drills barnacles or mussels (19). The dorsal varix, however, would not contribute to this stability and would tend to make the animal more sensitive to water movement. It is also quite possible that the varix arrangement of *C. foliatum* represents a combined response to several factors, of which fish predation is only one.

A linking of form with function is the closest approximation of adaptive significance that one can achieve for species whose evolutionary history is not precisely known. The correlated occurrence of *C. foliatum*'s unique falling behavior with a known source and specific type of mortality strongly suggests an adaptive response.

ALLISON R. PALMER
Department of Zoology, University of Washington, Seattle 98195

References and Notes

1. R. T. Abbott, *American Seashells* (Van Nostrand Reinhold, New York, 1974). Produced at the outer lip of the shell as the animal grows and often representing temporary cessations of growth, varices in muricids may take the form of conical nodes (*Ocenebra*, *Purpura*, *Thais*), blunt ribs (*Aspiella*, *Oceanebra*), delicate spines (*Homolocanthus*, *Murex*, *Poirieria*), or broad, thin blades (*Boreotrophon*, *Ceratostoma*, *Pteropurpura*, *Pterynotus*).
2. C. A. Hall, *J. Paleontol.* **33**, 428 (1959).
3. T. M. Spight and A. Lyons, *Mar. Biol.* **24** (No. 1), 77 (1974).
4. C. M. Eaton and L. Moulton, personal communication. P. K. Dayton [*Ecol. Monogr.* **41**, 351 (1971)] reported a density of 6.8 animals per square meter at Waadah Island on the outer coast of Washington.
5. L. Berner, *Bull. Inst. Oceanogr. Monaco* **816**, 1 (1942).
6. G. J. Vermeij, *Evolution* **28**, 656 (1974).
7. The individuals selected for these experiments were chosen because of their unworn, well-developed varices. Although no particular starting orientation is more likely than another in nature, preliminary trials indicated that, after the animal had fallen from three to six body lengths, the axis of coiling of all individuals including controls would orient perpendicular to the direction of the fall, regardless of starting orientation. Aperture up and aperture down with the axis of coiling parallel to the bottom were arbitrarily chosen because they represented the extreme positions of *C. foliatum*'s natural "flop" cycle and permitted more reliable replication. All the experiments were carried out in aquariums with running seawater or off the dock of Friday Harbor Laboratories. The substratum upon which the animals were dropped was flat and perpendicular to the direction of fall. "Landing success" refers to the precentage of all times dropped that an individual landed aperture down.
8. There is a significant negative correlation ($r = -.47$, $P < .05$, Spearman coefficient of rank correlation) between landing success when dropped aperture up and landing success when dropped aperture down for all individuals falling distances less than ten body lengths. This does not include the 27.9-mm individual which, over short distances, fell stably aperture down regardless of initial orientation.
9. What is increasing with the distance of fall is landing success independent of starting orientation rather than landing success per se. Hence, absolute length of fall is not important, only the position of the animal in the "flop" cycle when it reaches the bottom. Smaller individuals cover less distance over a complete cycle than larger ones.
10. Genera examined included *Acanthina*, *Bursa*, *Cantharus*, *Conus*, *Crassilabrum*, *Cymatium*, *Fasciolaria*, *Hexaplex*, *Latirus*, *Leucozonia*, *Littorina*, *Morula*, *Muricanthus*, *Pisania*, *Planaxis*, *Purpura*, *Searlesia*, *Strombus*, *Thais*, and *Vitularia*.
11. J. L. Hart, *Pacific Fishes of Canada* (Fisheries Research Board of Canada, Ottawa, 1973).
12. L. Moulton, personal communication.
13. T. Scott, *Annu. Rep. Fish. Bd. Scotland* **20** (No. 3), 486 (1901), *Gadus morhua* (Gadidae); L. R. Brightwell, *Proc. Zool. Soc. London* **123**, 61 (1953), *Squalus caniculus* (Squalidae); J. E. Randall, *Stud. Trop. Oceanogr.* **5**, 665 (1967), *Epinephelus striatus* (Serranidae), *Lutjanus analis* (Lutjanidae); E. S. Hobsen, *Natl. Oceanic Atmos. Adm. (U.S.) Fish. Bull.* **72**, 915 (1974), *Chaetodon lunula* (Chaetodontidae).
14. A. R. Palmer, personal observation.
15. That these fish are quite capable of removing firmly attached mollusks is dramatically supported by the finding of 31 chitons in the gut of a single *Hexagrammos* (L. Moulton, personal communication).
16. This sculptural pattern is perhaps most common in the Muricidae but also occurs among species of the Cymatiidae and Cerithiidae.
17. M. J. S. Rudwick, *Br. J. Philos. Sci.* **15**, 27 (1964). Circumstances where induced morphological changes occur in response to the presence or absence of a specific stress are exceptions to this generalization, for example, production of more and longer spines by a rotifer in the presence of a rotiferan predator [J. J. Gilbert, *Science* **151**, 1234 (1966)] and the presumed induction of thicker-shelled thaidid gastropod populations in the presence of crab predators [J. A Kitching, A. Muntz, F. J. Ebling, *J. Anim. Ecol.* **35**, 113 (1966); A. R. Palmer, unpublished data].
18. G. J. Vermeij, unpublished data.
19. R. T. Paine, *Veliger* **9**, 17 (1966).
20. Portions of this study were supported by NSF grant OCE 74-02307 A01 to R. T. Paine. I thank A. O. D. Willows, director of the Friday Harbor Laboratories, for allowing me use of the laboratory facilities. L. Moulton generously shared unpublished thesis data on stomach contents from kelp greenling. I thank R. T. Paine and A. J. Kohn for critically reading the manuscript. I also thank an anonymous reviewer for suggestions which have improved the manuscript.

