Auditory and Visual Determinants of Maternal Preference in Bobwhite Quail Neonates

by

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ABSTRACT

Imprinting studies have traditionally stressed the importance of visual features in the formation of early postnatal attachments. However, recent studies by Johnston & Gottlieb (1981, 1985) have demonstrated that visually imprinted preferences can be altered by the maternal call. Thus, in the present study the interaction between natural visual and auditory stimulation in the control of filial behavior was examined in bobwhite quail chicks during the first 4 days of postnatal life.

Previous research has revealed that bobwhite quail hatchlings are differentially responsive to their species-specific maternal call in the period right before and immediately following hatching (Heaton, Miller & Goodwin, 1978). Results from this study indicate that quail chicks begin to lose this naive preference for their maternal call over a non-conspecific call (a domestic chicken maternal call) by 72 hrs following hatch, and do not respond to either the bobwhite call or chicken call by 96 hrs following hatch. However, differential responsiveness to the bobwhite call can be reinstated in bobwhite chicks at 72 hrs and 96 hrs following hatching if the birds are provided

with integrated audiovisual stimulation (i.e., a quail hen model emitting the maternal call). These results suggest that in the initial stages of postnatal development, species identification in bobwhite quail is based primarily on the auditory component of maternal stimulation. Later in development, combined auditory and visual stimulation appears necessary to control species-specific filial behavior despite the fact that auditory cues remain dominant over visual cues.

These findings conform well to what is known about the neuroembryological development of sensory systems, in that the auditory system of birds (and mammals) develops in advance of the visual system. This prenatal sequence of sensory system development appears to influence the sequence of early postnatal perceptual preferences in precocial avian neonates.

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Chapter 1
Introduction

A close social attachment typically forms between young precocial birds and their hen upon exodus from the nest. It is generally supposed that this social attachment results from a process of visual imprinting. For example, drawing on naturalistic observations, Lorenz (1937) proposed that young hatchlings rely primarily on visual cues when attempting to discriminate between their mother and other conspecifics. This assumption on the part of Lorenz (1937) has led most students of imprinting to focus their attention on the visual characteristics of the mother and the developmental processes by which those characteristics become salient to the young (Bateson, 1966). However, in nature the mother presents the precocial hatchling with an array of sensory stimulation. For example, in most species the hen vocalizes a species- typical maternal assembly call while leading the young away from the nest (Collias & Collias, 1956; Joyner, 1977; Miller & Gottlieb, 1978). The role that this maternal call might play in determining the early social preference of precocial avian young has, however, received relatively little attention in the imprinting literature. In most cases, the maternal call has been thought to simply stimulate the young bird to follow its mother, thereby allowing the hatchling to become visually imprinted to her (Batesen, 1966; Fischer, 1966).

However, Gottlieb's (1971) studies on the effectiveness of species-specific auditory and visual stimulation in eliciting and

maintaining following behavior in precocial avian hatchlings yielded results which serve to question this view. He found that the auditory component of the maternal complement instigated a much higher incidence of 'following' behavior than did visual components in both domestic chicks and wild and domestic ducklings. Further, combined audio-visual stimulation elicited an even higher incidence of 'following' behavior on the part of ducklings during the early postnatal period. Interestingly, Gottlieb did not, however, find evidence for species-specificity of the 'following' response if the ducklings were presented with only visual features of the maternal hen (Gottlieb, 1971). More recent work by Storey and Shapiro (1979) also demonstrated that Peking ducklings show a distinct preference for the maternal assembly call over other forms of stimulation, even when presented with a silent live hen. In addition, ducklings prefered a combination of audio-visual stimuli over either auditory or visual stimuli presented alone. Field studies of mallard ducks by Miller and Gottlieb (1978) also suggest that the hen's call is an important component in eliciting and maintaining early 'following' behavior on the part of ducklings.

Porter and Stettner (1968) have presented evidence that suggests that auditory stimulation plays a dominant role over visual stimulation in eliciting 'following' behavior in young bobwhite quail chicks. In their study, subjects (bobwhite chicks) showed a stronger attachment response to a combined audio-visual stimulus than to a visual stimulus presented alone. However, it is important to note that Porter and Stettner (1968) used highly artificial, non-

species-typical forms of auditory and visual stimulation in their experiments.

