model and partial self-fertilization, as described in Crow and Kimura (*6*, pp. 92–94, 144, 152). There is a geometric approach to equilibrium, and at equilibrium, F, the fixation index of Wright, is related to h, the proportion of self-fertilization, by $F = h/(2 - h)$. In partial self-fertilization a fraction h of mates have unit correlation and the remainder zero, so that overall the correlation coefficient is h. In the model given here the correlation between mates is μ, and hence the relation between h and F is the same as that between μ and λ. Wright's F corresponds to λ, and h to μ.

However, there are two differences between the models. First, in Wright's model of self-fertilization F is essentially positive, whereas in the model given here λ can be negative. Second, and more important, the equilibrium mating frequencies are different in the two models. For example, if $q = \frac{1}{2}$, the genotype frequencies are $f_0 = f_2 = \frac{1}{4}(1 + \lambda)$, $f_1 = \frac{1}{2}(1 - \lambda)$, and the mating frequencies involving heterozygotes are as shown in Table 1.

The list of papers which have been written on assortative mating in relation to a single locus is too extensive to be given here, but a number of the more important ones are cited by Crow and Kimura (*6*, pp. 143, 161). Lewontin *et al.* (*7*) draw distinctions between assortative mating, inbreeding, and selective mating, which are relevant to the previous two paragraphs of this report. The equilibrium system given by Eq. 3 was introduced by Stark [see (*8*), where it is discussed in greater detail].

A. E. STARK
School of Community Medicine,
University of New South Wales,
Post Office Box 1, Kensington,
New South Wales, Australia 2033

References and Notes

1. R. A. Fisher, *Trans. R. Soc. Edinburgh* **52**, 399 (1918).
2. G. Malécot, thesis, University of Paris (1939).
3. O. Kempthorne, *An Introduction to Genetic Statistics* (Wiley, New York, 1957), pp. 493–498.
4. G. Malécot, *Colloq. Int. C.N.R.S.* **13**, 121 (1949).
5. S. Wright, *Evolution and the Genetics of Populations* (Univ. of Chicago Press, Chicago, 1969), vol. 2, p. 173.
6. J. F. Crow and M. Kimura, *An Introduction to Population Genetics Theory* (Harper & Row, New York, 1970).
7. R. Lewontin, D. Kirk, J. Crow, *Eugen. Q.* **15**, 141 (1968).
8. A. E. Stark, *Nature (London)* **259**, 44 (1976); *Ann. Hum. Genet.* **39**, 455 (1976).

9. I thank Prof. G. Malécot, head of the department (Mathématiques Appliquées, Université Claude Bernard, Lyon 1) where this work was completed, for his advice and hospitality, and two referees: the first pointed out the similarity of my model to that of partial self-fertilization, the second provided comments on the work of Fisher and a proof of the approach to equilibrium which I used to make a substantial improvement to my original manuscript.

9 December 1975; revised 24 May 1976

The Effect of Stimulus Sequence on the Waveform of the Cortical Event-Related Potential

Abstract. *The waveform of the cortical event-related potential is extremely sensitive to variations in the sequence of stimuli preceding the eliciting event. The waveform changes were manifested primarily in the amplitudes of the negative component of the potential that peaked at 200 milliseconds, the positive component that peaked at 300 milliseconds, and the slow-wave components. A quantitative model was developed relating the waveform changes to changes in event expectancy. Expectancy is assumed to depend on a decaying memory for events within the prior sequence, the specific structure of the sequence, and the global probability of event occurrence. For stimuli relevant to the task, the less expected the stimulus the larger the amplitudes of late components of the event-related potentials.*

The cortical event-related potential (ERP) associated with the rare outcomes of Bernoulli trials that are relevant to a task is different from that associated with the frequent outcomes (*1–3*). If, for example, a subject is instructed to count the occurrences of a few low-pitched tones embedded in a series of high-pitched tones, the low-pitched tones elicit ERP's characterized by a large negative component peaking at 200 msec (N200), a large positive component peaking at 300 msec (P300), and large slow-wave (SW) components (*3*). The distinction between the types of ERP waveforms made it possible for us to develop a discriminant function in which ERP's to individual tones were classified as "rare" or "frequent" (*4*). When a "correct" classification was defined as the categorization of an ERP elicited by a rare tone as "rare" and by a frequent tone as "frequent," the discriminant function formed from the ERP data of one group of subjects correctly classified 81 percent of all ERP's from a group of new subjects. Although the classification technique was successful, the reasons for misclassifying 19 percent of the trials remained unclear. An analysis of the waveforms associated with the misclassifications suggested that the erroneous classifications reflected systematic trial-to-trial variations in the ERP waveforms. Some of the "rare" events seemed to elicit a "frequent" waveform, and vice versa (*5*). Since the underlying assumption of research involving ERP's is that the ERP's elicited by all occurrences of a particular type of event are identical, such trial-to-trial variations in the ERP required further examination.

