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Somatic Inheritance of Habituation of Responses to Light in Planarians

Abstract. Planarians show long-lasting reversible decrease of responses to a photic stimulus repeated 25 times each day. This habituation was found to be significantly faster in regenerated offspring of previously habituated planarians, and was also transferred by cannibalization, thus resembling light-shock conditioning. Habituation provides a new situation in which to study the somatic inheritance of learning in planarians.

Previous descriptions of planarian behavior include their reactions to light (*1*), vibration, and to changes in pH, temperature, oxygen tension, and so forth.

Studies on classical conditioning (*2*) and instrumental conditioning (*3*) in planarians with light (conditioned stimulus) and shock (unconditioned stimulus) have greatly extended knowledge of their behavior. Of particular current interest is the inheritance and cannibal-transfer of learning in planarians (*4*), and the possible chemical basis of these memories (*5*). The significance of these

findings in view of the very simple nervous system planarians possess has been stressed (*2, 4, 5*).

The present study was undertaken to determine whether planarians show diminution or loss of responses to repeatedly applied sensory stimuli, that is, whether they show "habituation" (*6*). Light was chosen as the stimulus because there were earlier indications (*2, 7*) to suggest that habituation to this sensory modality might occur in planarians, in addition to the environmental familiarization demonstrated by Best (*8*).

Sixty-six planarians of the species *Dugesia dorotocephala* used in the study were kept in individual dishes of tap water in the laboratory. They were allowed normal diurnal light fluctuations and were fed every 4 days. The apparatus and procedures used were similar to those described by McConnell (*9*) except for the inclusion of a heat filter between light-source and animals. Transfer and handling were by gentle suction, water jet, and occasionally fine brush. Daily tests were given only between 1:30 and 5:00 P.M. to minimize diurnal rhythm effects. After 5 minutes of familiarization to the test trough each day, 25 presentations of incandescent light were given daily to each planarian, with intertrial intervals of 30 to 60 seconds. Each planarian was returned to its home dish after 25 trials. The light intensity during each 3-second stimulus reached 400 foot-lamberts from the previous level of 40 ft-lam with ambient room lighting. Testing in all groups was single blind, except for the cannibal habituation group in which double blind testing and matched pairs were used because of the small numbers in this group.

Naive planarians ($N = 35$) averaged 26 percent responses to light in this situation on the first 2 days. This is comparable to previous figures for light control groups during conditioning studies (*2*).

Figure 1 shows the time course of the habituation to light for 35 normal controls (group A), in which the percentage response to light on successive days declined with several small plateaus. The criterion of full habituation for a single planarian was arbitrarily set at 2 successive days (50 trials) with zero responses. Included in this group are eight planarians that were habituated in the manner described but in the absence of a heat screen, and seven

Table 1. Responses and habituation to light by *Dugesia dorotocephala*. Criterion of habituation is 50 consecutive trials with zero responses. *P* values refer to differences from the corresponding figure for group A, except in the case of group D, where *P* values refer to differences from their matched controls ($N = 6$), not shown in the table.

Responses in first 50 trials (Mean %, ± S.D.)	Time to criterion (Mean No. of trials, ± S.D.)
Group A (normal controls; N = 35)	
26 ± 10	386 ± 132
Group B (taildrop offspring; N = 15)	
15 ± 12 ($P < .01$)	218 ± 65 ($P < .001$)
Group C (regenerated cut tails; N = 10)	
16 ± 8 ($P < .001$)	245 ± 80 ($P < .001$)
Group D (cannibal habituation; N = 6)	
13 ± 9 ($P < .01$)	243 ± 87 ($P < .01$)

taildrop offspring of naive planarians, allowed to regenerate from 9 to 14 days and then habituated. Since there were no significant differences between results for either of these groups and the other naive planarians, all were
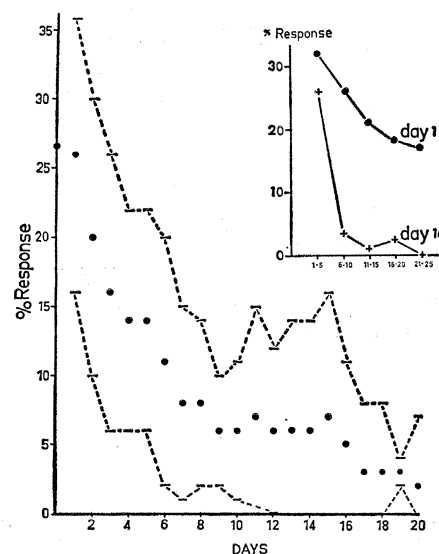

Fig. 1. Habituation of *Dugesia dorotocephala* to light. Each of 35 planarians received 25 presentations of light daily, each of 3 seconds duration. The ordinate shows the percentage of responses occurring each day, and training time in days is plotted along the abscissa. Each point is the mean of the percentages of responses of the 35 planarians on the day in question, and the horizontal bars above and below the points represent standard deviations of these means. The inset depicts receptor adaptation during 25 trials on day 1 (circles) and day 16 (crosses). Percentage response is shown on the ordinate for each of the five groups of five trials designated along the abscissa. Each circle is the mean of the percentages of responses of 35 planarians, and each cross is the mean of the percentages of responses of 16 planarians.

