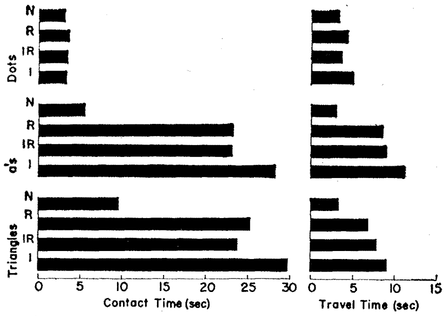

Fig. 1. Differences in response to different displacement conditions just after the critical period in development of the ability to perform under different conditions of inverted and reversed visual feedback.

12 to 13, four were able to make the inverted *a*'s but failed on the inverted triangles. None of the younger failures were able to make either inverted *a*'s or triangles.

Figure 1 shows the contact and travel times for the 12 subjects who completed all four visual conditions. Analyses of variance of the contact and travel times showed that there were significant differences between conditions. Subsequent tests found that the normal condition was the easiest, the reversed and inverted-reversed significantly harder than the normal but not different from each other, and the inverted condition significantly harder than the other three. Figure 1 shows also that the task of making triangles resulted in times of movement longer than either of the others.

The results conform to the expectations that guided the design of the study. That performance was related to age suggests that maturational factors may be involved in the behavior. The additional demonstration of differential organization and effectiveness of the response to inverted, reversed, and inverted-reversed vision provides systematic evidence that this developmental change is maturationally organized in terms of anistropic properties of the visual-feedback mechanisms of response.

The findings are of interest in relation to other studies which have suggested that a critical developmental period in behavioral or perceptual organization occurs sometime between the ages of 10 and 12 years. This period generally corresponds with the time at which relational thinking (*3*) and concepts of social relations (*4*) are believed to develop in the average child. Piaget (*5*) indicated that symbolic thinking developed around the years of 10 to 12. We believe this is also the time when handedness is stabilized in the child, and the beginning phase of highly refined manipulative skill.

The results are also of interest in relation to findings on development of perception (*6*) of the moon illusion, namely the decrease in apparent size of the moon as it moves from horizon to zenith; this development varies with chronological age, and reaches an adult level at about 10 or 11 years of age, and is attributed (*6*) to a learning process. The present results suggest this perceptual development may not be related to learning but to intrinsic development in the neurogeometric organization of the direct and compensatory reactions to displaced vision.

Overall, the findings suggest that maturational studies of space-displaced and delayed visual feedback in behavior (*7*) provide a fresh general area of experimental analysis of the development of organized behavior in the child. Interest is now being extended to maturational studies of reading, body-movement control, and to manual operations other than writing and drawing.

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1. Supported by the National Science Foundation and the National Institutes of Health.
2. Because failure was defined as inability to do one of the displacement conditions in the allotted time of the experimental period, the condition of displacement defining failure varied for different subjects.

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6 May 1963

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Stimulus Polarity and Conditioning in Planaria

Abstract. *Orientation in the monopolar pulse field used as the unconditioned stimulus was found to influence formation of a conditioned response to light in planarians. Planarians trained while oriented with the head toward the cathode reached maximal response rates rapidly, while those trained while oriented toward the anode showed no evidence of conditioned response formation.*

Recently it has been demonstrated that planarians can form conditioned responses in a classical light-shock conditioning situation (*1, 2*). These reports have suffered from a lack of precise definition of the physical variables of the experimental procedures, such as light intensity and the parameters of the electrical stimulus used.

It has already been shown (*3*) that light is not a neutral conditioned stimulus (CS) but can act as a weak aversive unconditioned stimulus (UCS), as might be expected from the negatively phototropic habits of planarians (*4*). Fortunately, most publications in this area have described the experimental equipment in sufficient detail to permit ready duplication of the CS.

Since these organisms have long been known to be strongly galvanotropic (*5, 6*), a thorough understanding of the electrical UCS used in conditioning experiments such as those referred to (*1, 2*) seemed equally essential to good experimental design. Unfortunately, these publications listed only the input voltage to the device used (the Harvard Inductorium) and gave indication of neither output voltage, nor, in some cases, the current density.

The purpose of this study was to define the effect of orientation in a monopolar UCS field on acquisition and retention of a conditioned response to light.

