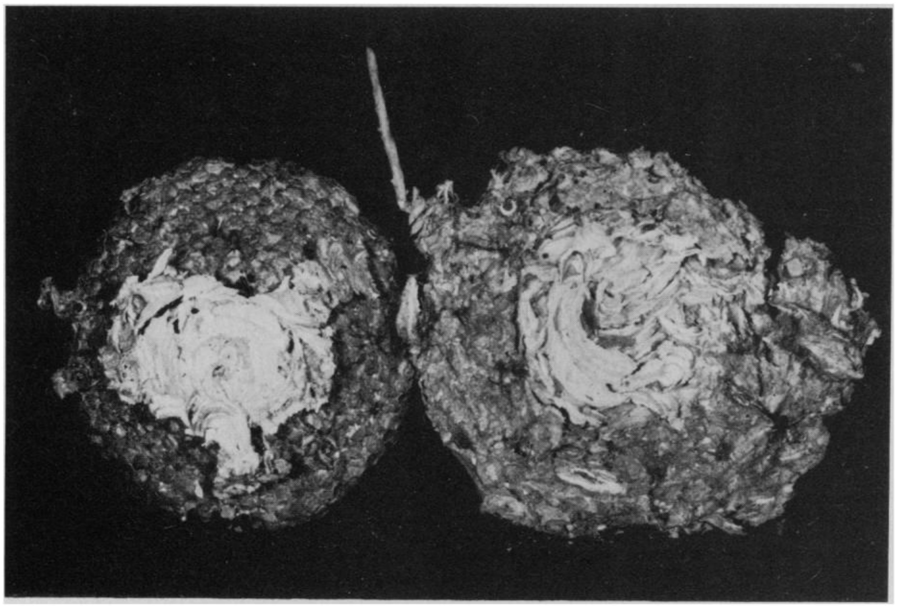

Fig. 1. Portion of a subterranean nest of *Vespula squamosa*. A typical mature nest would contain a stack of four to eight horizontal combs with cells opening downward, these being enclosed by a multilayered paper envelope. Nest expansion occurs laterally and downward, and the cavity is enlarged by workers as more space is needed. The dorsal surface of the oldest worker comb (left) and the inside of the envelope that covered it (right), which has been folded away from it, clearly show the lighter color and different texture of *V. maculifrons* paper in the center. This nest is approximately the size of a softball.

sent nests initiated by *V. squamosa* queens, in which case the parasitism is facultative. Since the smallest unequivocally usurped nest contained at least twice as many cells as a typical queen nest (*9*), *V. squamosa* queens may not discover host nests until after the first host workers become active. Alternatively, usurpation might occur so early in some colonies that it cannot be detected by study nest architecture. A precedent for the latter exists in another host-parasite *Vespula* pair; the inquiline *V. arctica* Rohwer queen and *V. arenaria* (F.) host queen are present together very soon after nest building and before emergence of host workers (*10*). Thus, the question of whether the socially parasitic behavior of *V. squamosa* queens is obligatory or facultative cannot be conclusively determined at this time (*11*).

Emery's rule, a general axiom regarding social parasitism, states that the closest relative of a social parasite tends to be the free-living species from which the parasite stock was derived (*1*, p. 360). According to one classification of Nearctic *Vespula*, *V. squamosa* and *V. maculifrons* are not closely related but are assigned to different species groups (*12*). Moreover, *V. squamosa* appears wrongly placed in the same species group with *V. vidua* (*13*). Thus, if reported parasitism of *V. vidua* by *V. squamosa* (*6*) in fact occurs, it seems that two distantly related species may be parasitized by a species not closely related to either host. This apparent violation of Emery's long-standing generalization suggests that pressures leading to the evolution of temporary, apparently facultative parasitism by *V. squamosa* may have been quite different from other cases of social parasitism, in which close association between two species would seem facilitated by common communicative channels and other shared behavioral patterns.

