decenyl)dihydro-2(3*H*)-furanone is a potent attractant for male Japanese beetles and appears to have considerable potential for survey and control of this serious pest.

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3. Ellisco traps were placed on the ground in areas where male beetles were active and baited by placing a stainless steel planchet (2.5 cm in diameter) containing the test sample in 0.25 ml of hexane in the bait well. All tests were run as randomized complete blocks with five or more replicates and 11 m between traps. Data were analyzed statistically, and mean captures were separated at the 5 percent level of significance by Duncan's multiple range test.
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6. Up to 250 live virgin female beetles were held in a 2800-ml Erlenmeyer flask. When additional beetles were available, 2150 to 3000 females were held in a glass chromatography jar (31 by 31 by 62 cm). Each morning, beetles were transferred to a clean vessel, and the vessel that had contained them overnight was rinsed three times with 15- or 30-ml portions of benzene for the flasks and chromatography jars, respectively. Each evening, the beetles were transferred to a clean vessel containing apple slices for food, and the vessel that had contained them during the day was rinsed three times. Neither benzene alone nor the benzene washings of flasks used to hold apples or male beetles plus apples were active in field bioassays.
7. The bioassay was similar to that used with the introduced pine sawfly by J. E. Casida, H. C. Coppel, and T. Watanabe [*J. Econ. Entomol.* **56**, 18 (1963)] and with the lesser peachtree borer by C. E. Yonce, J. H. Tumlinson, C. R. Gentry, and E. R. Mitchell [*Environ. Entomol.* **3**, 569 (1974)]; J. H. Tumlinson, C. E. Yonce, R. E. Doolittle, R. R. Heath, C. R. Gentry, E. R. Mitchell, *Science* **185**, 614 (1974).
8. A glass column (0.5-inch inside diameter) was packed to a height of 100 cm with a hexane slurry of Styragel (Waters Associates) and eluted with hexane at a flow rate of 5 ml/min. The active material eluted from this column in the 250- to 350-ml fraction. The column effluent was monitored with a refractive index detector.
9. Gas chromatography was performed on a gas chromatograph (Varian model 1400) equipped with a flame ionization detector. The column effluent was split so as to send 5 percent to the detector and 95 percent to a glass capillary collector [R. G. Brownlee and R. M. Silverstein, *Anal. Chem.* **40**, 2077 (1968)]. Stainless steel columns (2 m by 2.3 mm inside diameter) with a flow (N_2) rate of 20 ml/min were used with the other conditions noted; silanized Chromosorb W (120 to 140 mesh, acid washed) was used as the support in each column; the OV-101 (4.5 percent) column temperature was held at 150°C for 30 minutes and the temperature was then programmed at 8°/min to 225°C; the Carbowax 20M, (5.2 percent) column temperature was 190°C; the SP 2300 (7.6 percent) column temperature was 200°C; the SP 2340 (10.4 percent) column temperature was 200°C; and the Carbowax 20M (4.6 percent) column temperature was 190°C.
10. The infrared spectrum was obtained by washing the pheromone sample from the glass capillary collection tube into a NaCl microcavity cell (Barnes Engineering) with about 5 μl of carbon tetrachloride. The cell (0.5-mm path length) was placed in a 3X beam condenser (Barnes Engineering) in a Perkin-Elmer model 467 infrared spectrometer. The reference was CCl_4.
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12. The methyl 4-oxobutyrate was prepared as described [*Org. Synth. Collect. Vol. III* (1955), p. 630]. The acetylenic lactone was reduced to the olefinic lactones with H_2 over Pd/$BaSO_4$ (Lindlar catalyst) or to the saturated lactone with H_2 over Pd on charcoal.
13. The pure enantiomers of glutamic acid (Sigma) were deaminated either by the method of A. T. Austin and J. Howard [*J. Chem. Soc.* (1961), p. 3593] or by a modification of the method of M. Winitz, L. Bloch-Frankenthal, N. Izumiya, S. M. Birnbaum, C. G. Baker, and J. P. Greenstein [*J. Am. Chem. Soc.* **78**, 2423 (1956)]. This reaction is considered to proceed with full retention of configuration [K. Koga, M. Taniguchi, S. Yamada, *Tetrahedron Lett.* (1971), p. 263]. The conversion of the acid to the acid chloride with either thionyl or oxalyl chloride is considered to proceed with retention of configuration [C. Eguchi and A. Kakuta, *Bull. Chem. Soc. Jpn.* (1974), p. 1704]. The acid chlorides were reduced to the aldehydes in dry toluene at 65° to 70°C. The amount of *E* isomer produced in the Wittig reaction ranged from 10 percent when a mixture of tetrahydrofuran and hexamethyl phosphoramide (THF/HMPA) was used as the solvent to about 25 percent when a mixture of diethyl ether and methylene chloride was used. Undiluted THF gave about 15 to 20 percent of *E* isomer; THF/HMPA gave a higher overall yield and fewer by-products.
14. All concentrations given are in grams per 100 ml of chloroform. The rotations of the *R,Z* and *S,Z* enantiomers were measured at concentrations of 5.0 and 5.1, respectively. The rotations of the *R,E* and *S,E* enantiomers were $[\alpha]_D^{26°C} = -31.2°$ (concentration, 2.237) and $[\alpha]_D^{26°C} = +30.2°$ (concentration, 2.112), respectively. The *R*- and *S*-5-(1-decyl)dihydro-2(3*H*)-furanone enantiomers gave rotations of $[\alpha]_D^{26°C} = -31.8°$ (concentration, 2.387) and $[\alpha]_D^{26°C} = +30.0°$ (concentration, 2.739), respectively.
15. In cooperation with the Ohio Agricultural Research and Development Center, Wooster 44691. Approved for publication as Journal article No. 197-76. We thank the Animal and Plant Health Inspection Service (APHIS), U.S. Department of Agriculture, for locating sources of larvae and populations for bioassay. K. O. Lawrence and C. R. Buriff gave assistance in obtaining enough female beetles to complete this project. We thank R. R. Heath for NMR spectra, and J. M. DeVore, K. Allen, C. H. Johnson, C. R. Clark, M. Roth, K. P. Callahan, and B. Gold for technical assistance, and the management and members of the Buccaneer Country Club, Burgaw, N.C., for cooperation.