Planaria (species *Dugesia tigrina*) (*7*) were maintained in spring water at room temperature in the dark (except during conditioning trials) and were used within 7 days of receipt from the supplier.

The test apparatus and procedure was modified from that described by McConnell, Cornwall, and Clay (*8*). The trough was 30 cm long and was filled with spring water to give a right-triangular cross-sectional area of approximately 0.5 cm^2. Average level of illumination of the trough between trials was 0.17 ft-ca (about 1.87 lu/m^2) from an indirect 80-watt fluorescent unit 15 ft (about 4.57 m) away. The CS was provided by two 100-watt bulbs centered 6 inches (about 15.24 cm) over the trough, which produced an illumination of 1300 ft-ca (about 14,000 lu/m^2) during each trial.

A study of the waveforms produced by a Harvard Inductorium as used in previous studies (*1–3*) to provide the UCS showed that no control of pulse shape or frequency was possible and only poor control of stimulus intensity could be achieved, rendering accurate calculation of the stimulus current impossible (Fig. 1*A*). Therefore, a Grass stimulator, model S4, was used to produce a UCS of the following characteristics: frequency, 100 square waves per second; pulse width, 5 msec; and intensity, 25 volts. Silver alloy electrodes were used. The stimulus field measured in the trough was a true square wave with a voltage gradient of 833 mv/cm and a field strength of 0.57 ma/cm^2 (Fig. 1*B*). The direction of the field could be reversed by means of the polarity switch of the stimulator.

Subjects were studied individually. Trials were given only when subjects were gliding in a straight line toward either of the electrodes. Each trial was of 3 seconds' duration, manually controlled. For the first 2 seconds the light (CS) alone was present, and during the third second both the CS and the UCS (shock) were given. A minimum of 1 minute was allowed to pass between trials, and 25 trials, constituting one set and lasting an average of 35 minutes, were given per day. The UCS consistently evoked a longitudinal contraction of the animal. Stopping, turning the head at least 45° to the side, or longitudinal contraction occurring during the initial 2-second period of CS presentation was counted as a positive response. Since the experimenter had to administer UCS of the proper polarity to each subject, trials were not run in "blind" fashion.

The subjects were divided randomly into seven groups of five each. Several groups were crossed-over (orientation during UCS was reversed) after the sixth set (Table 1). A UCS sensitization control group (UCS presented without CS) was not included, since the pertinent experimental hazard has been fairly clearly eliminated by Thompson and McConnell (*1*). Groups analogous to C and D with anodal UCS crossed over to no UCS were also omitted because no significant difference in response was observed between these two situations (compare groups B, D, and F, set 6).

A plot of the average number of responses per subject in each set of trials (Fig. 2) showed rapid divergence of several of the groups. Because of these almost qualitative differences, the quantitative measure of "trials-to-criterion" was not applied. Statistical evaluation (Student's *t*-test) confirmed the development of statistically distinct populations at the end of the first group of sets (set 6) and at the end of the second group (set 9) as indicated in Table 1.

Table 1. Experimental design and results. (S.E. = standard error.)

Item	Group						
	A	B	C	D	E	F	G
Orientation during sets 1–6, head toward:	Cathode	Anode	Cathode	0 (no UCS)	Cathode	Anode	Alternating
Score*, set 6	22.2	3.8	21.5	3.0	22.4	3.3	5.0
S.E.	0.4	0.8	1.5	0.4	0.6	1.0	0.6
Statistical population,† set 6	I	II	I	II	I	II	II
Orientation during sets 7–9, head toward:	Cathode	Anode	0 (no UCS)	Cathode	Anode	Cathode	Alternating
Score*, set 9	23.2	3.0	6.8	14.7	4.1	19.0	3.0
S.E.	0.6	0.6	0.8	1.2	1.2	0.4	0.6
Statistical population,† set 9	I	II	III	IV	II	V	II

* Score: average number of conditioned responses per set of 25 trials. † Groups were considered to belong to different statistical populations (different Roman numerals) if $p < 0.01$, by Student's *t*-test.

