posterior phyllopods of the female and the anterior phyllopods of the male is 1 to 3 mm. Electrical recordings of synchronous couples yield sinusoidal potentials of 75 to 125 μv and 3 to 6 cycle/sec (Fig. 2B).

It is noteworthy that couples are not always synchronous. When potentials are recorded from asynchronous couples, the metachronal oscillations are superimposed on a much slower and larger oscillation representing the beat frequency of the unequal frequencies of male and female limb movements (Fig. 2C). When asynchrony occurs, it results from the female's momentarily running at a higher frequency than the male. This happens rarely and the frequency of the female soon returns to the lower rate of the male. I have not observed a female with a lower frequency than that of the male with which she is joined.

When a synchronous couple is separated, the male usually continues at a frequency similar to that of the couple and the female reduces her frequency to a lower value (Fig. 2, A and B). The males of most couples are smaller than the females (6.5 to 7.5 mm, males; 7.5 to 11 mm, females), and the frequencies of the separated individuals correspond to the relation of size and rate (Fig. 1). This observation together with the fact that each wave in the male precedes the wave in the female indicates that the male is the pacemaker for the couple and drives the female at a higher frequency than she exhibits alone.

The remote-recording method is also useful for measuring other behaviors of unrestrained *Artemia*. Shadow-induced escape responses can be measured by simultaneous recording of electrical fields and of the light level at the bottom of the chamber with a photocell. *Artemia* respond to shadows by contracting all limbs, nearly simultaneously, and producing potential changes well over 100 μv. Response times range between 100 and 240 msec. Shadow responses are observed in couples with each member simultaneously beginning vigorous swimming movements.

In the other arthropods for which synchronous rhythmic behavior has been reported, the behavior is involved with communication (*1*). In *Artemia* the rhythmic synchrony is primarily locomotor and its adaptive significance is obvious: the efficiency of metachrony in locomotion, feeding, and respiration is maintained during the period of coupling. Asynchrony would interrupt the smooth currents necessary for respiration and feeding and would reduce the efficiency of swimming. Even the escape response of the pair is synchronous; hence, sexually mature brine shrimp are not subject to adverse selection as a result of coupling.

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Auditory Evoked Potentials during Speech Perception

Abstract. *Neural responses evoked by the same binaural speech signal were recorded from ten right-handed subjects during two auditory identification tasks. One task required analysis of acoustic parameters important for making a linguistic distinction, while the other task required analysis of an acoustic parameter which provides no linguistic information at the phoneme level. In the time interval between stimulus onset and the subjects' identification responses, evoked potentials from the two tasks were significantly different over the left hemisphere but identical over the right hemisphere. These results indicate that different neural events occur in the left hemisphere during analysis of linguistic versus nonlinguistic parameters of the same acoustic signal.*

The relation between an acoustic speech signal and its phonetic message appears to be a complex and highly efficient code, which requires a specialized linguistic "decoder" for its perception (*1*). Dichotic listening experiments with normal (*2, 3*) and brain-damaged subjects (*4*) have further suggested that the specialized neural mechanisms required for the perception of speech are lateralized in one cerebral hemisphere, usually the left. This interpretation is consistent with clinical analyses of language disorders following brain damage (*5*), and may be related to anatomical differences between left and right temporal lobes (*6*).

In a recent review of hemispheric specialization for speech perception, Studdert-Kennedy and Shankweiler (*3*) concluded that ". . . specialization of the dominant hemisphere in speech perception is due to its possession of a linguistic device. . . . [W]hile the general auditory system common to both hemispheres is equipped to extract the auditory parameters of a speech signal, the dominant hemisphere may be specialized for the extraction of linguistic features from those parameters."

