BEHAVIORAL STUDIES ON LEARNING AND INTEROCULAR TRANSFER IN THE DOMESTIC CHICK

Thesis by

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ABSTRACT

Acquisition and interocular transfer of two kinds of visual learning, a pattern discrimination task and an illness-induced aversion to a colored food, were studied in young domestic chicks.

The experiment reported in Chapter I was designed to assess interocular transfer of a monocularly acquired operant pattern discrimination task reinforced by heat, and to determine whether the extent of transfer might vary with age and possible maturation of participiating interhemispheric connections. The results demonstrated that pattern discrimination learning failed to transfer from trained to untrained eye in intact chicks up to 16 days post-hatch, indicating that the monocular learning was stored in the form of a unilateral engram which was not available to the untrained hemisphere. This finding illustrates the extent to which the two halves of the chick brain are separately organized and able to function independently under certain conditions.

The series of experiments reported in Chapters II, III, and IV examined acquisition and interocular/interhemispheric transfer of a conditioned aversion to a colored food. It was found that 10-day-old chicks learned to avoid drinking a novel colored sucrose solution if their first experience with it was followed by illness induced by intraperitoneal injection of LiCl. Non-illness control subjects did not show an aversion. When novel taste and color were both present, the aversion was based on the visual (color) cue and not on taste. When color was eliminated, so that taste was the only novel cue available, then conditioning failed. Interocular transfer of this learning was evaluated by conditioning chicks with one eye closed and testing for an aversion to the colored sucrose with either the trained or the untrained eye open. The results showed that chicks avoided drinking the colored sucrose regardless of which eye was open during testing, indicating good interocular transfer of the monocularly acquired aversion.

To investigate further the roles of visual and gustatory cues in acquisition and transfer of the conditioned aversion, chicks were trained monocularly with novel color combined with either novel or familiar sucrose taste. They were then tested, with either the trained or the untrained eye open, for learned aversions to colored or uncolored sucrose. Chicks tested with the trained eye showed an aversion to the colored, but not the uncolored, liquid regardless of whether the taste was novel or familiar during training. This result confirmed that the aversion was mediated by the visual (color) cue and demonstrated that novel taste was not required for acquisition of the visual aversion. In contrast, chicks tested with the untrained eye open showed an aversion to either colored or uncolored sucrose, but in each case only if the taste was novel during training. The avoidance of uncolored sucrose was clearly a taste aversion acquired only by the so-called "untrained" hemisphere which was deprived of primary visual input during the training session. These findings demonstrated that interocular/interhemispheric transfer of the visual aversion failed in chicks trained with familiar taste; they did not, however, rule out the occurrence of transfer when novel taste was present.

Taken together, the results of this series of experiments on conditioned food aversions in chicks indicate that, while the visual system was normally dominant, eliminating primary visual input to half the brain somehow enhanced the effective significance of taste information and enabled that hemisphere to associate novel taste with the subsequent illness experience. It seems, then, that under certain conditions the two halves of the chick brain are capable of independent and concurrent avoidance learning based on different types of sensory information.

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GENERAL INTRODUCTION

In recent years, there has been accumulating evidence of numerous anatomical and functional homologies between avian and mammalian brains (Karten, 1969; Nauta & Karten, 1970). These findings suggest that analysis of central processes in birds may be a strategic approach to understanding brain function in mammals. Because of the nature of the avian visual system, birds are especially useful for studying issues related to interhemispheric transfer of information. In birds, unlike mammals, the retinal fibers from each eye cross at the optic chiasm[1] and synapse in the contralateral tectum or thalamus (Cowan, Adamson, & Powell, 1961; Cuénod, 1974; Meier, Mihailovic, & Cuénod, 1974). Since primary visual input can therefore be restricted to one hemisphere by covering one eye, and without cutting the chiasm, training a visual task through one eye and testing for retention through the other reveals the extent of interhemispheric transfer of information in intact birds.

The extensive interhemispheric fiber connections of mammals such as cats and monkeys permit essentially complete interocular transfer of learning even when primary visual input is lateralized to one hemisphere by section of the optic chiasm (for review, see Hamilton, 1980). While birds do not have a massive forebrain commissure comparable to the mammalian corpus callosum, several small fiber systems (most notably the tectal, anterior, and posterior commissures and the supraoptic decussation) interconnect the avian hemispheres at various levels and provide an anatomical substrate for transfer of information between the two half-brains (Cuénod, 1974).

Investigators using monocular training and testing procedures with intact birds have reported a variety of results ranging from good transfer to none at all (for reviews, see Cuénod, 1974; Zeier, 1975; Goodale & Graves, 1980). These findings have led to attempts to specify the factors which determine interocular, and by inference interhemispheric, transfer. Fairly substantial evidence indicates that transfer in birds depends at least partly on the portion of the visual field exposed to relevant stimuli (Levine, 1945a, 1945b, 1952; Goodale & Graves, 1980). Other proposed determinants of transfer, all of which are based on reasonable but limited data, include the type of response required and whether it is consistent with or counter to innate response tendencies (Zeier, 1970; Demarest, Brecha, & Bronstein, 1977); the type of reinforcement, including whether it is unilateral or bilateral (Stevens & Klopfer, 1977); the amount of training, strength of learning, previous experience, motivational and attentional factors; the extent of interhemispheric fiber connections of particular brain areas involved in different types of learning (Benowitz, 1974); and whether monocular training results in unilateral or bilateral engram formation (Benowitz, 1974).

In adult birds, primarily pigeons, operant discrimination tasks (color, brightness, movement, and pattern) generally show good interocular transfer, with a few notable exceptions apparently related to the portion of the visual field used to view the stimuli or to the position of the stimuli relative to the bird's open eye (see Cuénod, 1974; Goodale & Graves, 1980). Transfer is also found for conditioned withdrawal from a visual stimulus when the reinforcement is painful shock, but the same task fails to transfer when the noxious stimulus is auditory or visual; monocular extinction shows no transfer for any of these three cases (Stevens & Klopfer, 1977). Recent evidence indicates that interocular transfer of a color discrimination is inhibited in pigeons when conflicting information is presented to the two eyes simultaneously (Palmers & Zeier, 1974), whereas complementary pieces of information presented to each eye separately can be integrated in order to solve a discrimination problem (Graf & Zeier, 1979). The supraoptic decussation, an interhemispheric fiber system which projects from the dorsal thalamus to the contralateral Wülst of the telecephalon, is required for transfer of at least appetitive color and pattern discrimination learning in pigeons (Cuénod, 1974).

In the last decade, an increasing number of investigators interested in interocular/interhemispheric transfer in birds have been using young domestic chicks as experimental subjects. The use of domestic chicks for behavioral studies of brain function has a number of theoretical and practical advantages. These advantages derive from the fact that chicks are small precocial birds which from the time of hatching are capable of an impressive amount of learning and a wide variety of well-organized behaviors. As a result, large numbers of newly-hatched chicks can be tested with a limited commitment of time, money, and laboratory space. Furthermore, it is easy to control chicks' early experience (even pre-hatch, if desired) and therefore to study innate behaviors and developmental trends. The reported work on interhemispheric transfer in chicks has focused primarily on three questions: What types of visual information transfer? What interhemispheric fiber connections are involved when transfer occurs? Does interocular transfer reflect formation of bilateral engrams during monocular training, or does it result from interhemispheric readout of a unilateral engram during testing? The data relevant to these issues are limited and to some extent contradictory.

The types of learning reported to show interocular transfer in chicks include a passive avoidance task (Cherkin, 1970), an object discrimination (Bondy & Harrington, 1978), a colored food discrimination (O'Connell, 1978), and sometimes imprinting (Horn, Rose, & Bateson, 1973). Failure of transfer has been reported for extinction of the passive avoidance habit (Benowitz, 1974), for habituation to the "deep" side of a visual cliff (Zeier, 1970), and sometimes for imprinting (Bell & Ehrlich, 1979). The supraoptic decussation is apparently necessary for transfer of the passive avoidance learning (Bell & Ehrlich, 1979), imprinting (Horn, Rose, & Bateson, 1973), and colored food discrimination (O'Connell, 1978) in chicks.

Since interocular transfer fails on occasion in intact chicks as well as other birds, it seems that monocular training sometimes produces a unilateral engram which is confined to the hemisphere contralateral to the trained eye. There is also some evidence that interocular transfer in chicks is accomplished by the untrained hemisphere tapping a unilateral engram in the trained hemisphere. For example, transfer of passive avoidance learning is eliminated if a memory-disrupting drug is injected into the trained hemisphere (Bell & Gibbs, 1977) or if the supraoptic decussation is cut after monocular training (Bell & Ehrlich, 1979). In contrast, good interocular transfer of passive avoidance has been found after large lesions of the trained hemisphere (Greif, 1976), and cutting the supraoptic decussation after monocular training does not impair transfer of a colored food discrimination (O'Connell, 1978). These latter findings support the view that interocular transfer occurs because bilateral engrams are formed as a consequence of monocular training. In mammals, as well, the issue of unilateral versus bilateral memory formation has been controversial. Experiments with chiasm-sectioned cats and monkeys have produced conflicting results which have been variously interpreted as evidence for unilateral engrams or for duplicate bilateral engrams (see Cuénod, 1972). Recent findings, however, seem to resolve the controversy and indicate that bilateral memory formation is the usual case, with the secondary engram in the "untrained" hemisphere often somewhat weaker than that in the trained hemisphere (Hamilton, 1977).

There are additional issues related to interocular/interhemispheric transfer which could profitably be investigated using the chick model, but on which there are little or no reported data. These include questions about how the extent of transfer may vary with post-hatch development or with experience; how transfer is influenced by changes in such variables as arousal, motivation, amount, type or schedule of reinforcement, and response requirements; and the extent to which the two half-brains are separately organized and capable of independent function.

In the work reported here, the chick model has been used to study acquisition and interocular transfer of two kinds of visual learning, a pattern discrimination task and an illness-induced aversion to a colored food. Good interocular transfer of simultaneous pattern discriminations is found in adult pigeons key-pecking for food (e.g., Cuénod, 1974; Green, Brecha, & Gazzaniga, 1978). While it is difficult to use food as a reinforcer for newly-hatched chicks, they will learn a pattern discrimination if pecking the correct key produces heat reward (Lee-Teng & Butler, 1971). The experiment reported in Chapter I was designed to assess interocular transfer of an operant pattern discrimination task reinforced by heat, and to determine whether the extent of transfer might vary with age. The purpose here was, first, to discover whether pattern discrimination learning, which is known to transfer in adult pigeons, should be included in a list of visual learning tasks which transfer in newly-hatched chicks. If the results were to demonstrate interocular transfer, further experiments would be required in order to identify the fiber connections involved and to distinguish between bilateral engram formation and interhemispheric tapping of a unilateral engram as the mechanism of transfer. Results indicating failure of interocular transfer, on the other hand, would strongly suggest the formation of a unilateral engram which was not accessible to the untrained hemisphere. Chicks of three different age groups were studied to evaluate the possibility that capacity for interhemispheric/interocular transfer develops post hatch with increasing visual experience and/or with progressive maturation of participating interhemispheric connections.