A naive auditory preference for their species-typical maternal assembly call has, in fact, been demonstrated in young domestic chicks, ring-billed gulls, Peking, mallard and wood ducks, and bobwhite quail (Gottlieb, 1971a; Evans, 1973; Heaton, Miller & Goodwin, 1978). This naive auditory preference appears to be the result of specific auditory stimulation embryos receive while in the air space of the egg before hatching. For example, Gottlieb (1971a) was able to show that mallard embryos show an activation of bill clapping when stimulated by its maternal call at 26-27 days of age (while still in the egg). These studies and those described above suggest that the maternal call can indeed serve as an important cue by which the young precocial bird discriminates its mother from other conspecifics, as well as birds of other species, in the period immediately following hatching.

Nonetheless, the nature of the relationship between auditory and visual cues available during the first days following hatching is not well understood. While several investigators have proposed that auditory stimulation is overwhelmingly important in establishing an early social preference for the maternal hen on the part of the hatchling (Gottlieb, 1971a; Johnston & Gottlieb, 1981, 1985), little is known about the role of combined audio-visual stimulation to the subsequent maintenance of a maternal preference. Recently, however, several studies have shown that the attractiveness of the species-typical maternal assembly call is such that previously visually imprinted ducklings that are exposed to

their maternal call (for the first time) will readily approach it in preference to a previously presented, familiar visually imprinted object (Johnston & Gottlieb, 1981, 1985).

In a synthesis of embryological research, Gottlieb (1971b) examined the sequence of development of the sensory modalities of a number of diverse species. Gottlieb was able to show that the sequence of sensory development is cutaneous->vestibular->auditory->visual in rats, deermice, rabbits, cats, opossums, birds and man. While these results would lead one to believe that the development of sensory modalities is potentially determined by evolutionary and/or genetic considerations, Gottlieb stressed two additional features which may also contribute to developmental outcome: a) cellular function plays a role in regulating the species-typical rate of structural maturation and in completing sensory development, especially with respect to fully adaptive or adjustive behavior, b) sensory stimulation also plays a role in regulating the species-typical rate of maturation and in completing sensory development, especially in perfecting perceptual development. Therefore, amount of stimulation can affect the amount of maturation, and deprivation of such stimulation may lead to later onset or incomplete development of a given sensory system; alternatively, extra stimulation may lead to earlier onset of the sensory system function. Gottlieb (1968) also reports that normally occuring auditory stimulation is necessary for the proper development of species-typical auditory perception in ducks. He noted that partial deprivation of normally available auditory stimulation produced a lag in the development of their species-

typical auditory discriminative abilities. These finding all support the idea that relevent stimulation plays an essential role in the development of adaptive sensory-motor functions.

Of course, under normal postnatal circumstances, precocial hatchlings receive information in several sensory modalities. As reviewed above, two modalities known to be important for the control of filial behavior are the visual and auditory modalities, although it is not clear how they interact in the course of development. Recently, Johnston and Gottlieb (1985) have proposed that hatchlings use auditory rather than visual information when choosing where to direct their early filial behavior. However, if auditory cues are ambiguous, they argue that hatchlings then choose on the basis of visual cues. Johnston and Gottlieb (1985) have termed this interaction between auditory and visual stimulation the "cue hierarchy" hypothesis. Research with ducklings lends empirical support to this view. When ducklings can make a choice on the basis of species-typical auditory cues, they typically ignore available visual information (Johnston & Gottlieb, 1981). It is not known, however, if such a "cue hierarchy" also exists in other avian species.

The specific purpose of this study, therefore, was to investigate the relationship between auditory and visual stimulation in eliciting and maintaining a maternal preference in young bobwhite quail (Colinus virginianus) hatchlings. Quail are particularly appropriate subjects for the investigation of such early perceptual preferences, in that previous studies have demonstrated a naive auditory preference for their species-typical maternal

assembly call both prenatally and postnatally (Heaton, Goodwin & Miller, 1978; Heaton & Gallaher, 1981). In addition, bobwhite quail are known to receive ongoing auditory stimulation from themselves and from clutchmates in the days immediatly prior to hatching (Vince, 1972). These factors suggest that their auditory system is more fully developed and functional than the visual system in the period immediatly following hatching. What is known about the embryological development of sensory systems in precocial birds would support this view. We know that the auditory system of birds (and mammals) develops in advance of the visual system (Gottlieb, 1968), suggesting that hatchlings should initially prefer auditory over visual stimulation. Later in development, as the visual system becomes more experienced, it seems likely that combined audio-visual stimulation would be necessary to control early perceptual and social preferences.