Inspection of the trial-to-trial waveform measures suggested that the variations might have been due to short-term sequential dependencies. Remington (*6*) and others (*7–10*) have demonstrated sequential dependencies in choice tasks, in which reaction time (RT) on any given trial is sensitive to the specific sequence of preceding events. These sequential effects have been attributed by some to trial-to-trial changes in the subject's expectancies (*9, 10*). Since expectancy has been implicated as one determinant of the ERP waveform, we attempted to determine whether the waveform of the ERP exhibits similar sequential dependencies.

Seven subjects listened to series of regularly presented tone bursts. On each trial a high-pitched and a low-pitched tone were equally likely to occur (*11*). The subject was instructed to count the high-pitched tones silently and to report the count after each block of 200 trials. In a second condition, the probabilities of the high- and low-pitched tones were changed to .3 and .7, respectively (*12*). Each subject was tested on 800 to 1600 trials, depending on the condition.

During testing, the subject was comfortably seated in a reclining chair in a well-lighted experimental room. The electroencephalogram (EEG) was recorded with Burden Ag-AgCl electrodes from F_z, C_z, and P_z (according to the 10-20 system) which were referred to a linked mastoid electrode, with a wrist ground. The band pass of the amplifier system was set for a time constant of 0.8 second and an upper half-amplitude frequency of 35 hertz. Additional electrodes (Beckman) were situated above and on the outer margin of the right eye to record eye movement and blink potentials. On each trial, a 768-msec epoch of the EEG, beginning 100 msec before the stimulus onset, was digitized from each of the recording channels (at a rate of one sample every 3 msec) and stored on digital magnetic tape. The EEG epochs contaminated with eye movement or blink artifacts were excluded from the subsequent waveform analysis. All trials entered into the tabulations of sequences.

Remington's terminology (*6*) will be followed. An "A" represents whichever stimulus event occurred on trial *N* (a first-order sequence). For the second-order sequences there were two possible patterns of stimuli on trials $N - 1$ and N, "AA" or "BA." Similarly, there were four possible third-order patterns ("AAA," "BAA," "ABA," or "BBA"), eight fourth-order patterns, and 16 fifth-order patterns. When the sequences terminated with a high-pitched tone, an A in a sequence represents the occurrence of a high-pitched tone and a "B" that of a low-pitched tone. When the sequences terminate with a low-pitched tone, the labels are reversed. A waveform measure can be plotted for each of the possible sequences and a tree diagram constructed by connecting the points in each order to the related points in the higher and lower orders. For instance, the third-order sequences ABA and BBA are related to the second-order sequence BA by the occurrence of either an A or a B on trial $N - 2$. Branches at each node, which systematically diverge to high orders, indicate differential effects of the preceding stimuli in the sequence on the dependent variable on trial N (Fig. 1).

The averaged ERP waveforms (from C_z) for the sequences of the outer limbs of the tree structure are shown for one subject in Fig. 2. Large discriminant scores reflect large P300 components (and the associated N200 and SW components). There is systematic variation in the waveform of the ERP as a function of the sequence of preceding stimuli. The size of the P300 complex elicited by an A increases with the number of B stimuli that precede it (the ascending limb of the tree), and the size of the P300 complex decreases as runs of A stimuli of increasing length precede a given A. The influence of preceding stimuli on the ERP elicited on trial N extends at least to trial $N - 4$ (Fig. 1a) (*13*). The discriminant score variations seem to result mainly from amplitude changes of the waveform components and not from large shifts in latencies of the components (Fig. 2) (*14*).

In the unequal probability condition (.3/.7), the tree structures for the high- and low-pitched tones are displaced (Fig. 1, b and c). The discriminant scores for each sequence are generally larger for the stimuli with a low probability and smaller for those with a high probability (*15*). The average displacement, however, is no larger than the range of the discriminant scores observed for fifth-order sequences in each of the panels (Fig. 1). The sequential determinants of waveform variability seem to be at least as potent as the determinants of the ERP waveform associated with changing levels of stimulus probability.

