CONDITIONED MODIFICATION OF PHOTOTACTIC BEHAVIOR IN *HERMISSENDA*

I. Analysis of Light Intensity¹

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Abstract

Psychophysical experiments examined the control of phototactic behavior by light intensity in the nudibranch mollusk *Hermissenda* by measuring the time that *Hermissenda* remained in an illuminated area. This measure of phototactic behavior exhibits a closer correspondence to changes in test light intensity than other previously examined measures of phototaxis. Changing the intensity of a test light in a series of increasing steps resulted in a graded increase in positive phototactic behavior. Behavioral responses to different light intensities were examined in conditioned and control animals. Conditioning resulted in a significant suppression of phototactic behavior at all light intensities examined. Random control procedures did not produce suppression of phototactic responding. These behavioral results provide a data base to examine how well neural correlates produced during conditioning fit the behavior.

One of the major goals of neurobiologists is to identify the neural loci for cellular mechanisms of associative learning. Associative learning has now been demonstrated in a number of different molluscan preparations (Mpitsos and Davis, 1973; Mpitsos and Collins, 1975; Gelperin, 1975; Crow and Alkon, 1978; Crow and Offenhach, 1983; Walters et al., 1979; Davis et al., 1980; Sahley et al., 1981a, 1981b; Carew et al., 1981a, 1983). In some of these preparations, neural correlates of the conditioning have been examined in identified neurons that make up the neural circuitry mediating the behavior (Davis and Gillette, 1978; Crow and Alkon, 1980; Chang and Gelperin, 1980; Carew et al., 1981b; Crow, 1982, 1983a, 1983b; Davis et al., 1983; Hawkins et al., 1983; Walters and Byrne, 1983).

The Pacific nudibranch *Hermissenda* is one preparation in which neural correlates of associative learning have been identified and a mechanism of learning has been proposed. The conditions that produce associative suppression of phototactic behavior are well documented (Crow and Alkon, 1978; Crow and Offenhach, 1979, 1983; Crow, 1983c) and various neural correlates of conditioning in the B-type photoreceptors have now been studied in several laboratories (Crow and Alkon, 1980; Alkon et al., 1982; Crow, 1982, 1983a, 1983b). Recently, it has been suggested that an enhanced photoresponse from the type B photoreceptors is critical for producing the behavioral modification (Farley and Alkon, 1982; West et al., 1982; Alkon, 1983). However, it is not yet firmly established how the changes in the B-photoreceptors produced by conditioning result in the

generation of a change in phototactic behavior. The relationship between the enhanced photoresponse in the B-type photoreceptors and the behavior that is modified presents an interesting paradox. Since *Hermissenda* is positively phototactic and the conditioning procedure results in a decrease in the normal phototactic response (Crow and Alkon, 1978), how can an enhanced photoresponse produced by conditioning generate a decrease in phototactic behavior?

There are at least three possible explanations that might account for the apparent paradox. One possibility is that after conditioning there are complex circuit interactions that cause an enhanced photoresponse to lead to decreased phototactic behavior (Alkon, 1983). A second possibility is that there is a nonlinear relationship between light intensity and behavior so that brighter lights (and with conditioned animals larger photoresponses) actually decrease positive phototactic behavior. Finally, it may be possible that the proposed correlates (enhanced photoresponses) are not causally related to the behavior and that other processes or aspects of the photoresponse are involved. In this and the following paper, these latter two issues are addressed. The first paper describes the results of behavioral studies showing that increasing light intensity produces increased positive phototactic behavior over a broad range of light intensities and that conditioning results in a decrease in this behavior. The second paper provides evidence for a new relationship between conditioned changes in the B-photoresponse and changes in phototactic behavior following conditioning.

Some of the results of these experiments have been reported in preliminary abstracts (Crow, 1983a, 1983b).

Materials and Methods

Animals. Adult *Hermissenda crassicornis* were obtained from Sea Life Supply Co., Sand City, CA. The animals were maintained in an

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artificial seawater aquarium at $14 \pm 1^\circ\text{C}$ on a 12-hr light, 12-hr dark cycle. Animals were fed small pieces of muscle gonad (*Mytilus edulis*).