8 March 1977; revised 3 May 1977

Auditory Evoked Potentials as Probes of Hemispheric Differences in Cognitive Processing

Abstract. *The amplitude of auditory evoked potentials recorded from the cerebral hemispheres to pairs of task-irrelevant tones was related to differential hemispheric engagement in ongoing cognitive activity (for example, verbal versus musical). The hemisphere hypothesized to be most engaged in the ongoing cognitive task, as compared to the unengaged hemisphere, produced a greater potential difference between the temporal and reference electrode to the second of the tone pairs. These findings are related to "fast habituation" and "recovery cycle."*

Evidence from clinical and behavioral studies has indicated that, for the majority of right-handed people, the left hemisphere plays the more active role in the processing of analytical (for example, linguistic) information, and the right hemisphere plays the more active role in holistic (for example, spatial and musical) information processing (1). Recently, attempts have been made to study this lateralization of brain function in intact subjects by using neurophysiological techniques such as the electroencephalogram (EEG) and evoked potential (2–5). Although these investigations have tended to support the clinical-behavioral observations, the results have not been overwhelmingly convincing and many have been criticized for their methodological shortcomings (6). For example, Galambos *et al.* (7, p. 282) concluded, "The interhemispheric electrophysiological differences reported to date, however, are so tiny as to be barely believable. Hence, either the evoked response method is virtually blind to the crucial events we believe must be there, or the hemispheric differences are barely present in the conditions under which the measurements are currently being made."

In previous auditory evoked potential (AEP) studies of cerebral lateralization, AEP's were elicited directly by relevant speech or nonspeech stimuli (2, 3, 6, 7). Further, most previous studies had little control over the subject's level of arousal or his involvement in the task. For example, subjects may have been told to simply listen to the incoming stimuli (2, 4).