The subsequent chapters contain a series of investigations on acquisition and interocular/interhemispheric transfer of a conditioned aversion to a colored food. Much of the recently reported work on learning, memory, and interocular transfer in chicks has involved a one-trial passive avoidance task requiring day-old chicks to inhibit an innate tendency to peck at a shiny metal lure which is coated with an unpleasant tasting liquid (see Cherkin & Lee-Teng, 1965; Lee-Teng & Sherman, 1966). The present purpose was to address these issues from the perspective of a different, and perhaps more "prepared", type of avoidance learning. It has been shown repeatedly that animals learn to avoid a novel food if they become sick after sampling it for the first time (Garcia, Ervin, & Koelling, 1966; Kimeldorf & Hunt, 1965). This phenomenon is variously referred to as a conditioned aversion, an illness-induced aversion, or experimental baitshyness. Some of its characteristics have suggested that animals are especially prepared for this adaptive kind of learning (e.g., see Seligman, 1970). For example, a strong aversion is often demonstrated after a single pairing of food and illness, even over an interval of up to several hours (Garcia, Ervin & Koelling, 1966). Further, the type of food-related cues most readily associated with illness depends on the animal studied and whether it normally relies more on taste or on vision in its selection of food (Revusky & Garcia, 1970; Seligman, 1970; Rozin & Kalat, 1971; Garcia, Hankins, & Rusiniak, 1974). Studies with weanling rats (Grote & Brown, 1971) and infant guinea pigs (Kalat, 1975) indicate that, in rodents, this learning ability is mature shortly after birth. These findings support the view (Rozin & Kalat, 1971) that the capacity for illness-based avoidance learning over long delays is an evolutionary specialization which does not depend on "learning to learn".

The series of experiments contained in Chapter II was designed to extend these observations to young precocial birds by determining whether chicks would learn in one trial an illness-induced aversion to a novel liquid and, if so, whether this avoidance learning would be preferentially based on visual or gustatory information. Briefly, the results showed that young chicks did acquire an aversion and that it was mediated by a novel visual cue (color) and not by taste. A subsequent study, reported in Chapter III, evaluated interocular transfer of this special type of visual learning. After monocular training, chicks were found to display a marked aversion whether tested with the trained or the untrained eye open. In light of the evidence from binocularly trained chicks (Chapter II) that the aversion was based on color and not taste, these results indicated good interocular/interhemispheric transfer of the visual learning. It was considered possible, nevertheless, that the presence of novel taste during training might be an important factor in promoting learning and/or interhemispheric transfer. Chapter IV therefore consists of further investigations into the roles of novel visual and gustatory cues in acquisition and transfer of the conditioned aversion.

FOOTNOTE

[1] There is some recent evidence that a small contingent of uncrossed optic nerve fibers projects to the ipsilateral thalamus (Repérant, J., cited in Donovan, W. J., Structure and function of the pigeon visual system, *Physiol. Psychol.* 6, 403-437, 1978).

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Lack of interocular transfer of pattern discrimination learning in chicks*

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Complete optic decussation in birds restricts direct visual input from each eye to the contralateral half-brain[4]. Interocular transfer of visual learning therefore depends on interhemispheric connections. By testing birds for interocular transfer, one can assess the extent to which these fiber cross-connections communicate various kinds of information from one hemisphere to the other. The influence of experiential and developmental factors on this communication can be evaluated by studying subjects under different conditions and at different ages. Good interocular transfer in young birds has been reported for a one-trial passive avoidance task[1,3], a pebble–grain object discrimination[2], a conditioned food aversion[7], and usually imprinting[6,9,12]. In contrast, transfer fails for adaptation to the 'deep' side of a visual cliff[13], extinction of the passive avoidance habit[1], and sometimes imprinting[10]. Lee-Teng and Butler[11] showed that very young domestic chicks could learn a simultaneous pattern discrimination in a situation which entailed key-pecking for heat reward. The present experiment was designed to assess interocular transfer of this pattern discrimination learning in chicks pecking for heat. A second purpose was to determine whether the extent of transfer might vary with age, possibly as a result of progressive maturation of participating interhemispheric fiber systems.

Subjects were 72 White Leghorn cockerels. They were housed individually, with standard chick mash and drinking water freely available. The training apparatus, located in a dimly lit room, was an automated operant chamber with interior dimensions that varied from 6.5 × 11.5 × 17.5 to 13 × 17 × 26.5 cm, depending on the chick's size. The chamber was chilled to approximately 13 °C by a thermostatically controlled refrigeration unit (FTS Systems, Inc., Model SLC-20). Heat reward was provided by a 250 W infrared lamp located 10 cm above the top of the chamber. Stimulus patterns could be back-projected onto either or both of two plastic keys positioned vertically in the center of one wall of the chamber.

Each chick was shaped to peck the stimulus keys. During shaping, both keys were lighted and a peck at either key turned on the overhead heat lamp for 5 sec.

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When the key-peck response was well established, one key was darkened and the chick was required to discriminate between the two keys. A peck at the lighted key produced 5 sec heat (reward); a peck at the dark key resulted in a 5 sec 'time out' in the dark cold chamber (non-reward). The position of the light alternated between top and bottom keys according to a balanced pseudo-random schedule which recycled every 32 responses. When the chick had made at least 36 correct responses in 4 successive blocks of 10 trials on this light/dark discrimination, the pre-training procedure was repeated with each eye occluded in turn. Prior to pre-training, a ring of black Velcro was glued with flexible collodion to the feathers around each of the chick's eyes. Another ring of Velcro was covered with a thick piece of felt and was used as an occluder by pressing it firmly onto the ring around an eye. Chicks with both eyes occluded in this way were shown to be behaviorally blind.

Three groups of 24 chicks were trained at 3–6, 7–10, and 11–16 days of age, respectively. With one eye occluded, a chick was required to discriminate between two simultaneously presented patterns projected on the stimulus keys. A peck at the correct pattern (S^{POS}) produced 5 sec heat reward; a peck at the incorrect pattern (S^{NEG}) produced 5 sec non-reward. The positions of S^{POS} and S^{NEG} were, again, alternated between top and bottom keys according to a balanced pseudo-random schedule which recycled every 32 trials. Discrimination training continued until the chick reached a 90% criterion of at least 36 correct responses in any 4 successive blocks of 10 trials. Animals which failed to reach this criterion within 90 min (about 25%) were eliminated from the experiment. For half the animals in each age group, the positive (negative) stimulus was a cross (+) and the negative (positive) stimulus, a triangle (△). Half of each of these subgroups was trained with the left eye and half with the right. Thirty minutes after the end of the monocular training session, each chick was retrained to the 90% criterion on the pattern discrimination with either the same eye (monocular retention test) or the other eye (interocular transfer test).

Data analyses were performed on initial performance (errors in the first 40 trials), trials to criterion, and errors through criterion for training and testing sessions. In addition, a percentage savings score for each of the above 3 variables was calculated for each chick according to the formula (Training–Testing/Training + Testing) × 100. Since analyses of variance on initial performance, trials, and errors revealed no significant differences during training or testing as a function of which eye was trained first or which pattern was S^{POS}, the data for these conditions were pooled. There were also no significant differences between groups during training on the basis of age or of subsequent eye tested. Analysis of the test data, however, revealed that chicks tested for retention with the trained eye (MR groups) performed significantly better by all measures than those tested for interocular transfer (IOT groups) (Initial Performance: $F = 38.16$, df = 1,66, $P < 0.001$; Trials: $F = 20.16$, df = 1,66, $P < 0.001$; Errors: $F = 24.57$, df = 1,66, $P < 0.001$). There were also significant effects of age (Initial Performance: $F = 3.13$, df = 2,66, $P < 0.05$; Trials: $F = 5.01$, df = 2,66, $P < 0.01$; Errors: $F = 5.69$, df = 2,66, $P < 0.01$), reflecting somewhat poorer test performance of older chicks. There were no significant interactions.

Individual *t*-tests comparing mean percentage savings with zero revealed that the

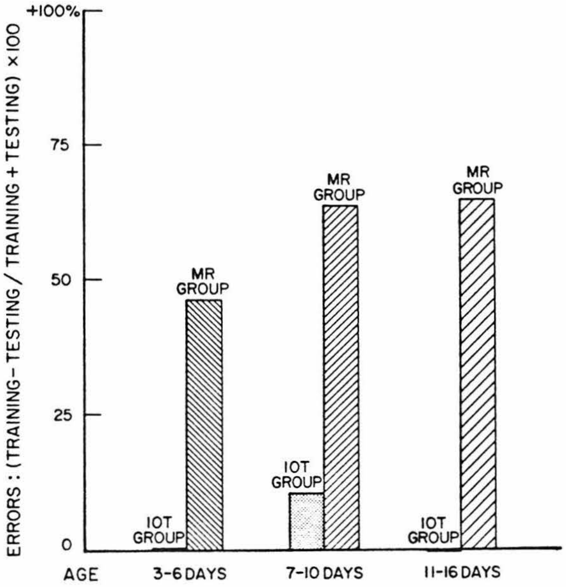

Fig. 1. Mean percentage savings: errors through criterion.

3 IOT groups had no significant savings with the second eye by any measure. In marked contrast, all 3 MR groups had excellent retention of the discrimination with the trained eye, as shown by large and significant percentage savings scores for all measures (Initial Performance: 3–6 days, $t = 2.46$, $df = 11$, $P < 0.05$; 7–10 days, $t = 4.47$, $df = 11$, $P < 0.01$; 11–16 days, $t = 5.57$, $df = 11$, $P < 0.01$; Trials: 3–6 days, $t = 2.51$, $df = 11$, $P < 0.05$; 7–10 days, $t = 6.72$, $df = 11$, $P < 0.01$; 11–16 days, $t = 5.96$, $df = 11$, $P < 0.01$. Errors: 3–6 days, $t = 2.94$, $df = 11$, $P < 0.02$; 7–10 days, $t = 7.17$, $df = 11$, $P < 0.01$; 11–16 days, $t = 7.33$, $df = 11$, $P < 0.01$). Mean percentage savings for errors are shown in Fig. 1.