Despite the large body of behavioral and clinical evidence for specialization of one hemisphere in speech perception, there is no evidence which clearly distinguishes neural activity specifically related to linguistic processing from that which occurs during the processing of any auditory stimulus (*7, 8*). Empirical evidence for such a distinction requires a direct comparison of neural activity during linguistic and nonlinguistic processing conditions with other sources of variation in neural activity eliminated between conditions. We have therefore compared neural activity evoked by the same consonant-vowel syllable during two auditory identification tasks: one that required analysis of acoustic parameters which provide linguistic information (Stop Consonant task) and one that required analysis of acoustic parameters which provide no linguistic information at the phoneme level (Fundamental Frequency task). For convenience, we shall use the terms "linguistic and nonlinguistic parameters" to refer to those acoustic parameters that do and do not, respectively, provide linguistic information at the phoneme level.

In the Stop Consonant task, subjects were required to indicate which of two possible stimuli had occurred on each trial: /ba/ or /da/. The stimuli were generated by the parallel resonance synthesizer (Haskins Laboratories), and were prepared to be identical in duration (300 msec), initial fundamental frequency ($F_0 = 104$ hz), frequency contour (falling), and intensity contour (falling). Thus, the two syllables differed only in those acoustic cues important for distinguishing between voiced stop consonants, namely, the direction and extent of the second (*9*) and third (*10*) formant transitions. Stop consonants were selected for the linguistic task since they appear to be the most highly encoded of all phonemes (*1*).

In the Fundamental Frequency task, subjects were again required to indicate which of two possible stimuli had occurred on each trial. In this task, however, the two stimuli had identical linguistic information, namely, formant transitions appropriate for the syllable /ba/. They differed only in fundamental frequency: /ba/-low (initial $F_0 = 104$ hz) versus /ba/-high (initial $F_0 = 140$ hz). Both stimuli were 300 msec in duration and had frequency and intensity contours matched to those of stimuli in the Stop Consonant task. Variations in fundamental frequency were selected for the nonlinguistic task since absolute fundamental frequency provides little or no linguistic information at the phoneme level in English. Thus, the two tasks employed three acoustic stimuli, with the syllable /ba/-low (initial $F_0 = 104$ hz) common to both tasks and used for comparison of evoked potentials. Spectrograms of the three stimuli are shown in Fig. 1, arranged according to identification task.

Ten right-handed subjects (ages 18 to 20) were each tested during two separate sessions (*11*). Both sessions consisted of six blocks of 64 stimuli, three blocks each of the Stop Consonant and Fundamental Frequency tasks. A block of 64 stimuli contained 32 each of the two possible stimuli for that task, presented in random order with 5-second intervals between stimuli. The two tasks were presented in alternating order during each session. Five subjects began session 1 with the Stop Consonant task and session 2 with the Fundamental Frequency task; the remaining five subjects began the two sessions in the reverse order. Subjects were required to indicate which of the two possible stimuli they heard on each trial as soon as possible after stimulus onset. In both tasks, subjects pressed button No. 1 with the right index finger when they heard /ba/-low and button No. 2 with the right middle finger when they heard the other stimulus. Thus, both identification tasks contained an identical acoustic stimulus (/ba/-low), which occurred an equal number of times (32 per run of 64), with equal presentation probability on each trial ($p = .5$), and which required an identical motor response (pressing button No. 1 with the right index finger). Before session 1, subjects were asked to listen to the three acoustic stimuli and report what they heard. All subjects correctly identified each of the three syllables. They were then allowed to practice each task under conditions identical to those of the experiment until reaction times were stable. All subjects made fewer than five errors per run of 64 stimuli, and errors did not differ significantly between tasks. Therefore, error scores will not be considered.

Electrical activity was recorded from temporal and central 10-20 system (*12*) scalp locations over the left hemisphere (T3 and C3) and from corresponding locations over the right hemisphere (T4 and C4), each referred to a linked-ear reference with silver disk electrodes. Impedances of all electrodes were monitored regularly during each session and were less than 2.5 kilohms paired with the linked-ear reference. Particular care was taken to equalize impedances of the two ear reference electrodes: in all subjects both reference electrodes were equal at less than 3.0 kilohms, paired with each of the other electrodes.

