dividuals of each of these species and of *Ips yohoensis* are gynogenic; in fact all five "species" probably should be considered a single species with polymorphic females; all males are indistinguishable cytologically or morphologically, but the females differ morphologically.

Matings of males whose sisters are of one morphological form to normal females of another form result in bisexual progeny containing females that are morphologically highly variable. Without exception, however, SR females produce broods of daughters almost exactly like themselves, whether mated to males whose sisters were of the same or a different morphological form, or even to males of two distinctly different species such as *Ips borealis* and *Ips perturbatus*. Regardless of the type of mating, hatchability in SR broods approaches 100 percent, whereas normal bisexual *Ips tridens* mated to *Ips borealis* or *Ips perturbatus* produce eggs of which none hatch. Females, both SR and normal, fail to oviposit unless mated.

This gynogenic condition appeared spontaneously in two laboratory matings of females from bisexual broods. There was no history of gynogenesis in either of the parent lines and outmatings of brothers produced bisexual progeny. Genes for gynogenesis may be floating in certain populations and may be occasionally expressed; once induced, the condition is probably obligatory for the duration of that particular line.

One may wonder how widely spread is the SR condition in the Scolytidae. In addition to the species mentioned, we have discovered gynogenic strains of *Ips borealis* and *Ips perturbatus* and a SR condition in a species of *Pityophthorous*, similar to that in *O. latidens*. Several species of *Xyleborus* are reported to have 15 to 20 females per male in the usual colony (*14*). Nevertheless, not a single SR strain was encountered while we reared several hundred thousand *Ips confusus*.

G. N. Lanier
J. H. Oliver, Jr.
Division of Entomology and Acarology, University of California, Berkeley

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14 April 1966

Evoked Potential Correlates of Generalization

Abstract. *Late components of evoked potentials recorded during the occurrence and nonoccurrence of generalization are different. During generalization the evoked response waveshapes resembled those elicited by the conditioned stimulus during correct performance. The differences are statistically significant.*

When an animal learns to perform a conditioned response upon presentation of a particular conditioned stimulus, we assume that a neural representation of this experience is stored somewhere in the brain. If a novel, but similar, stimulus is subsequently presented to the trained animal, performance of the previously learned response sometimes occurs and is referred to as generalization. To explain this phenomenon, it seems reasonable to suggest that the novel stimulus recalls a stored representation of prior experience.

Electrophysiological recordings, taken from electrodes chronically implanted in cat brains, have been reported (*1*) to contain rhythmic activity at two frequencies, when generalization occurs to a novel stimulus at one frequency (F_2) after training with a rhythmic conditioned stimulus at another frequency (F_1). One of the observed frequencies corresponds to the novel stimulus which is actually present (F_2), while the other is approximately that of the conditioned stimulus actually used during training (F_1). Since no physical event at frequency F_1 is present in the environment of the animal, electrical rhythms at F_1 have been assumed to reflect the recall of a neural representation of prior experience from storage in the brain. This interpretation is supported by the observation that rhythms at F_1 are no longer present during F_2 stimulation, after the animal has been taught to differentiate stimuli at the two frequencies.

This report presents some results obtained in more recent studies in which computer analysis was applied to electrophysiological data recorded during generalization. Studies were carried out on four cats, each bearing 34 electrodes chronically implanted in numerous cortical and subcortical brain regions. These animals were trained in performance of a lever-press to avoid shock within 15 seconds after onset of a flickering light (10 cy/sec). After appreciable overtraining, the animals were subjected to test sessions in which occasional trials with a 7.7-cy/sec flicker were interspersed among presentations of the conditioned stimulus of 10 cy/sec. If generalization occurred, the test stimulus was terminated when the lever was pressed. If no behavioral response occurred after 30 seconds, the test stimulus was terminated without electrical shock. Electrophysiological responses obtained in all sessions were