It is apparent from these results that the rate of conditioning in the situation described was strongly influenced by the orientation of the subjects in a monopolar UCS field. It should be emphasized that the UCS intensity used was just sufficient to produce a brisk unconditioned response (UCR) whether orientation was toward the anode or toward the cathode. It was observed that larger specimens have lower thresholds than smaller ones. We have not yet determined whether it is possible by much more extensive training to demonstrate conditioning with anodal UCS. Extinction occurred as expected after cessation of cathodal UCS application (group C) but was also noted after cross-over to anodal UCS (group E), suggesting that anodal stimulation could neither produce nor maintain the conditioned response. On the other hand, anodal UCS could not be considered equivalent to "no UCS" since cathodal UCS after six sets of anodal UCS (group F) resulted in significantly faster conditioning ($p <$ 0.01) than after six sets of no UCS (group D). This would suggest that anodal stimulation sensitized the subjects to subsequent cathodal stimulation. However, when anodal and cathodal trials were alternated during each set (group G) no conditioning was demonstrable, which suggests that in these circumstances the anodal trials actively

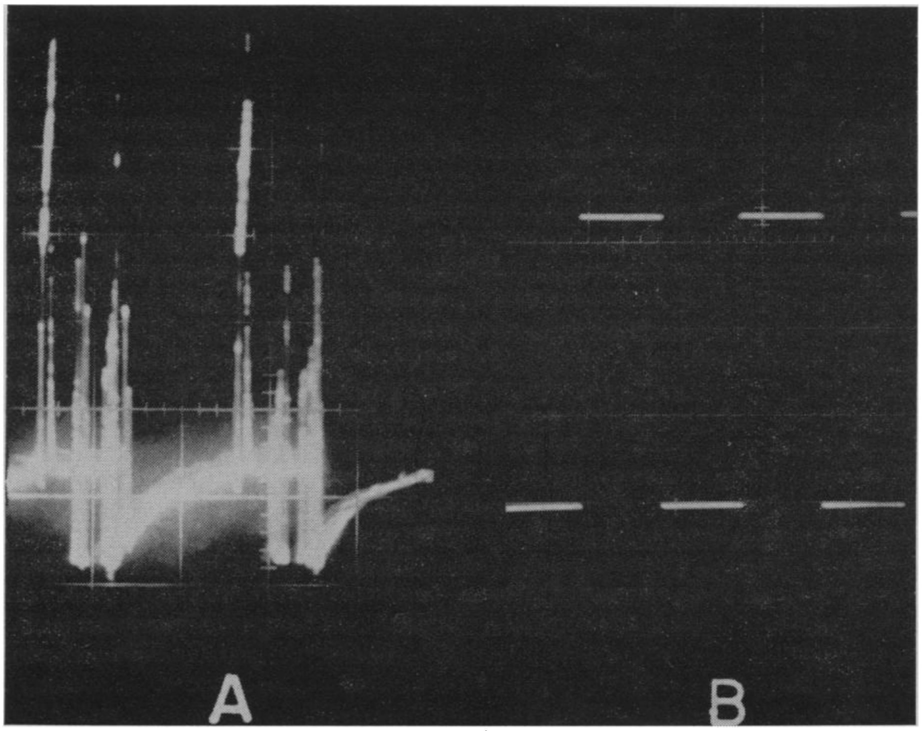

Fig. 1. The wave forms produced by (*A*) Harvard inductorium with an input of 6 volts, and (*B*) Grass model S4 stimulator at 100 cy/sec with 5 msec duration and 25-volt output; measured by electrodes 1 cm apart at the center of the trough.

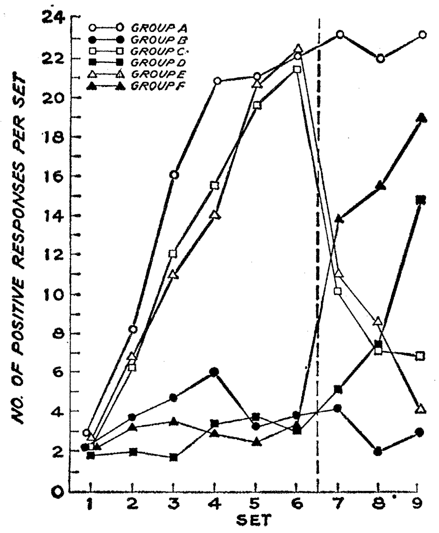

Fig. 2. The mean of each group per set on consecutive days for a total of 225 trials. The series for each group was divided into the first six sets (150 trials) and the last three sets (75 trials) according to the subject's orientation during the UCS. Group A, cathodal-cathodal; group B, anodal-anodal; group C, cathodal-no UCS; group D, no UCS-cathodal; group E, cathodal-anodal; and group F, anodal-cathodal.

inhibited conditioning. Further analysis of the effects of anodal UCS and its interaction with cathodal conditioning is needed.