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Augmenting Mental Chronometry: The P300 as a Measure of Stimulus Evaluation Time

Abstract. *A technique for measuring the latency of the P300 component of event-related brain potentials on individual trials is described. Choice reaction times and the latency of the P300 were compared under speed-maximizing and under accuracy-maximizing instructions. The choice stimuli required different levels of semantic categorization. The data support the proposition that the latency of P300 corresponds to stimulus evaluation time and is independent of response selection.*

In his 1938 survey of experimental psychology, Woodworth (*1*) ventured the hope that "brain waves" might be used in the timing of mental events: "the 'speed of thought' we say; but as soon as we set about measuring the time occupied by a thought we find that the beginning and end of any measurable time must be external events. We may in the future use 'brain waves' as indicators of the beginning and end of a mental process . . . but in general it has seemed necessary to let the timed process start with a sensory stimulus and terminate with a muscular response." In the decades that followed, it became clear that while the electroencephalogram (EEG) can be a useful index of neural pathology and global changes in a subject's state, it cannot support studies of the timing of specific mental events; the suggestion that brain waves may play such a role is absent from the second edition of Woodworth's book (*2*).

Yet, the need for an index of the timing of mental processes, independent of response selection and execution time, is as acute now as in the earliest days of mental chronometry (*1*). Much of contemporary cognitive psychology (*3*) is concerned with the analysis of mental events into their presumed stages. The traditional approach to this problem using reaction time (RT) could be complemented by a measure of stimulus processing that is independent of overt motor responses. In this report we present evidence that the P300 component of the human event-related brain potential (ERP) can serve as such an index for measuring stimulus evaluation time.

The P300 is elicited by a class of task-relevant events (*4*, *5*). Its amplitude has been shown to be directly proportional to the "surprise value" (the reciprocal of expectancy) of a stimulus (*6*). However, before a stimulus can surprise it must be identified. As P300 commonly appears as a discriminative response to specific stimuli within a series, its elicitation must be preceded by an adequate evaluation of the stimulus at some level of pro-