We now report a study in which we have successfully assessed lateralization of brain function by using the AEP as a "probe" of ongoing cognitive processing of information. We were able to obtain reliable AEP changes that were related to the subject's mode of ongoing cognitive processing by using pairs of task-irrelevant auditory tone pips superimposed on linguistic and musical auditory information presented to the subject. We were also able to confirm independently each subject's involvement in the task to assure us of his or her continuous cognitive processing of the information presented during the recording period.

The use of tone pairs allowed us to investigate hemispheric AEP differences in what has been described by Callaway (8) as "fast habituation." Essentially, fast habituation is defined as a reduction in AEP amplitude that occurs when less than 10 seconds elapses between pairs of stimuli; it is generalized to AEP components from 100 to 300 msec, shows response decrements from 30 to 80 percent or more of maximum depending on the interstimulus interval, shows less decrement to stimuli that are relevant to a task the subject is performing or to stimuli the subject cannot anticipate, is a form of learning, and is probably independent of peripheral control. Other investigators have referred to this phenomenon as "recovery cycle" (9). The choice of terms often reflects investigator bias. Use of the term "habituation" reflects a behavioral bias, whereas "recovery cycle" reflects a more physiological bias (8, 9). In our study, we hypothesized that if a hemisphere can be engaged by the processing requirements of a task, it will produce a pattern of fast habituation or recovery to pairs of "probe" stimuli different from that of the relatively unengaged hemisphere.

The subjects were five female and seven male right-handed (10) volunteers between the ages of 21 and 28 years with no known neurological or hearing deficits. The AEP's to pairs of irrelevant tone pips between T_4–C_z and T_3–C_z (11) were recorded for each subject under two experimental conditions and one baseline condition (12). Each condition consisted of four 3-minute segments separated by a 30-second rest period. Conditions were separated by 5-minute rest periods. The AEP's were recorded separately for tone 1 and tone 2 of the pairs of tone pips. For each of the three conditions, the AEP was the result of averaging the responses to 80 stimuli (20 pairs for each of the four segments).

For the baseline condition, four 3-minute segments of taped white noise along with randomly occurring clicks were presented to the subjects over stereophonic headphones. For each segment, 20 pairs of 600-hertz, 100-msec tone pips (with an interstimulus interval of 2 seconds and an interpair interval of 6 seconds) were superimposed on the white noise and clicks (13). The subject was instructed to relax with eyes closed, ignore the tone pips, and indicate that he or she heard the random clicks in the white noise by simultaneously pressing two microswitches with the index fingers of both hands. The presentation of the tone pips started 10 to 15 seconds after the task was begun in order to allow the subject to become adequately involved in the task before presenting the "probe" stimuli.

For the left-hemispheric or verbal condition, subjects were presented with four verbal passages. The passages were selected for their analytical content and their lack of imagery (14). Each subject was required to identify specified "key" words in each of the four passages, and to press the microswitches as described for the baseline condition each time a key word in the passage was heard. Subjects were informed of the key word before the start of each passage; they were also instructed to attend to the content of the passage and to be prepared to answer written questions pertaining to the content at the end of each passage.

For the right-hemispheric or music condition, subjects were presented with four musical selections. Before each selection, subjects were presented with a simple melody or musical theme, which was part of the selection. Each subject was required to identify this theme when it occurred in the musical selection by pressing the microswitches.

The subject's scores on the written questions, as well as his performance in identification of the key words in the verbal passages and themes in the musical selections, were used as indices of his involvement in the cognitive tasks presented. Data were evaluated only for those subjects showing greater than chance performance across the experimental conditions.