Two-way analyses of variance on percentage savings scores revealed a significant effect of eye tested for each of the 3 dependent variables (Initial Performance: $F = 14.69$, $df = 1,66$, $P < 0.001$; Trials: $F = 22.10$, $df = 1,66$, $P < 0.001$; Errors: $F = 25.74$, $df = 1,66$, $P < 0.001$), indicating that the MR groups had significantly greater savings than the IOT groups by all measures. There were no significant effects of age on percentage savings and no significant interactions (*F*s all < 1.0).

The results clearly demonstrate that pattern discrimination learning failed to transfer from the trained to the untrained eye in chicks pecking for heat reward. Further there was no evidence that transfer was developing in progressively older chicks up to 16 days post-hatch. These findings indicate that the pattern discrimination learning in one side of the chick brain was not available to the other hemisphere. Similar lack of interocular transfer in normal chicks has been reported for monocular adaptation to a visual cliff[13] and for monocular extinction of a passive avoidance habit[1]. Thus, in the intact avian brain as in the surgically bisected mammalian brain, restricting visual input to one eye may result in learning which remains confined to one hemisphere. Such findings show the extent to which the two sides of the avian brain are separately organized and able to function independently under certain conditions. In contrast to earlier evidence favoring bilateral memory storage in chicks[8], the present results suggest that monocular visual learning can be stored in the form of a unilateral engram which is not retrievable through the untrained hemisphere.

The failure of interocular transfer, even in chicks more than two weeks old, might be viewed as surprising in light of the positive transfer found for many other learning tasks in chicks[1–3,7,9,12] and the good transfer of simultaneous pattern discriminations reported for adult pigeons[5]. Critical systems for mediating interhemispheric transfer of this type of learning may not exist in the chicken brain or may not become functionally mature until some later age. It is also possible, however, that the observed failure of transfer resulted from the nature of the experimental procedure and/or the nature of the task itself, and that the same visual information might show good interocular transfer under different conditions. In this experiment, for example, the chicks had no experience with either monocular training or pattern discrimination learning prior to the single day of training and testing. If, as is possible, birds must 'learn' to transfer the visual information from one hemisphere to the other, these conditions may have deprived them of an adequate opportunity to do so. Alternatively, interocular transfer may be influenced by the nature of the reinforcer or the relationship between response and reinforcer. In the typical interocular transfer experiment with pigeons, key-pecking is reinforced with food. In the present experiment, pecking was rewarded by heat. This may be considered an 'unnatural' association for a chick to learn: pecking is not normally related to keeping warm as it is to obtaining food. Perhaps an animal's capacity for interhemispheric transfer of a particular kind of learning varies directly with the information's adaptive importance to the species.

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An Illness-Induced Conditioned Aversion in Domestic Chicks: One-Trial Learning with a Long Delay of Reinforcement[1]

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Four experiments were run to determine whether 10-day-old domestic chicks would acquire a one-trial illness-induced aversion to the visual and/or taste properties of an unfamiliar liquid. Immediately following a 1-hr exposure to a novel green sucrose solution, experimental subjects were injected with 0.2 *M* LiCl and control animals with normal saline. Results of a two-jar preference test (green sucrose, uncolored water) 24 hr later demonstrated that chicks which drank green sucrose prior to LiCl treatment developed a strong aversion to this solution. Controls displayed no preference. Chicks trained and/or tested without the color cue (uncolored sucrose) failed to show a conditioned taste aversion. These findings indicate that, for chicks, an association between a visual (color) cue and subsequent illness is readily established; a taste–illness association could not be demonstrated. When the sucrose taste cue was eliminated and only the color stimulus was available, LiCl-treated and control animals alike exhibited an apparent aversion to the green water (or preference for uncolored water). Thus, taste properties may account for control subjects' willingness to drink the original green sucrose solution. The long-delay avoidance learning demonstrated by LiCl-treated chicks appears to be mediated by the visual, not the gustatory, cue.

Animals learn to avoid a novel food or liquid if they become ill within several hours after sampling the unfamiliar substance (Garcia *et al.*, 1966). An unusual characteristic of this long-delay conditioned aversion learning is that it may occur after a single experience. Further, it appears to require a special relationship between the food cues and the illness. Illness-induced aversions are most readily acquired when the distinctive stimuli associated with the novel substance are of a type normally used by the species in its identification of food (see Revusky and Garcia, 1970; Seligman, 1970; Rozin and Kalat, 1971; Garcia *et al.*, 1974, for reviews). Rats, which rely mainly on gustatory stimuli for feeding, associate a novel taste with delayed illness but do not easily acquire a food aversion mediated by visual, auditory, or tactual cues (Garcia and Koelling, 1966;

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Garcia *et al.*, 1968). On the other hand, animals which depend on visual cues for food selection rapidly learn an illness-induced aversion to an unfamiliar food or liquid on the basis of its appearance (Brower, 1969; Wilcoxin *et al.*, 1971; Braveman, 1974; Johnson *et al.*, 1975).

Since experimental treatments may readily be introduced during the interval between sampling of the novel food and onset of illness, conditioned food aversion learning provides a unique and useful paradigm for the study of memory formation. Investigators in several laboratories have chosen to study memory in the domestic chick, a precocial bird offering a number of experimental advantages. The organization of the avian brain is less complicated than that of the mammalian brain, and accumulating evidence of anatomical and functional homologies (Karten, 1969; Nauta and Karten, 1970) suggests that analysis of central processes in birds may be a strategic approach to understanding learning and memory in mammals. Most of the chick memory experiments reported previously have employed a one-trial passive avoidance task requiring 1-day-old chicks to inhibit an innate tendency to peck at a shiny metal lure which is coated with an unpleasant tasting liquid (see Cherkin and Lee-Teng, 1965; Lee-Teng and Sherman, 1966).

The investigations reported here were undertaken in an effort to develop an illness-induced aversion paradigm for use in the study of memory in young domestic chicks. It was found that naive 10-day-old chicks acquired a one-trial aversion to a distinctively flavored and colored novel substance when this was paired with delayed illness. Further tests indicated that this learning was supported by visual, but not gustatory, cues.

SUBJECTS AND APPARATUS

Subjects were 245 White Leghorn cockerels[2] obtained when 1 day old from Pacesetter Hatcheries, Cucamonga, California. On the morning of their arrival, the chicks were housed individually, either in 1-gal white cardboard ice cream cartons fitted with wire-mesh lids or in 18-cm^3 white Plexiglas compartments with wire-mesh floors and lids. The chicks remained in these compartments at all times during the course of the experiments, except when hand-held by the experimenter. The room was maintained at 90°F and 45% relative humidity; overhead lighting was on between 8:00 AM and 8:00 PM daily. Standard chick mash and drinking water were available *ad libitum* except as noted. All food, water, and experimental solutions were presented in 56.7-ml clear glass jars, each fitted with a black plastic lid having a 2.54-cm diameter hole in the center. This arrangement made the food and liquids visible and accessible to the chicks, while minimizing spillage.

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[2] 19 chicks died during the course of the experiments; all data for these animals were discarded.

The specific subject groups used in Experiments 1 through 4 below are summarized in Table 1. Experiment 1 investigated illness-induced conditioning of an aversion to a green sucrose solution. In Experiments 2, 3, and 4, the roles of the component taste and color stimuli were evaluated separately.

TABLE 1
Description of Experimental and Control Groups for Experiments 1, 2, 3, and 4

Experiment	Group[a]	*n*	Day 10 solution[b]	Day 11 test solutions
1	E-1	56	GSS	GSS/UW
	C-1	51		
2	E-2	20	USS	USS/UW
	C-2	19		
3	E-3	37	GW	GW/UW
	C-3	23		
4	E-4	10	GSS	(a) USS/GW
	C-4	10		(b) GSS/UW

[a] All E (experimental) groups received LiCl injections, all C (control) groups saline injections.
[b] GSS = green sucrose solution; USS = uncolored sucrose solution; GW = green water; UW = uncolored water.

EXPERIMENT 1

Procedure

One hundred and sixteen chicks were maintained on *ad libitum* food and water for 6 days after their arrival. On Days 7, 8, and 9, the animals were accustomed to the experimental schedule in a series of three adaptation sessions. For each chick, the sessions began at the same time each day (between 10:00 AM and 12:00 PM for all subjects) and consisted of 2 hr of food and water deprivation followed by access to 25 ml of water for 1 hr. At the end of the hour, each animal was hand-held for a few seconds. Food and water were returned 1 hr later.

On Day 10 (Conditioning Day) subjects were randomly assigned to the experimental group (E-1, *n* = 56) or the control group (C-1, *n* = 51). A 2-hr deprivation period began at the same time as on the preceding days and was followed by 1-hr access to 25 ml of an unfamiliar green 15% (w/v) sucrose solution (4 drops of green Schilling vegetable dye per 100 ml of solution).[3] Intake was measured to the nearest 0.2 ml. After this drinking session, the experimental subjects were hand-held and injected i.p. with

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[3] The 15% concentration of sucrose was used because preliminary tests indicated chicks have an approximately equal preference for this solution and for water. Green coloring was selected arbitrarily; in pilot work, similar results were obained using blue or red coloring.

1.0 ml of 0.2 *M* LiCl.[4] Control subjects were given 1.0-ml ip injections of isotonic saline. All injections were given between 3 and 10 min after the drinking session ended. The LiCl treatment reliably produced symptoms of illness (diarrhea, lethargy), which were apparent within 10 to 15 min and generally lasted 40–45 min. Saline injections never caused observable signs of illness. Food and water were returned to all animals 1 hr after the injections.

On Day 11 (Test Day), subjects were deprived of food and water for the same 2-hr period, then given a two-jar preference test consisting of access for 1 hr to 25 ml of the green sucrose solution (GSS) and 25 ml of familiar uncolored water (UW).[5]

Data Analysis

The results were analyzed in several ways. Experimental (LiCl) and Control (saline) Groups were compared on the basis of how much GSS they drank on Day 10 and on Day 11, and on the difference scores between the two days. A Test Day preference score was calculated for each chick,[6] and the preference scores of experimental and control subjects were compared. Amounts of UW intake on Test Day and total liquid consumption during testing were also analyzed for differences between groups. Finally, comparison was made of the number of subjects in each group which preferred GSS to UW (i.e., the amount of GSS consumed was more than half their total intake during testing). All data were discarded for subjects which drank less than 1.0 ml of GSS during the Day 10 conditioning session (11% overall, no significant difference between groups).