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References and Notes

1. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
2. The four genera include *Polistes*, *Mischocyttarus*, *Vespa*, and *Vespula*. *Vespula* is divided into two subgenera based on adult morphology and nesting habits; *V. (Dolichovespula)* construct aerial nests and *V. (Vespula)* construct subterranean nests.
3. Among Nearctic *Vespula*, obligatory permanent social parasites include *V. (D.) arctica* Rohwer in nests of *V. (D.) arenaria* (L.) and *V. (V.) austriaca* (Panzer), whose Nearctic host has not been documented but which parasitizes *V. (V.) rufa* (L.) in Europe (*1*, p. 378).
4. C. D. F. Miller, *Can. Entomol. Suppl.* **22**, 1 (1961).
5. A. N. Tissot and F. A. Robinson, *Fla. Entomol.* **37**, 73 (1954); A. T. Gaul, *Bull. Brooklyn Entomol. Soc.* **42**, 87 (1947). Our study finds that *V. squamosa* colonies persist late into autumn and typically consist of 2000 to 4000 workers. Mature nests contain up to 10,000 cells.
6. L. H. Taylor, *Ann. Entomol. Soc. Am.* **32**, 304 (1939).
7. One nest contained 1360 tan cells, the other 2186 (31 percent and 48 percent of the total worker cells, respectively). Thus, although most nest usurpation seems to occur early in the season, *V. squamosa* queens are apparently able to invade even well-established *V. maculifrons* colonies. Moreover, repeated usurpations of the same nest may occur; three nests collected in late July and early August 1974 contained from 3 to 25 *V. squamosa* queen carcasses in the nest cavity together with a live queen in each. Similarly, June excavations of very young *V. maculifrons* nests in 1975 suggest conspecific supersedure, the first stage in the evolution of social parasitism as postulated by Taylor (*6*); from one to three freshly killed *V. maculifrons* queens were found beneath nests of some *V. maculifrons* colonies.
8. S. F. Sakagami and K. Fukushima, *Insectes Sociaux* **4**, 1 (1957).
9. Documented queen nest sizes of the subgenus *Vespula* are few, but most have contained 20 to 40 cells [J. P. Spradbery, *Wasps* (Univ. of Washington Press, Seattle, 1973)].
10. H. E. Evans, *Insect World Dig.* **2**, 6 (1975).
11. Obligatory, temporary social parasitism between species, so common in the ants, has not been documented in the social wasps (*1*, *6*).
12. J. C. Bequaert, *Entomol. Am.* **12**, 78 (1931). The subgenus *Vespula* is divided on the basis of adult morphology and biology into at least two species groups, *V. vulgaris* (L.) and *V. rufa* (L.).
13. Comparative nest architectural, behavioral, morphological, and electrophoretic data currently under study strongly indicate that *V. squamosa* is wrongly aligned with the *V. rufa* group to which *V. vidua* is assigned.

3 July 1975; revised 4 August 1975

On Evoked Potentials, Cognition, and Memory

Begleiter and Porjesz (*1*) report a study of the effects of decision-making processes on event-related brain potentials (ERP) recorded at the vertex. They have obtained data which "demonstrate the relationship between specific components of the ERP to a sensory stimulus and a cognitive decision about the physical attributes of that stimulus." From this finding they derive the suggestion "that these patterns of neural activity might reflect the activation of memory traces about the specific experience." The relation between evoked potential components and cognitive activity which Begleiter and Porjesz report is well known. The data they present suggest that the principal decision-related ERP component they record is the P300 component. This being the case, the conclusions that they draw concerning memory are unwarranted.

A brief survey of the literature will put matters in perspective. In *Science* alone there have appeared in the last decade numerous reports (*2–4*) which have unequivocably established "a relationship between specific components of the ERP to a sensory stimulus and a cognitive decision . . ." (*1*). The component of the evoked response to which these reports refer is a positive-going potential, with a peak latency in the range of 250 to 350 msec. This component, often labeled P300 or P_3, is currently the focus of much active research. A recent bibliography by Price and Smith (*5*) contains 145 items. Considerable detail has accumulated on the relationship of P300 to cognitive activity and has been published in several major journals (*6–10*). Of this vast literature Begleiter and Porjesz cite a single paper—Sutton *et al.* (*3*).

Had they considered the relevant literature Begleiter and Porjesz would have realized that most, if not all, of the enhanced

P_2 component they measure is likely to be P300. While Begleiter and Porjesz define their N_1-P_2 component as measured at peaks occurring at 140 to 200 msec, respectively, the peaks they label as P_2 in their figure 2 have latencies of 200, 240, and 300 msec. Because they have given themselves such latitude in defining and measuring their peaks, the bar graph they present in figure 1 is hard to interpret. It is difficult to see how data such as that in their figure 2 can lead to the bar graph.