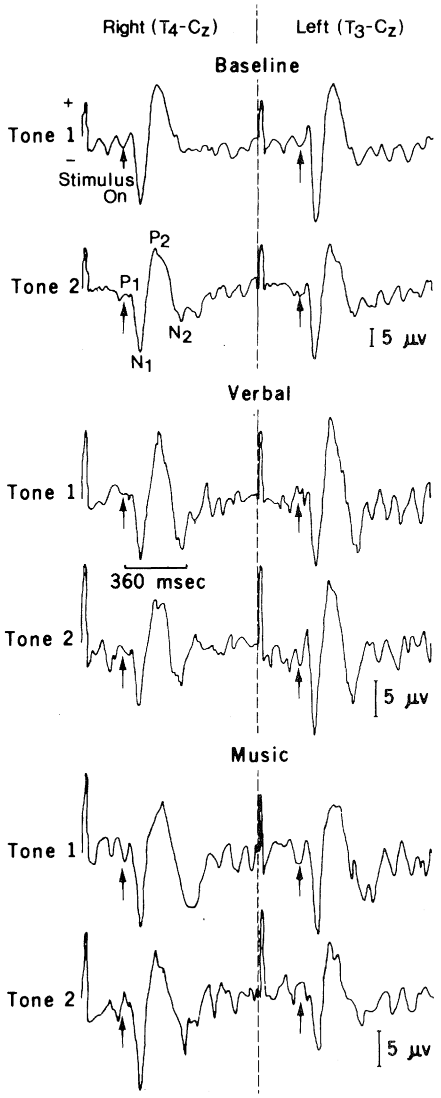

Fig. 1. Auditory evoked potentials to pairs of tone pips for baseline, verbal, and music conditions recorded from homologous right- and left-hemisphere locations in a normal female adult. The vertical arrows indicate stimulus onset. The peak at the beginning of the tracing (before the stimulus onset) is the calibration signal. Peaks 1, 2, and 3, as defined in the text, refer respectively to the negative-going peak from P_1 to N_1, the positive-going peak from N_1 to P_2, and the negative-going peak from P_2 to N_2. Positivity at C_z with respect to T_4 or T_3 is up.

There were approximately eight clicks, key words, and musical themes that occurred during each 3-minute task segment of baseline, verbal, and music conditions, respectively. Thus, the number of required button presses was equated across each task. The baseline condition was always presented first, and the verbal and music conditions were counterbalanced for order across subjects.

Three reliable AEP peaks were identified for each subject. The mean latencies and standard deviations in milliseconds for these peaks across all conditions for all subjects were: peak 1 (negative-going) latency = 106.5 [standard deviation (S.D.) = 11.3]; peak 2 (positive-going) latency = 195.1 (S.D. = 23.6); peak 3 (negative-going) latency = 304.3 (S.D. = 35.4). The AEP's for one subject across baseline, verbal, and music conditions are illustrated in Fig. 1.

Amplitude scores for each peak were obtained by computing the peak-to-trough or trough-to-peak distance in millimeters and, on the basis of the calibration signal, converting this distance to microvolts. In addition, an overall amplitude measure was obtained by summing the amplitudes across all three AEP peaks.

A condition-by-tone-by-hemisphere analysis of variance was done on the overall amplitude score. The results yielded a significant condition effect [F (2, 22) = 62.1, $P < .001$], tone effect [F (1, 11) = 49.1, $P < .001$], condition-by-tone effect [F (2, 22) = 10.4, $P < .001$], condition-by-hemisphere effect [F (2, 22) = 4.2, $P < .03$], and condition-by-tone-by-hemisphere effect [F (2, 22) = 4.7, $P < .02$]. The Duncan multiple range test (15) was used to more closely evaluate these effects. This analysis indicated that (i) left-hemisphere bipolar AEP's were significantly greater in amplitude than right-hemisphere bipolar AEP's during the verbal condition and (ii) right-hemisphere AEP's were higher in amplitude than left during the music condition (Fig. 2A) (16). These differences were more pronounced for the AEP's to tone 2 of each pair ($P < .01$ verbal, and $P < .005$ music). The baseline condition showed no such laterality effect. In addition, there was an overall decrease in AEP amplitude from tone 1 to tone 2. The most dramatic amplitude decrement ($P < .001$) occurred for the baseline condition, with the right and left hemispheres showing virtually identical responses. For the verbal condition, there was no significant decrement in AEP amplitude for the left hemisphere, whereas the right hemisphere showed a significant decrement from tone 1 to tone 2 ($P < .001$). The music condition showed a decrement from tone 1 to tone 2 for both hemispheres, with the right producing less of a decrement than the left ($P < .01$ right, 12 percent decrement; $P < .001$ left, 16 percent decrement).