Results and Discussion

The results of the two-jar preference test, summarized in Table 2, clearly demonstrate that the experimental group formed an aversion to the green sucrose (88% preferred uncolored water), whereas 57% of the saline-injected controls displayed a preference for the green sucrose (χ^2 (1) = 23.52; $P < 0.001$). The number of control subjects preferring GSS did not differ significantly from chance. One-way analysis of variance on Test Day preference scores revealed that Group E-1 had a reliably lower preference for GSS (mean = −62.04) than Group C-1 (mean = +16.80) (F (1, 94) = 48.6; $P < 0.01$). A days × drugs analysis on amount of GSS consumed showed significant main effects of days (F (1, 95) = 29.94; $P <$ 0.01) and drugs (F (1, 95) = 4.92; $P < 0.05$) and a significant interaction (F

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[4] In pilot studies, various doses of LiCl were used; 1.0 ml of 0.2 *M* LiCl was found to be the most reliable dose, in terms of consistently producing nonfatal illness.

[5] Pilot work had indicated that shorter drinking sessions (30 min) or one-jar tests did not reveal significant differences between groups.

[6] Preference score = $[(t - c)/(t + c)] \times 100$, where t = test solution (green sucrose in this case) and c = control solution (uncolored water, in this case).

TABLE 2
Summary of Results

Group	Mean intake of Day 10 solution (ml)	Mean intake of Day 11 test solution (ml)	Mean intake of Day 11 control solution (ml)	Mean total intake, Day 11 (ml)	Mean preference, Day 11 test solution	Subjects preferring Day 11 test solution (%)
E-1	4.79	1.51	5.91	7.32	−62.04	12
C-1	5.03	4.07	2.47	6.78	+16.80	57
E-2	7.73	5.68	3.40	9.08	+ 1.48	53
C-2	3.87	1.85	1.59	3.44	+ 1.58	53
E-3	2.55	0.86	5.73	6.59	−70.84	8
C-3	1.78	0.51	1.69	2.20	−56.18	13
E-4	2.66	(a) 3.54	(a) 0.62	(a) 4.16	(a) +64.80	(a) 90
		(b) 0.24	(b) 3.60	(b) 3.84	(b) −82.40	(b) 10
C-4	2.18	(a) 3.92	(a) 0.80	(a) 4.72	(a) +63.20	(a) 100
		(b) 1.80	(b) 2.74	(b) 4.54	(b) −11.80	(b) 50

(1, 95) = 8.45; *df* = 1, 95; $P < 0.01$). These statistics reflect the fact that the E-1 subjects greatly decreased their GSS intake from Day 10 to Day 11 (means = 4.79 and 1.51), in contrast to Group C-1, whose GSS intake did not change significantly (means = 5.03 and 4.07). Group E-1's Test Day GSS consumption was significantly lower, and its UW intake higher, than that of the controls. Total fluid consumption during testing was not reliably different for the two groups (see Fig. 1).

Thus, one experience with green sucrose, followed by LiCl-induced illness, was sufficient to condition an aversion to the green sucrose solution. In the next experiment, the visual (color) cue was eliminated in order to determine whether the unfamiliar taste of sucrose would be sufficient to mediate this illness-induced aversion learning.

EXPERIMENT 2

Procedure and Data Analysis

The procedure for this experiment was identical to that described for Experiment 1, except that uncolored 15% sucrose solution (USS) replaced the green 15% sucrose solution on both Days 10 and 11. Subjects were 39 chicks, 20 assigned to the LiCl group (E-2) and 19 to the saline control group (C-2). The results were analyzed as described previously.

Results and Discussion

In distinct contrast to the results of Experiment 1, the animals which drank USS prior to LiCl illness did not display an acquired aversion to the sucrose (see Table 2 and Fig. 2 for a summary of results). There were no significant differences between Groups E-2 and C-2 or between either of these groups and Group C-1, in terms of the percentage of subjects

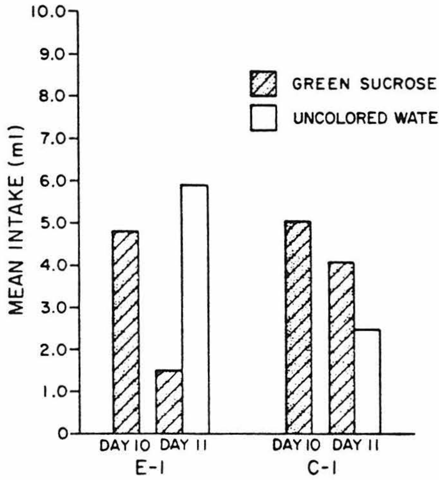

FIG. 1. Mean intake of green sucrose (Day 10) and of green sucrose and uncolored water (Day 11) by Groups E-1 (LiCl) and C-1 (saline).

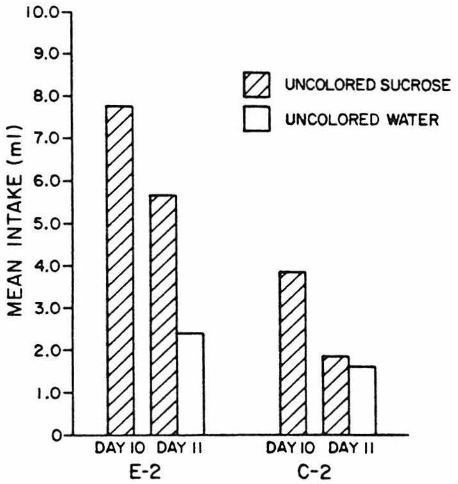

FIG. 2. Mean intake of uncolored sucrose (Day 10) and of uncolored sucrose and uncolored water (Day 11) by Groups E-2 (LiCl) and C-2 (saline).

preferring sucrose on Test Day or in terms of mean sucrose preference scores. In fact, E-2 subjects drank significantly more USS than the controls on both Day 10 (F (1, 36) = 6.46; $P < 0.05$) and Day 11 (F (1, 36) = 5.94; $P < 0.05$) and showed a smaller percentage decrease from one day to the next.

That the pairing of unfamiliar clear sucrose solution with delayed illness failed to produce a conditioned aversion suggested that the learned aversion demonstrated by E-1 subjects was mediated by the visual (color) cue rather than by the taste of the sucrose. For chicks, the distinctive appearance of a liquid seems to be more readily associated with subsequent internal discomfort than is an unfamiliar flavor. It is possible, however, that 10-day-old chicks cannot detect the taste of sucrose and that the color cue was the only one available to them in the first experiment. Uncolored sucrose and uncolored water may not taste discriminably different. If this is the case, then the color cue alone is sufficient to mediate conditioning of an illness-induced aversion, and green water should be treated like the green sucrose of Experiment 1; that is, chicks experiencing LiCl illness after drinking green water for the first time should display an aversion to the green water when tested the next day, while saline-injected controls should demonstrate a nearly equal preference for green and uncolored water during testing. Experiment 3 tested these predictions.

EXPERIMENT 3

Procedure and Data Analysis

Sixty chicks were used as subjects in this experiment. The procedure was identical to that described for the preceding experiments, except that the Day 10 novel solution was green water (GW) (4 drops of green

Schilling vegetable dye per 100 ml of water) and the Day 11 two-jar preference test consisted of access to green water and uncolored water. Data analysis has been described.

Results and Discussion

The results for the LiCl (E-3, $n = 37$) and saline (C-3, $n = 23$) subjects are summarized in Table 2 and strongly suggest that green water was aversive to the chicks irrespective of drug treatment. A solutions × drugs analysis of variance comparing green solution preference scores for the GSS (E-1 and C-1) and GW (E-3 and C-3) groups revealed significant main effects of solutions ($F\,(1, 163) = 13.82$; $P < 0.01$) and of drugs ($F\,(1, 163) = 37.76$; $P < 0.01$), and a significant solutions × drugs interaction ($F\,(1, 163) = 4.92$; $P < 0.05$). Overall, Experiment 1 subjects had a reliably greater preference for GSS on Test Day than Experiment 3 subjects had for GW, and LiCl-injected chicks displayed a significantly lower Test Day preference for green solution than did control subjects. However, the differential effects of LiCl and saline injections occurred only when the green solution was sucrose, not when it was water. Inspection of mean preference scores for the four groups (see Fig. 3) shows that E-3 and C-3 chicks had as negative a preference for GW as E-1 chicks had for GSS and that all three of these groups had a much lower preference score than Group C-1. Analysis of the amount of green solution consumed during testing revealed that GW intake of Groups E-3 and C-3 did not differ significantly from Test Day GSS intake of Group E-1 and that both groups drank reliably less green solution than did Group C-1 (E-3 vs C-1: $F\,(1, 79) = 17.72$; $P < 0.01$; C-3 vs C-1: $F\,(1, 66) = 14.90$; $P < 0.01$). These data are depicted in Fig. 4. Finally the percentage of subjects preferring the green

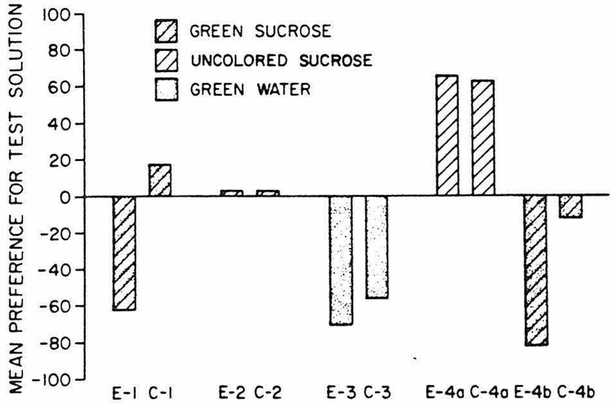

FIG. 3. Mean Day 11 preference scores of Experimental (E) and Control (C) groups, Experiments 1, 2, 3, 4. Preference score = $[(t - c)/(t + c)] \times 100$, where t = test solution and c = control solution. Day 10 solutions and Day 11 control solutions for each group are given in Table 1.

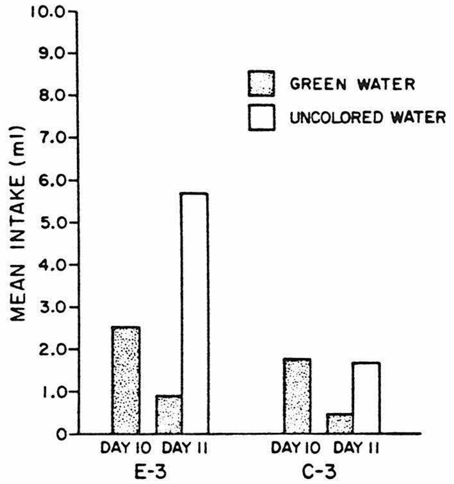

FIG. 4. Mean intake of green water (Day 10) and of green water and uncolored water (Day 11) by Groups E-3 (LiCl) and C-3 (saline).

solution to uncolored water during testing was 15% or less for Groups E-1, E-3, and C-3, as compared with 57% of Group C-1 (χ^2 (3) $= 39.5; P < 0.001$).