Subjects were seated comfortably in a sound-attenuating and electrically shielded chamber illuminated at moderate intensity. The electroencephalogram (EEG) was recorded with a Grass model 7 polygraph with Grass model 7P5A wide-band a-c EEG preamplifiers (system gain $= 2 \times 10^4$), and was monitored visually throughout each run. Half-amplitude low- and high-frequency settings were 0.3 hz and 500 hz, respectively. Amplified signals were entered into a LINC computer for analog-to-digital conversion and signal averaging. Sampling epochs were 490 msec with 256 time points per epoch (*13*). The LINC controlled the stimulus presentation order, averaged evoked potentials separately for each of the two stimuli in each task, and stored the averaged responses on magnetic tape for off-line data analysis. Subjects' identification responses and reaction

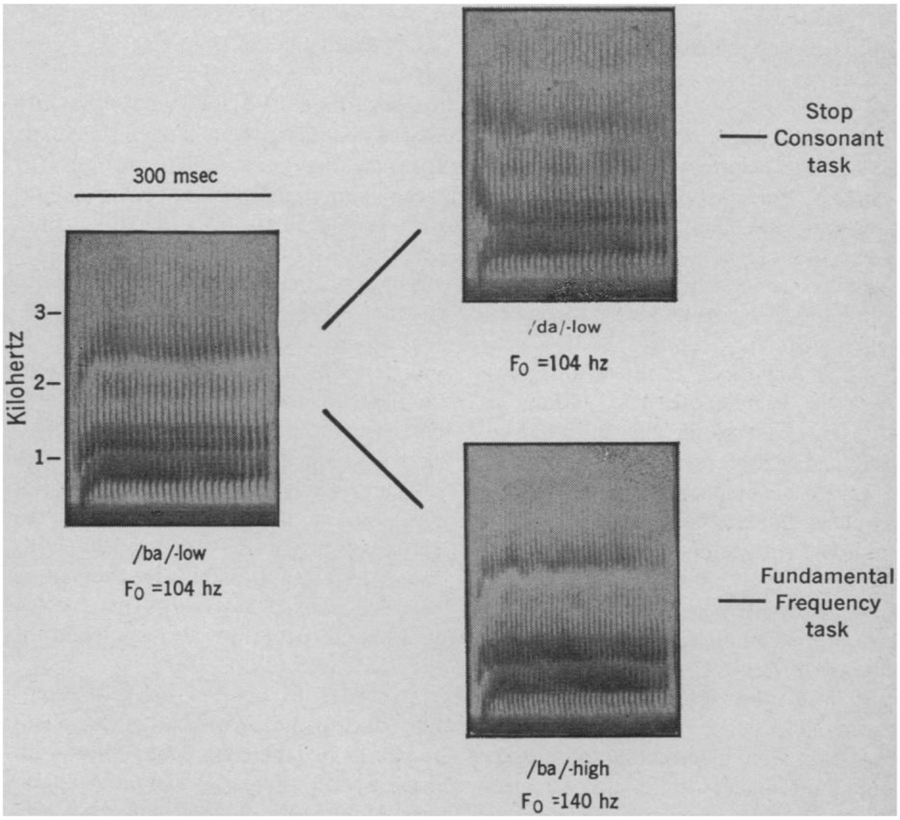

Fig. 1. Spectrograms of the three stimuli. The syllable /ba/-low ($F_0 = 104$ hz) was identical for both tasks. In the Stop Consonant task, stimuli differed only in those acoustic cues important for distinguishing between voiced stop consonants (direction and extent of the second and third formant transitions). In the Fundamental Frequency task, stimuli had identical linguistic information and differed only in fundamental frequency.