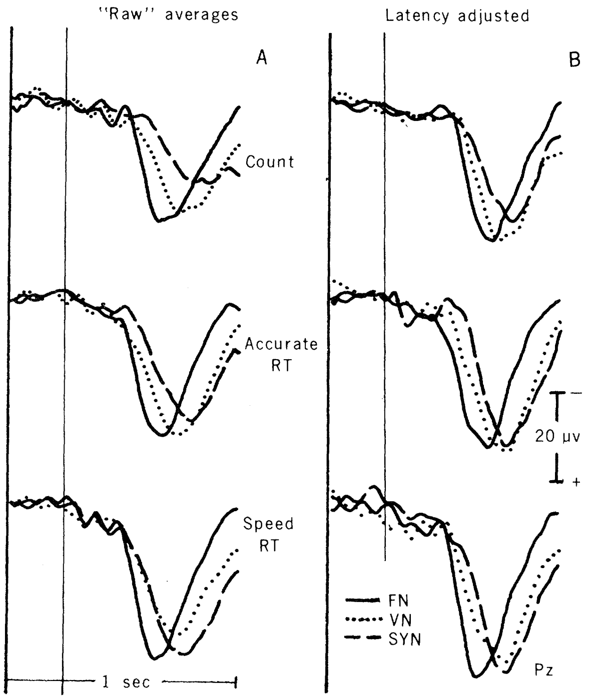

Fig. 1. Event-related potentials, recorded at the parietal electrode, and averaged over all subjects for the three different semantic categorizations obtained during the three different response regimes. (A) Raw averages time-locked to the stimulus onset; (B) latency-adjusted averages obtained by the technique described in the text.

cessing. Several investigators (*5*, *7*) have, in fact, suggested that the endogenous process manifested on the scalp by P300 is associated with stimulus evaluation rather than with response selection. If so, then P300 latency should bear some relation to the time required for stimulus evaluation.

This proposition has been tested, with mixed results, by the assessment of the covariation between RT and P300 latency. Many report a large positive correlation (*8*); others, however, find the two variables to be uncorrelated (*9*). This contradiction may be due to the fact that RT is multiply determined and only some of the variables influencing it also affect the P300. That is, if P300 latency represents stimulus evaluation time, then when the variance of the RT is largely determined by stimulus evaluation, the correlation between P300 latency and RT will be large and positive. On the other hand, whenever the variance of RT is determined by response selection processes, the P300-RT correlation may be small. Kutas and Donchin (*10*) have, in fact, reported that when subjects are instructed to maximize their response speed, the correlation between the latency of mean RT and mean P300 was substantially lower than under accuracy-maximizing instructions.

This assertion, however, is based on a comparison of a small number of mean RT's and latencies. Clearly, the study of the correlation between these two measures of processing time would benefit from a procedure that permits a comparison of P300 latency and RT for each trial of an experiment. Determining peak latencies from the average ERP is problematic because the amplitude of the peak used for estimating latency is itself dependent on the variability of the latencies from trial to trial. Ritter *et al.* (*11*) estimated single-trial latencies of visually identified peaks. This, however, is a laborious technique impractical for experiments involving hundreds of trials. Woody (*12*) proposed a technique which augments signal averaging through an estimate of the latency jitter. We utilized this technique for measuring the latency of the P300 component on the single trials acquired in the experiment described by Kutas and Donchin (*10*).

Five University of Illinois students viewed series of words presented on the screen of a Plato terminal (*13*). The words appeared, one at a time, every 2000 msec. Three series were used. In the fixed names (FN) series the word Nancy appeared on 20 percent of the trials and the word David on 80 percent of the trials. In the variable names (VN) series the subject was presented with one of several female names on 20 percent of the trials and with one of several male names on 80 percent of the trials. Finally, in the synonym (SYN) series, synonyms of the word prod appeared on 20 percent of the trials and other words on the remaining trials (*14*). Each series was used in three different experimental conditions which differed in the response required. Subjects either counted the number of times words from the infrequent category were presented (count) or pressed one of two buttons, depending on the stimulus category. There were two choice RT conditions. In one, the subjects were instructed to respond as fast as they could (speed RT). In the other, subjects were instructed to respond as quickly as they could while avoiding errors (accurate RT). The EEG was recorded from Fz, Cz, Pz, C3, and C4 referred to the chin (*15*).

A large P300 component (>25 μv) was elicited by the rare words; the P300 associated with the frequent words was minute (*10*). In the count and accurate RT conditions the latency of the P300 was shortest for the FN series, longest for the SYN series, and intermediate for the VN series. This was not the case for the speed RT condition, where the P300 had similar latencies for the VN and SYN series, although both were longer than the FN latency (*16*). The amplitude of P300 varied with the subject's task and with the stimulus series.