Conditioning procedures. The conditioning procedure and apparatus have been described in detail in previous publications (Crow and Alkon, 1978; Tyndale and Crow, 1979) and will be described only briefly in this report. The animals were trained and tested in glass tubes that were attached to clips on the top surface of a rotating turntable. During the training periods, the animals were confined to the ends of the tubes by a small foam plug inserted into an aperture in the tube located 4 cm from the end. The conditioning paradigm consisted of pairing illumination (conditioned stimulus (CS)) with high speed rotation (nominal unconditioned stimulus) of the turntable (95 rpm). The 30-sec light stimulus preceded maximum rotation by 500 msec and rotation terminated with light offset. The average intertrial interval was 2.25 min. The light (CS) was provided by two 60-W lamps housed in enclosures and projected through Corning blue-green color filters. The lamp housings were positioned at the perimeter of the turntable (see Fig. 1). The light intensity of the CS was $28.5 \times 10^{-4} \text{ W/cm}^2$ measured with a photodiode at the perimeter of the turntable. Nonassociative effects were assessed by examining the behavior of random control groups that received light and rotation programmed on independent random schedules. The conditioning and control sequences were automated as

Figure 1. Apparatus used for training and testing of phototactic behavior. The training and testing apparatus is enclosed inside an incubator. Test illumination is provided by a fiber optic bundle contained inside the central post positioned over the center of the turntable. The holder attached to the end of the central post contains neutral density filters and an interference filter (510 nm). Training lights (CS) containing Corning blue-green filters are enclosed in the light housings positioned over the lateral edge of the rotating table. The behavior of the *Hermisenda* in the test light at the center of the table is recorded by a video camera shown in the photograph mounted at the back of the incubator. Diffuse red light is provided by a fiber optic shown at the upper right.

described previously (Crow and Alkon, 1978; Tyndale and Crow, 1979). The conditioning and testing apparatus was inclosed inside an incubator that maintained the temperature at $14 \pm 1^\circ\text{C}$. The different groups received multiple training sessions consisting of 50 conditioning trials each day for 3 consecutive days. Conditioning effects were assessed 24 hr following the last conditioning session.

Behavioral methods: initiation of locomotion. Testing the time taken by individual animals to initiate locomotor behavior in response to light before and after conditioning was accomplished by detecting the movement of the animals between an infrared emitter and a phototransistor located at the starting end of the glass tube (see Fig. 1). The output of the phototransistors was amplified and connected to a 20-channel event recorder.

Behavioral methods: time in light. The following procedures were used to measure phototactic behavior before and after conditioning. Light provided by a fiber optic (Dolan-Jenner) was positioned at the center of the turntable. Attached to the end of the fiber optic guide was a filter holder that held a narrow band interference filter (510 nm; half-band width, 10 nm) and when appropriate, neutral density filters to attenuate the light. The unattenuated light at the center of the turntable was $9.3 \times 10^{-4} \text{ W/cm}^2$ at 510 nm as measured with a calibrated photodiode. The position and movement of the animals near and at the center of the turntable in both dim red light and in light of different intensities were recorded on tape by a video camera mounted inside the incubator and connected to a time-lapse video recorder (Panasonic model NV-8050) equipped with a time generator (see Fig. 1). The pretraining (pretest) and post-training measure of phototactic behavior consisted of dark adapting the *Hermisenda* for 12 min and then measuring the amount of time that each animal remained in the central illuminated area during a 10-min observation period under the different conditions of illumination. The time in light during the 10-min period was recorded as described on videotape for subsequent analysis. In order to provide sufficient background illumination for the video camera, a diffuse red light was placed inside the incubator (see Fig. 1). The intensity of the red light measured at the center of the turntable was $1.6 \times 10^{-5} \text{ W/cm}^2$. Photoreceptors exhibit diminished sensitivity to light at this wavelength (640 nm) although small changes in photoreceptor activity can be detected at this wavelength and intensity. The small photoresponses evoked by the dim red light were not considered to be a problem in interpreting these behavioral results since the intensity was below the threshold for evoking changes in phototactic behavior (see Fig. 2) and control experiments using an infrared filter which transmits wavelengths that do not evoke a photoresponse in B-type photoreceptors produced similar behavioral results (see Fig. 2).

Phototactic responses were initially measured in increments of 1 log unit of attenuation, i.e., -6.0, -5.0, -4.0, -3.0, -2.0, -1.0, 0. In order to facilitate the analysis, a sample of light intensities was selected for the conditioning experiments. Only animals that responded to all three of the test light intensities were selected for the conditioning experiments. Phototactic behavior was measured before and after conditioning to unattenuated light at 510 nm, referred to as 0 attenuation, light-attenuated -2.0 log units and -4.0 log units. As a control procedure, the behavior of the animals was measured in the dim red light (condition R) before each ascending series of light intensities. The following sequences of light stimuli were used in the experiments: R, -4.0, 0, -2.0; R, -4.0, -2.0, 0. After completion of behavioral observations at a given light intensity, the animals were removed from the tubes and the inside of the tubes was scrubbed to remove mucus trails before replacing the animals in the tubes. Following replacement, the animals were again dark adapted 12 min between the ascending series of light intensities.