The tree structure reported here is similar to the RT trees of Remington (*6*) and Falmagne *et al.* (*7*). The analogous effects in the two cases are the enhancement of the P300 complex and the prolon-

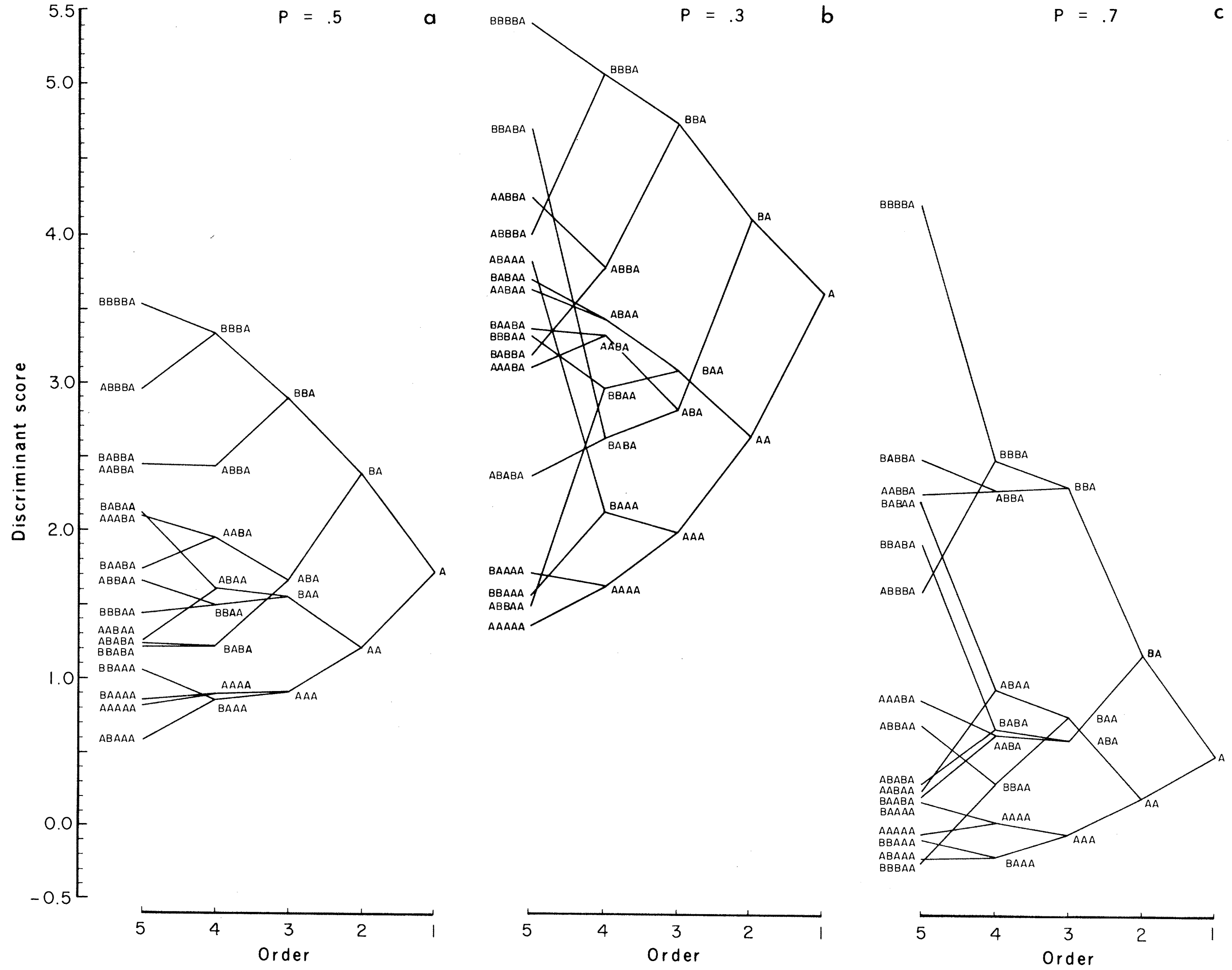


Fig. 1. Tree diagrams of discriminant scores [a composite measure of the ERP waveform elicited on trial N (*24, 25*)] as a function of the sequence of preceding stimuli. The discriminant score is given in arbitrary units. Within each order (1 to 5), the stimulus sequence is labeled, and related sequences are connected across orders. (a) Mean of all occurrences of each sequence with stimulus probabilities of .5/.5 (*26*). (b) Probability of stimulus presentation equal to .3 (A represents the high-pitched tone). (c) Probability of stimulus presentation equal to .7 (A represents the low-pitched tone).

gation of RT with longer sequences of preceding B's. If, as has been argued (*9*), RT increases as an inverse function of expectancy, a similar relationship between expectancy and ERP waveforms can be assumed. We proceeded, therefore, to develop a model, based on the concept of expectancy, to describe the sequential dependencies in ERP waveform.