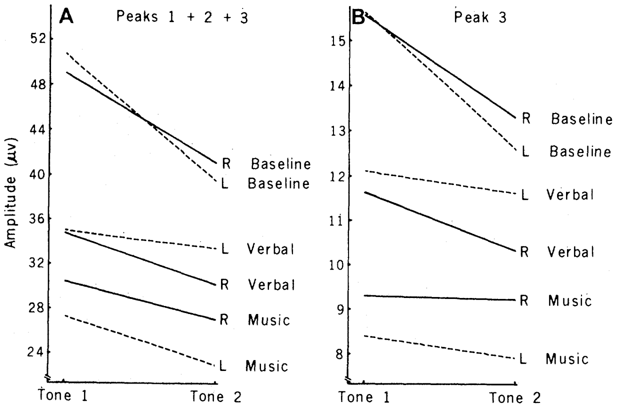

Fig. 2. Right- and left-hemisphere AEP amplitudes in microvolts to pairs of tone pips for baseline, verbal, and music conditions. Each data point is the mean of the averaged AEP's to 80 stimuli for each of 12 subjects. (A) Results for the overall amplitude measure. (B) Results for N_{300}.

In order to examine more closely the contribution of each AEP peak to this amplitude laterality effect, condition-by-tone-by-hemisphere analyses of variance were also done separately for each AEP peak. The results of these analyses and the paired comparisons (Duncan) indicated that although the relationships described for the overall amplitude measure held for each peak individually, the most potent effect was seen for peak 3 and was again most pronounced for the second tone (Fig. 2B). Again, there were no hemispheric differences in AEP amplitude during the baseline condition. The left hemispheric tone 2 bipolar AEP was significantly higher in amplitude than the right for the verbal condition ($P < .005$); whereas the right was significantly higher than the left for the music condition for both tone 1 and tone 2 ($P < .005$). Again, as for the overall measure, there was a marked decrement in AEP amplitude between tone 1 and tone 2 in the baseline condition ($P < .001$), with no significant difference between the hemispheres. The verbal and music conditions produced hemispheric differences in the AEP amplitude decrement from tone 1 to tone 2. During the verbal condition, the left hemisphere showed no significant amplitude decrement between the two tones, whereas the right hemisphere showed a decrement from tone 1 to tone 2 ($P < .005$). In the music condition, the right hemisphere showed virtually no amplitude decrement, while the decrement for the left hemisphere was not significant ($P < .20$).

The results of the analyses indicated that the left hemisphere responded with higher bipolar AEP amplitude than the right to task-irrelevant tone pips presented while subjects were processing verbal information. The right hemisphere responded with higher bipolar AEP amplitude than the left when subjects were processing music. This effect was most pronounced for the second of the paired tones. In addition, the decrement in the bipolar response from the first to the second tone occurred to a lesser degree from the hemisphere hypothesized to be most engaged in processing the incoming information.

It is important to note that the obtained AEP's reflect voltage *differences* between T_3 and C_z and T_4 and C_z electrodes, and that the C_z site produces the higher-amplitude response to auditory stimuli. Therefore, a higher AEP amplitude recorded from one hemisphere indicates a greater potential difference between the temporal electrode of that hemisphere and the C_z reference. Thus, a higher-amplitude left-hemisphere AEP during the verbal condition is probably a result of a lower-amplitude response at the T_3 recording site compared with the T_4 site. Conversely, a higher-amplitude right-hemisphere response during the music condition probably indicates a lower-amplitude response at the T_4 site compared with the T_3 site.