The chicks in this experiment displayed a strong aversion to green water on Day 11, regardless of drug treatment. The behavior of the C-3 subjects toward the green water in no way resembles the behavior of Group C-1 toward green sucrose, indicating that in Experiment 1 distinct taste properties of the green sucrose solution counteracted a preference for uncolored liquid. The failure of E-2 subjects to acquire an aversion to uncolored sucrose must not, then, have been due to inability to detect the novel taste of the sucrose.

The other question of interest in this experiment was whether a visual (color) cue would be sufficient to mediate conditioning of an illness-induced aversion. Unfortunately, because of a floor effect, the results do not clarify this issue. The small amounts of green water consumed by all these animals, before as well as after injection, suggest a general aversion to green water[7] and obscure any conditioned difference between groups during testing.

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[7] Since the preparation of this manuscript, preliminary data have been collected which indicate that this "green water aversion" depends on the chicks' previous experience being limited to uncolored water. When 24 naive 1-day-old chicks were housed with both green water and uncolored water freely available, 24-hr intake, measured for 4 days, failed to reveal a significant preference for either liquid. This finding argues against the possibility that, for chicks, green coloring has a detectable and unpleasant taste in water and suggests instead that the observed aversion depends on the chicks learning that "water is uncolored." Perhaps chicks will avoid a substance to a greater extent and more persistently if it is perceived as an "adulterated" familiar-tasting liquid (GW) than they will a more thoroughly novel substance (GSS). This possibility is currently being investigated.

EXPERIMENT 4

The results of Experiments 2 and 3 indicate that 10-day-old chicks do not learn in one trial to avoid an unfamiliar sucrose solution when this learning depends on an association between the distinctive flavor and delayed illness. On the other hand, chicks acquired a strong aversion to sucrose when both color and taste cues were available (Experiment 1). Moore and Capretta (1968) reported similar results using painful leg shock to modify food preferences in 2-week-old chicks. Repeated pairing of shock with preferred color or preferred flavor of food decreased the chick's preference for the preferred color only. However, if the preferred flavor of food was distinctively colored during training, then decreased preference for the flavor was observed (Capretta and Moore, 1970). Thus, an aversive association between pain and taste was established indirectly through a mediating visual cue.

The present experiment investigated the possibility that an association between sucrose flavor and delayed illness might be similarly established if the flavor was combined with a color cue during the initial exposure to sucrose. This association would be expressed as an aversion to clear sucrose after a pairing of green sucrose with delayed illness.

Procedure and Data Analysis

Twenty chicks were used for this experiment. The general experimental procedure was as described for the preceding experiments, but Day 11 testing was somewhat different. The Day 10 conditioning session consisted of a 1-hr access to 25 ml of GSS, followed by injection with either LiCl (Group E-4, $n = 10$) or saline (Group C-4, $n = 10$). On Day 11, two preference tests were conducted. The first consisted of a 1-hr access to 25 ml of USS and 25 ml of GW. After an additional 3 hr of food and water deprivation, both groups were tested again, with 25 ml of GSS and 25 ml of UW available for 1 hr.

Results and Discussion

The results of the first preference test (see Table 2) showed that Groups E-4 and C-4 did not differ significantly in terms of amount of GSS consumed on Day 10, amount of USS or GW consumed during testing, or USS preference scores. One-way analyses on amounts of USS and GW, and on amounts of GSS and USS, revealed that both groups had a strong preference for the USS over GW (F (1, 38) = 33.28; $P < 0.01$) and both drank more USS during testing than they had GSS on Day 10 (F (1, 19) = 5.40; $P < 0.05$). The lack of significant differences between groups indicates that the presence of a color cue during the Day 10 exposure to sucrose did not establish an association between sucrose flavor and illness.

The second preference test was conducted to verify the assumption that E-4 subjects had learned an aversion to the green sucrose solution, and the results, summarized in Table 2 and Fig. 5, clearly demonstrate such an aversion. Whereas Groups E-4 and C-4 had not differed significantly either before injection or during the first preference test, during the second test the E-4 animals drank reliably less GSS than the controls (F (1, 18) = 6.95; $P < 0.05$), and the mean GSS preference score for Group E-4 (−82.4) was significantly lower than that of Group C-4 (−11.80) (F (1, 18) = 9.95; $P < 0.01$).

GENERAL DISCUSSION

Ten-day-old chicks learned an aversion to a palatable colored sucrose solution when their initial sampling of the sucrose was followed by LiCl-induced illness. Young domestic chicks can therefore be included in the growing list of animals which are capable of one-trial conditioned aversion learning with a long delay of reinforcement. This offers a promising paradigm for the study of memory processes in chicks.

The results have implications for a number of issues. Studies with weanling rats (Grote and Brown, 1971) and infant guinea pigs (Kalat, 1975) suggest that, in rodents, this specialized learning ability is mature shortly after birth. The present finding extends this observation to a precocial avian species, lending further support to the suggestion made by Rozin and Kalat (1971) that long-delay avoidance learning is an adaptive evolutionary specialization which does not depend on "learning to learn."

While conditioned aversions to both the taste and the appearance of

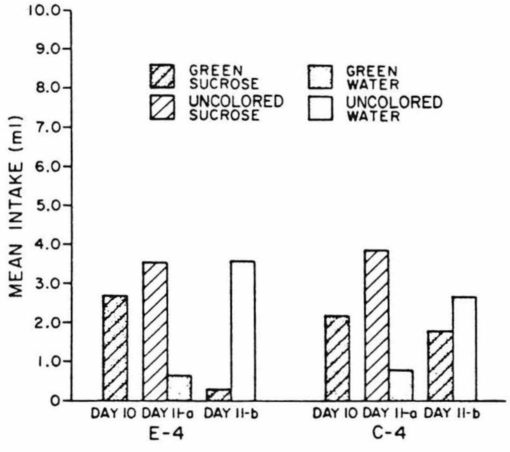

FIG. 5. Mean intake of green sucrose (Day 10), of uncolored sucrose and green water (Day 11(a)), and of green sucrose and uncolored water (Day 11(b)) by Groups E-4 (LiCl) and C-4 (saline).

food or liquid have been reported previously for chicks, none of these studies involved a delay of reinforcement (Capretta, 1961; Moore and Capretta, 1968; Capretta and Moore, 1970). In the present experiments, there was an interval of at least several minutes between sucrose consumption and illness. Under these conditions, the association between green sucrose and illness appeared to depend entirely on the visual (color) cue. The LiCl chicks displayed an aversion to sucrose only when it was colored during both initial sampling and the preference test. That the color cue was apparently necessary for learning does not, however, eliminate the possibility that the sucrose flavor was somehow involved in mediating the color–illness association.

The failure of the LiCl chicks to display any evidence of an acquired taste aversion is difficult to interpret. Chicks are able to detect the distinctive flavor of sucrose (see Experiment 3; also Kare *et al.*, 1957; Jacobs and Scott, 1957) and they are able to inhibit drinking when presented with uncolored but unpalatable liquids (Shettleworth, 1972). Capretta and Moore (1970) were able to decrease the flavor preferences of 2-week-old chicks with repeated painful leg shock, but only if a color cue was added to the food during training. They suggested that the exteroceptive color stimulus mediated an association between an external consequence (shock) and an interoceptive gustatory stimulus. In the present instance, an association between the exteroceptive color stimulus and the internal consequence (illness) was readily established in one trial, while a taste–illness association was never displayed. It is possible that the sucrose flavor would support long-delay avoidance learning under different experimental conditions. Alternatively, the ability to form taste–illness associations over long delays may be undeveloped or absent in young chicks. The separate roles of color and taste cues warrant further examination, in view of the strong effect obtained in Experiment 1 with the combined stimuli.

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BRIEF REPORT

Interocular Transfer of a Visually Mediated Conditioned Food Aversion in Chicks

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Young chicks with one eye occluded were subjected to a food aversion conditioning procedure in which an unfamiliar colored liquid (the conditioned stimulus) was paired with delayed LiCl-induced illness (the unconditioned stimulus). In a subsequent preference test, chicks displayed marked avoidance of the liquid whether tested with the trained or the untrained eye open, demonstrating substantial interocular transfer of the monocularly acquired visual food aversion after the single conditioning session and despite the long interstimulus interval. A possible role of the unconditioned stimulus in determining interocular transfer of avoidance habits in birds is discussed.

In the typical conditioned food aversion experiment, animals are made sick after they have sampled a novel food. A single pairing of food and illness, even over intervals of up to several hours, is often sufficient to establish a strong aversion (Garcia *et al.*, 1966). Animals which use mainly taste cues in their normal selection of food readily learn to avoid a novel taste which has been paired with illness (Garcia and Koelling, 1966; Garcia *et al.*, 1968), whereas animals which rely on vision for food identification are more likely to acquire an aversion to the color or other visual characteristics of a food (Brower, 1969; Wilcoxin *et al.*, 1971; Braveman, 1974; Johnson *et al.*, 1975). Illness-induced aversions display unusual resistance to extinction and are not readily disrupted by brain lesions, electroconvulsive shock, and other such manipulations (see Gaston, 1978).

These findings suggest that animals are uniquely prepared for food aversion learning (see Seligman, 1970, for review of prepared learning). This prepared learning may be based on specialized, prewired brain mechanisms which favor the formation of associations between food-

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related cues and illness and mediate this associative learning over unusually long delays. Such prewired mechanisms may be easier to discover than the neural processes underlying other, less prepared, types of learning and may therefore serve as a valuable model for investigations of associative learning.

A previous study (Gaston, 1977) demonstrated that young domestic chicks acquired an aversion to a novel green sucrose solution which was paired once with delayed LiCl-induced illness. Further, this conditioned aversion was found to be mediated by the visual (color) cue and not by taste. Similar visually mediated conditioned food aversions have been reported for chicks by Ionescu and Bureš (1976) and by Martin *et al.* (1977).

In birds, unlike mammals, the sensory input from each eye crosses completely in the optic chiasm (Cowan *et al.*, 1961). Recrossing of visual information is reported to occur via the supraoptic decussation (Cuénod, 1974). By occluding one eye, primary visual information may be restricted to the contralateral half-brain without surgical intervention. Training with one eye open and testing for retention with the other reveals the extent to which monocularly acquired learning is available to the untrained hemisphere in intact birds. This approach can be combined with brain lesions to provide information about the areas involved in processing and storing particular types of visual learning.