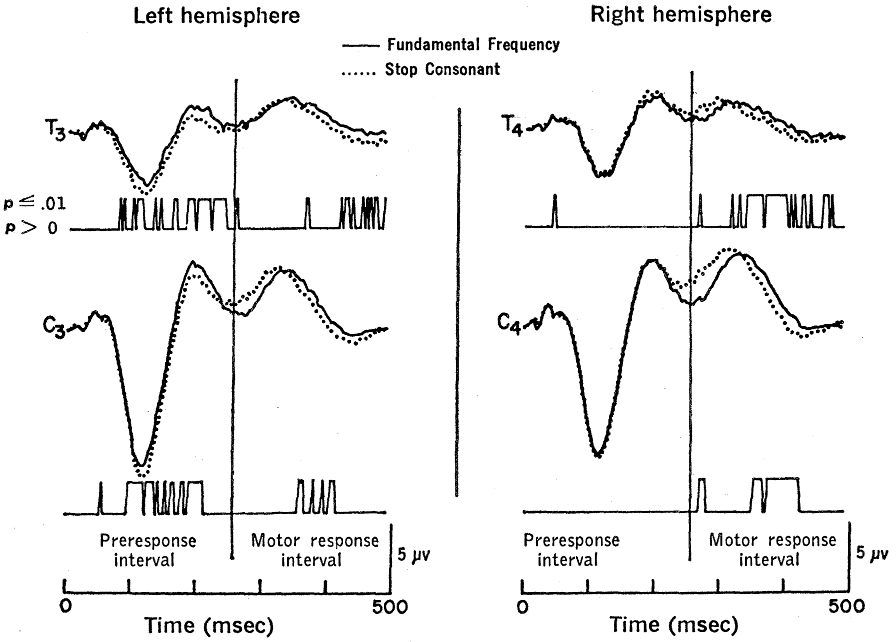

Fig. 2. Electrical activity evoked by the identical stimulus in both tasks, /ba/-low ($F_0 = 104$ hz). Averages of 1920 responses for the Fundamental Frequency (solid lines) and Stop Consonant (dotted lines) tasks are shown for left (*T3* and *C3*) and right (*T4* and *C4*) hemisphere locations. Positivity at the scalp electrode relative to the linked-ear reference is upwards. Time scale: 500 msec. Vertical calibration: 5 μv. Results of the Wilcoxon statistical tests (*15*) for each of the 256 individual sample points are shown below the evoked potentials at each electrode location. Upward deflections of the statistical traces indicate that the difference between evoked potentials at that individual time point is significant at the $P < .01$ level.

times were recorded with a Beckman-Berkeley model 7531R Universal Counter-Timer.

The synthetic stimuli were played to the subjects from a Precision Instrument FM tape recorder (frequency response: ± 0.5 db, d-c to 10 khz at 30 inch/sec). They were presented binaurally at a 65-db sensation level against a 30-db white noise through a Grayson-Stadler model 829D electronic switch to G. C. Electronics earplug-type earphones. The timing of all events, including the initiation of LINC sampling epochs, was controlled by pulses on a separate channel of the frequency-modulated tape recorder synchronized with stimulus onset.

Averaged potentials evoked by the identical stimulus in both tasks (/ba/-low) were combined across subjects to obtain averages of 1920 responses for each task and electrode location as shown in Fig. 2. Evoked potentials from the Stop Consonant and Fundamental Frequency tasks are superimposed at each electrode location to facilitate visual comparison. Reaction times did not differ significantly between tasks according to a Wilcoxon test (*14*) (median ± semi-interquartile range: Stop Consonant = 502 ± 75 msec, Fundamental Frequency = 493 ± 70 msec; $T = 15$, $N = 10$, $P > .10$). To determine the statistical reliability of differences between evoked potentials from the two tasks, Wilcoxon tests (*14*) were computed between evoked potentials at each of the 256 individual time points in the sampling epoch (*15*). Results of the statistical analyses are shown in Fig. 2 below the evoked potentials at each of the four electrode locations. Upward deflections from baseline in the statistical traces indicate that the difference between evoked potentials at that time point was significant at the $P < .01$ level. For significance at the $P < .01$ level, the computation procedure for the Wilcoxon tests requires that the differences between evoked responses for a given time point occur in at least eight of the ten subjects.