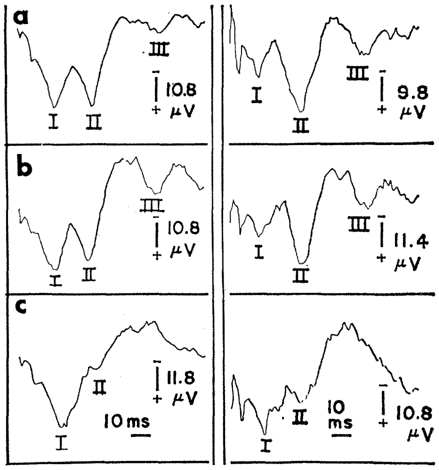

Fig. 1. Average evoked potentials recorded from lateral geniculate body (left) and nucleus reticularis (right) during behavioral trials that resulted in conditioned response performance (*a*) to 10-cy/sec flicker, and generalization (*b*) and no response (*c*) to 7.7-cy/sec flickers. Generalization and no-response averages are based on 42 evoked potentials, and conditioned-response averages on 100 evoked potentials. Analysis epoch is 90 milliseconds.

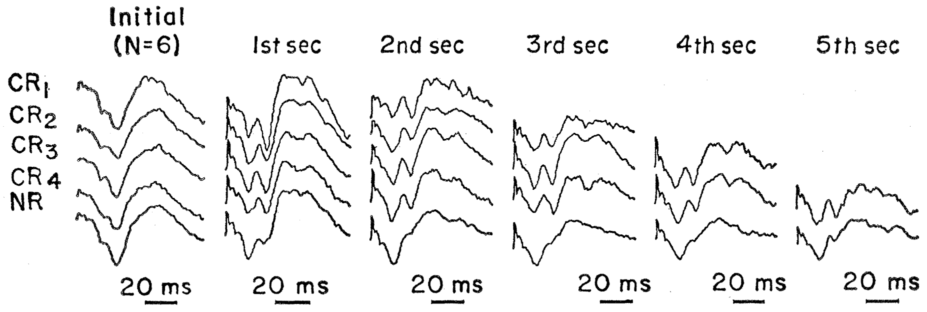

Fig. 2. Averaged responses obtained from the lateral geniculate body during 27 tests of generalization to 7.7-cy/sec flicker, after training to 10-cy/sec flicker. Upper four rows of data are taken from 21 trials that resulted in generalization, distributed as follows with respect to latency: CR_1, three trials, 2-second latency; CR_2, six trials, 3-second latency; CR_3, six trials, 4-second latency; and CR_4, six trials, 5-second latency. Bottom row of data comes from a group of six trials in which 30 seconds of stimulation failed to elicit any performance (*NR*). First column of waveshapes represents average of initial evoked response in each of six trials, with the exception of CR_1. First column of CR_1 represents average of the first and second evoked responses in three trials of that group. Other columns represent second by second averages, each based upon 48 evoked potentials. Analysis epoch is 125 milliseconds.

permanently recorded on magnetic tape for subsequent analysis.

If generalization occurred, average evoked responses from many, but not all, of the structures in all four animals were different from those observed when generalization did not occur.

We selected test trials obtained in one session from one of these animals for detailed analysis, because of the unusually large size of the sample and the spread of response latencies. Twenty-four of these test trials resulted in generalization and six in no behavioral response. With the use of a general purpose digital computer, average evoked responses and standard deviations throughout the averaging epoch were computed for a portion of these data.

Of the eight structures that were monitored during this session, the most striking differences during generalization were displayed by the lateral geniculate body and the nucleus reticularis (*2*). These results are illustrated in Fig. 1, which shows clearly that late components, labeled II and III, were large during generalization and essentially absent during no-response trials. The response evoked by the test stimulus during generalization closely resembled that elicited by the training stimulus during correct performance.

For the lateral geniculate, components II and III first appeared shortly after onset of the trial, and the time of appearance was independent of the latency of performance (Fig. 2). The initial evoked potential was essentially the same for all trials, which indicates similar initial excitability. A more detailed analysis of the first second of each trial has shown that components II and III usually appeared on the third evoked potential. Comparable results were obtained for nucleus reticularis. The fact that components II and III appear long before any overt movement occurs, and that the time of appearance does not correlate with response latency, indicates that these components do not arise as a consequence of movement.

