

tion, but reflect rather the discriminative function possessed by the stimulus. For this reason these responses, when they occurred during the extinction tests, were recorded separately from the responses to the unlighted key. This made possible the study of the generalization of "superstitious" responding to a discriminative stimulus at the same time that we were investigating the generalization of conditioned reinforcement.

Two measures of conditioned reinforcement were used in this study: the number of responses made to the unlighted key to produce the conditioned reinforcer and the number of minutes spent while responding to produce the conditioned reinforcer until the extinction criterion was reached. Generalization gradients obtained with each of these measures are presented in Fig. 1. In this figure, for each measure, both the generalization gradient obtained on the first extinction test and the mean of the gradients obtained on all four tests are presented. The values in the first-test gradient are based on independent groups of ten each, whereas all values in the pooled-across-tests gradient are based on the same group of 40. The similarity between the first-test and pooled-across-tests gradients indicates that aside from the reduction in response level on repeated extinction tests, the procedure of retraining and retesting does not distort the gradients obtained. The pooling of the data across tests does reduce error variance sufficiently to produce statistical reliability, whereas first-test performance for both measures only approaches an acceptable confidence level ( $.05 < p < .10$ ). For data from all tests, however, the gradient for responses to extinction is significant [ $F(3/117) = 5.27, p < .01$ ] as is the gradient for time spent responding to produce the different stimulus values [ $F(3/117) = 6.31, p < .01$ ].

The analysis of "superstitious" responding to the different test stimuli was performed as follows: since the time to extinction varied with the test stimulus, the different test stimuli were not presented equally often. For this reason the measure of responding used was the mean number of responses per minute during stimulus exposures. Because these responses were made during the presentation of the different stimuli, these data reflect the discriminative function, as opposed to the reinforcing function of the stimulus.

In Fig. 2 two gradients are presented: the first-test gradient and the pooled-

across-tests gradient. The similarity of the two is evident. With this measure, the first-test gradient is significant [ $F(2/27) = 26.85, p < .01$ ] as is each of the four separate test gradients (not shown here). The pooled-across-tests gradient is also significant: [ $F(2/28) = 28.92, p < .01$ ]. In general, the variability of the individual gradients reflecting the discriminative function of the stimulus (measured in the presence of that stimulus) was strikingly less than the variability of the gradients of conditioned reinforcement (measured during periods of stimulus absence).

Responding to a stimulus which precedes the presentation of a reward generalizes lawfully to similar stimuli despite the fact that reinforcement was in no way contingent upon such responding. Furthermore the presentation of such stimuli strengthens (or maintains) ongoing behavior to the degree that the stimulus is similar to the original (conditioned reinforcer.) Thus, reinforcement is seen as a stimulus function and is subject to the same laws and principles (for example, generalization) as are other functions of stimuli (5).

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### Spontaneous Electrical Activity in the Brains of Diapausing Insects

**Abstract.** *The spontaneous electrical activity in cerebral ganglia of several insect species does not disappear during diapause. Some recordings of electrical activity in pupae of the cecropia silkworm (in which the brain is considered to be electrically "silent" during diapause) suggest that at least some activity is maintained, but possibly it is restricted to certain regions of the brain.*

Most thorough research on diapause has been performed on pupae of *Hyalophora cecropia* (L.). The complete loss of spontaneous electrical activity in the brain as well as the inability to respond to electrical stimulation appear to be

features of its diapause (1). These changes in the cerebral ganglia were consistent with the altered biochemical relations; the amount of cholinesterase had diminished drastically whereas the titer of cholinergic substance increased steadily. Accordingly, a temporary retardation of development in pupae of *Phalaenoides glycine* Lew. was evoked (2) by inhibiting its cholinesterase activity through injection of eserine.

Diapausing pupae of *Bupalus piniarius* L. have been shown to possess spontaneous electrical activity in the brain (3). In order to establish whether the case of *Hyalophora* or *Bupalus* represents the "normal" situation, electrical activity during diapause in a number of insect species has been investigated.

The device for these recordings consisted of an unsharpened silver wire (diameter, 20  $\mu$ ) with glass insulation as the active electrode (4), connected with a Tektronix a-c preamplifier (100 $\times$ ) and a Tektronix oscilloscope type 502. Action potentials with an intensity of  $> 50\mu\text{v}$  were easily distinguished on a noise level which amounted to about 20  $\mu\text{v}$ .

The insect species tested were: *Leptinotarsa decemlineata* Say (Coleoptera, Chrysomel.), *Panolis flammea* Schiff. (Lepid., Noct.), *Hyloicus pinastri* (L.) (Lepid., Sphing.), *Bupalus piniarius* L. (Lepid., Geometr.), and *Hyalophora cecropia* (L.) (Lepid., Saturn.). Some relevant details about their diapause may be mentioned. (i) Diapause was induced in *Leptinotarsa* by rearing from the egg stage at 20°C under short-day conditions. The beetles tested were dug up from the soil immediately before the experiment, 3 to 6 weeks after entering diapause. Nondiapausing beetles were obtained from a culture exposed to long-day conditions at 25°C. (ii) *Panolis* pupae contain adults within 2 to 3 weeks after pupation. These moths hibernate inside the pupal cuticle. From 32 pupae kept at 20°C for 12 weeks none of the moths emerged. Electrical activity in the brain was investigated in pupae kept at 20°C for 4 to 7 weeks. One day before this experiment the oxygen consumption of the insects amounted to  $49 \pm 12 \mu\text{l g}^{-1} \text{ hr}^{-1}$  at 25°C. (iii) The *Hyloicus* pupae, which spent 7 to 14 weeks at 20°C after the pupal moult, did not show any sign of adult development at the time of the experiment. (iv) *Bupalus* pupae, which were investigated after a chilling treatment of 44 to 48 weeks at 3°C, showed distinct characteristics of adult develop-

Table 1. Occurrence of spontaneous electrical activity in the cerebral ganglia of diapausing and active insects.