The literature on interocular transfer in intact birds includes reports of good transfer for one-trial passive avoidance learning (Cherkin, 1970; Benowitz, 1974), conditioned color and pattern discriminations (see Cuénod, 1974), active avoidance of a stimulus that had been paired with shock (Stevens and Klopfer, 1977), and usually imprinting (Moltz and Stettner, 1962; Horn *et al.*, 1963; Demarest *et al.*, 1977; but cf. Klopfer, 1973), and reports of no transfer for some active avoidance learning (Stevens and Klopfer, 1977), visual cliff habituation (Zeier, 1970), and the extinction of passive (Benowitz, 1974) and active avoidance responses (Stevens and Klopfer, 1977). To date, attempts to specify principles which govern whether or not transfer occurs have been unsuccessful.

As an approach to investigating the neural mechanisms underlying food aversion conditioning over long delays in chicks, the present experiment examined interocular transfer of this exceptional kind of visual learning. Of interest was the extent to which a monocularly acquired aversion to green sucrose solution is available to the untrained hemisphere. Subjects were a total of 117 newly hatched White Leghorn cockerels. They were housed individually throughout the experiment, with drinking water and standard chick mash available *ad libitum* except as noted. Food, water, and experimental solutions were presented in clear glass jars. The procedure was similar to that described previously (Gaston, 1977). On Days 7, 8, and 9, the animals were accustomed to the experimental schedule in a series of three adaptation sessions, each consisting of 4-hr of food and water deprivation followed by 1-hr access to 25 ml of water. After the last (Day 9) adaptation session, each animal had the lids of one eye closed with a drop of collodion in preparation for monocular training.[2] On Day 10, a 4-hr deprivation period was followed by 1-hr access to 25 ml of an unfamiliar green 15% sucrose solution (4 drops of green Schilling vegetable dye per 100 ml of solution). Intake was measured to the nearest 0.2 ml. Thirty-seven subjects (31%) which failed to drink at least 1.0 ml of the green sucrose solution were eliminated from the experiment. Remaining animals were randomly designated experimental (E) or control (C) subjects. Five to ten minutes after the end of the drinking session, experimental subjects were injected ip with 1.0 ml of 0.2 *M* LiCl. Controls were injected ip with 1.0 ml of isotonic saline. The LiCl treatment reliably produced symptoms of illness (diarrhea, lethargy) which were apparent within 10 to 15 min and generally lasted 30 to 45 min. Saline injections never caused observable signs of illness. E and C animals were each divided into two equal groups of 20: Groups E-T and C-T were assigned to be tested the next day with the same (trained) eye and Groups E-UT and C-UT with the opposite (untrained) eye. Approximately 2 hr after the end of the conditioning session, the untrained eye of E-UT and C-UT animals was opened by softening the collodion cap with a small amount of acetone, and the lids of the trained eye were closed with a drop of collodion. E-T and C-T chicks had acetone applied around, but not on, the closed eye. On Day 11 (Test Day), 4 hr of food and water deprivation were followed by a preference test consisting of simultaneous access for 1 hr to 25 ml of the green sucrose solution (GSS) and 25 ml of familiar uncolored water (UW).

Results of the preference test, summarized in Table 1, demonstrate that the experimental animals had clearly formed an aversion to the GSS (87.5% preferred UW). This was true of chicks tested with the trained eye (E-T: 90% preferred UW) and of those tested with the untrained eye (E-UT: 85% preferred UW). In contrast, 52.5% of the Controls displayed a preference for GSS [$\chi^2(1) = 14.58$; $P < 0.001$]. Both E groups showed selective suppression of GSS intake during the preference test, drinking reliably less GSS than the control groups [$F(1, 76)=6.71$; $P < 0.05$]. All four groups drank similar total amounts of liquid during testing (*F*'s all < 1.0). A percentage preference index was computed for each chick[3] and individual *t* tests comparing the mean percentage preference of each group with zero preference (which represents equal consumption of the two liquids during testing) demonstrated that both experimental groups

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[2] Chicks with *both* eyes closed in this manner are behaviorally blind, i.e., they do not peck at a shiny object or orient to a flashing light.

[3] Percentage preference = (GSS − UW/GSS + UW) × 100.

TABLE 1
Summary of Results

	Mean intake					
Group	Day 10 GSS (ml)	Day 11 GSS (ml)	Day 11 UW (ml)	Mean total intake, Day 11 (ml)	Mean percentage preference, Day 11 GSS[a]	Subjects preferring Day 11 GSS (%)
E-T (*n* = 20)	4.37 ± 2.32	1.14 ± 1.37	4.33 ± 3.07	5.47 ± 3.00	−56.1 ± 48.8	10.0
E-UT (*n* = 20)	3.72 ± 2.40	1.91 ± 3.29	3.25 ± 2.34	5.16 ± 3.60	−37.0 ± 53.3	15.0
E (mean)	4.04	1.53	3.79	5.32	−46.6	12.5
C-T (*n* = 20)	4.06 ± 1.40	2.58 ± 3.48	2.25 ± 2.05	4.83 ± 4.17	−14.4 ± 66.6	40.0
C-UT (*n* = 20)	2.78 ± 1.23	3.88 ± 3.12	1.63 ± 1.75	5.51 ± 2.85	+28.2 ± 70.3	65.0
C (mean)	3.42	3.23	1.94	5.17	+7.0	52.5

[a] Each mean percentage preference represents an average of percentage preferences calculated for individual chicks.

had a significant aversion to the GSS (E-T: $t = 5.13$; $P < 0.01$; E-UT: $t = 3.1$; $P < 0.01$). Neither control group displayed a statistically significant preference.

A two-way analysis of variance on percentage preferences revealed significant main effects of drugs [$F(1, 76)=15.72$; $P < 0.001$] and of eyes [$F(1, 76)=4.82$; $P < 0.05$]. The drug effect indicates that experimental animals had a reliably lower preference for GSS than control subjects. Scheffé tests for comparisons between means (Winer, 1962) showed that this effect obtained whether testing was done with the trained eye (E-T vs C-T: $F(1, 76)=4.82$; $P < 0.05$] or with the untrained eye [E-UT vs C-UT: $F(1, 76)=11.63$; $P < 0.01$]. Overall, animals tested with the trained eye had a reliably lower preference for GSS than those tested with the untrained eye. A Scheffé test revealed that Group C-T had a significantly lower GSS preference than Group C-UT [$F(1, 76)=4.89$; $P < 0.05$]. While the average magnitude of the aversion expressed by Group E-UT was only about 66% of that demonstrated by Group E-T, this difference between the two experimental groups was not statistically significant [$F < 1.0$).

The significantly lower preference for GSS of Group C-T as compared with Group C-UT could have resulted from a mild saline-induced aversion which was not available to the untrained hemisphere. Alternatively, the C-UT animals may not have remembered seeing the GSS prior to testing and may have been responding to it as a novel stimulus. However, results from additional control groups did not support either explanation, and the reason for the difference between the two saline control groups remains unclear.

The results of this experiment are consistent with the previous report (Gaston, 1977) that one experience with green sucrose followed by LiCl-induced illness is sufficient for chicks to acquire an aversion to the GSS. Further, it is shown that monocularly trained chicks display a marked aversion whether tested with the trained or the untrained eye open. Substantial interocular transfer of the visually mediated aversion learning was found to occur after a single conditioning session, despite an interstimulus interval of at least 10 min. While chicks do not exhibit any evidence of an acquired taste aversion under these experimental conditions (Gaston, 1977), it remains possible that the novel sucrose taste has a role in mediating acquisition and/or interocular transfer of the visual aversion.

The factors which govern whether or not interocular transfer of learning occurs in birds are not clear. Even if the issue is restricted to avoidance learning, there have been reports both of positive transfer, such as in the present experiment, and of no transfer. Cherkin (1970) and Benowitz (1974) found that chicks which learned in one trial to inhibit pecking of a bad-tasting object demonstrated good interocular transfer of the passive avoidance task. Stevens and Klopfer (1977) have recently reported a series of active avoidance experiments with adult birds. They found good interocular transfer of conditioned withdrawal from a visual stimulus when the unconditioned stimulus was painful shock to the wings, but failure of transfer when the unconditioned stimulus was a loud noise or a monocularly presented looming object. Thus, research to date on interocular transfer of avoidance learning in birds has failed to find transfer for responses established through distance receptors, i.e., visual or auditory, whereas positive transfer has been found for responses established through somesthetic or visceral receptors. It is suggested here, then, that a crucial factor involved in determining interocular transfer of avoidance learning in birds may be the organism's perception of the unconditioned stimulus as an internal, rather than external, event.

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Evidence for Separate and Concurrent Avoidance Learning in the Two Hemispheres of the Normal Chick Brain

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Previous studies have shown that young chicks avoid drinking a novel liquid (green sucrose solution) which has been paired once with delayed LiCl-induced illness. This conditioned aversion was found to be mediated by the visual (color) cue and not by taste, and tests with monocularly trained chicks demonstrated good interocular transfer of learning. The present experiment examined the possibility that novel sucrose taste might play some role in acquisition and/or interocular transfer of the aversion. Chicks with one eye occluded were made sick with LiCl after drinking green sucrose solution, which combined novel color with either novel or familiar sucrose taste. The animals were tested the following day, with the trained or the untrained eye open, for learned aversions to green or uncolored sucrose. Chicks tested with the trained eye displayed a marked aversion to the colored sucrose, but not to uncolored sucrose, regardless of the taste variable. In contrast, animals tested with the untrained eye showed a significant aversion to either colored or uncolored sucrose, but in each case only if the taste was novel during training. These findings indicate that, in monocularly trained chicks, each half-brain can independently acquire an illness-induced food aversion, with learning in the seeing and nonseeing hemispheres mediated by novel color and taste cues, respectively.

Animals acquire an illness-induced food aversion most readily when the available cues are both novel and of the type normally used by the species for food selection (Revusky & Garcia, 1970; Seligman, 1970; Rozin & Kalat, 1971; Garcia, Hankins, & Rusiniak, 1974). Thus, rats quickly learn to avoid an unfamiliar taste which has been paired with illness (Garcia & Koelling, 1966; Garcia, McGowan, Ervin, & Koelling, 1968), while birds and other animals which rely more on vision for identification of food easily learn an aversion to a distinctive visual characteristic such as color (Brower, 1969; Wilcoxin, Dragoin, & Kral, 1971; Johnson, Beaton, & Hall, 1975; MacKay, 1977). When a novel cue of the preferred type is not

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available, however, learning may sometimes be based on other sensory information (Garcia, Kimeldorf, & Hunt, 1961; Rozin, 1969; Wilcoxin et al., 1971; Braveman, 1974, 1975).