A measure of P300 latency for all the individual trials was obtained by using the following procedure. The single trials from Cz and Pz for each of the nine experimental conditions and five subjects were treated separately. There were thus 90 separate analyses, approximately 20 trials per analysis. Each analysis proceeded as follows. All single-trial EEG records were low-pass filtered (filter attenuating by 3 db at 6.29 hertz) to reduce alpha activity (*17*). An ensemble average was computed; this average provided the initial template for the latency measurement procedure. To restrict latency measures to the component of interest, a subepoch of the total record was chosen which bounded the P300 latency range (as determined by examination of the filtered trials). For these analyses the subepoch ranged from 280 to 780 msec after stimulus. The cross-correlation function between each individual trial and the template was computed over this subepoch. All the single-trial records were then aligned at their point of maximum correlation with the template. These realigned records were averaged to form a new template. New cross-correlation functions were computed and the trials were realigned. After each iteration, the template provided a "better" estimate of the average ERP. The iterations continued until no further improvement was observed in the template (*18*). The final template is an estimate of the ERP waveform adjusted for latency variability. After the final iteration, each single trial record was associated with a number which indicated the temporal shift required to yield the maximum correlation between this trial and the final template. This number is an estimate of the latency

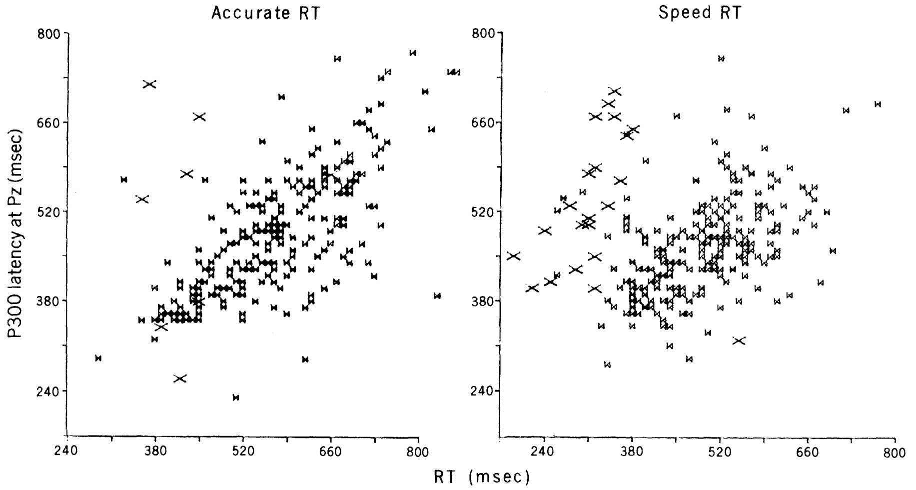

Fig. 2. Single-trial P300 latency plotted against reaction time, on the same trials, for the accurate and speed RT conditions. The *X*'s mark trials on which errors were committed. The observed error rate was 3 percent for the accurate RT condition and 9 percent for the speed RT condition. As a binary choice was required, it is reasonable to assume that the observed error rate is approximately half the actual rate. The linear regressions describing these data were $y = 0.57x + 156$ with $r = .66$ ($F = 185.65$, d.f. $= 240$) for the accurate RT condition and $y = 0.38x + 276$ with $r = .48$ ($F = 69.86$, d.f. $= 239$) for the speed RT condition.

of P300 on that trial. It is important to emphasize that the efficacy of this procedure depends on the quality of the data. For a discussion of the precautions that must be observed see Ruchkin and Sutton (*19*).

Figure 1 shows the average ERP's for each of the three conditions for each of the three word series averaged over all five subjects for the rare stimuli. The raw averages for the parietal location are shown in Fig. 1A and the corresponding latency-adjusted versions of these ERP's in Fig. 1B. There is a reduction in the variability of the P300 amplitudes after latency adjustment. Such changes in P300 amplitude are consistent with the estimates of latency variability for the different conditions based on trial-by-trial measures of P300 latency. The larger the variance observed in a condition, the greater the effect of latency adjustment on the amplitude of the average ERP (*20*). When the amplitude of P300 is thus adjusted for latency, there appears to be no systematic relationship between P300 amplitude and any of the experimental variables.

That the latency adjustment reduced the amplitude variability across conditions and that the amplitudes were affected in the same manner for all subjects suggest that the latency estimates provided by the algorithm are valid. Further evidence is provided by a comparison of the latency estimates obtained independently from the data recorded at the parietal (Pz) and central (Cz) sites. These estimates are positively correlated ($r = .61$). In other words, when the algorithm is applied to two sources of information about P300 latency, similar estimates are obtained.