Physiological stage	Electrical activity (No. of insects)	
	+	-
<i>Bupalus piniarius</i>		
Diapause	8	1
Development	8	1
<i>Hylocius pinastri</i>		
Diapause	3	
<i>Leptinotarsa decemlineata</i>		
Active	5	
Diapause	7	
<i>Panolis flammea</i>		
Diapause	8*	2
<i>Hyalophora cecropia</i>		
Diapause†	2	1
Diapause‡	1	2
Diapause§	2	

\* One pupa did not show any sign of adult development. † After storage at 25°C the insects were kept at 3°C for 5 weeks and subsequently at 10°C for 2 days before being tested. ‡ These pupae spent 2 weeks at 3°C immediately before the experiment. § These insects did not form a cocoon before the pupal moult, but there was no indication of an abnormal diapause.

ment and thus were considered as "developing." Diapausing insects kept for 1 to 2 weeks at 25°C after pupation showed a respiration intensity of  $106 \pm 16 \mu\text{l}$  of oxygen per gram per hour. This value is somewhat lower than that for specimens of this species tested for electrical activity previously (3). (v) The *Hyalophora* pupae were obtained from larvae reared on lilac at 25°C and under long-day conditions. After pupation the insects were stored at 25°C for 12 weeks. Subsequently, some of them were chilled for 2 to 5 weeks before being tested.

Electrical activity was determined by inserting the active electrode into the brain at several places successively. Electrical activity during one or more penetrations was considered positive (+, Table 1). With the electrodes used, the values of the recorded action potentials were between 50 and 150  $\mu\text{v}$ . Occasionally higher potentials (up to 600  $\mu\text{v}$ ) were recorded.

There was spontaneous electrical ac-

Table 2. Cholinesterase activity in the brains of *Bupalus*, both pupae and adults. The brains were excised from diapausing pupae which were kept after pupation at 25°C for 0 to 2 days (I) or for 12 to 25 days (II). The brains of the adults were collected 2 to 4 days after emergence.

Developmental stage	Cholinesterase activity per brain ( $\mu\text{mole acetylcholine hr}^{-1}$ )
Pupae (I)	0.036
Pupae (II)	.036
Adults	.250

tivity during diapause in all insect species mentioned (Table 1). In the cecropia pupae this phenomenon occurred in five of the eight specimens. Even in these, often only one of the insertions gave a positive reaction. However, with this method of recording, more stress should be laid upon a positive than on a negative result because in the latter case the possibility remains that an active center was present but that it was missed by the insertion. The chance of a miss is probably greater in cecropia. It seemed much more difficult to penetrate the brain of cecropia without causing great damage than it was to penetrate the brains of the other species, possibly because of differences in mechanical properties of the perilemma. But also quantitative differences in activity between cecropia and other species may result in a lower number of positive insertions in cecropia. The latter view is favored by the observation that, in contrast to the other species, electrical activity from cecropia was never recorded when the active electrode was applied to the brain surface only.

If there is a quantitative difference in brains of diapausing and nondiapausing insects, it is not very conspicuous in *Bupalus* and *Leptinotarsa*. In *Hyalophora*, however, it is conceivable that in diapausing brains the records were obtained from active regions, whereas other parts of the brain may be characterized by the disappearance of all electrical activity (and in this case the total amount of cholinesterase may be very low). This hypothesis might explain the discrepancy between the data of Van der Kloot (1) and our observations on cecropia. As an alternative explanation one may assume an incomplete diapause in our cecropia pupae. In this context, it is interesting to note that, possibly because of the rearing conditions of the larvae, cecropia pupae are sometimes able to start adult development without any chilling (5).

After the demonstration of electrical activity in the brains of *Bupalus*, the concentration of cholinesterase in diapausing and active *Bupalus* specimens was determined. Brains of 105 pupae and 16 adults were excised and cholinesterase was measured manometrically (Table 2). A measurable amount of enzyme is present during diapause, but its concentration rises appreciably in the adult.

In cecropia, a study of the brains of diapausing pupae showed that the activity of the enzyme was less than 0.05

$\mu\text{mole}$  of acetylcholine per brain per hour (1). In *Bupalus*, the activity per brain in diapausing pupae appeared to be somewhat lower. However, considering the smaller dimensions of this brain, it may be concluded that the cholinesterase activity during diapause exceeds that in cecropia.

That cholinesterase is present in *Bupalus* in the brains of diapausing pupae fits well with the observed spontaneous electrical activity. The demonstration of this electrical activity in the other insect species allows the conclusion that this nerve activity in the brains of diapausing insects seems a rather common phenomenon. Thus cecropia may represent an exceptional case because of the disappearance (partial?) of electrical activity.

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#### Gastric Content of Fasted Primates: A Survey

Abstract. The acidity of the gastric contents of fasted members of seven families of primates was measured, and no relationship was found between acid concentration and phylogenetic development; in general, however, gastric acidity was higher in New World monkeys than in Old World monkeys. The administration of histamine increased gastric acidity.

More and more primates are being used in research, and biological studies in several species of monkeys formerly uncommon to the laboratory have become desirable. Gastroenterologists have recently shown that certain New World species have a markedly different gastric acid pattern from the more widely used rhesus monkey (1, 2). Hence we surveyed several species to determine whether there was any relationship between the phylogenetic development, or the habitat of the animals, and the amount of acid in the gastric juice.

Twenty-seven monkeys were housed