Gaston (1977) conditioned domestic chicks to avoid an unfamiliar liquid (green sucrose solution) which was paired once with delayed illness. When novel gustatory and visual stimuli were both available, the aversion was mediated by the visual (color) cue and not by taste. When only the novel taste cue was available, conditioning failed. Other investigators have shown that chicks can acquire an illness-induced aversion when color is the only novel stimulus (Ionescu & Bureš, 1976; Martin, Bellingham, & Storlein, 1977; Genovese & Browne, 1978).

A later study (Gaston, 1978) evaluated interocular transfer[2] of the conditioned aversion to green sucrose. After chicks with one eye occluded had sampled novel green sucrose, they were made sick with LiCl. The following day, the chicks displayed marked avoidance of the liquid whether tested with the trained or untrained eye open. Since the earlier study with binocularly trained chicks demonstrated that animals conditioned in this way formed an aversion only to the colored solution, and not to the taste alone (Gaston, 1977), this finding indicated good interocular transfer of the monocularly acquired visual aversion.

In order to examine the possibility that novel taste might nevertheless play some role in acquisition and/or interocular transfer of the aversion, the present experiment evaluated the effects of training with novel color in combination with either novel or familiar sucrose taste. The chicks were tested, with the trained or the untrained eye open, for learned aversions to green or uncolored sucrose. Preliminary observations[3] indicated that novel taste was not necessary for monocular conditioning but that it was required for interocular transfer of the aversion. Two alternative explanations for such a situation seem plausible and predict different outcomes for the present investigation. First, a novel taste during training might nonspecifically promote interhemispheric communication of visual information by increasing arousal or activation of the nonseeing hemisphere. According to this interpretation, chicks tested with the untrained

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[2] Since complete optic decussation in birds restricts direct visual input from each eye to the contralateral half-brain (Cowan, Adamson, & Powell, 1961), interocular transfer of visual learning in monocularly trained birds depends on interhemispheric communication via fiber cross-connections.

[3] In a pilot study (unpublished), chicks were accustomed to drinking uncolored sucrose (taste adaptation) prior to the monocular conditioning procedure which paired green sucrose with LiCl-induced illness. For these animals, then, only the color of the solution was novel during conditioning. Taste adaptation did not interfere with monocular conditioning: Those subjects tested with the trained eye displayed a large learned aversion to the green sucrose. In contrast, animals tested with the untrained eye did not demonstrate an aversion to the colored solution. In other words, there was no interocular transfer of the visual aversion when chicks were preadapted to the taste.

eye would display an aversion to colored sucrose only after being trained with novel taste, but would not show an aversion to the taste alone (uncolored sucrose). On the other hand, the hemisphere receiving no direct visual input might independently learn a taste aversion when novel taste information is available (e.g., Gaston, 1978). When it is not, no learning would occur in the nonseeing hemisphere. By this latter view, the two hemispheres of the chick brain are capable of separately but concurrently acquiring illness-induced aversions to the most salient food-related sensory information *directly* available—color in one case, taste in the other. If this is true, then chicks trained with novel taste and tested with the untrained eye would be expected to avoid uncolored as well as colored sucrose.

SUBJECTS AND APPARATUS

Subjects were 170 White Leghorn cockerels, obtained from Pacesetter Farms, Cucamonga, California, on the day of their hatching. They were housed individually throughout the experiment in 18 cm^3 white Plexiglas compartments with wire-mesh floors and lids. The room was maintained at approximately 90°F and 45% humidity; overhead lighting was on between 8:00 AM and 8:00 PM daily. Drinking water and standard chick mash were available ad libitum except as noted. Food, water, and experimental solutions were presented in 56.7-ml clear glass jars, each fitted with a black plastic lid having a 2.54-cm diameter hole in the center.

PROCEDURE

The general procedure has been described in detail previously (Gaston, 1977, 1978). On Days 7, 8, and 9, the animals were accustomed to the experimental schedule in a series of three pretraining sessions, each consisting of 4 hr of food and water deprivation followed by 1 hr access to 25 ml of uncolored water (novel taste groups, N) or uncolored 15% sucrose solution (familiar taste groups, F). Following the third (Day 9) pretraining session, each chick had the lids of one eye closed with a drop of collodion in preparation for monocular training.[4] On Day 10 (Training Day), 4 hr food and water deprivation were followed by 1 hr access to 25 ml green 15% sucrose solution (four drops of green Schilling vegetable dye per 100 ml of solution). Intake was measured to the nearest 0.2 ml. Forty-two subjects (24%) which failed to drink at least 1.0 ml of the green sucrose solution were eliminated from the experiment. The remaining 128 animals were randomly designated experimental (E) or control (C) subjects, so as to create 4 equal groups: EN, EF, CN, and CF. Five to ten minutes after the end of the drinking session, all experimental subjects were injected ip with 1.0 ml of 0.2 *M* LiCl. Controls were injected ip with

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[4] Chicks with both eyes closed in this manner are behaviorally blind.

1.0 ml of isotonic saline. The LiCl treatment reliably produced symptoms of illness (diarrhea, lethargy) which were apparent within 10 to 15 min and generally lasted 30 to 45 min. Saline injections never caused observable signs of illness. Each E and C group was then divided into two equal subgroups, matched for green sucrose consumption during training, with one subgroup assigned to be tested the next day with the trained (T) eye and the other with the untrained (Ut) eye. Approximately 2 hr after the end of the conditioning session, the untrained eye of each animal in the four Ut groups was opened by softening the collodion cap with a small amount of acetone, and the lids of the trained eye were closed with a drop of collodion. Chicks in the four T groups had acetone applied around, but not on, the closed eye. On Day 11 (Test Day), 4 hr of food and water deprivation were followed by a preference test consisting of simultaneous access for 1 hr to 25 ml of familiar uncolored water (UW) and 25 ml of the test solution. For half of the animals, the test solution was *green* sucrose solution (GSS) and for the other half, it was *uncolored* sucrose solution (USS).

Thus, a complete four-way factorial design was formed with 16 groups of eight chicks each. The four variables, each with two levels, were Drug Treatment (LiCl, Saline), Taste (Novel, Familiar), Eye Tested (Trained, Untrained), and Test Solution (GSS, USS). The experimental design and group designations are shown in Table 1.

TABLE 1
Summary of Results, Day 11 Preference Test

		Drug treatment			
		LiCl experimental (E)		Saline control (C)	
		Taste		Taste	
Eye tested	Test solution	Novel (N)	Familiar (F)	Novel (N)	Familiar (F)
Trained (T)	GSS (G)	ENTG	EFTG	CNTG	CFTG
		1.77[a]	1.85	3.60	4.22
		5.45	5.50	3.15	1.38
Trained (T)	USS (U)	ENTU	EFTU	CNTU	CFTU
		5.57	4.85	4.45	4.42
		4.08	4.17	1.50	3.58
Untrained (Ut)	GSS (G)	ENUtG	EFUtG	CNUtG	CFUtG
		1.90	3.20	1.57	2.40
		6.75	4.32	2.03	1.47
Untrained (Ut)	USS (U)	ENUtU	EFUtU	CNUtU	CFUtU
		1.22	3.97	3.22	2.07
		3.08	2.95	1.25	1.78

[a] For each group, the top number is the mean amount of test solution consumed (ml) and the bottom number is the average amount of uncolored water consumed (ml).

RESULTS

The results of the Day 11 preference test are summarized in Table 1. Analysis of variance revealed that, overall, chicks drank more of the test solution if tested with the trained rather than the untrained eye [$F(1, 112) = 8.47$; $p < .01$] and if the test solution was USS rather than GSS [$F(1, 112) = 5.83$; $p < .02$]. Analysis of total liquid consumed during testing (GSS or USS + UW) showed that experimental animals, which had been made sick with LiCl the previous day, drank more overall than saline controls [$F(1, 112) = 16.96$; $p < .001$] and that chicks tested with the trained eye drank more than those tested with the untrained eye [$F(1, 112) = 13.18$; $p < .001$].

In order to evaluate the chicks' relative preferences for the test solution, whether GSS or USS, the test results for each animal were converted to a percentage preference index according to the formula [(test solution − UW/test solution + UW) × 100]. The range of this index is from +100% (chick drank only test solution, no UW) through zero (chick drank equal amounts of the test solution and UW) to −100% (chick drank no test solution, only UW). Mean percentage preferences for the experimental and control groups are depicted in Fig. 1.

A four-way analysis of variance on percentage preferences revealed significant main effects of drug treatment [$F(1, 112) = 7.30$; $p < .01$] and of test solution [$F(1, 112) = 7.94$; $p < .01$] and a significant drug treatment × taste interaction [$F(1, 112) = 3.97$; $p < .05$]. Overall, experimental (LiCl) animals had a reliably lower preference for the test solution than did the saline controls, and chicks tested with GSS had significantly lower preference scores than those tested with USS. For the experimental subjects, novel taste during training led to lower test preferences than did familiar taste, whereas the taste variable did not influence the test results of controls.

Individual t tests compared the mean percentage preference of each of the eight experimental and eight control groups with zero preference (see Fig. 1). These tests confirmed that none of the saline control groups showed an aversion to the test solution. In fact, only one of these groups displayed a statistically significant preference for either solution, and that was in favor of the test solution (Group CNTU: $t = 3.44$; $p < .02$). In contrast, four of the experimental groups were found to have a significant aversion to the test solution, while the remaining four groups showed no reliable preference. The experimental animals tested with the trained eye displayed a significant aversion to GSS, but not to USS, regardless of the taste variable (Group ENTG: $t = 2.86$; $p < .05$; Group EFTG: $t = 2.56$; $p < .05$). Experimental animals tested with the untrained eye, on the other hand, showed a significant aversion to either GSS or USS, but in each case only if the sucrose taste was novel during training (Group ENUtG: $t = 3.05$, $p < .02$; Group ENUtU: $t = 2.99$, $p < .02$).

