a rather complex environment, with many events happening concurrently. We hypothesized that it was the reward, given for imitative behavior, which was crucial to the learning. To test this hypothesis, the adult uttered the sounds as during the training and the children received the same number of rewards as before. However, the rewards were contingent upon time elapsed since the last reward, regardless of the child's behavior.

The data show a deterioration in imitation behavior whenever rewards are shifted from response-contingent to time-contingent delivery. It is concluded, therefore, that reward immediately following correct, imitative behavior (and withholding of reward following incorrect responding) is a crucial variable in maintaining imitative behavior in these children. The same finding has been reported by Baer and Sherman (*3*) who worked with imitative behavior in normal children.

Since the child was rewarded whenever he responded like the adult, *similarity* was consistently associated with food. Because of such association, similarity should become symbolic of reward. In other words, imitative behavior, being symbolic of reward, should eventually provide its own reward (Baer and Sherman, *3*). To test this hypothesis, both children were exposed to Norwegian words which they were unable to reproduce perfectly when first presented. The adult simply stated the Norwegian word and the child always attempted to repeat it; no extrinsic rewards were delivered. However, occasionally the child was presented with English words which the adult rewarded when correctly imitated. This procedure was necessary to maintain the hypothesized symbolic (learned) reward function of imitation.

The children improved in the imitation of the Norwegian words over time. It is as if they were rewarded for correct behavior. In view of the data pointing to the need for rewards in maintaining imitative behavior, and in the absence of extrinsic rewards, we would argue that the reward was intrinsic and a function of the prior imitation training. There is one implication of this finding which is of particular interest for therapeutic reasons: children may be able to acquire new behaviors on their own. (This finding contrasts with the frequent stereotype of a conditioning product, namely, that of an automaton unable to function independently.)

Currently, three new schizophrenic children are undergoing the same speech training program as Billy and Chuck. After 3 days of training, one of these children achieved a level of imitative behavior similar to that shown by Billy and Chuck after 26 days. It should be pointed out that schizophrenic children are a very heterogeneous group with respect to their speech histories and symptomatology in general, and that Billy and Chuck had failed in development to a profound degree. Insofar as one works with such a diverse population, it is likely that numerous procedures could be helpful in establishing speech.

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Unconditioned Response to Electric Shock: Mechanism in Planarians

Abstract. *Some implications of a mathematical theory relating neuronal geometry to the parameters of excitation in unconditioned response of planarians to electric shock are experimentally verified. The regions and patterns of primary neural excitation depend on the relation between the distribution of neural sizes and the waveform of the electric stimulus.*

Thompson and McConnell's classical conditioning paradigm for planarians (*1*) has been used, with several modifications, for a number of interesting and provocative experiments on the mechanisms of memory storage (*2*). In this paradigm the planarian is placed in a narrow plastic trough equipped with an electrode at each end and filled with water. Several seconds of brilliant illumination, constituting the conditioned stimulus, are followed by approximately a second of electric shock, the unconditioned stimulus, administered through the water by way of the end electrodes. Response of the planarian during the lighted period preceding the shock is scored as a conditioned response, and response during the period of shock is scored as an unconditioned response. Interpretation of the results of these experiments has been equivocal because of apparent discrepancies in the results of various laboratories (*3*, *4*) employing this paradigm. It must be emphasized that the discrepancies reported entail not merely a difference between the McConnell group and those critical of their results but also discrepancies among the results of the critics' experiments. Such fundamental variations suggest that one or more critical variables in the situation have not been adequately controlled; in some obvious instances, the experiments of the critics are among the most vulnerable.

The study of Barnes and Katzung (*4*) intimates that the kind of electric current pulse used for the unconditioned stimulus may be one such variable; they use a monopolar square-wave train instead of the inductorium output used by Thompson and McConnell and others (*1*, *2*). But while this study indicated relevancy of the electrical stimulus waveform it did not lead to reproducible results in other laboratories (*3*) or in our own.