Conditioning effects were assessed 24 hr following the last conditioning session by computing from the videotapes the percentage of time that the animals remained in the center area under different light intensities. Post-training scores were compared with the pretraining measures of phototactic behavior. The time taken by individual animals to initiate locomotion in the red light or in the presence of light (510 nm) of different intensities was also collected and compared with previously published results (Crow and Offenbach, 1983) to verify that animals exhibited behavioral suppression using a different measure of phototactic behavior.

Statistical methods. A one-way analysis of variance was used to compare the behavioral responses to the different light intensities before and after conditioning for both the random controls and paired groups (Winer, 1962). Within group comparisons of start latencies in

response to different light intensities and comparisons between pre-training and post-training percentages were made with difference scores using a *t* test for correlated means. Tests of significance of the different light intensities following a significant overall *F* test employed Newman-Keuls procedures (Winer, 1962). Comparisons between post-training measures of phototactic behavior for paired and random controls involved a two-way analysis of variance with repeated measures (Winer, 1962).

Results

Phototactic responses to light gradients. The initial studies were conducted in order to examine the effect of different light intensities on the control of phototactic behavior of *Hermisenda*. Can *Hermisenda* discriminate between different light intensities? In order to test this, a psychophysical experiment was conducted where animals ($N = 15$) were first dark adapted for 12 min and then phototactic behavior was measured at different light intensities. As a control procedure, the time that the animals remained at the ends of the tubes in red light and infrared light during a 10-min observation period was recorded as described (see "Materials and Methods"). Following the initial pretest measurements in red or infrared light, phototactic behavior was examined in response to the following ascending series of light intensities: -6.0 , -5.0 , -4.0 , -3.0 , -2.0 , -1.0 , 0 . The light intensities are expressed in log units of attenuation. Before the response to the next intensity was examined, all animals were removed from the tubes, the tubes were scrubbed, and then animals were placed back into the tubes and dark adapted as described in "Materials and Methods." The pooled data from three independent replications are shown in Fig. 2.

The relationship between the increase in the intensity of the test light and stronger positive phototactic behavior is indicated by the significant overall effect of light intensity ($F_{6,84} = 13.45$; $p < 0.01$). These results indicate that, with increases in the intensity of the test light, *Hermisenda* spends more time during the observation period in the test light at the end of the

glass tubes (see Fig. 2). The evidence that different light intensities show proportional control of phototactic behavior is provided by the significant increase in the percentage of time during the observation period that the *Hermisenda* remained at the end of the tubes with brighter intensities as compared to the measures collected both in red light and dim light. Within group comparisons using the Newman-Keuls procedure (Winer, 1962) showed that behavior in response to light-attenuated 2 log units was significantly different from behavior in light-attenuated 3 and 4 log units ($p < 0.05$). Behavior was significantly different in response to 1 log unit as compared to 3 and 4 log units ($p < 0.01$), and 0 attenuation as compared to 2 log units ($p < 0.01$). These results show that the animals can discriminate between levels of illumination that vary by one log unit of attenuation.

The next experiment examined the effect of light intensity on another measure of phototactic behavior, the initiation of locomotion. An analysis of the effect of the different light intensities on the time taken to initiate locomotion (start latency) and the time in the light showed an inverse relationship between the two measures of phototactic behavior (Fig. 3). The animals started faster in response to bright light (0 attenuation) as compared to the start latencies in dim light (-4.0) ($p < 0.025$) and light-attenuated 2 log units ($p < 0.05$) ($n = 20$) (see Fig. 3). However, the start latencies in response to light-attenuated -4.0 log units were not significantly different from the start latencies in the red light. Taken collectively, these results show that two different measures of phototactic behavior of *Hermisenda* are controlled by the intensity of illumination. Furthermore, the animals can discriminate between light intensity that varies by 1 log unit of attenuation.