pooled in the control group. Table 1 gives the mean time taken to reach criterion for the four experimental groups. Natural taildrops (group B) and surgically divided tails (group C) of planarians that had been habituated to a criterion level were allowed to regenerate for 10 days. Both these groups gave results differing significantly from group A. Regenerated offspring (groups B, C) of fully habituated planarians showed a significantly lower level of responsiveness to light in the first 2 days of testing and reached the habituation criterion more quickly than the initially naive controls (group A).

The pooled cannibal habituation group ($N = 6$) were fed two fully habituated planarians every fourth day for 20 days. These were shared by the group and all were observed to be eating at each feeding. Then the course of their habituation to light was compared with controls ($N = 6$) fed in the same manner with planarians naive to light but otherwise handled in the same way as the habituated planarians that were eaten. The cannibal habituation group (D) showed fewer responses to light over the first 50 trials and reached criterion significantly sooner than their controls (Table 1). Five out of the six planarians in group D reached criterion before the first of their matched controls had done so.

The gradual quantitative change of response leading to the loss of responses (called habituation) persists, at least in part, from day to day. It is slowly reversible. Ten planarians that showed 28 percent (±10) responses in their first 50 trials, were then fully habituated (zero responses in 50 consecutive trials). They still showed a significant reduction in responsiveness to light after 3 and 7 weeks without intervening testing, namely: at 3 weeks postcriterion, 12 percent (±8) responses ($P < .01$), and at 7 weeks, 16 percent (±7) ($P < .01$).

Habituation to light occurs exclusive of changes of stimulus or qualitative changes of response. The latter is shown by the fact that planarians habituated to light in the normal position still responded when presented with a light stimulus differing both qualitatively and quantitatively from that to which they were habituated (10).

The results for day 1 (Fig. 1, inset) demonstrate that for one planarian on a given day the frequency of response to a single light trial is related to the position of that trial in the day's

sequence of 25 light presentations. This, together with the electrophysiological findings of Behrens (11), suggests that adaptation of the photoreceptors occurs. Responsiveness of planarians on day 16 is greatly reduced by habituation, but still shows evidence of adaptation, as graphically shown by Fig. 1, inset.

There is evidence (6, 12) that habituation in mammals is a central phenomenon with overall inhibitory effect which utilizes pathways and is dependent upon synaptic mechanisms common to learning and conditioning. The suggestion (6, 12) that habituation is a fundamental physiological mechanism of adaptation is borne out by the ability of planarians to habituate. Past (6, 12) and present results distinguish habituation from adaptation of sensory receptors.

A possible chemical basis for inheritance and transfer of conditioning in planarians has been suggested (5). The present results are of interest because habituation is an extinction of response or a learned failure to respond. Though quite distinct from conditioning, it shows very similar transfer by

cannibalism. Such habituation in planarians may differ sufficiently from other learning situations to require a molecular coding different from that for conditioning, to be transferred in the manner described (13).

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Electroencephalographic Desynchronization during Deep Sleep after Destruction of Midbrain-Limbic Pathways in the Cat

Abstract. *Lesions which interrupt the ascending limb of the midbrain-limbic circuit in the cat at different levels, or which even destroy it completely, do not prevent electroencephalographic desynchronization at the beginning of periods of deep sleep, nor do they affect the maintenance of desynchronization throughout the sleep episodes. The pontine mechanisms responsible for these electroencephalographic patterns can apparently exert their influence through ascending pathways other than those directly impinging on the hypothalamus and the limbic system.*

A behavioral pattern, characterized by postural atonia with sudden loss of neck muscle tone and rapid jerks of eyeballs and body muscles, and paradoxically associated with an electroencephalographic change from synchronization to the desynchronized rhythms generally considered typical of arousal, has recently been described as deep sleep in mammals (1). The neural mechanisms which induce these episodes appear to be located in the pons (1, 2), but little is known about their ascending connections. However, these connections have been tentatively identified (1) with the ascending limb of the so-called "midbrain-limbic circuit," which connects the caudal and rostral midbrain tegmentum with hypothalamic and limbic structures (3). Since evidence on this topic is scanty

and since the functional significance of the midbrain limbic pathways is uncertain (4), we undertook experiments to clarify the issue (5).

Screw-electrodes were implanted in the skull of cats for monitoring electrical activity from the right and left hemispheres, and in both orbits for recording eye movements. The electromyogram of the neck was obtained through two needles permanently inserted into the paravertebral cervical musculature. The animals were placed in a soundproof, electrically isolated, lighted cage and were observed through a large glass window. Graphic recordings were made on a multichannel inkwriter (6). After a sufficient number of deep sleep episodes in the intact animals had been observed, various types of midbrain lesions were made