In serial RT tasks, when the intertrial interval is less than 2.0 seconds, the effect of a stimulus sequence on the expectancy of a stimulus event is presumed to function as follows. The subject forms a local (as opposed to a global) subjective probability distribution that reflects event frequency within a "sliding window." The more frequently an event occurs within that window, the greater is the subjective probability (expectancy) that the event will recur. When the next event in the sequence confirms the expectations induced by the probability distribution, RT is shorter than if the less expected event occurs.

In our experiment, the amplitude of the P300 complex (as measured by the discriminant score) seems to be larger when the expectation is disconfirmed than when it is confirmed by the eliciting event. Thus, a model accounting for the waveform data should estimate the expectancy the subject has for an event as a function of the preceding sequence of stimuli. We assume expectancy to be determined in a linear additive fashion by three factors: (i) the memory for event frequency within the prior stimulus sequence, (ii) the specific structure of the prior sequence, and (iii) the global probability of the event.

The assumption that the locally operating, subjective probability distribution depends on a sliding window implies that the magnitude of the effect of a stimulus on the expectancy for succeeding stimuli is a decaying function of sequential position (or time) (*10*). We assume that the effect of a stimulus on responses to succeeding stimuli is governed by an exponential decay process (*9*). The specific form of the "memory" (M) expectancy function for event A on trial N as a function of the sequence of past events S_i is assumed to be

$$M_{AN} = \sum_{i=N-1}^{N-m} \alpha^{N-i} S_i \qquad (1)$$

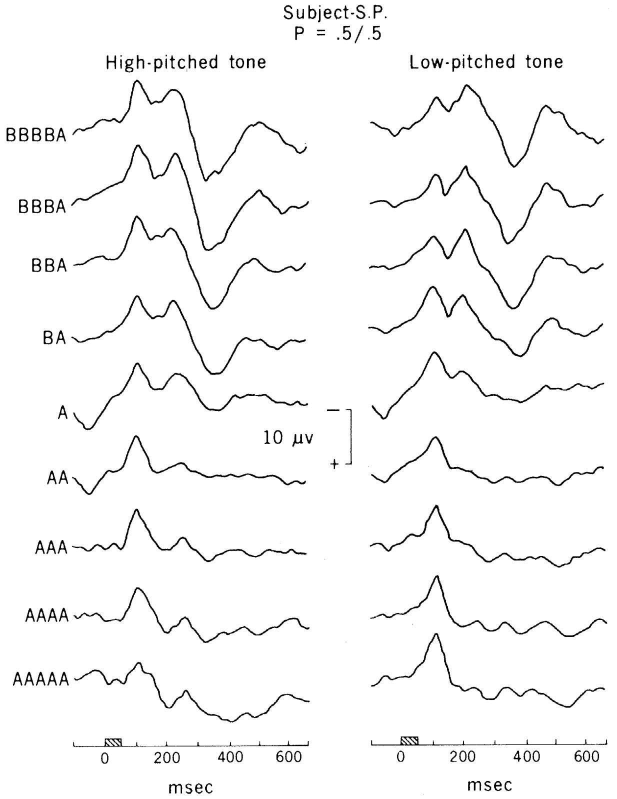
where

$$S_i = \frac{0 \text{ for } (S_i = \text{B})}{1 \text{ for } (S_i = \text{A})}$$

and where m equals the order of the sequence (here, $m = 5$). The constant α corresponds to the rate of decay in memory of prior stimulus information ($0 \leq \alpha \leq 1$); small values of α indicate that only very recent events contribute to expectancy (*16*).

Alternations in the stimulus sequence generate expectancies that the alternation pattern will continue (*10*, *17*). With regard to alternations, our model assumes that (i) a positive expectancy is generated for the stimulus on trial N that fits the alternation pattern, and a negative expectancy is generated for one that breaks the pattern; (ii) the magnitude of the alternation factor should grow (linearly) with the number of consecutive prior alternations; and (iii) a minimum of two prior alternations are necessary to induce an alternation set. Thus, each stimulus sequence was assigned an alternation factor $A(S_i)$, whose value (-3 to $+3$) was generated by these assumptions (*18*).