The results appear to be due, in part, to hemispheric differences in fast habituation or recovery cycle as a function of task demands. In the engaged hemisphere, there may be fewer neurons available to respond to the "probe" stimuli; thus, a low-amplitude response at the engaged recording site occurs and results in a higher-amplitude bipolar AEP compared with that obtained for the unengaged hemisphere. These active neurons in the engaged hemisphere may also be more refractory to the second member of the tone pair; hence the bipolar response to tone 2 from that hemisphere remains relatively large compared with that of the less engaged hemisphere.

Another possible explanation for the obtained asymmetries to tone 2 is that engaging a hemisphere by a particular task may make that hemisphere more receptive to all incoming (auditory) stimuli and, thus, better able to anticipate the sequential relationship between the irrelevant tone pairs. This would produce less orienting to the tone pairs by the engaged hemisphere and would result in a higher bipolar AEP for tone 2 for the engaged hemisphere than for the unengaged hemisphere. This explanation appears to be consistent with Kinsbourne's activation hypothesis (*17*).

These findings lend further support to previous clinical-behavioral studies and to the hypothesis that the cerebral hemispheres may at times have the ability to function and respond independently of one another (*18*). It appears that the "two-tone probe technique" is sensitive to differential engagement of the cerebral hemispheres in ongoing information processing, and it thus offers a promising approach for studying cerebral lateralization in humans.

D. W. SHUCARD
J. L. SHUCARD
D. G. THOMAS

EEG and Neurophysiology Laboratories,
Department of Behavioral Sciences,
National Jewish Hospital and Research
Center, Denver, Colorado 80206, and
Department of Psychiatry,
University of Colorado Medical Center,
Denver 80220

References and Notes

1. D. Kimura, *Can. J. Psychol.* **15**, 166 (1961); *Q. J. Exp. Psychol.* **16**, 355 (19 → R. W. Sperry, *Am. Psychol.* **23**, 723 (1968); N. Geschwind, *Science* **170**, 940 (1970); R. D. Nebes, *Cortex* **7**, 333 (1971); M. Durnford and D. Kimura, *Nature (London)* **231**, 394 (1971); M. S. Gazzaniga, *Am. Sci.* **60**, 311 (1972); A. R. Luria, *The Working Brain* (Basic Books, New York, 1973); D. E. Broadbent, in *The Neurosciences Third Study Program*, F. O. Schmidt and F. G. Worden, Eds. (MIT Press, Cambridge, Mass., 1974), pp. 31–41.
2. R. Cohn, *Science* **172**, 599 (1971).
→ L. K. Morrell and J. G. Salamy, *ibid.* **174**, 164 (19 → C. C. Wood, W. R. Goff, R. S. Day, *ibid.* **173**, 1248 (1971); S. A. Shelburne, Jr., *Electroencephalogr. Clin. Neurophysiol.* **32**, 17 (1972); D. L. Molfese, R. D. Freeman, Jr., D. S. Palermo, *Brain Lang.* **2**, 356 (1975).
4. M. Buchsbaum and P. Fedio, *Physiol. Behav.* **5**, 207 (1970).
5. D. W. McAdam and H. A. Whitaker, *Science* **172**, 499 (1971); D. Galin and R. Ornstein, *Psychophysiology* **9**, 412 (1972); G. McKee, B. Humphrey, D. McAdam, *ibid.* **10**, 441 (1973); J. C. Doyle, R. Ornstein, D. Galin, *ibid.* **11**, 567 (1974); D. Galin and R. R. Ellis, *Neuropsychologia* **13**, 45 (1975).
6. D. Friedman, R. Simson, W. Ritter, I. Rapin,

