **1**, 1 (1967).
3. R. W. Briggs, E. Amano, H. H. Smith, *Nature* **207**, 890 (1965).
4. D. Schwartz and T. Endo, *Genetics* **53**, 709 (1966).
5. I thank E. O. Smith for technical assistance. Supported by NSF grants GB-4178 and GB-8107.

17 January 1969

Auditory Sequence: Confusion of Patterns Other Than Speech or Music

Abstract. *Accurate perception of temporal order is essential for many auditory tasks. Yet the temporal pattern of four successive sounds (for example, hisses, buzzes, and tones) could not be recognized even when the duration of each sound was considerably longer than either the average phoneme in normal discourse or the notes of melodies. Although each of the stimuli was perceived, their order remained frustratingly elusive.*

Realization of the importance of sequence recognition to normal auditory function led Hirsh (1) to state that any theory of auditory perception requires "... the concepts of sequence and temporal pattern to play the same role that Gestalt or form or shape has played in visual perception." The ease and assurance with which temporal order is perceived are especially obvious for speech and music, and it has been assumed that this ability could be applied to sequences of other sounds as well.

However, during a psychophysical experiment involving a repeated sequence of three successive sounds (1000-hz tone, broad-band noise, 600-hz tone), we found that, although listeners perceived each of the separate sounds clearly, they could not tell the order in which they occurred, even

with continued listening. It was impossible to tell if the low-pitch tone followed the noise or the high-pitch tone. Yet the duration of each sound was 200 msec, considerably longer than the 70 to 80 msec for the average speech sound in normal discourse, and the 50 msec required for perceiving the sequence of successive notes in music (2).

Previous studies on perception of the order of three or more different sounds have involved only speech or music. However, when pairs of electrically generated sounds (for example, a tone and a buzz) were presented, subjects identified which of the two sounds came first (stimulus duration, as short as 20 msec) (3). The difficulties which our subjects had in recognizing sequences of three arbitrarily selected sounds suggested that we were not

using some special cues necessary for the ordering of stimulus pairs. For example, remembering which member of the pair was present at either onset or termination of stimulation could allow correct answers without direct recollection of sequence. Broadbent and Ladefoged (4), in a similar evaluation, suggested that the "quality" of pairs rather than sequence itself might have been responsible for correct ordering.

Our series of experiments involved 150 undergraduate students divided into five groups of 30 subjects. Each subject made only one judgment. All sounds were delivered through matched headphones at an intensity of 80 db (0.0002 dyne/cm²). The first group verified and extended our preliminary observations. They heard four sounds consisting of a high tone (1000 hz), a hiss (2000-hz octave band of noise), a low tone (796 hz), and a buzz (40-hz square wave), each sound lasting 200 msec and followed immediately by the next in the order listed. The last named (buzz) was followed by the first (high tone) without pause, so that the sequence continued without interruption. These subjects were told the names of the sounds in advance, and asked to state their order of occurrence, starting with any sound they chose. They were allowed to listen as long as they wished (most responded within 10 to 30 seconds). At the time of response, most subjects perceived each of the successive sounds, but were uncertain of their order and felt that their responses were guesses. Only five of the 30 reported the order correctly (the most probable chance score, since there is one chance in six of guessing correctly).

To insure that the observed inability to perceive temporal order reflected a basic perceptual limitation rather than special characteristics of the experimental procedure, the additional 120 students were tested (four groups of 30 subjects).

To test the possibility that confusion concerning the appropriate names prevented correct responses, one group heard each sound separately, along with its name, before listening to the experimental tape used in the previous experiment. Nevertheless, correct responses remained at the chance level.

Although the high and low tones were readily discriminated, they were qualitatively similar, and this resemblance of the two sounds might have contributed to the confusion. Therefore, another group was tested with the

vowel sound "ee" replacing the low-pitch tone. Again, responses were not significantly different from chance.