With such trial-by-trial estimates of latency it is possible to compare the RT obtained on each trial with the latency of P300 on the same trial. The data are presented in Fig. 2 in the form of scatter plots, one for the speed RT task, the other for the accurate RT task. Data obtained from all five subjects for the three word lists are presented: The following aspects of the results are notable. The correlation between P300 latency and RT for all trials is low during the speed RT condition ($r = .26$) and higher during the accurate RT condition ($r = .61$). Removal of trials on which errors were committed increased the correlations for both the accurate RT ($r = .66$) and speed RT ($r = .48$) conditions. These trends hold for all subjects in all experimental conditions.

These data support the notion that at least two processes are initiated by a stimulus, a response selection and execution process indexed by the overt response and a stimulus evaluation process indexed by the P300 component. Under accuracy instructions where response selection is contingent on stimulus evaluation the two processes are tightly coupled, with RT frequently longer than P300 latency. When subjects operate under speed instructions, stimulus evaluation is more loosely coupled with response selection; responses may be generated before the stimulus has been fully evaluated.

These speculations are consistent with a striking feature of the data revealed by the large X's in Fig. 2. On these trials the subject pressed the button indicating the frequent category even though the stimulus was one of the rare words. Most of these trials occurred, as expected, during the speed RT condition. The interesting feature of these data, given that on most of the "correct" trials P300 latency preceded reaction time, is that on the "error" trials P300 latency exceeded reaction time. It is as if the subject continued to process the information provided by the stimulus even though the overt response had been generated (*21*). Clearly, we have no direct knowledge that the subject continued to process the stimuli. Nevertheless, some process manifested by the P300 persisted well past the response selection.

An examination of the mean deviation of RT and P300 latencies (P300 minus RT) provides more information concerning the relative timing of stimulus evaluation and response generation under the different instructional regimes. During the speed RT condition the RT exceeded P300 on the average by 26 ± 88 msec (mean ± standard deviation), while during the accurate RT condition the RT exceeded P300 by an average of 91 ± 88 msec. However, the RT measured by microswitch closure overestimates the time at which response selection occurs, 100 msec being a reasonable estimate (*22*). If so, response selection was terminated before the P300 was elicited in the speed RT condition but was coincident with P300 in the accurate RT condition. By contrast, during the error trials P300 latency exceeded RT by 179 ± 148 msec, indicating that on these trials the reaction process was initiated long before the process associated with P300 was terminated.

The processes revealed by these data were described as early as 1895 by Kulpe (*23*), who noted that when a person is instructed to respond to a stimulus as rapidly as possible there is "in consciousness . . . a somewhat indistinct sensation of the initiating stimulus. Oftentimes this sensation does not become fully clear until the reaction has been performed." This point was also made by James (*24*): "the whole succession [of the reaction process] is so rapid that perception seems to be retrospective and the time order of events to be read off in memory rather than known at the moment."

That reactions to a stimulus often precede its complete processing is a phenomenon intuitively obvious, but difficult to study. The insights articulated by

Kulpe and James have not been tested experimentally because processing occurring after the motor response is opaque to a research technology depending exclusively on overt reactions (*25*).

It is the thesis of this report that the P300 component of the human ERP can serve to augment mental chronometry by providing the index required for studying such processes. In Woodworth's terms, "brain waves" can be useful as indicators (at least of the end) of a mental process.