I have superimposed the curves they present for medium stimuli judged "bright" and judged "dim" (Fig. 1). For subject M.K. the curves are virtually identical except for a small difference 300 msec following the stimulus, the "bright" judgments yielding a slightly larger P300. For subject M.D., the fairly large wave peaking at 250 msec in association with the "bright" stimuli may be a P300. Data for D.G. are difficult to interpret, as the amplitude differences appear across the time axis. If these data are "typical," then they are reporting yet another demonstration that, under conditions in which subjects are to make decisions in the face of uncertainty, some decisions will manifest themselves by an enhanced P300 component. It is not immediately apparent why the medium intensity stimuli which were judged "bright" yielded a larger P300 than those judged "dim." The meager data Begleiter and Porjesz provide on their procedures make it difficult to arrive at an explanation. However, they continued to present "medium" stimuli until they accumulated 16 judgments in each category. Under such circumstances the relative probability of any stimulus-response combination can vary, and the relative probability of stimuli has a strong effect on P300 amplitude (*3, 4, 6, 10*). Proper experimental design requires careful attention to the frequency with which specific brightness judgments are made. The authors were amiss in not providing this information in their report. To determine whether P200 differences are masked by the P300 differences, it is further necessary to record at several scalp loci so as to capitalize on the different scalp distributions of these two components.

Once the source of the observed differences is identified as P300, it should be noted that the literature suggests that while P300 clearly manifests an *act* of decision-making it provides little information as to the *contents* of that decision. Thus, the differences observed by Begleiter and Porjesz may indeed reflect the fact that a decision concerning stimuli of medium brightness was made by the subject. However, these differences cannot be considered related to the specific physical attributes which the subject has ascribed to the stimuli. In other words, the ERP waveforms cannot be considered as carrying the specific "memory traces" for stimulus brightness. On the evidence at hand, all that can be said is that the subject (perhaps) searched his memory. While it might be the case that neural patterns such as P300 reflect "the activation of memory traces about specific experience," there is no evidence for this proposition in Begleiter and Porjesz's report.

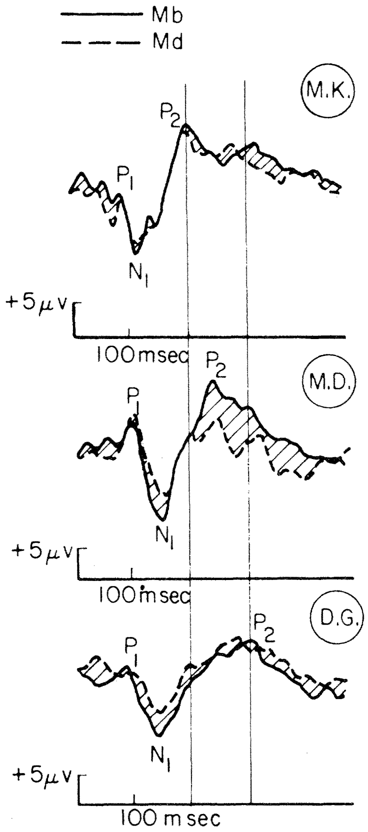

Fig. 1. Superimposition of curves for medium stimuli judged "bright" (*Mb*) and judged "dim" (*Md*) from (*1*).

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11 April 1975

Begleiter and Porjesz' report (*1*) on indications of decision-making in visual evoked responses (VER's) to bright, dim, and medium intensity flashes is ambiguous on the following important point: They say that the effect was "independent of the preceding stimulus," yet their experimental protocol required "a minimum of 32 medium flashes," which were presented "until each subject had judged 16 . . . to be 'bright' and another 16 to be 'dim.' " If the total number of bright and dim flashes was held constant at 32 each, it is unclear how they ensured statistical independence of each medium flash from the preceding sequence of bright, dim, and medium flashes. In other words, if it became necessary to deliver a large number of medium flashes to obtain the requisite number of judgments, was the same independent sequence of flash intensities adhered to throughout the experiment? Without such independence it would be hard to ensure the absence of light or dark adaptation effects, even with their long interstimulus intervals of 3 to 6 seconds. Accordingly, it seems possible that their amplitude differences could have resulted from peripheral receptor as well as central effects. The "decisions" may have occurred in the retina, rather than in the thalamus or visual cortex.

In this context, it is interesting that, in two of their published VER records (M.K. and M.D.), the amplitude of P_1 for medium flashes judged as "dim" increased relative to either the preceding early negative wave or the start baseline. This suggests a more complex interpretation of their overall P_1-N_1-P_2 amplitude changes. When trying to evaluate somatosensory evoked response (SER) differences for nonnoxious and noxious tactile stimulation of glabrous skin, we have found changes in the relative amplitudes of the early and later time domains of the SER (25 to 60 msec and 60 to 200 msec) to be the most reliable indicators of correlated stimulus and sensory changes (*2*).