In order to analyze evoked potentials during the identification processes required by the two tasks, the 490-msec evoked potential sampling epoch was empirically divided into the *preresponse* and *motor response* intervals shown in Fig. 2. Since the identification process must be complete at or before the identification response is made, only the preresponse interval is appropriate for the analysis of evoked potentials during the identification process (*16*). Differences between evoked potentials during the motor response interval will be considered below.

If the analysis of linguistic and nonlinguistic parameters of an acoustic signal consists of the same neural events, then evoked potentials should be the same (within the limits of normal variation) for both tasks during the preresponse interval. Evoked potentials from the right hemisphere (T4 and C4) were indeed identical for both tasks during the preresponse interval, as shown in Fig. 2. However, statistically significant differences in evoked potentials occurred at left hemisphere locations (T3 and C3) during the same time interval. By chance variation, 1.77 significant time points would be expected at each location during the preresponse interval. At temporal and central locations over the left hemisphere 30 and 34 significant points were obtained, while 1 and 0 significant points were obtained at corresponding right hemisphere locations. These results indicate that neural events in the right hemisphere were identical for both tasks during the preresponse interval, regardless of the task requirements. In contrast, different neural events occurred in the left hemisphere during the same time interval, depending upon whether the task required analysis of linguistic or nonlinguistic parameters of the acoustic signal.

We have been careful to eliminate factors which could produce artifactual differences in evoked potentials between tasks. There is, however, one additional source of possible artifact. Since the occurrence of a motor response (*17*) and the speed of that response (*18*) can alter the neural activity evoked by sensory stimulation, it is possible that even nonsignificant differences in reaction time produced the results shown in Fig. 2. To examine this possibility, the evoked potentials at each electrode location were recategorized. Instead of averaging the six Stop Consonant and six Fundamental Frequency blocks for each subject, the six fastest and six slowest reaction time blocks were averaged to maximize reaction time differences. Evoked potentials from the fast and slow reaction time blocks were then analyzed statistically in the same way as those in Fig. 2.

If the evoked potential differences during the preresponse interval in Fig. 2 were produced by nonsignificant differences in reaction time, then similar or larger differences should be produced by averaging the blocks with slowest and fastest reaction times. Such a result did not occur. No more significant differences than would be expected by chance occurred at any electrode location during the preresponse interval: one significant point was obtained at each left hemisphere location, and one and two significant points, respectively, were obtained at right hemisphere locations. During the motor response interval, evoked potentials from the slow and fast reaction time blocks were significantly different in the same direction as those during the motor response interval in Fig. 2. Thus, we cannot rule out the possibility that slight differences in reaction time may have produced the effects during the motor response interval shown in Fig. 2. However, differences in reaction time could not have produced the significant differences in evoked potentials during the preresponse interval.

In summary, this experiment demonstrates that: (i) differences in neural responses evoked by the same speech signal occurred between tasks which required analysis of linguistic versus nonlinguistic parameters of that signal; (ii) such differences occurred only at left hemisphere locations; and (iii) these differences are not related to differences in the acoustic signal, its presentation probability, the subjects' motor response, or reaction time. These results indicate that different neural events occur in the left hemisphere during analysis of linguistic versus nonlinguistic parameters of the same acoustic signal. Further, they provide strong support for the idea that a unilateral neural mechanism is specialized to perform those linguistic processes necessary for speech perception.