Statistical significance of the differences between waveshapes of the average evoked potential for no-response and for generalization trials was evaluated by use of the two-tailed *t*-test. Results are summarized in Table 1. For both sites, differences are not significant for the initial component I, which appears regardless of the behavioral outcome, but are highly significant for component II; for component III, the difference is significant for nucleus reticularis but equivocal for the lateral geniculate.

A distinct late component which appeared during generalization but was absent when generalization failed to occur, similar in latency to component II, was clearly observed in one brain structure in two of the other three animals. This phenomenon was observed in the visual cortex of one of these cats and in the mesencephalic reticular formation of the other. Analogous phenomena have subsequently been observed in a number of other animals subjected to somewhat different behavioral procedures.

We propose that component I, which displays constant characteristics independent of the behavioral outcome, may reflect the registration of afferent input to the structure. Components II and III, which vary according to behavioral outcome, may reflect recall from memory of the appropriate response.

D. S. Ruchkin
E. R. John
Brain Research Laboratories, Department of Psychiatry, New York Medical College, New York 10029

Table 1. Significance of differences between average evoked potentials from generalization and no-response trials. Significance is evaluated by the two-tailed *t*-test; df is 82; σ_{CR} and σ_{NR} are the standard deviations in microvolts, for the generalization and no-response cases, respectively; and $t = | CR_{av} - NR_{av} | N^{1/2}/(\sigma^2_{CR} + \sigma^2_{NR})^{1/2}$, where CR_{av} is the amplitude of the average response waveform for the generalization case at the time the particular component is at its maximum deflection, and NR_{av} is amplitude of the no-response average at the corresponding instant of time. The base line from which amplitudes are measured is the time average of the waveform, computed over the full 130-msec interstimulus interval. (All recordings were made through a-c coupled amplifiers.) *N* is the number of evoked potentials used to compute the average response, and σ^2 is the unbiased estimate of variance. Since the differing late components did not appear until the third evoked potential, the first two evoked potentials were excluded from all averages. *N* was 42 for all averages. To ensure that background noise was uncorrelated, averages were computed by taking every other evoked potential from a trial, thereby making the minimum time between any two samples equal to 260 msec. Estimates of the noise correlation function indicated that this was adequate. Boneau (*3*) has demonstrated that assumptions of normality and equality of variance may be related without affecting validity of the two-tailed *t*-test, so long as the number of samples in each average is the same.

Component	Latency (msec)	σ_{CR}	σ_{NR}	*t*	*P* (%)
		Right lateral geniculate			
I	18	13.9	20.0	0.856	50
II	35	18.0	20.0	5.11	0.1
III	67	16.6	22.5	2.10	5
		Right nucleus reticularis			
I	16	16.8	28.0	1.08	50
II	34	23.5	24.8	3.86	0.1
III	67	20.3	28.0	3.38	.1

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28 March 1966

Cerebral Concussion in the Monkey: An Experimental Model

Abstract. *A statistically significant experimental model has been developed for reproducing head injury by impact in the monkey. Results with 80 monkeys subjected to occipital impact under specified conditions (duration of phenomena, 1 to 10 milliseconds) enable the construction of curves relating the production of experimental cerebral concussion in 10, 50, and 90 percent of the monkeys to the average impulse of the blow in pounds·seconds, as well as to the average linear acceleration of the head. These curves are proposed as a baseline from which blows to various parts of the head, as well as nonimpacting impulsive loads, can be studied under various conditions of protection and according to various time regimes.*

Despite many attempts to describe the mechanical and physiological responses of the central nervous system to head impact (*1–4*), little is known about the relation of impact to response; still less about the response itself. The impact-response relation is fundamental to design of rational head protection—only one of the practical needs for such knowledge. However, there is a more basic aspect to the understanding of brain response to impact. The sudden abolition of consciousness after a blow on the head—cerebral concussion—includes, as may be expected, a multitude of events occurring simultaneously or in sequence. There is reason to suspect that study of some of these events—their functional disorganization and reorganization during and after impact—could lead to better understanding of the functions of the nervous system.