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14. Female names presented were Nancy, Alice, Ellen, Milly, Marie, Cindy, Betty, Carol, Susan, Debby, Janet, Jenny, Sally, Patty, Clara, Doris, Laura, Ethel, Helen, and Rhoda. Male names presented were David, Barry, Larry, Louis, Henry, Aaron, Billy, Allan, Bobby, Brian, Thomas, Howie, Oscar, Simon, Roger, Linus, Jacob, Gordy, Derek, and Teddy. The synonyms of prod presented were goad, poke, shove, urge, nudge, push, prompt, spur, and press. Other words presented were knob, grasp, void, clear, bare, book, yarn, clasp, seize, door, tale, grudge, rough, myth, snatch, blank, torn, cook, chair, and hook.
15. The EEG was amplified by Brush amplifiers (model 11-4307-02) with a 2-second time constant and 30-hertz high-frequency cutoff (one-half amplitude). The electrooculogram was recorded between supraorbital and canthal positions. Trials contaminated by eye movements were not included in any analyses. Data were digitized at 10 msec per point.
16. The mean P300 latencies computed from the average parietal ERP's in milliseconds were FN = 400, VN = 500, and SYN = 580 for the count condition; FN = 430, VN = 500, and SYN = 550 for the accurate RT condition; and FN = 400, VN = 500, and SYN = 500 for the speed RT condition.
17. D. S. Ruchkin and E. M. Glaser, in *New Perspectives in Event-Related Potential (ERP) Research*, D. Otto, Ed. (Government Printing Office, Washington, D.C., in press). Note that the filter uses an equal number of equally weighted values preceding and following each time point and is therefore free of phase shifts.
18. The criterion for improvement was obtained as follows. The maximum correlations for all trials were averaged at each iteration and compared to the corresponding average correlation on the previous iteration. The process was terminated if the increase in the average maximum correlation did not exceed 0.005.
19. D. S. Ruchkin and S. Sutton, in *Progress in Clinical Neurophysiology*, J. Desmedt, Ed. (Karger, Basel, in press).
20. The mean P300 latencies computed from the single-trial parietal ERP's in milliseconds were FN = 450 ± 56, VN = 516 ± 74, and SYN = 559 ± 99 pooled over response types, and count = 592 ± 98, accurate RT = 502 ± 71, and speed RT = 483 ± 60 pooled over stimulus categories.
21. As the subjects pressed a button on all RT trials, it is possible to interpret the potentials we record as the P2 of the "motor potential" rather than as P300. We reject this explanation for the following reasons. (i) The same ordering of P300 latency and variability for the different word series held for the count condition, which required no overt motor reaction (means: FN = 527, VN = 587, and SYN = 662 msec). (ii) The ERP's elicited by the frequent stimuli have a substantially smaller positivity (*10*). (iii) The correlation between P300 latency and RT is higher at Pz than at Cz. Correlations for error-free trials between Cz and RT are $r = .55$ in the accurate RT condition and $r = .35$ in the speed RT condition. (iv) The fact that the P300 latency–RT correlation depends on the instructional regime (speed versus accuracy) suggests that the relation is not controlled by the motor response. (v) The P300 often preceded the button press, especially in the correct-accuracy trials.
22. F. C. Donders, in *Attention and Performance*, W. G. Koster, Ed. (North-Holland, Amsterdam, 1969), vol. 2, p. 412 (this is a translation of an article published in 1869). Ritter and Vaughan (*5*) assumed that response selection precedes switch closure by 150 msec. This estimate implies that response selection precedes the peak of the P300 on accurate as well as on speed RT trials. It is impossible to measure directly when response selection occurs; all estimates are conjectural. But even the longer of the two estimates is consistent with our interpretation. While the peak of P300 is a convenient landmark for measuring latencies, it does follow the inception of the component by many milliseconds.
23. O. Kulpe, *Outlines of Psychology* (Swan Sonnenschein, London, 1895), p. 407 (this is E. B. Titchener's English translation of the 1893 German edition).
24. W. James, *The Principles of Psychology* (Dover, New York, 1950), p. 88.
25. Within the reaction time tradition it is possible to allow the subject to make an error detection or correction response [for example, see P. M. A. Rabbitt, S. M. Vyas, S. Fearnley, in *Attention and Performance*, P. M. A. Rabbitt and S. Dornic, Eds. (Academic Press, New York, 1975), vol. 5, p. 395]. This, however, may confound the interval of interest with further unrelated processing.

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Progressive Brain Damage Accelerates Axon Sprouting in the Adult Rat

Abstract. *An entorhinal cortical lesion causes undamaged fibers in the deafferented hippocampus to sprout and form new connections within 4 to 7 days after the lesion was made. When a partial lesion of the entorhinal cortex precedes a second, more complete entorhinal lesion by a few days, the rate of axon sprouting is accelerated so that the response to the second lesion occurs within only 2 days. This priming effect is present within 4 days, lasts for a few weeks, and eventually subsides. This acceleration may explain, in part, the faster recovery and reduced deficits seen in behavioral studies that have followed serial lesion paradigms.*

Brain lesions administered serially over a few days create less functional deficit and allow faster recovery than single-staged lesions, even though the general location and volume of tissue removed is equivalent (*1–3*). Many hypotheses have been suggested to account for this difference (*1, 2, 4*), but the underlying cellular mechanisms are not understood at present. It seemed to us that axon sprouting might be one of the underlying events that reduce behavioral deficits and accelerate recovery in serial lesion paradigms. Lesions of certain nerve pathways can cause the remaining afferents sharing the same terminal field to "sprout" and create new functional circuitry. In some cases these adjustments appear to minimize performance deficits and aid in recovery of normal function (*5*). Accordingly, the initial lesion in a serial lesion paradigm might ini-