Electroencephalogr. Clin. Neurophysiol. **38**, 13 (1975).
7. R. Galambos, P. Benson, T. S. Smith, C. Schulman-Galambos, H. Osser, *ibid.* **39**, 279 (1975).
8. E. Callaway, in *Habituation: Physiological Substrates*, H. V. S. Peeke and M. J. Herz, Eds. (Academic Press, New York, 1973), pp. 153–174.
9. T. Allison, *Electroencephalogr. Clin. Neurophysiol.* **14**, 331 (1962); H. Davis, T. Mast, N. Yoshie, S. Zerlin, *ibid.* **21**, 105 (1966).
10. Subjects were considered right-handed if they had a right-sided preference for batting, writing, and kicking and if all immediate family members were right-handed.
11. Position C_z is an active electrode site that elicits the clearest response to auditory stimuli [W. R. Goff, Y. Matsumiya, T. Allison, G. D. Goff, in *Average Evoked Potentials: Methods, Results and Evaluations*, E. Donchin and D. B. Lindsley, Eds. (National Aeronautics and Space Administration, Washington, D.C., 1969), pp. 95–141]. Studies using the AEP that were not concerned with lateralization effects have typically recorded between C_z and one or more ear references. Pilot experiments in our laboratory, using different electrode sites, including a reference with the ears linked, indicated that the temporal-to-C_z placement produced the clearest lateralized responses to the different task requirements and allowed the averaging of fewer responses to obtain scoreable AEP peaks. Even though C_z probably produces a larger evoked response than the lateral sites used in this study, it is possible that for this reason the response amplitude is potentially more variable than it is with other electrode arrays; it would thus be more sensitive to the lateralizing effects of the tasks. Further, since C_z is common to both temporal placements, differences in electrical activity at the temporal recording sites would still be discernible from the bipolar response.
12. Grass Gold-plated electrodes (Grass) were used to record the AEP's between T_4–C_z and T_2–C_z (according to the 10-20 International System), with a ground electrode located on the forehead. Electrode impedance was maintained below 5000 ohms and was checked and recorded at the beginning of each condition. Two amplifier channels of a polygraph (Grass model 78) with a bandpass of 0.3 to 300 hertz and a sensitivity of 7.5 μv/mm were used to record the EEG. The AEP's for tone 1 and tone 2 were summed separately on a signal averager (Nicolet 1072) and printed out on an X-Y plotter (Hewlett-Packard 7004b). Two calibrators (Bioelectric CA5) in series with the subject's scalp were used to place a 10-μv, 20-msec calibration signal on the left- and right-hemisphere AEP's.
13. All of the material for each condition, including the instructions, was prerecorded on audiotape and presented to subjects through stereophonic headphones while they were seated in a reclining chair in a sound-attenuated, electrically shielded room. A mixer (Sony MX-14) was used to control intensity ratios between tone pips and the task material presented in each of the three conditions. Tone pips were produced by a waveform generator (Interstate Electronics Corporation). Tone-pip intensity as measured by an impulse precision sound level meter (Brüel and Kjaer) was approximately 84 db sound pressure level, according to the C-weighting network specified by International Electrotechnical Commission recommendation 179. The average intensity of the white noise, verbal passages, and musical selections was 76 db ± 5 bd. Stimulus intervals, stimulus duration, and triggering of the averager and calibration equipment was controlled by a Siliconix System.
14. Passages were taken from the reading test section of E. C. Gruber, *The Complete Study Guide for Scoring High: Graduate Record Examination* (Arco, New York, 1970).
15. A. L. Edwards, *Experimental Design in Psychological Research* (Holt, Rinehart & Winston, New York, 1960), pp. 136–140.
16. The general AEP amplitude differences between baseline, verbal, and music conditions were probably due to subjective differences in the intrusiveness of the tone pips on incoming white noise, verbal, and musical stimuli. Most subjects, when questioned at the end of the experimental session, indicated that during the music condition, the tone pips were less intrusive than they were during the verbal condition; they were most intrusive during the baseline condition. Thus, it appears that a contextual effect between the tone pips, and ongoing white noise, verbal, and musical stimuli produced AEP's of generally higher amplitude during the baseline condition, and higher-amplitude AEP's for the verbal compared with the music condition.
17. M. Kinsbourne, in *Attention and Performance IV*, S. Kornblum, Ed. (Academic Press, New York, 1973), pp. 239–256.
18. D. Galin, *Arch. Gen. Psychiatry* **31**, 572 (1974).
19. We thank M. Andrew for his technical assistance with the audio stimuli and Drs. A. Friedman, J. Campos, and S. Hoffman for their helpful comments. Supported in part by NIH grant MH 28513 to D.W.S.