It has been assumed thus far that sequence perception of speech sounds could be accomplished readily under the conditions used. To verify this assumption, a group of subjects listened to a repeated sequence of four spoken digits (one, three, eight, two), each statement of the four items taking the same 800 msec as the other series. Despite the fact that individual phonemic orders must be established within digits, the correct identification of all digits and their sequence was made very quickly by all after only one or two repetitions.

It is known that repetition of verbal signals over and over can disrupt perception under certain circumstances (5). Although repeated sequences were identified under our conditions for words (digits), repetition itself may have a hitherto unreported effect on perception of nonspeech sounds, and hence sequence might be identified properly if repetition were avoided. Therefore, a group was told that they would hear a high tone, a low tone, a hiss, and a buzz presented in a certain order just once. After hearing each stimulus separately along with its name, they heard the 200-msec sounds in a single sequence. Their task was facilitated by the possibility that the first and last sounds may be identified by their unique position at onset and termination. At the same time, the difficulty was increased by the single opportunity to hear the sequence, and the fact that there was now a correct response for the first sound named (changing the probability of a correct guess from one in six to one in 24). The sequence was reported correctly by five subjects, which, although significantly better than chance ($P < .01$ by binomial expansion), nevertheless indicated that the task was not possible for the great majority of listeners.

Current work on sequences shows that the duration of each item must be increased from 200 to about 700 msec before half the inexperienced subjects can verbally identify the correct order. For experienced listeners such as the experimenters, identification of order remains extremely difficult or impossible at 200 msec, but can be accomplished at 300 msec.

Our experiments have indicated that perception of temporal order is unexpectedly difficult for some sounds. A

determination of the critical attributes of sequences permitting accurate pattern recognition should be of interest to theories of auditory perception.

RICHARD M. WARREN

CHARLES J. OBUSEK

RICHARD M. FARMER

Department of Psychology,

University of Wisconsin, Milwaukee

ROSLYN P. WARREN

Department of Zoology

References and Notes

1. I. J. Hirsh, in *Brain Mechanisms Underlying Speech and Language*, C. M. Millikan and F. J. Darley, Eds. (Grune & Stratton, New York, 1967), p. 22.
2. F. Winckel, *Music, Sound, and Sensation* (Dover, New York, 1967), p. 54.
3. For a review of this literature, see W. H. Fay, *Temporal Sequence in the Perception of Speech* (Mouton, The Hague, 1966), p. 29 and following.
4. D. E. Broadbent and P. Ladefoged, *J. Acoust. Soc. Amer.* **31**, 1539 (1959).
5. R. M. Warren, *Psychol. Bull.* **70**, 261 (1968).
6. Supported in part by NIH grant NB 05998 and by a University of Wisconsin graduate school research grant.

25 November 1968; revised 4 March 1969

Sound Velocity in Carbon Suboxide

Carbon suboxide is one of a number of small polyatomic molecules which have one very low vibration frequency, in particular the bending of the central CCC group at about 63 cm⁻¹. Studies of vibration-translation energy transfer suggest that in such a case two relaxation times may be expected; the shorter one is associated with the mode where $\nu_7 = 63$ cm⁻¹, and the longer relaxation time is associated with all other vibrational degrees of freedom.

Ultrasonic dispersion studies (Fig. 1) with a novel optical method have revealed the longer of the two expected relaxation times as $\tau = 48$ nanoseconds at 1 atmosphere. The values of the heat capacity predicted by statistical thermodynamics are (i) $C_p/R = 7.078$ and (ii) $C_p/R = 4.485$ for (i) static

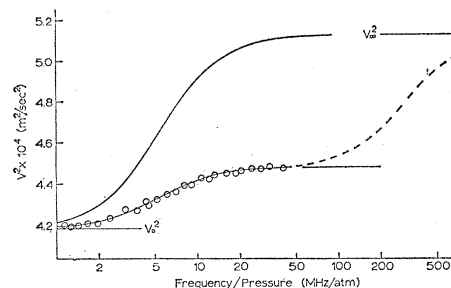


Fig. 1. Ideal sound velocity in O=C=C=O.