The probability (P) that a stimulus will occur affects the discriminant score independently of sequential effects (Fig. 1). It may be conceived of as a reflection of long-term memory, or as a nonzero asymptote of the decaying short-term memory process that governs the more recent sequential effects. Similar effects of global probability operate on reaction times (*6*, *7*). We assumed that the three determinants of expectancy [$M(S_i,\alpha)$,



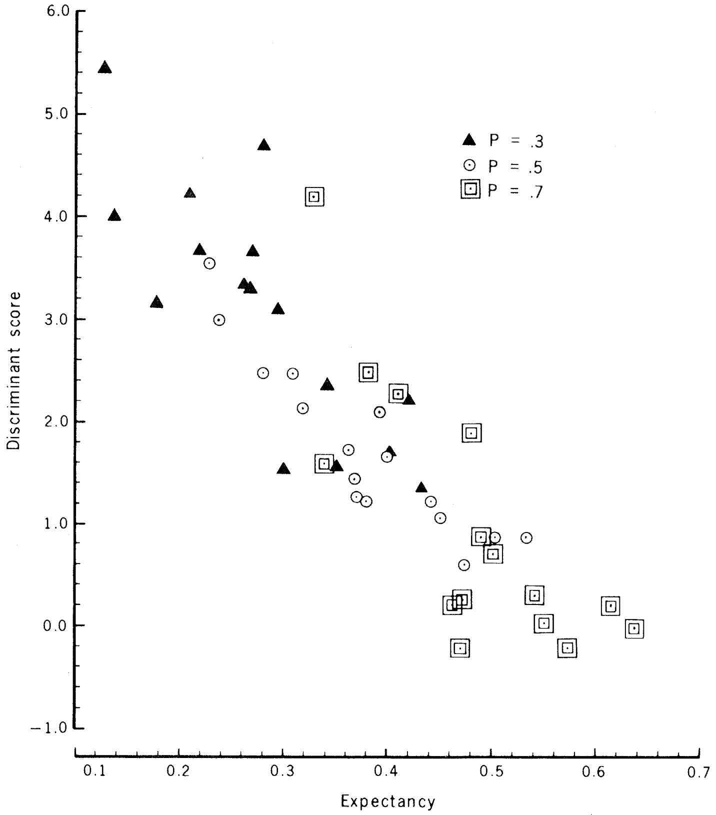


Fig. 2 (left). Averaged ERP waveforms from the vertex (C_z) lead for sequences that form the outer limbs of a tree diagram with the probabilities of occurrence of each signal equal to .5. Vertex negativity is plotted upward. Fig. 3 (right). Observed discriminant score plotted as a function of the predicted expectancy score for stimulus presentation at three probabilities of stimulus occurrence.

$A(S_i)$, and P] combine linearly and in an additive fashion to contribute to overall event expectancy and, therefore, to predict the magnitude of the discriminant score.

We first determined the memory decay constant α in Eq. 1 that would provide the best linear relationship between discriminant scores and the memory expectancy factor for the probability conditions, P = .3, .5, or .7. The value of α that maximized the linear correlation between M and the discriminant scores did not differ among the three conditions (*19*). The mean value of α, 0.6, was thus selected as the memory decay rate for all conditions. We performed a multiple linear regression analysis in order to determine the equation relating the values of the fifth-order discriminant scores to M, P, and A:

$$\text{Expectancy} = 0.235M + 0.033A + 0.505P - 0.027 \qquad (2)$$

In Fig. 3, the observed expectancies (measured as discriminant scores) for all three probability conditions are plotted as functions of the expectancy values derived from Eq. 2 (*20*). The regression equation accounted for approximately 78 percent of the variance (R = .881) (*21*).

The multiple regression analysis was repeated with pairs of factors to evaluate the incremental proportion of variance accounted for by each factor. The largest gains were added by including the P (38 percent) and M (49 percent) factors; a small predictive increase was gained by including A (5 percent) (*22*). Alternations occurred in only a small number of sequences (4 of 16) and their effect on the ERP waveform counters attempts to explain these results in terms of habituation. If the mere occurrence of a stimulus affects all subsequent stimuli through habituation, the precise pattern of stimuli within a sequence should not materially affect the results.

Our model extends hypotheses previously advanced to account for the effects of event probabilities on the waveform of ERP's (*23*). The amplitude of the P300 complex increases as the expectancy of a stimulus decreases, and multiple factors combine to determine the expectancy that the subject associates with individual stimuli. Moreover, the effect of expectancy can be inferred to be related to dynamic processes that develop over short progressions of stimuli spanning time intervals of only a few seconds. Thus, caution should be exercised in the interpretation of changes in the waveform of the average ERP. The validity of the common assumption that the average is computed over a homogeneous data set must be carefully evaluated for each experiment. For example, whenever the global probability of an event is increased, there is a corresponding increase in the number of runs of that stimulus in the series. If trials in such a series are averaged without regard to their serial position, the increased proportion of trials following long runs of like stimuli may well reduce the amplitude of the P300 complex. Also, an examination of the behavior of the discriminant scores obtained in our previous work on the classification of single-trial ERP's (*4*) suggests that many of the errors of classification may have been due to sequential effects.

It is hardly surprising to find that the organism's response to "identical" stimuli is in flux. The nervous system is not a passive recipient of inputs that are obediently switched to outputs; rather it is a dynamic system that continuously generates hypotheses about the environment. The P300 seems to be associated with the evaluation of such contextual hypotheses.