8 November 1976; revised 22 April 1977

Sympatric Speciation Based on Allelic Changes at Three Loci: Evidence from Natural Populations in Two Habitats

Abstract. *Allelic changes at three loci largely explain* Chrysopa downesi*'s sympatric speciation from a* Chrysopa carnea*-like ancestor. Disruptive selection first produced a stable polymorphism based on a single pair of alleles that adapted individuals to two habitats, and second, it established seasonal asynchrony in reproduction through allelic substitutions at two loci.*

A central problem in evolutionary biology concerns the amount and type of genetic change and the procession of events that produce independent evolutionary units—species. Genetic divergence of geographically isolated populations (allopatric speciation) is generally accepted as the primary mode of speciation in bisexual animals (*1*). In contrast, the concept of speciation through the action of disruptive selection on an interbreeding population (sympatric speciation) remains an area of considerable controversy. In the selection experiments around which the modern theory of sympatric speciation was built, the physiological and genetic basis for the reproductive isolation produced in the laboratory is unknown, and the artificial forces of disruptive selection are not related to field conditions (*2*). Therefore, these experiments have provided relatively limited insight into the question of sympatric speciation in natural populations.

As a testable hypothesis, Maynard Smith (*3*) offered a general theoretical model for sympatric speciation through disruptive selection. This model's attractiveness resides in its simplicity—a few, simple genetic changes underlie the proposed process of speciation. Until now, the most convincing field and laboratory evidence for this model has come from monophagous insects in which simple genetic changes produce divergent host races that lead to new species (*4*). Indeed, it has been suggested that sympatric speciation through disruptive selection is restricted to host-specific, phytophagous or parasitic animals (*5*). In contrast, we report experimental evidence herein that disruptive selection can act through habitat differences in the speciation of non–host-specific animals. In our example, a single gene difference underlies a divergence in habitat association, and allelic substitutions at two loci underlie the subsequent evolution of an effective reproductive barrier. This study illustrates that Maynard Smith's theoretical model for sympatric speciation, rather than being restricted to monophagous or parasitic species, has broad application among bisexual animals.

Our experimental animals were the sibling species *Chrysopa carnea* Stephens and *Chrysopa downesi* Banks (Insecta: Neuroptera: Chrysopidae), which occur sympatrically in northeastern United States. They share many important features in their biology; for example, the larvae of both species prey on a variety of soft-bodied arthropods, and the adults feed on honeydew and pollen and have similar dietary requirements for reproduction (*6*). Under laboratory conditions these species hybridize and produce fully viable and fertile F_1 and F_2 offspring. However, in nature the two species are reproductively isolated through differences in habitats and in seasonal periods of reproduction (*7*).

The species *C. carnea*, which is multivoltine (producing several generations each summer), occurs mainly in grassy areas and meadows during its annual reproductive period (late spring to the end of summer). At this time the pale green adults are cryptically colored against a background of light green foliage. At the end of summer, when reproduction ceases, the adults enter reproductive diapause and move to the senescent foliage of deciduous trees. This movement by the *C. carnea* adults is accompanied by a change in color, from light green to reddish-brown, thus maintaining the adults' camouflage in their overwintering site. In contrast to *C. carnea*, *C. downesi* is a univoltine, early-spring breeder, and it is restricted to conifers throughout the year. The very dark green color of *C. downesi* adults camouflages them in their coniferous habitat during both reproduction and diapause.