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7. Three experiments concerning neural activity evoked by speech sounds have been reported. H. J. Greenberg and J. T. Graham [*J. Verb. Learn. Verb. Behav.* **9**, 274 (1970)] reported larger amplitudes of the evoked potential's "largest amplitude spectral component" from left- than right-hemisphere locations during a consonant-vowel syllable learning task. No statistical evidence was included to show that the obtained results differed significantly from those expected by chance variation. W. T. Roth, B. S. Kopell, and P. E. Bertozzi [*Electroencephalog. Clin. Neurophysiol.* **29**, 38 (1970)] reported no significant differences in activity recorded at the vertex to "sense and non-sense" monosyllables. In a paper published after the present experiment was submitted, R. Cohn [*Science* **172**, 599 (1971)] reported "differential cerebral processing of noise and verbal stimuli." Cohn's major result was a "prominent positive-going peak with a latency of around 14 msec in the right brain derivation" in response to "click" stimuli generated by 10-msec pulses, but not in response to "single syllable words" generated and presented in an unspecified manner. There are three major difficulties with the Cohn experiment: (i) No statistical evidence was presented to demonstrate that the obtained results differed significantly from chance variation. (ii) Cohn's "verbal" and "noise" stimuli differed in many acoustic parameters such as duration, frequency composition, rise-time, total amplitude, and amplitude contour. Differences in neural activity evoked by such stimuli could be related to any or all of such acoustic differences, none of which need have any direct bearing upon the issue of speech versus nonspeech perception which Cohn wished to address. (iii) It is possible that auditory evoked potentials of 14-msec latency are of nonneural origin. In previous reports of potentials recorded under conditions similar to those used by Cohn, the shortest latency potentials recordable from the human scalp and considered to be of neural origin do not occur until approximately 30 msec [T. E. Mast, *J. Appl. Physiol.* **20**, 725 (1965); H. Ruhm, E. Walker, H. Flanigin, *Laryngoscope* **77**, 806 (1967); W. R. Goff, Y. Matsumiya, T. Allison, G. D. Goff, in *Average Evoked Potentials*, E. Donchin and D. B. Lindsley, Eds. (NASA, Washington, D.C., 1969), p. 95]. Potentials in the 14-msec latency range have been considered to be nonneural artifacts [R. G. Bickford, J. L. Jacobson, D. T. Cody, *Ann. N.Y. Acad. Sci.* **112**, 204 (1964); T. E. Mast, *J. Appl. Physiol.* **20**, 725 (1965); W. R. Goff *et al.*, in *Average Evoked Potentials*, Donchin and Lindsley, Eds. (NASA, Washington, D.C., 1969)].
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13. The 256 time points were distributed throughout the 490-msec epoch at three sampling rates: 1 point every 0.5 msec for the first 60 points, 1 point every 1 msec for the next 66 points, and 1 point every 3 msec for the remaining 130 points.
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15. This procedure was designed to (i) determine the statistical reliability of differences between evoked potentials from the two tasks, and (ii) determine the precise distribution of significant differences in time relative to stimulus onset and subjects' identification responses. Our procedure computed statistical significance for each of the 256 evoked response time sample points, using a standard nonparametric paired comparison technique (Wilcoxon matched-pairs signed-ranks test). At every sample point, the difference between amplitudes of responses from Stop Consonant and Fundamental Frequency tasks was obtained for each of the ten subjects. The differences between tasks were then ranked and the Wilcoxon T statistic was calculated in the usual manner (*14*). Thus, a value of the T statistic for the difference between evoked potentials from the two tasks was obtained for each of the 256 individual time points in each pair of responses.
16. On a single trial the motor identification response unambiguously ends the time interval during which the identification process must have occurred. However, in the average of large numbers of trials required for comparison of evoked potentials, the proper end of the "processing interval" is less clear. Our criterion for distinguishing the preresponse and motor response intervals was the time point after which 99 percent of the motor responses occurred. The 99 percent point was selected instead of the 100 percent point because it disregards those few trials with extremely short reaction times which cannot be meaningfully related to the identification tasks.
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