KENNETH C. SQUIRES*
CHRISTOPHER WICKENS
NANCY K. SQUIRES
EMANUEL DONCHIN†
Cognitive Psychophysiology Laboratory,
Department of Psychology,
University of Illinois, Champaign

References and Notes

1. J. M. Ford, W. T. Roth, S. J. Dirks, B. S. Kopell, *Science* **181**, 465 (1973); S. A. Hillyard, R. F. Hink, V. L. Schwent, T. W. Picton, *ibid*. **182**, 177 (19 → W. Ritter and H. G. Vaughan, Jr., *ibid*. **164**, 326 (1969); L. Karlin and M. J. Martz, Jr., in *Attention and Performance*, S. Kornblum, Ed. (Academic Press, New York, 1973), vol. 4, p. → T. W. Picton and S. A. Hillyard, *Electroencephalogr. Clin. Neurophysiol*. **36**, 191 (1974); W. Ritter, R. Simson, H. G. Vaughan, Jr., *ibid*. **33**, 547 (1972); D. B. D. Smith, E. Donchin, L. Cohen, A. Starr, *ibid*. **28**, 146 (1970); R. T. Wilkinson and M. V. Lee, *ibid*. **33**, 411 (1972).
2. P. Tueting, S. Sutton, J. Zubin, *Psychophysiology* **7**, 385 (1970).
3. N. K. Squires, K. C. Squires, S. A. Hillyard, *J. Exp. Psychol.: Hum. Percept. Perform*. **1**, 268 (1975); K. C. Squires *et al*., *Electroencephalogr. Clin. Neurophysiol*., in press.
4. K. C. Squires and E. Donchin, *Electroencephalogr. Clin. Neurophysiol*., in press.
5. It is unlikely that the variations were due to sensory factors since the two auditory stimuli were supraliminal and clearly distinguishable. It is also unlikely that they were due to gross changes in attention level since, over the short blocks of trials, procedural and task parameters remained identical.
6. R. J. Remington, *J. Exp. Psychol*. **82**, 250 (1969).
7. J. C. Falmagne, S. P. Cohen, A. Dwivedi, in *Attention and Performance*, P. M. A. Rabbitt and S. Dornic, Eds. (Academic Press, New York, 1975), vol. 5, p. 296.
8. S. Kornblum, in *Attention and Performance*, S. Kornblum, Ed. (Academic Press, New York, 1973), vol. 4, p. 259.
9. R. J. Audley, in *ibid*., p. 509.
10. D. R. J. Laming, *Mathematical Psychology* (Academic Press, New York, 1973), p. 197.
11. A tone burst was presented every 1.3 seconds through TDH-39 earphones. Each stimulus had a total duration of 60 msec, including 10-msec rise and fall times, and was gated in random phase. The frequency of the high-pitched tone was 1500 hertz and that of the low-pitched tone was 1000 hertz. Both stimuli were 60 db sound pressure level (SPL) against a continuous background of wide-band noise at 55 db SPL. The sequence of stimuli was completely random except for the constraint that each stimulus occurred with a probability of .5.
12. Subjects were tested in the unequal probability condition either in a second experimental session or after a break in testing during which the subject left the experimental chamber. The separation between conditions was designed to eliminate confusion about the probabilities of occurrence of each tonal stimulus. The subjects were thoroughly briefed about the stimulus probabilities and the mode of random selection of stimuli.
13. The tree structure continued to diverge at least back to trial $N - 6$. As the number of preceding B stimuli increased to five and six, the mean discriminant scores increased to 3.7 and 4.07 units, respectively. For increasingly long runs of preceding A stimuli the corresponding scores were 1.21 and 1.15.
14. Since the observed changes in waveform statistics as a function of order duplicate the variations in choice RT in analogous tasks, latency shifts in the evoked components which were comparable to the RT latency variations might have been expected. Latency shifts of components such as P300 would yield variations in the discriminant score since it is calculated for fixed latencies. Remington (*6*) reported changes in the RT of about 20 msec between first-order (A) sequences (290 msec) to fifth-order sequences (BBBBA, 310 msec) and about 37 msec between the extreme fifth-order sequences (mean RT for sequence AAAAA was 273 msec). Similar variations in the latency for P300 were not seen in the averaged ERP waveforms, but such small latency shifts are probably beyond the resolution possible with these data. Furthermore, it has been argued (*8*) that sequentially related latency differences in RT are primarily a consequence of repetitions and alternations of the response rather than of the stimulus. Thus, if the speed of processing a stimulus remains relatively unaffected by sequential effects (particularly with simple stimuli) in the RT paradigm, we can assume that such would also be the case in the current paradigm, and therefore the differences in the discriminant scores primarily reflect differences in amplitude rather than in latency.
15. Repeated measures analysis of variance showed significant main effects of both sequence [$F(30,180) = 6.61$, $P < .001$] and stimulus (or probability) [$F(1,6) = 8.91$, $P < .025$]. The interaction of sequence and stimulus was not significant.
16. In Eq. 1, only A's contribute to the value of M. Thus, in the case of the prior sequence containing only B's (BBBBA), the values of all S_i and the resultant memory factor will be equal to zero.
17. When the discriminant score was plotted as a function of the memory factor alone, certain sequences had discriminant scores which did not fall at their orderly, predicted position. For example, the last A in the sequence ABABA had a much smaller discriminant score than predicted. However, with this particular sequence expectancies for another A would be elevated because the event A on trial N is consistent with the pattern of alternations set up by the sequence.
18. Of the 16 fifth-order sequences, four met requirement (iii) and thus had nonzero alternation factors; they were BBABA (+2), ABABA (+3), BABAA (−3), and AABAA (−2).
19. The three obtained values of α were 0.58, 0.60, and 0.61 for P = .3, .5, and .7, respectively.
20. To evaluate the extent to which the expectancy function fit the data for individual subjects, linear correlation coefficients were calculated for each subject in each condition. The mean correlation coefficient values were −.333, −.578, and −.536 for P = .3, .5, and .7, respectively.
21. Regression analyses were also performed on the individual-subject data, yielding statistically significant multiple R values in all cases, ranging from .426 to .840 with a mean of .628.
22. In Eq. 2, only the first-order terms have been used. A better fit might have been obtained had interactions between factors or higher order terms been included (Fig. 3). For example, if separate regression lines were fit for the three probability values, the slope of the line for the P = .7 condition would be greater than that of the other two. Furthermore, the degree of predictive linear fit seems to differ between conditions, being maximum for the P = .5 condition (for this condition a multiple regression of the discriminant score upon the M and A factors produced a multiple R value of .916).
23. K. C. Squires, S. A. Hillyard, P. H. Lindsay, *Percept. Psychophys*. **13**, 25 (1973); Tueting *et*