No specific mechanism for the dependence of conditioning rate on orientation in the UCS field can be proved at this time, but several alternatives can be considered. Viaud (*6*) has shown that the stimulus threshold to an electrical field depends on the orientation in the field and that the planarian is, in fact, more "sensitive" in cathodal orientation than in anodal orientation. Viaud also confirmed the earlier evidence (*5*) that planarians always migrate toward the cathode and showed that this applies to segments as well as to the intact animal. Halas *et al.* (*9*) have recently shown that more shocks of presumably aversive intensity are required to cause a planarian to reverse his direction of travel when moving toward a cathode than when moving away from the cathode. These results may be a reflection of the galvanotropism of planarians. However, neither galvanotropism nor a difference in sensory threshold can explain our results, since the conditioned response achieved was cessation of motion toward and active turning away from the cathode. A related explanation, that the planarian "perceives" anodal and cathodal UCS as qualitatively different stimuli, appears doubtful in view of the active interference between the two types of UCS in the alternated group (group G). Furthermore, at the stimulus intensity used, all subjects showed a distinct UCR, regardless of orientation in the field. Nevertheless, this hypothesis deserves further study, since the planarian UCR consistently begins with a withdrawal of the end of the body nearest the anode (*6*, and our own observations); conversely, according to the reports of human subjects partially immersed in water (*10*), a shock is always felt in the portion of the body nearest the cathode, regardless of orientation. The recent paper of Shafer and Corman (*11*) adds further support to previous observations of differential sensitivity and motor responses to direct current depending on orientation, and emphasizes the importance of stimulus intensity.

Another explanation is that the formation of the physical correlate(s) of the conditioned response is directly affected by the polarity of the electrical UCS. There is ample direct evidence that d-c fields applied directly to the central nervous system of higher animals have a very strong influence on conditioning (*12*). It would be of considerable interest to know whether a pulsed or constant d-c field could influence the rate of learning of an operant response by planarians (*13*; *14*).

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Cerebral Cortex: A Sensorimotor Amalgam in the Marsupialia

Abstract. ***In the cerebral cortex of the opossum and the wallaby there is a complete and coincident overlap of the sensory and the motor representations of the body. Within this sensorimotor area it is not possible to draw the line which in other mammals separates a primarily sensory area from a primarily motor area.***

Since Sherrington and Grünbaum (*1*) demonstrated in anthropoid apes that the central fissure demarcates the "precentral" motor area which lies in front of it, and since Cushing (*2*) demonstrated in humans that a "postcentral" sensory area lies behind it, it has been possible to establish a dividing line homologous with the central fissure in all mammals investigated. This dividing line was confirmed when it became possible with electrical recording techniques to map in detail the sensory areas in animals; Woolsey (*3*) then showed that organization within the sensory area behind was a mirror image of that within the motor area in front. Although movements have been elicited on stimulation of the "sensory" area and tactile impulses have been recorded from the "motor" area, the existence of two spatially separate areas, each with a pre-eminent function, is not challenged.

These facts of organization of the sensory and motor areas of the cortex were established entirely in placental mammals. That the mode of cortical representation is different in marsupial mammals was shown by a recent study in our laboratory (*4*) of the details of cortical localization in 40 opossums (*Didelphis virginiana*). It was found that a single area contained both the sensory and the motor representations of the various body parts, and that this area was not divisible into a more sensory portion and a more motor portion as in previously studied mammals.

Systematic exploration of the cortex was made with points of observation 2 mm apart. Motor systems were studied by stimulation with bipolar electrodes using 60-cycle current. Successive stimuli at 2-minute intervals were given with increasing milliamperage until a threshold movement was obtained. Sensory systems were investigated with the evoked potential tech-