For purposes of the present analysis the central nervous system of the planarian can be thought of as an ensemble of neurons and the neurons, in turn, as tubes with sealed ends and impermeable surfaces, containing an aqueous axoplasmic solution of ions. The use of electric shock as an unconditioned stimulus in the paradigm is equivalent to placing this ensemble of neurons in a spatially uniform, but temporally varying, electric field. The direct consequence of imposing an electric field on these neurons is to produce an ionic migration leading to a shift in the ionic distribution of the axoplasm from its resting state. If the perturbation induced in this ionic distribution by the electric field exceeds some threshold value in any surface region of the axoplasm of a neuron, then excitation occurs in that neuron.

If a field of intensity E is imposed on a solution of ions of charge q per mole and diffusion coefficient D, the flow, J, of these ions in a one-dimensional system will be

$$J = -D\,\mathrm{d}C/\mathrm{d}x + DqEC/RT \quad (1)$$

where C is the concentration, R the gas constant, T the absolute temperature, and dC/dx the derivative of C with respect to the position variable x.

The maximum perturbation in the ionic distribution occurs at the extremities of such a neuron with respect to the axis of the field. Thus, if L is the half-length of the neuron, the maximum perturbation occurs at $\pm L$ so the condition of excitation is that

$$y^* \leq \frac{C(L) - C(0)}{C(0)}$$

where y^* is the threshold value of the relative perturbation.

It can be shown (*7*) that, for a pulse stimulus of a single, monophasic square wave of amplitude E and duration t, these statements are equivalent to the requirement that

$$1 \leq (EL/\lambda)[1 - \exp(-2Dt/L^2)] \qquad (2)$$

for excitation of a neuron of half-length L. The rheobasic potential, λ, is assumed to be the same for all neurons of the ensemble comprising the planarian nervous system. Similarly it can be demonstrated that for a train of monophasic, square-wave pulses of duration t, separation τ, and amplitude E, the excitation condition is that

$$1 \leq \frac{EL}{\lambda}\left\{\frac{1 - \exp(-2Dt/L^2)}{1 - \exp[-2D(t+\tau)/L^2]}\right\} \qquad (3)$$

These relations imply that the rheobasic value of the field intensity, E_r, for a neuron of half-length L is

$$E_r = \lambda/L \qquad (4)$$

while its chronaxie, t_c, is

$$t_c = (L^2/2D)\ln 2 \qquad (5)$$

Thus long neurons of the planarian's nervous system have a low rheobasic value of field intensity and long chronaxie, whereas short neurons have a high rheobasic field intensity and short chronaxie.

Electron microscope studies of the planarian nervous system (*6*) show that the brain is primarily comprised of short neurons and the ventral nerve cords are made up of long ones. Short pulse durations, with the amplitude E adjusted to response threshold, would therefore excite brain in preference to longitudinal nerve cords, whereas longer pulse durations with E at response threshold would excite longitudinal nerve cords in preference to brain.

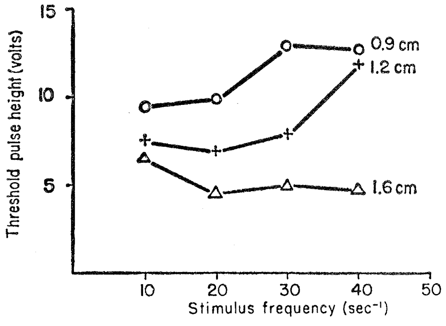

Fig. 1. Threshold pulse height of stimulus signal impressed on trough electrodes as a function of length of planarian and pulse frequency. For all points the stimulus was a 1-second, monophasic, square-wave pulse train in which pulse separation equaled pulse duration. ○, 0.9 cm; +, 1.2 cm; △, 1.6 cm.

Let t_{c1} and t_{c2} denote the chronaxies of the brain and longitudinal nerve-cord neurons, respectively. L_1 and L_2 denote the half-lengths subtended on the longitudinal axis of the planarian by brain and longitudinal cord neurons, respectively. Let L_p signify the length of the planarian. Denote by E_{t1}, E_{t2}, and E_p the respective amplitudes of the threshold pulses for excitation of brain neurons, excitation of longitudinal cord neurons, and evocation of some behavioral response. In keeping with the above, it would follow that

$$E_p = \text{Min}(E_{t1}, E_{t2}) \qquad (6)$$

where Min means "the minimum of."