al. (*2*) also noted effects of both repeated and alternated events and related their results to the "unexpectedness" of the outcome.

24. The discriminant score is a combined measure of the N200, P300, and SW components of the ERP at the three electrode sites that was developed according to a stepwise discriminant analysis procedure (*26*), which optimally discriminates between ERP's elicited by rare and frequent stimuli (*3, 4*). The use of such a statistic has certain advantages; since it is a combined measure of several ERP amplitudes, it is less susceptible to EEG noise than individual base-to-peak amplitudes, it includes more waveform information, and it is a measure that can be applied to any subject's data without adjustment. The latencies at which ERP amplitudes were taken for inclusion in the discriminant score were 104, 188, 248, 320, 356, and 380 msec for F_z; 128, 236, 332, 356, 380, and 668 msec for C_z; and 224, 344, 380, 476, 536, and 572 msec for P_z.
25. E. Donchin, *IEEE Trans. Biomed. Eng.* **13**, 131 (1966); *NASA Spec. Publ. SP-191* (1969), p. 199; ______ and R. Herning, *Electroencephalogr. Clin. Neurophysiol.* **38**, 51 (1975); E. Donchin, E. Callaway, R. Jones, *ibid.* **29**, 429 (1970).
26. Combining data across stimuli was justified, because the tree structures for each were essentially identical. A repeated measures analysis of variance yielded a significant sequence effect [$F(30,180) = 106.5$, $P < .001$], but the effect of differing signals was nonsignificant, as was the signal by sequence interaction. High-pitched tones (counted by the subject), however, tended to yield larger discriminant scores than the low-pitched tones. This counting effect was significant ($P < .01$) when we tested it using difference scores for matched pairs of fifth-order sequences, but it was small relative to the sequence effect.

27. Supported by the Advanced Research Projects Agency of the Department of Defense under contracts DAHC 15 73 C 0318 and ONR US NAVY N-0002 to E.D. The technical assistance of T. Dunn and S. Petuchowski and the helpful comments of G. McCarthy and R. Horst are gratefully acknowledged.

* Present address: Department of Medicine, University of California, Irvine 92668.

† Reprint requests should be addressed to E.D.