Chapter 2

General Method

Subjects:

Three hundred and seventy-three experimentally naive bobwhite quail chicks (Colinus virginianus) were used in the following studies. Fertile, unincubated eggs were received weekly from a commercial supplier. The eggs were placed in a refrigerator for 48 hrs to allow for the synchronization of hatching; they were then placed in a Petersime Model I incubator, which was monitored twice daily for proper temperature and humidity. Temperature was maintained between 37-38 degrees celcius and the humidity between 75-85% to mimic natural incubating conditions. After 20 days of incubation the eggs were moved to a hatching tray located at the bottom of the incubator. When the eggs were in the hatching tray, they were checked every hour to allow the experimenter to accurately assess the time of hatch and the subjects' developmental age. Only those eggs which hatched on day 22 were used as subjects. Time of hatching was recorded on a prepared hatching chart and the chick's leg was banded for individual identification. Chicks were housed in 20.5 cm by 30.8 cm plastic tubs, placed under heat lamps. Each rearing tub contained 12 chicks (to duplicate natural brood conditions). Food and water was provided continuously.

Apparatus:

Testing was conducted in a circular arena, 160 cm in diameter, constructed out of wood and painted flat black. The

arena was surrounded by a wall 24 cm in height, lined with foam to attenuate echoes. Speakers were set into opposing sides of the wall and the entire wall was covered by a black curtain to shield the observer from the subject's view. Two rectangular approach areas were outlined by green tape on opposite sides of the arena. These approach areas comprise less than 2% of the total area of the arena. A third area, equidistant from both the speakers, was demarcated as the point at which the subjects are introduced into the arena at the beginning of the study (See Fig. 1).

Each of the two speakers in the arena was connected to a Tascam model 122-B cassette tape recorder located at the observer's control table. Two stopwatchs and one timer were also located on the control table to aid in the scoring. A 162 cm by 82 cm mirror was suspended at an angle from the ceiling above the testing arena. This allowed the experimentor to observe the subject in the testing arena without being seen by the subject.

Procedure:

All testing was done in a sound-attenuated room. Each chick was taken individually from its rearing room and transported to the testing room in a small plastic container. At the onset of a trial, the chick was placed at the start point, midway between the two speakers. The location of the stimuli provided to the subjects during each of the simultaneous choice tests was alternated between trials to prevent any side bias from affecting results. Three testers were used to prevent against possible experimentor bias affecting the results. During the 5 minute test, each subject was scored on both latency of approach and duration of time spent

in each of the approach areas (see Fig. 2a & 2B for a sample of data recording sheets).

Latency was scored as the amount of time (in seconds), from the begining of the trial, taken by the subject to approach each approach area. Duration was scored as how long (in seconds) the subject remained in each of the delineated areas. The subject had to remain in an approach area for at least 10 consecutive seconds for the score to be counted as a duration score; this criterion prevented any random movements from being counted as a response to the stimuli. If the subject did not enter one of the areas, the subject received a score of 300 seconds for latency (the length of the trial) and 0 seconds for duration for that stimulus. To determine if a preference was exhibited, the duration score on one side had to be more than double the score accrued on the other side. If the subject did not meet these criteria, "no preference" was scored.

Data Analysis:

The data of primary interest in each experiment was the measures of preference as scored by duration, for one or the other of the presented stimuli. Three measures were analyzed: 1) an individual preference, assigned to any subject that had a duration score for one side more than double the score on the other side. The significance of the preference shown by a group according to this criterion was evaluated by the binomial test. 2) difference in the latency and 3) duration of response to each type of stimuli. This data was evaluated by the Wilcoxon matched-pairs signed-ranks test. Mean and interquartile ranges of latency and

duration scores were also determined (see Lickliter & Gottlieb, 1985, 1987 for examples). The same scoring format was used in all experiments. Significance levels of $p < .05$ (two-tailed) were used throughout the study to evaluate results.

Chapter 3

Experiment I

Heaton, Miller and Goodwin (1978) demonstrated that incubator hatched bobwhite quail chicks show a high degree of responsiveness to their species-typical maternal call in both single call and simultaneous auditory choice tests. However, in the Heaton, Miller and Goodwin (1978) study, chicks were tested at only 24 hrs. following hatching. The purpose of this experiment was twofold: 1) to attempt to replicate the finding of Heaton et. al (1978), and 2) to assess whether the naive responsiveness of the quail chick to the species-specific maternal assembly call persists into later stages of postnatal development.

Methods:

Tapes of a bobwhite and a chicken maternal assembly call were used in this experiment. The tapes are copies of the original tapes used by Heaton et. al (1978) in their study. The bobwhite maternal assembly call has a repetition rate of 1.7 notes per second, with a major peak at 2350 Hz and minor peaks at 625, 750 and 4500 Hz. The duration of the call is 3.0 seconds. This call was recorded in a field near the nest around the time of nest exodus. The recording of the chicken maternal assembly call is comprised of a duration of 2.8 seconds, a repetition rate of 2.5 notes per second, and has a major peak at 775 Hz. This call was originally recorded by N.E. Collias (1956) in the context of a domestic chicken hen leading her chicks away from the nest. Prior

to testing the calls were adjusted using a General Radio Model 1933 sound level meter to a peak amplitude of 65 dB, measured at the point where the chick was introduced into the arena.