Conditioned modification of phototactic behavior. The next series of experiments was designed to examine the range of light intensities over which the animals would exhibit modified phototactic responses after conditioning. Conditioning studies

Figure 2. Phototactic behavior in response to illumination of increasing intensity. Light intensity at 510 nm is expressed in log units of attenuation (-6.0 , -5.0 , -4.0 , -3.0 , -2.0 , -1.0 , 0). The behavior of the animals in response to dim (1.6×10^{-5} W/cm²) diffuse red light was used as a control procedure. As an additional control procedure, behavior was measured with an infrared filter substituted for the red filter in the fiber optic bundle. Illumination (510 nm) of increasing intensity resulted in a significant increase in the amount of time that the animals remained in the central illumination area. This measure of phototactic behavior results in a behavior-intensity curve that closely parallels the intensity-photoresponse amplitude of B-type photoreceptors of *Hermisenda*. The curve was fitted by hand ($n = 15$). The data in this figure and subsequent figures are expressed as means $\pm$ SEM.

Figure 3. The relationship between two measures of phototactic behavior: time in light ($n = 20$) and time to initiate locomotion in response to light ($n = 20$). The relationship between the two measures is inverse. Animals start significantly faster in response to bright (0) ($p < 0.025$) and moderately bright light (-2.0) ($p < 0.05$) as compared to the red light and dim light (-4.0).

with vertebrates have shown that conditioned animals respond to a broad range of CS intensities (stimulus generalization) if a nondiscrimination training procedure is employed. In order to facilitate the behavioral analysis only three (-4.0 , -2.0 , 0) of the seven ascending series of light intensities were examined before and after training. Figure 4 shows the percentage of time that the animals remained at the end of the tubes in the dim red light (Fig. 4A) and in the test lights (Fig. 4B) of increasing intensity before training (pretest) and 24 hr after conditioning (post-training). These results represent the pooled data from two independent replications ($n = 20$) from two different animal shipments. The replicates were not significantly different from each other although there was more variability between the two samples in response to light-attenuated -4.0 log units as compared to the brighter intensities.

As shown in Fig. 4B, test lights of increasing intensity resulted in a significant increase in the animals pretest and post-training positive phototactic behavior. The behavior of the animals in response to the dim red light used as a control procedure before and 24 hr after multiple session training is shown in Figure 4A. These results show that behavioral responses to the dim red light are not changed by conditioning and provide additional evidence for the specificity of the stimuli used in this training paradigm as shown previously for the modification of start latencies in response to illumination following training (Crow and Offenbach, 1979). The effect of light intensity on behavior was demonstrated by the results of the analysis of variance (Winer, 1962) for the three different light intensities before and after conditioning. Light intensity had a significant effect on phototactic behavior for both the pretest ($F_{2,38} = 13.54$; $p < 0.01$) and post-training ($F_{2,38} = 9.04$; $p < 0.01$) behavioral analysis (Fig. 4B).

Newman-Keuls tests (Winer, 1962) showed that, for the pretests, light-attenuated -2.0 log units resulted in a more positive phototactic response than light-attenuated -4.0 log units ($p < 0.05$), and 0 attenuation showed more positive behavioral effects than -2.0 log units ($p < 0.01$) or -4.0 log units ($p < 0.01$). Following conditioning, light intensity was again effective in controlling behavior. Post-training effects showed that 0 attenuation was significantly different from -4.0 log units ($p < 0.01$) and -2.0 log units ($p < 0.05$). Conditioning

resulted in a suppression in the behavioral response to the three light intensities (see Fig. 4B). The suppression of phototactic behavior was indicated by significant differences between the pretest and post-training measures of behavior at the three different light intensities. Conditioning resulted in a significant decrease in phototactic behavior in response to light-attenuated -4.0 log units ($t_{19} = 1.80$, $p < 0.05$), -2.0 log units ($t_{19} = 1.88$, $p < 0.05$), and 0 attenuation ($t_{19} = 2.59$, $p < 0.01$).

Since conditioning resulted in phototactic suppression at all test light intensities as compared to each animal's pretest measures, additional experiments were conducted to test if the effects were associative. In order to test the associative contribution to the measure of phototactic behavior, separate groups of animals received random presentations of light and rotation as described in "Materials and Methods." The results shown in Figure 5 represent the pooled data from two independent replications ($n = 20$). As previously described for the conditioned groups, the relationship between phototactic behavior and test light intensity was significant for both pretest ($F_{2,38} = 9.83$; $p < 0.01$) and post-training measures ($F_{2,38} = 17.13$; $p < 0.01$). Newman-Keuls tests (Winer, 1962) showed that bright light (0 attenuation) resulted in more positive phototactic responses than light-attenuated 2.0 log units ($p < 0.01$) or 4 log units ($p < 0.01$) for both pretest and post-training experiments. The behavioral response to dim red light did not change significantly as a result of the random procedures as shown in Figure 5A. However, in contrast to the results of conditioning, random controls did not show significant phototactic behavior suppression to any of the test light intensities after multiple random presentations of the light and rotation (Fig. 5B).