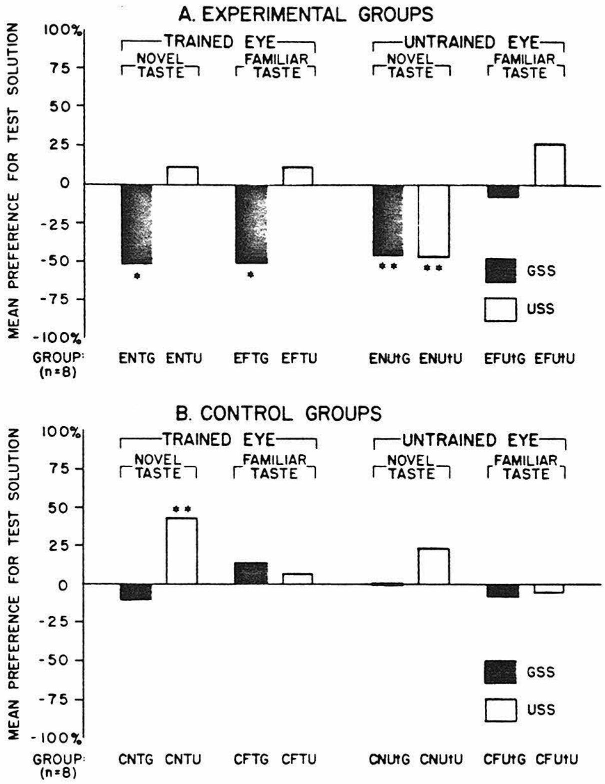

FIG. 1. Mean Day 11 percentage preference scores for Experimental and Control groups. A percentage preference score was computed for each chick according to the formula $[(t - UW)/(t + UW)] \times 100$, where t = test solution (GSS or USS) and UW = uncolored water. *, $p < .05$; **, $p < .02$.

The eight saline control groups were included in the experimental design to confirm that any aversion displayed during testing was a product of LiCl poisoning and could not be attributed to the trauma of injection or to any of the other experimental variables, either singly or in combination. Since the results described above clearly demonstrate that none of the control groups displayed an aversion, and since the primary intent of the experiment was to reveal differences between the various experimental groups, an additional statistical test was performed using just the data of the experimental animals.

A three-way analysis of variance on percentage preferences of the experimental subjects revealed significant main effects of test solution [$F\ (1, 56) = 8.58$; $p < .005$] and taste [$F\ (1, 56) = 4.25$, $p < .05$] and a significant taste X eye tested interaction [$F\ (1, 56) = 4.32$; $p < .05$]. Overall, the experimental chicks tested with GSS had reliably lower percentage preference scores than those of animals tested with USS, and subjects who had novel taste during conditioning had significantly lower preference scores than those for whom the sucrose taste was familiar. However, these differential effects of novel and familiar taste obtained only for chicks tested with the untrained eye.

DISCUSSION

The present results demonstrate that chicks made sick after drinking green sucrose and tested with the trained eye show a marked aversion to green sucrose (GSS) but not to uncolored sucrose (USS). This replicates the findings with binocularly trained chicks (Gaston, 1977) and confirms that the aversion is mediated by the visual (color) cue and not by taste. The pronounced aversion to GSS displayed by animals which were tested with the trained eye after training with familiar sucrose taste (Group EFTG) demonstrates that taste adaptation did not interfere with monocular learning and that novel taste is not required for acquisition of the visual aversion.

Experimental chicks which were preadapted to sucrose taste and tested with the untrained eye showed no evidence of an acquired aversion to either GSS or USS (Groups EFUtG and EFUtU). In contrast, chicks trained with novel sucrose taste and tested with the untrained eye demonstrated a significant aversion both to GSS (Group ENUtG), as found previously (Gaston, 1978), *and also to USS* (Group ENUtU). This avoidance of uncolored sucrose clearly represents an acquired aversion to the taste of the liquid. Equally clearly, this taste aversion was learned only by the (''untrained'') hemisphere which was deprived of direct visual information (cf. Groups ENTU and EFTU, which failed to demonstrate a taste aversion when tested with the ''trained'' eye), and then only if the taste was novel during training (cf. Group EFUtU). Since all the animals in this experiment were trained with novel color, it is not known whether it in any way affects taste aversion learning in the nonseeing hemisphere.

Taken together, the results strongly support the view that each hemisphere can independently acquire an illness-induced food aversion, with learning in the seeing and the nonseeing hemispheres mediated by novel color and taste cues, respectively. These results do not, however, rule out some interhemispheric transfer of the visual aversion in chicks trained with novel taste (i.e., the aversion to GSS shown by Group ENUtG might be based either on taste alone or on a combination of taste and color). It therefore remains possible that novel taste has an activating effect which facilitates interhemispheric communication of visual information. On the other hand, the evidence clearly indicates that reverse transfer, of taste aversion from nonseeing to seeing hemisphere, did not occur. This can be seen by comparing Groups ENUtU and ENTU: chicks tested with the untrained eye open displayed a significant taste aversion, whereas chicks trained under identical conditions but tested with the trained eye did not.

When the present results are considered in combination with those of the previous related studies, it is apparent that the seeing whole or half-brain of the chick was able to utilize only the novel visual information for acquisition and expression of an illness-induced aversion. That is, it could associate color with subsequent illness, whether novel taste was present or not, but showed no evidence of learning a taste aversion even when sucrose taste was the only novel cue available during training. However, when one eye was occluded and vision through that eye thus eliminated, then the corresponding half-brain was able to utilize novel taste information (ignored by the seeing half-brain) in acquiring an aversion. It thus appears that, while the visual system was normally dominant, elimination of direct visual input to half the brain enhanced the effective significance of gustatory information and enabled that nonseeing hemisphere to associate the novel taste cue with illness. It is possible that similar nonvisual learning occurs only in the visually deprived hemisphere during other types of monocular training and that, if undetected, it may be mistaken as evidence for interhemispheric transfer of visual information.

It has been shown here that, under certain conditions, the two halves of the chick brain are capable of independent and concurrent avoidance learning based on different types of sensory information. While the generality of this capacity remains to be determined, the present instance is a clear illustration of the extent to which the two hemispheres can function separately in the intact avian brain.

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GENERAL DISCUSSION

The experiments which have been presented here address several aspects of learning and interocular/interhemispheric transfer in the domestic chick. The work reported in Chapter I demonstrated that an operant pattern discrimination task reinforced by heat failed to transfer from the trained to the untrained eye in newly hatched chicks. Furthermore, there was no evidence that transfer was developing in progressively older chicks up to 16 days post-hatch. Other investigators have reported lack of eye-to-eye transfer in chicks for habituation to the "deep" side of a visual cliff (Zeier, 1970), extinction of a learned passive avoidance habit (Benowitz, 1974), and imprinting (Bell & Ehrlich, 1979). Interocular transfer has also been found to fail for some tasks in adult birds (e.g., see Stevens & Klopfer, 1977; Goodale & Graves, 1980). Such results indicate that, in intact birds, monocular visual learning can be stored in the form of a unilateral engram which is not retrievable through the untrained hemisphere, and they illustrate the extent to which the two halves of the avian brain are separately organized and able to function independently under certain conditions.

The present failure to find interocular transfer of pattern discrimination learning, even in chicks more than two weeks old, is in contrast to reports of good transfer for similar discriminations in adult pigeons (e.g., Cuénod, 1974; Green, Brecha, & Gazzaniga, 1978). The discrepant findings may reflect a fundamental difference in the capacity of chicken and pigeon brains to transfer information interhemispherically. Alternatively, differences in experimental conditions (e.g., type and schedule of reinforcement, amount of training, previous experience) may account for the conflicting results. One testable possibility, discussed in more detail in Chapter II, is that the critical difference between the two cases has to do with the "naturalness" of the relationship between response and reinforcer.

This hypothesis predicts that chicks would show transfer of the pattern discrimination if they were pecking to obtain food rather than heat.

The series of experiments reported in Chapters II, III, and IV examined acquisition and interocular/interhemispheric transfer of a conditioned food aversion. Ten day old chicks avoided drinking a novel colored sucrose solution when their first experience with it was followed by experimentally induced illness; non-illness control subjects did not show an aversion. When novel taste and color were both present, the aversion was found to be based on the visual (color) cue and not on taste. When the color was eliminated, so that taste was the only novel cue available, then conditioning failed. Interocular transfer of this learning was evaluated by conditioning chicks with one eye closed and testing for an aversion to the colored sucrose with either the trained or the untrained eye open. The results showed that the chicks avoided drinking the colored sucrose regardless of which eye was open during testing, indicating good interocular transfer of the monocularly acquired aversion. This behavioral evidence of transfer did not distinguish between alternative possible underlying mechanisms. Here, as in the experiment on pattern discrimination learning, monocular training may have produced a single, unilateral engram in the trained hemisphere. In the present case, however, such a unilateral engram must have been accessible to the untrained hemisphere. Alternatively, interocular transfer may have occurred because monocular conditioning resulted in bilateral memory formation.

While the data from chicks trained with both eyes open had demonstrated that the conditioning procedure resulted in an aversion only to the colored solution, and not to the taste alone, it seemed possible that the presence of novel taste during conditioning might nevertheless play some role in acquisition and/or interocular transfer of the aversion. This possibility was investigated by training chicks monocularly with novel color combined with either novel or familiar sucrose taste.

They were then tested, with either the trained or the untrained eye open, for learned aversions to colored or uncolored sucrose. Chicks tested with the trained eye showed an aversion to the colored, but not the uncolored, liquid regardless of whether the taste was novel or familiar during training. This result confirmed that the aversion was mediated by the visual (color) cue and also demonstrated that novel taste was not required for acquisition of the visual aversion.

In contrast, chicks tested with the untrained eye open showed an aversion to either colored or uncolored sucrose, but in each case only if the taste was novel during training. The avoidance of uncolored sucrose was clearly a taste aversion, acquired only by the so-called "untrained" hemisphere which was deprived of primary visual input during the training session and apparently stored in the form of a unilateral engram which was unavailable to the other half of the brain. As discussed in Chapter IV, the results demonstrate that interocular/interhemispheric transfer of the visual aversion failed in chicks trained with familiar taste, again indicating unilateral memory formation, but they do not rule out the occurrence of transfer when novel taste was present. Other investigators have shown that chicks and other birds can acquire an illness-induced aversion when a visual cue is the only available stimulus (Wilcoxin, Dragoin, & Kral, 1971; Brett, Hankins, & Garcia, 1976; Ionescu & Bureš, 1976; Martin, Bellingham, & Storlein, 1977; Genovese & Browne, 1978). Unfortunately, there are as yet no reported studies on interocular transfer of these aversions[1].

Taken together, the results of the present series of experiments on conditioned food aversions in chicks indicate that, while the visual system was normally dominant, eliminating primary visual input to half the brain enhanced the effective significance of taste information and enabled that hemisphere to associate novel taste with the subsequent illness experience. It seems, then, that under certain conditions, the two halves of the chick brain are capable of independent and concurrent avoidance learning based on different types of sensory information.

FOOTNOTE

[1] Pounds, Williamson, & Cheney have recently found evidence for interocular transfer of an illness-induced aversion to colored water in pigeons (personal communication).

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