4 February 1976; revised 19 April 1976

Drag Reduction by Formation Movement in Spiny Lobsters

Abstract. *Movements of spiny lobsters (*Panulirus argus*) in formation reduce drag during locomotion; such movement is of particular significance during mass migration. Queues (single-file lines) of spiny lobsters sustain less drag per individual than do individual lobsters moving at the same speed. It is proposed that queuing behavior conserves energy and is a consequence of the evolutionary role of migration in this particular species.*

A wide variety of animals assemble in stable aggregations or formations, either stationary or moving. The immediate adaptive significance of such formations is often far from obvious, despite its self-evident germaneness to current concern with the evolution of social behavior.

Schooling of fish, herding of mammals, flocking of birds, and swarming of insects seem to provide protection against predation (*1*). Other advantages of aggregation relate to thermoregulation, mating efficiency, finding food, pooling of orientational information, learning, and reducing aggression. An advantage occasionally suggested but infrequently demonstrated is that energy is saved during long-distance locomotion, for example, that V formations of geese and some other birds reduce drag and increase lift; this hypothesis is supported by mathematical models but remains unconfirmed (*2*). We now present experimental evidence that precise, single-file line formations or queues conserve energy by reducing drag during group migratory movements of the spiny lobster, *Panulirus argus* (*3*).

Queuing is most prevalent during autumnal mass migrations during which thousands of spiny lobsters traverse open bottom, day and night, for periods of at least several days (*4, 5*). Queues of as many as 65 individuals are maintained through tactile contact by the antennular rami and first pereiopods of each lobster with the extended abdomen of the lobster ahead. Queuing and clustering of lobsters may deter predatory fish by presenting them with a barrier of antennae. Queuing may also facilitate the pooling of orientational information and the leadership by the best-oriented individuals at any instant. But a basic physical advantage may result from improved hydrodynamic performance through reducing drag.

From an analysis of film and field data, we constructed a model of a typical queue. Walking speed, proper interlobster positioning, and posture were determined from 35-mm color slides and 16-mm color cine film taken during mass migrations near Bimini, Bahamas. Measures of queue size and length of migratory lobsters were based on field data (*4, 5*). Carapace lengths (CL) of migrating lobsters at Bimini ranged from 55 to 126 mm with a mean of approximately 83 mm (1969, 84.6 mm; 1971, 82.1 mm). There was no apparent correlation between lobster size and position within a queue. The interlobster distance was measured between the trailing edge of the lead lobster carapace and the base of the rostral horns of the following lobster (range, 7 to 34 cm; $\bar{X} = 16$ cm). This distance is limited by the length of the inner rami of the follower's antennules and the length of the abdomen of the lobster ahead. The angle between antennae, which the slowly moving lobsters constantly waved, was approximately inversely proportional to queue speed ($\bar{X} = 150°$ at 15 cm/sec; $\bar{X} = 92°$ at 28 cm/sec; minimum recorded angle, 30° at 28 cm/sec).

Queues ranged from 2 to 65 individuals during migrations, although isolated individuals and small queues (fewer than six lobsters) often resulted when long queues were fragmented by intense fishing with nets by lobstermen. Lobsters maintained larger queues in undisturbed areas. While marching on level substrate, lobsters stand erect, with the body axis held horizontal approximately 5 cm (85 mm CL lobster) above the substrate.

Lobsters migrate at a rate that ranges from 15 cm/sec for queues just forming to 35 cm/sec for well-formed queues moving over open areas ($\bar{X} = 28$ cm/sec). During ultrasonic tracking studies, average walking speeds of 28 cm/sec were recorded for individual lobsters over distances up to several kilometers. Individual lobsters walked at maximum rates of 30 to 34 cm/sec for 10 to 30 m during orientation experiments ($\bar{X} = 21$ cm/sec, $N = 23$).

A plywood tow tank (10 m long by 1 m wide by 0.75 m deep) filled with freshwater was used to test the drag-reduction hypothesis. A variable-speed electric capstan was used to pull preserved lobsters on a nylon monofilament line (0.6 mm diameter). A weighted pendulum with an idler pulley, through which the towline was threaded, measured force in degrees of deflection, which was then converted to newtons (*6*).

For test models, lobsters with all appendages were preserved in 10 percent solution of formalin in seawater. Pieces of Styrofoam were placed inside the carapace dorsal to the approximate center of gravity so that the average density of each lobster was slightly greater than that of freshwater, and friction with the tank floor was essentially eliminated. Lobsters of the appropriate size range were connected in queues with thin stainless steel wire.

Two sources of error arose from using preserved specimens. We could not determine the drag associated with movements of the walking legs or antennae during locomotion, and our models could not make instantaneous trim adjustments, which, in living animals, might normally influence both lift and drag. However, neither of the inaccuracies seems sufficiently large to influence the interpretation of the data.

In initial experiments, we measured both individual drag and queue drag at varying speeds, keeping antennal angle and interlobster distance constant at