

on the night of 5 July when the minimum air temperature was 3°C. This was not preceded by inclement weather that would have confined the hen to her nest. However, the synthetic egg and recorder had been installed in the afternoon of the previous day, just after the first egg hatched. Possibly because of the disturbance, the frequency of nest departures for the remainder of the day was 22 percent less than for the same time period the following day, not followed by torpor. Thus a similar pattern of reduction of foraging can be suggested as the cause for resorting to hypothermia. Both chicks from this nest fledged normally. When the local nectar supply was declining at the end of the season, hypothermia occurred twice in a fourth nest (containing chicks), as indicated by the same temperature patterns as those in Fig. 1, a and c.

The pattern of these first observations of hypothermia during nesting and the correlations with reduced opportunity for feeding suggest that the duration of the hypothermia is consistent with the relation between food intake and duration of torpor observed for rodents in the laboratory (15). Because arousal and reattainment of normal body temperature appears to be timed for a first-light search for more food, it must be the onset of torpor that is geared to the extent of depletion of energy reserves, an interaction between "biological clock" and "biological fuel gauge."

Tiny hummingbirds, nesting in the chilling nocturnal climate of the Rocky Mountains, are succeeding in near-marginal energetic conditions. A reduction in feeding opportunity by inclement weather or by demands of nest protection may lead to an energy crisis. Unlike man, the nesting hummingbird reduced the rate of depletion of energy reserves, rather than crying for "more!"

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Nonvisual Photoc Responsiveness in Newly Hatched Pigeons (*Columba livia*)

Abstract. Overt behavioral arousal was elicited by light stimulation in pigeon hatchlings. The sensitivity is not mediated via the retina or by direct stimulation of the brain, but rather it is most likely a dermal sensitivity.

The effects of unconventionally mediated sensory stimulation upon the behavior of organisms have always been as interesting as they are mystifying. There have been several reports in the literature of extraretinally mediated effects of light on avian circadian and reproductive cycles, for example, *Zugunruhe*, fat deposition, and testicular growth (1). These effects of light stimulation on behavior are of a relatively long latency and lack a direct indicator of the relation between the stimulus and immediate behavior. More direct effects on behavior have been observed in studies with chick embryos in which light stimulation alters the motility patterns (for example, number of movements and temporal distribution of activity) of 4- to 9-day-old embryos (2). This early sensitivity occurs prior to any evidence of visual function (3).

In the course of our investigation of the onset of visual function in the altricial pigeon embryo, as indicated by the pupillary reflex (4), we discovered a nonvisually mediated response to light stimulation in newly hatched pigeons. We were attempting to devise an overt behavioral measure of visual responsiveness (in order to amplify our earlier findings), and intermittently presented hatchling pigeons with 5 seconds of light stimulation. The characteristic response we observed consisted of a squab raising its head and vigorously wagging it from side to side. Often these movements would be accompanied by wing fluttering and leg extensions,

which resulted in raising the body from the substrate. On occasion we also noted vocalization. This entire behavioral pattern is similar to the normal feeding pattern of newly hatched doves and pigeons (5). The pattern can also be elicited by gentle bilateral tactile stimulation of the bill (6), which is roughly analogous to the procedure employed by the parent pigeon.

As a routine control procedure for possible nonretinally mediated photic sensitivity, we covered the eyes of the hatchlings to make certain that the behavioral responses we were observing were in fact visual. Under these conditions, with the eyes covered, the squabs continued to respond to the light onset, and we began to investigate the actual nature of this curious and unexpected responsiveness.

For this purpose, fertile pigeon eggs were incubated in a forced draft incubator at 37.5°C and 60 to 70 percent relative humidity. They were turned automatically eight times daily. Within 6 to 24 hours after hatching, the birds were observed individually in a Plexiglas observation box (temperature and humidity controlled as above). The hatchling was placed in a small plastic container (6.5 by 6.5 cm) located 20.0 cm directly below the stimulus light (500-watt photoflood lamp, General Electric No. EBV2). Two glass heat filters and a petri dish filled with a saturated copper sulfate solution, acting as a further heat filter, were positioned between the Plexiglas and the lamp. The temperature in the plane of the

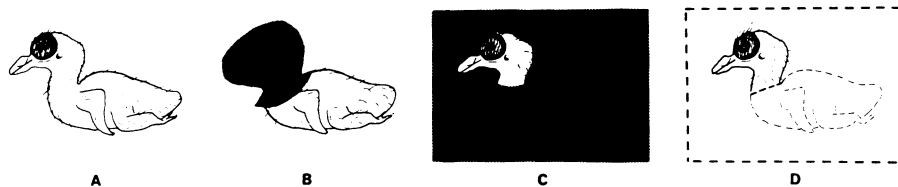


Fig. 1. Schematic representation of the four experimental conditions: (A) no hood, (B) hood, (C) opaque cape, and (D) clear cape.