We now report a technique whereby the injurious aspect of head impact can be quantitatively determined and related to the occurrence of concussion. We used 80-odd rhesus monkeys (*Macaca mulatta*) in these experiments. The value of using primates in such work has been discussed (*5, 6*); it is argued that the anatomical similarities between monkey and man are more likely to permit valid extrapolation of data than information obtained from quadrupeds.

Adult rhesus monkeys, anesthetized with Nembutal and seated in a specially designed chair, received blows to the occipital region of the head. The blows were delivered by a piston actuated by compressed air; it weighed 3.8 lb (1.4 kg) and had a 1 in.^{2} (6.45-cm^2) hard-rubber cap at the impacting end. By control of the air pressure behind the piston, impacts could be varied from a gentle tap to a fatal, crushing blow. The posture of the monkey was such that the head could move freely forward after impact, although the body was restrained by waist, lap, arm, and leg belts.

The impact and response of the head were measured directly. The applied force as a function of time was sensed by a bonded strain-wire dynamometer fitted in series between piston and impacting rubber tip; piston velocity was recorded as the voltage generated as a magnet, encased in the piston body, passed through a surrounding coil.

Responses of the head were measured by means of photography and accelerometers. Displacement of the head with time was determined from high-speed motion pictures taken at 4000 frames per second, in which a selected point on the skin, at an estimated projection of the center of gravity of the monkey's head, was compared with a stationary background grid. Linear acceleration–time history of the head was sensed by piezoelectric crystal accelerometers weighing 1 g and fixed rigidly to the skull.

Changes in intracranial fluid pressures with time were sensed at various sites by low-impedance semiconductor strain-gage pressure transducers; they were placed in holes bored in the skull and attached so that the 5 mm-diameter sensitive surface was flush with the inner wall of the cranial vault; they were secured to the bone with self-tapping screws, and a layer of dental cement assured water-tight closure of the skull. The outputs of the various gages and transducers were fed into amplifiers and recorded by a tape recorder that could be played back into a direct-writing string oscillograph. Timing impulses were provided by a tuning-fork oscillator (1000 cy/sec).

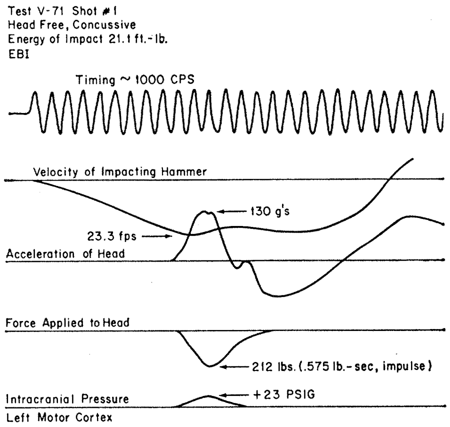

Fig. 1. Oscillographic record of physical measurements during impact; traces for velocity, acceleration, force, and intracranial pressure with a 1000-cy/sec time trace are displayed.

The level of anesthesia in each monkey was carefully controlled so that aversive response to noxious stimuli, especially ear pinch, was consistently present; abolition by impact of such response was the criterion of concussion, and the duration of abolition was the duration of cerebral concussion. This criterion proved significantly more reliable than suspension of the corneal and palpebral reflexes or changes in other physiological indices such as the electroencephalogram, electrocardiogram, arterial blood pressure, respiration, and cerebrospinal fluid pressure, which were also recorded before, during, and after impact.

Impact force and velocity of the piston, the displacement-time history of the head relative to a fixed grid, the linear acceleration of the head, and intracranial pressures were measured during most of the tests on the 80 monkeys. Data from experiments in which skull fracture was produced and from tests in which multiple blows were given are not included in this study. A typical record (Fig. 1) shows that the applied force–time curve is roughly triangular; total duration is about 6 msec and it reaches a peak in about 2 msec. As would be expected, the acceleration and intracranial-pressure pulses follow about the same pattern. In all records, the duration of the force was between 1 and 10 msec, averaging 4 msec.

The data describing input and re-