The results show that conditioning produces phototactic suppression at all of the light intensities tested. In order to assess the associative effects of conditioning, direct comparisons of the time that animals remained in the central illuminated area during the post-training 10-min observation period were made between conditioned animals and random controls. The analysis of variance revealed a significant overall difference between the paired animals and the random controls for the test light intensities ($F_{1,38} = 6.33$, $p < 0.05$). Significant overall effects of light intensity on phototactic behavior were observed for the post-training measures ($F_{2,76} = 18.29$; $p < 0.01$). Tests on the differences between means at each light

Figure 4. Conditioning of phototactic behavior. Effect of multiple session training on suppression of phototactic behavior measured at three light intensities (-4.0 , -2.0 , 0). A, behavioral response to dim diffuse red light before and after 150 paired trials ($n = 20$). The response to the red light did not change significantly following conditioning. B, suppression of phototactic behavior 24 hr after 150 conditioning trials was significant at test light intensity -4.0 ($p < 0.05$), -2.0 ($p < 0.05$), and 0 ($p < 0.01$) ($n = 20$).

Figure 5. Absence of an effect of random conditioning procedures on phototactic behavior measured at three light intensities (-4.0 , -2.0 , 0). A, behavioral response to dim red light before and after 150 random presentations of light and rotation ($n = 20$). The response to the red light after the random procedure was not significantly different from pretest responses. B, the random procedures did not significantly change phototactic behavior measured at the three light intensities (-4.0 , -2.0 , 0).

intensity using the Newman-Keuls method (Winer, 1962) revealed significant differences between the paired group and random controls for light-attenuated -4.0 log units ($p < 0.05$), -2.0 log units ($p < 0.05$), and 0 attenuation ($p < 0.01$). The differences in behavior between groups are only expressed in the presence of light (510 nm) since the results of control studies showed that there were no significant differences between the random and paired groups when tested after training in the dim red light (see Figs. 4 and 5). These results show that the conditioning procedure produces an associative suppression of normal positive phototactic behavior at all three levels of illumination tested in these experiments. Moreover, the behavioral suppression is not due to nonspecific changes in motor activity since the modification of phototactic behavior is only expressed in the presence of illumination.

Discussion

Light intensity discrimination. The results of these psychophysical experiments show that the behavior of *Hermisenda* can be controlled by changes in the intensity of illumination. Using the time that the animals remain in the test light as the measure of phototactic behavior, the results indicate that the animals can discriminate between light intensities that vary by 1 log unit of attenuation (see Fig. 2). The phototactic behavior of *Hermisenda* in response to the ascending series of light intensities results in the generation of a behavior-light intensity curve that closely resembles the light intensity-generator potential amplitude function of the B-type photoreceptor (Alkon, 1976). The close correspondence between phototactic behavior and the light response of the B-type photoreceptors indicates that the measure of phototactic behavior employed in these studies will be useful for future studies of cellular correlates produced by conditioning (see companion paper). In fact, the time that the animals remain in light both before and after training shows a closer correlation with the test light intensity than other measures of phototactic behavior previously examined in conditioning studies of *Hermisenda* (see Crow and Alkon, 1978; Crow and Offenbach, 1983).

Conditioning and sensory generalization. The finding that behavior in the presence of dim red light did not change significantly after conditioning demonstrates that this measure of phototactic behavior (time in light) exhibits stimulus specificity. These results along with previously published studies (Crow and Offenbach, 1983) again demonstrate that this example of conditioning in *Hermisenda* produces a change in the animals response to light. Therefore, the behavioral suppression found after training is not due to a nonspecific change in activity (see Figs. 4A and 5A).

Previously, Crow and Offenbach (1983) found that conditioned animals remained in the central illumination area of the turntable in the presence of bright light significantly less during a post-training observation period as compared to pretest measures. The results of this study confirmed the original observation and in addition show that behavior changes in the presence of a wide range of test light intensities (Fig. 4B).

The phototactic suppression found in this study was associative as shown both by the change in behavior after conditioning relative to pretest measures and the absence of a change in behavior following random control procedures (Fig. 5B). Direct comparisons between the paired groups and random controls showed that, using this measure of phototactic behavior, conditioning produced significant behavioral suppression relative to pretests as well as to the random controls at all of the test light intensities.