hatchling did not vary more than 0.14°C during the entirety of each 5-second light stimulation. The intensity of the stimulus light with the three heat filters in place, measured at the point at which the hatchling was placed, was 2.4 mw/cm^2 and 0.39 ma (as measured, respectively, by a Yellow Springs Instrument model 65 radiometer and a photoelectric cell connected across a Simpson model 260-6 VOM meter). A piece of opaque cardboard was used as a peripheral shield around the heat filters on the top of the observation box, so that all of the stimulus light impinging on the pigeon passed through the filters. Background illumination during no-stimulation trials was 0.55 mw/cm^2 and 0.08 ma , measured as above.

Four test conditions were employed to elucidate the locus of responsivity to light:

1) No-hood: Entire body of hatchling was exposed to stimulation (Fig. 1A).

2) Hood: Head of hatchling placed in a hood made of black corduroy material through which no measurable light was transmitted. This condition controlled for retinal sensitivity (Fig. 1B).

3) Opaque cape: Entire body *except* the head was covered with the black opaque material. This controlled for dermal sensitivity (Fig. 1C).

4) Clear cape: Entire body *except* the head was covered with a clear sheet of plastic film. This controlled for a possible restraining effect of the opaque cape (Fig. 1D).

Each experimental condition was presented in a series of ten trials in the following sequence: ten stimulations, ten no-stimulations, ten stimulations (five trials were given for the no-hood condition). Since the response also occurs spontaneously in the absence of any specifiable stimulus and since light stimulation enhances its rate of occurrence, the latency of response from an arbitrary time zero was chosen as the dependent variable. Stimulation was presented for 5 seconds every 30 seconds and a timer was simultaneously

activated by the observer at the onset of either a stimulus or no-stimulus period. The timer was deactivated at the onset of a response, thus providing a response latency. If the bird did not respond within 15 seconds, it was scored as no response.

The no-hood condition was always presented first, followed by a random presentation of the other three conditions to each subject. When a bird failed to be clearly responsive in the no-hood condition, it was excluded from further analysis (only 7 out of a total of 80, or 8.75 percent, of the birds examined were discarded).

Light stimulation elicited a rate of overt behavioral responsiveness with a latency two to three times as fast as the normal (nonstimulated) rate of activity whether the head of the hatchling was hooded or not ($P = .01$, Wilcoxon test), as seen in Fig. 2. When only the head and upper neck were stimulated (opaque cape) there were no differences in onset of activity between stimulation and no-stimulation trials (Fig. 2). The response was reinstated in the clear cape condition, indicating that the effect found in the opaque cape test was not due to a restraining factor ($P = .01$) (Fig. 2). The possibility of

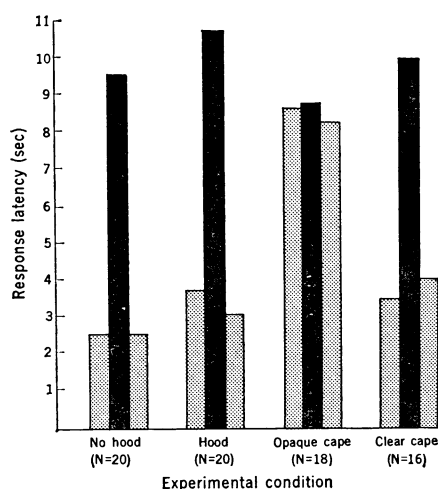


Fig. 2. Latency of response to photic stimulation in the four experimental conditions (stippled area, stimulation; dark gray area, no stimulation).

temperature change due to stimulation as a contributing factor is ruled out by the clear demonstration of a lack of responsiveness in the opaque cape condition. In addition, the response latencies were always faster than the maximal rise time for the temperature change (7).

The no-stimulation trials for all conditions did not differ significantly, demonstrating that the experimental treatments per se did not affect baseline activity rates. Except in the hood condition ($P = .05$), the first and second stimulation series did not differ significantly. It is possible that the shorter latency in the second stimulus period of the hood condition was an experimenter artifact, since identification of response onset was sometimes difficult when the hood covered the head, and perhaps became progressively easier in viewing a given bird. In addition, this difference may also indicate a possible summation effect of light and tactile stimulation. Tactile stimulation of the bill elicits a response almost identical in form to that elicited by light stimulation and would probably be increased in the hooded condition.

It is clear from these findings that newly hatched pigeons are sensitive and reactive to light, a sensitivity not dependent upon retinal or direct brain mediation. Rather, some form of dermal mechanism appears to account for this phenomenon. Electrophysiological and behavioral evidence of dermal light sensitivity has been described in invertebrates and tadpoles (8). Electrical responses have been recorded in the skin of frogs, guinea pigs, rats, axolotls, and black mollies (9). The exact locus and identification of the dermal sense organs and neural mechanisms involved in the nonvisual light responsiveness in pigeons await further investigation.