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3 March 1975; revised 29 August 1975

Stowell's criticism is well taken, as our report (*1*) lacked some procedural details, which can easily be provided. The stimulus order was fixed for each subject, in order to ensure that the same number of bright and dim stimuli preceded each medium flash, for the first 32 presentations of each. Thereafter, the identical order was repeated, but with bright stimuli substituted for dim and vice versa, until the necessary number of "bright" and "dim" responses to medium flashes was obtained. As all evoked potentials, stimulus codings, and response codings were stored on tape, it was possible to retrieve the first 16 of each stimulus-response combination to average the evoked potentials for the bright, dim, medium judged "bright," and medium judged "dim" categories. Thus, the same independent sequence of flash intensities was adhered to throughout the experiment, which precludes the possibility of light-dark adaptation effects. It is therefore unlikely that our amplitude differences could be explained in terms of peripheral reception retrieval effects.

The thrust of Donchin's argument is that the decision-related evoked potential we report (*1*) is the P300 component. He, therefore, disregards all aspects of our study that do not conform to already existing data and ideas concerning P300. He overlooks statistically significant findings obtained in the P_1-N_1 component, with peak latencies of 100 and 140 msec, respectively. This early component difference certainly can neither be subsumed under the rubric of a P300 phenomenon, nor can it be ignored, particularly in light of the fact that evidence confirming this result has been independently obtained in similar experimental designs by Buchsbaum *et al.* (*2*) and Puschinskaya (*3*). They report early component differences that correspond exactly to ours, both in time and effect: namely, that amplitude differences occurring at 100 to 140 msec are evidently sensitive to different decisions.

Donchin states that had we considered the "relevant literature, Begleiter and Porjesz would have realized that most, if not all, of the enhanced P_2 component they measure is likely to be P300." In support of this statement, he cites a vast body of literature that has been accumulated in the last decade, dealing with the relationship between sensory stimuli, cognition, and the evoked potential, and claims that these papers deal with "a positive-going potential, with a peak latency in the range of 250 to 350 msec." However, included among his list of papers is one by Johnston and Chesney (*4*), with an experimental paradigm quite similar to ours. Their study examines evoked potential events occurring up to 250 msec after stimulus presentation, and nothing is mentioned about P300. Their major effect, which starts at around 160 msec, is quite consistent with ours; that is, they obtain different evoked potentials to identical stimuli depending on the context of the stimulus.

In our study only one subject (D.G.) out of 18 had a P_2 latency within the range of 250 to 350 msec, the range Donchin attributes to P300. Furthermore, while Donchin exercised great caution in measuring the latency of the P_2 components illustrated in our report, he first reports a P_2 latency of 240 msec for subject M.D.; then, a few sentences later, he reports that the same P_2 latency for M.D. is 250 msec. In point of fact, the actual P_2 latency for M.D. is 236 msec, which, according to Donchin's criterion for P300, does not qualify at all as P300. It is puzzling for us to imagine how data occurring predominantly around 200 msec and quite often as early as 140 msec can be so easily incorporated or interpreted as a P300 peak by Donchin, particularly as he stringently assigns a narrow band of 100 msec from 250 to 300 msec to the P300 component. It should be mentioned, however, that while this P300 peak has been reported to occur as late as 300 to 600 msec (*5*), 300 to 450 msec (*6*), and 260 to 450 msec (*7*), it does not occur before 250 msec.

The curves for "bright" and "dim" stimuli were superimposed by Donchin with respect to the first point on the trace. This assumes that this single arbitrary point is in fact a true baseline, which is not at all the case. Amplitude measurements in our experiment were calculated in terms of the perpendicular peak-to-peak distance between P_1 and N_1 and N_1 and P_2 so that aligning the curves in this fashion (yet reducing the scale) merely serves to obscure our amplitude differences and does not add any new or significant information. By focusing solely on specific differences in individual subjects, which are shown for purely illustrative purposes, Donchin totally disregards the more important statistical differences that we obtained with 18 subjects.

The reason why it is not "immediately apparent why the medium intensity stimuli which were judged 'bright' yielded a larger P300 than those judged 'dim' " is that our findings and those of aforementioned investigators are obviously not related to the P300 component. While the P300 literature (by Donchin's own admission) "clearly manifests an *act* of decision-making it provides little information as to the *contents* of that decision." Our results and those of others clearly demonstrate that significantly different evoked potentials to the same stimulus were obtained in trials that resulted in *different* decisions and, hence, behavioral outcomes. Therefore, it is not only reasonable to assume that such cognitive decisions must precede behavioral actions, but that they may be reflected in the electrical activity of the brain.

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