Consider the situation in which a monophasic square-wave pulse train, satisfying jointly the following conditions, is used as a stimulus.

$$\text{(I)}\quad t = \tau \ll t_{c2} = (L_2^2/2D)\ln 2$$

$$\text{(II)}\quad t \text{ is such that } E_{t2} < E_{t1}$$

where, from condition I, and the equation

$$E_{tj} = \frac{\lambda}{L_j}\left\{\frac{1 - \exp(-4Dt/L^2_j)}{1 - \exp(-2Dt/L^2_j)}\right\} \qquad (7)$$

$j = 1, 2$. Condition I causes Eq. 7 to reduce to

$$E_{t2} \cong 2\lambda/L_2 \qquad (8)$$

and condition II in conjuction with Eq. 6 causes $E_p = E_{t2}$. Since L_2 could be expected to be proportional to the length of the planarian, one would anticipate that, for a frequency range satisfying conditions I and II,

$$E_p \propto 1/L_p, \qquad E_p \text{ independent of frequency.} \qquad (9)$$

In addition, since the longitudinal nerve cords would be the direct mediators of a longitudinal contraction, the behavioral response to a threshold pulse of this height within such a frequency range should be a longitudinal contraction.

An approximate estimate of the frequency range in which one can be assured that conditions I and II will be fulfilled can be calculated from histological information. In electron micrograph montages of planarian brain (*6*) a neural process subtending a length of more than 8 μ on the long axis of the worm is rarely observed. Electron micrographs of the ventral nerve cords (*6*) exhibit a number of relatively large-diameter axons which can be traced for distances of 20 to 30 μ before they run off the edge of the photograph or leave the plane of the section. The ventral cord axons are therefore probably much longer than 30 μ. One can thus assert that $L_1 < 4\ \mu$ and $L_2 > 15\ \mu$. With a value for D of 10^{-5} cm²/sec, this yields $t_{c2} > 80$ msec. Condition I would therefore be adequately satisfied for pulse trains in which $t = \tau \leq 50$ msec, that is, for any pulse train in which the pulse separation was equal to the pulse width and in which the frequency was greater than 10 pulses per second. Similarly, a numerical solution of Eqs. 7 and 8 shows that $E_{t1} > E_{t2}$ for all frequencies from 10 to 100 pulses per second. Condition II would therefore be satisfied for the range of 10 to 40 pulses per second used in the present experiment.

Planarians of the species *Dugesia tigrina* were tested in a plastic trough similar to that used by Barnes and Katzung (*4*) with a Grass model S-4 stimulator as the source of the electrical stimulus. The trough was illuminated at 11 lu/m² so the subjects could be observed for scoring. Thresholds were determined by a modified up-down method with a set of 8 to 10 test shocks, each of 1-second duration, administered 2 minutes apart to each worm. The water used for maintenance and the water used to fill the trough yielded the following in parts per million: total solids, 64; alkalinity, 16; calcium, 32; magnesium, 1; chlorides, 2; sulfates, 3; iron, 0.01; and its *p*H was 7.1. The planarians were maintained and tested at 22°C. Troughs were coated with slime before the experiment started each day. Shock was administered only when the worm was extended and parallel to the long axis of the trough. To avoid electrical skin-conduction effects, no test was administered when a worm was on the air-water interface.

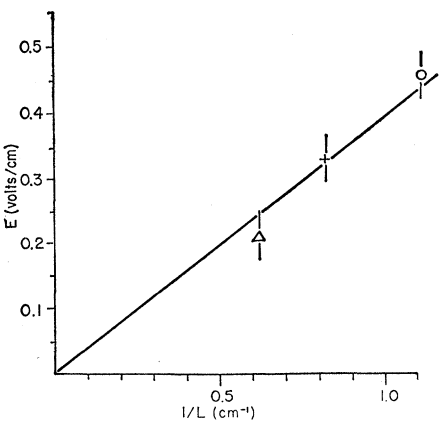

Fig. 2. Threshold field intensity as a function of the reciprocal of the length of the planarian. The theoretical curve was obtained with Eq. 7. Experimental points were computed from the data of Fig. 1.