Implications for cellular correlates of conditioning. In *Hermisenda*, light evokes a depolarizing generator potential in the B-type photoreceptors (Dennis, 1967). The generator potential of B-photoreceptors consists of a number of phases described as

an initial depolarizing transient peak, a hyperpolarizing dip, a plateau phase, and a depolarizing tail that occurs at the offset of light (Detwiler, 1976). These various phases of the generator potential have been subsequently shown to be produced by several ionic conductances (Alkon, 1979). Conditioning results in a number of changes in the components of the light response of the photoreceptors (for a discussion, see accompanying paper). One such change has been reported for the depolarizing tail (referred to as the long-lasting depolarization (LLD)), which is expressed following conditioning by a longer time period for the membrane potential to return to base line following light offset (West et al., 1982).

A number of proposed mechanisms of conditioning in *Hermisenda* have been reported to alter the LLD (see Alkon (1983) for a review). However, it is unclear how this component of the light response (LLD) could be involved in the expression of the change in phototactic behavior since the LLD occurs *after* the termination of light. The results presented in this paper as well as in previous publications have shown that behavior changes in the presence of light following conditioning and behavior in the dark does not significantly change (Crow and Offenbach, 1979, 1983). The results of this study showing that the behavioral response to dim red light was not changed by conditioning (see Fig. 4A) is consistent with the previous findings showing that latencies (time taken to locomote into the central area of the turntable) in the presence of red light are not significantly altered by conditioning (Crow and Offenbach, 1983).

However, using a different measure of behavior, the shadow response, Lederhendler and Alkon (1984) have suggested that conditioning alters the ability of *Hermisenda* to detect light-dark intensity differences. Moreover, it was suggested that there may be a common underlying mechanism related to the LLD for the various components of modified phototactic behavior. According to this hypothesis, the LLD would be involved in the expression of the behavior since the prolonged depolarization after the light terminates would not provide information to the animal regarding the decrease in illumination. However, the results reported in this paper are inconsistent with such an interpretation. First, conditioned animals are capable of discriminating between the different light intensities used in the present experiments (see Fig. 4) since animals remained in the brightest lights (0 and -2.0) significantly longer than the dim light (-4.0) (see Fig. 4B). Second, the LLD would not be expected to alter the behavior of animals moving in an illuminated gradient from areas of dim illumination into areas of greater intensity, which is much closer to the conditions of illumination that the animals experience under the testing procedures used by a number of different investigators of phototactic behavior (Crow and Alkon, 1978; Alkon et al., 1982; Farley and Alkon, 1982).

Furthermore, since conditioned animals showed behavioral suppression in the presence of all test light intensities (see Fig. 4) and did not exhibit a decrease in the number of entries into the illuminated area after conditioning (unpublished observations), it is unlikely that the change in behavior over such a broad range of stimulus intensities would reflect a reduced ability to discriminate light-dark differences. Finally, phototactic suppression in response to the -2.0 test light could not be explained by the LLD since it was previously reported that conditioning did not result in an enhanced LLD in response to light of a similar intensity (Farley and Alkon, 1982). In fact the only intensity at which conditioning resulted in an enhanced LLD (24 hr, horizontal orientation) was the brightest test light (0 attenuation) (Farley and Alkon, 1982). Therefore, conditioning produces changes in phototactic behavior over a broad range of light intensities where the LLD is either absent or not affected by conditioning. This suggests that if the primary change is in the B-type photoreceptor then other com-

ponents of the photoresponse must provide the information necessary for the expression of the altered behavior in the presence of light (see accompanying paper for discussion).

Taken collectively, the results reported in this study have important implications for any proposed mechanism of conditioning in *Hermisenda*. Just as the nature of cellular changes in a neural network that mediates a behavior imposes constraints on the expression of the behavior, the nature of the behavior imposes constraints on the proposed cellular mechanism(s). In the case of *Hermisenda* a mechanism that implicates the involvement of the B-type photoreceptors must explain the phototactic suppression in response to a broad range of test light intensities found in these experiments. Clearly, the dependence of the LLD on large depolarizing generator potentials produced by bright light indicates that it would not be a reasonable mechanism to explain the results of this study. The challenge for future studies of *Hermisenda* is to explain the relationship between photoreceptor changes and behavioral changes. A new way of addressing this issue is discussed in the accompanying paper (Crow, 1985).

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