Although the biological significance of this nonvisual photic sensitivity in pigeons is presently not known, it is interesting that the intensity of light stimulation utilized in our experiments is *lower* than the intensity of sunlight which can penetrate an intact shell (2.4 mw/cm^2 or 0.39 ma stimulus light versus 3.7 mw/cm^2 or 3.8 ma sunlight through shell, as measured above). This suggests a potential source of prenatal sensory stimulation which could affect embryonic development (10). We are currently engaged in evaluating the embryonic behavioral response to light stimulation and have been able so far to trace responsiveness back as early as 11 days of incubation, or only 61

percent of the total incubation period. By contrast, the earliest measured retinally mediated response (the pupillary reflex) does not occur until day 15 (4).

A potential postnatal function of such sensitivity, if it is in fact maintained into adulthood, could be involved in the homing ability of pigeons. We are presently engaged in determining how widespread this form of photic sensitivity is in birds, but have thus far clearly demonstrated it only in the pigeon (11). Perhaps such a nonvisually mediated photic sensitivity aids in the orientation to the home loft. Experiments in which adult pigeons still return to the loft area when their visual input has been interfered with might be partially accounted for by this mechanism (12).

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Prism Adaptation: Control of Intermanual Transfer by Distribution of Practice

Abstract. Correction of errors in localizing movements produced by laterally displacing vision by means of wedge prisms has been termed "prism adaptation." Intermanual transfer of prism adaptation from an exposed to an unexposed hand, with subject's head immobilized, has been reported not to occur. However, it was found that a standard learning variable, distribution of practice, controls the occurrence or nonoccurrence of transfer. When practice is massed, there is no transfer of adaptation; when it is spaced, the transfer is extensive. Spacing of practice also influences the amount of aftereffect displayed by the exposed hand.

When wedge prisms are placed before the eyes, vision is displaced in the direction of the apex of the prisms. As a result, visually guided movements deviate at first to that same side. Under suitable conditions, the initial mislocalization can be corrected; this is termed "prism adaptation." When the prisms are then removed, this correction in orientation (now inappropriate) persists for a time, leading to errors in the opposite direction. The latter has been termed "prism aftereffect."

It has been reported that prism adaptation does not transfer from an exposed arm to an unexposed arm if the head is immobilized during the prism-exposure period (1-5). In contrast, several other studies have indicated that intermanual transfer can take place in the absence of head movement (6-10). An analysis of adaptation to sensory rearrangement in terms of a learning approach (11) allows us to account for this discrepancy.

In all experiments in which intermanual transfer has unambiguously occurred, a prism-exposure condition involving "terminal display" was employed; that is, the subject first pointed at a visual target with an unseen arm and was then allowed to view the terminal position of his responding finger in relation to the target. On the other hand, in the experiments of Hamilton (2) and of Mikaelian (4, 5), in which intermanual transfer with head immobilized was not observed, the prism-exposure period involved "continuous display," in which (i) the subject was provided with continuous view of self-produced hand movements and (ii) there were no targets to be pointed at; that is, the subject had no tasks other than to view his hand moving back and forth within a structureless visual field.

A number of explanations have been advanced for the disparity in results between the two sets of conditions, but none have been able to account ade-

quately for all of the data (12). However, analysis of the two experimental designs within a learning context reveals that continuous display could be considered a type of massed-practice procedure. That is, the subject continually views his moving hand and is therefore being continuously trained. In contrast, the terminal-display procedure is, by definition, a spaced-practice procedure; that is, the hand is not always in view and, thus, training is not continuous.

If this difference in distribution of practice were responsible for the two conflicting sets of data, it follows that it should be possible to obtain intermanual transfer with a continuous-display procedure by introducing rest or blackout periods between periods of training, thereby spacing the practice. We report here confirmatory evidence.

The procedure involved measurement of the accuracy of pointing at visual-target positions with unaided vision before and after viewing self-produced, continuous movements of a hand through a 20-diopter prism which displaced vision 11.3° laterally. The hand could be seen only during the prism-exposure period and not when accuracy of pointing was tested. Half of the subjects (the nontransfer groups) were tested with the same hand that had been viewed through the prism, while the remaining subjects (the transfer groups) were tested with the unexposed hand. All testing and viewing were with the right eye (left eye occluded) and with the head stabilized by a biteboard. The deviation from baseline pointing values after prism removal provided a measure of the prism aftereffect.

Subjects (96 female undergraduates) were given one of three treatments during the exposure period. The first treatment consisted of spaced practice in contrast to the massed practice employed in previous continuous-display