The results are shown in Figs. 1 and 2. The data show satisfactory agreement with the predictions of the theory.

Although in the present discussion and study only two major size classes have been delineated, there probably are other neurons of intermediate length. Experiments were performed (*8*) in which a single, monophasic, square-wave pulse was used as the stimulus. The pulse duration was set at various values, and the kind of behavioral response to a pulse with the amplitude adjusted to response threshold was observed. Pulses of short duration evoked a small local contraction restricted to the head region. Pulses of intermediate duration evoked contraction of the anterior quarter of the planarian. Longer pulses evoked a longitudinal contraction of the entire planarian.

The assumption that these contractions were the result of excitation of the neurons of the affected region by the stimulus pulse permits another test of the theory. Since the values for D for the various ions which might plausibly be involved in excitation are all approximately 10^{-5} cm^2/sec, values for the chronaxies, t_c, to be anticipated for various neuronal lengths can be calculated from Eq. 5. For lengths of 2, 6, 10, and 50 μ the values of t_c would be 0.35, 3.1, 8.8, and 219 msec, respectively. In a general way these values correspond to the neuronal lengths predominating in the regions which contracted.

The correspondence between the quantitative predictions of the theory and experimental results suggest that the theory is essentially correct. The theory predicts also that the sets of neurons subjected to excitation depend in a critical, and known manner on the waveform of the electrical stimulus used as the unconditioned stimulus. In our experiments the pulse trains employed had a pulse separation equal to pulse duration. Although this particular pulse-train configuration was more or less arbitrary as far as testing the theory is concerned, it was chosen for comparability with the Barnes and Katzung experiments (*4*), in which a similar waveform, but different frequency, was employed. The lengths of the planarians employed in their study was not reported but, on the basis of the intensities of electric field which they used as stimuli and the results of the present study, it would appear that their subjects must have been much smaller than either our own or those normally used. Therefore, the distribution of neuronal sizes would be different, and consequently the pattern of primary excitation produced by the same stimulus frequency and waveform would be different. The discrepancy between their original results and those later obtained in Calvin's laboratory (*3*) might be accounted for on such a basis. The situation is analogous to higher-animal experiments in which intracranial stimulation is the reinforcement, except that here the relations between waveform and distribution of neuronal sizes are functionally analogous to electrode placement in determining which regions of the central nervous system will be excited. Whether a particular laboratory obtained the reported behavioral modifications or not would thus have depended upon their more or less fortuitous choice of stimulus waveform in relation to planarian size. The Harvard inductorium has probably led to the most consistent success precisely because its waveform is "dirty"—that is, it contains a mixed-frequency spectrum. For shooting in the dark at an unknown target a shotgun is better than a rifle. Learning in a planarian, as in any other animal, probably entails activation of some specific subset of neurons in a specific temporal order. In the absence of certain knowledge about this requisite subset and order, the probability of producing them is improved, though only inefficiently, by activating a variety of neuronal subsets in a multiplicity of firing orders.

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Catecholamines in Human Plasma

The data on catecholamines and consequently the conclusions in the report by J. F. O'Hanlon, Jr. (*1*), are open to question for the following reasons:

1) The indicated values for plasma noradrenaline (NA) and adrenaline (A) in his subjects are about 8 and 2 times as high, respectively, as the values now accepted as normal (*2*). In fact, the NA values are in the range which we have seen only in patients with pheochromocytoma and neuroblastoma.

2) The validity of the method used for the analyses of the catecholamines has been seriously questioned (*3*), the 1959 rebuttal by Weil-Malherbe (*4*) and Manger (*5*) notwithstanding. In fact, Weil-Malherbe, whose method O'Hanlon used, now recognizes that his previously reported values for plasma catecholamines in humans were much too high, and has modified his method with a additional resin treatment of the aluminum oxide extract. As a consequence, the values he now reports are in the accepted normal range. The points are emphasized by Weil-Malherbe himself in the publication (*6*) cited by O'Hanlon. Until about 5 years ago there may have been some question about the upper limit of catecholamines in normal human plasma. Sufficient data are now available, however, including those of Weil-Malherbe (*6*), to show that this figure is less than 1.5 μg/liter for the combined values of NA (not more than