Two groups of naive chicks (one of 80, one of 87) were individually tested at 24, 48, 72 and 96 hours (20 chicks tested at each age group) following hatching. Group one was presented with the bobwhite maternal only. Group two was presented with the bobwhite maternal assembly call on one side of the testing arena and the chicken assembly call on the other side. The position of the call or calls were counter-balanced across subjects to prevent a possible side bias from affecting the results. Two groups (single test and simultaneous choice test) were tested because Gottlieb (1971a) proposed that the simultaneous choice test is a stronger test of preference than the single call test, since in a simultaneous choice test the chick must be able to demonstrate a preference for one call over the other, while in a single choice test, the chick may respond to the mere presence of auditory stimulation. Latency and duration of responsiveness to the calls were scored as described in the General Methods section.

Results and Discussion:

Chicks in Group 1 displayed a strong preference for the bobwhite maternal assembly call at 24, 48, 72 and 96 hrs. of testing (Table 1). These results clearly indicate that the maternal exodus call is able to elicit preferential responsiveness in naive bobwhite quail neonates, at least when no other competing

auditory stimulus is presented. However, this preference decreased over time.

Chicks in Group 2 displayed a significant preference for the bobwhite maternal call over the chicken call at both 24 and 48 hrs. of age. However, a significant preference was not seen at either 72 or 96 hrs. following hatching (see Tables 2 and 3). These results indicate that a naive auditory preference for the maternal call is reliably demonstrated by chicks in the period immediately following hatching as originally reported by Heaton, et al. (1978). However, this naive preference is apparently lost by 72 hrs. after hatching, suggesting that auditory stimulation is no longer sufficient, in and of itself, to elicit a maternal preference at later stages of postnatal development.

TABLE 1. Preference of Subjects in Choice Tests in Experiment I, Group 1.

Experimental Condition	Age (in hrs)	n	Preference: Bobwhite Call	Preference: No Preference
Naive Auditory tests for bobwhite call	24	20	18	2
	48	20	16	4
	72	20	12	8
	96	20	13	7

TABLE 2. Preference of Subjects in Simultaneous Choice Tests in Experiment I, Group 2.

			Preference		
Experimental Condition	Age (in hrs)	n	Bobwhite Call	Chicken Call	No Preference
Naive Auditory test between bobwhite call & chicken call	24	21	17*	0	4
	48	22	14 *	1	7
	72	23	7	5	11
	96	21	0	0	21

* $p < 0.001$ (binomial test)

TABLE 3. Medians of Latency and Duration of Response by Subjects in Simultaneous Choice Tests in Experiment I, Group 2.

Age (in hrs)	n	Latency (in sec)		Duration (in sec)	
		Bobwhite Call	Chicken Call	Bobwhite Call	Chicken Call
24	21	88*** (29-127)	240 (251-300)	109*** (56-178)	0 (0-0)
48	22	137** (39-300)	248 (255-300)	94*** (0-182)	5 (0-0)
72	23	190 (41-300)	232 (169-300)	34* (0-93)	14 (0-24)
96	21	264 (293-300)	270 (300-300)	0 (0-0)	0 (0-0)

Medians and interquartile ranges are given as summaries of group performance only. Significance levels are based on the Wilcoxon test, which compares distribution of scores, not median values.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

(Wilcoxon tests; shorter latency and longer durations are indicated.)

Chapter 4

Experiment II

Experiment IIA:

The results of Experiment I indicate that the bobwhite quail chick displays a naive auditory preference for its species-typical maternal assembly call, at least during the first 48 hrs. following hatching. However, no studies have specifically investigated whether a naive visual preference for features of the maternal hen also exists. Thus, in this experiment chicks were assessed for their naive responsiveness to visual features of the maternal complement.

Methods:

Two taxidermically prepared natural models of quail hens were used in this experiment. One was a stuffed model of an adult bobwhite hen, the other a stuffed model of a scaled quail hen (Callipepla squamata), a species of quail which is often found in the same locale as the bobwhite quail.

Eighty-three naive chicks were individually tested at either 24, 48, 72, or 96 hrs. after hatching in a simultanous choice test between the two hen replicas. The side of presentation of each of the models was counter-balanced across subjects to prevent any possible side bias from affecting the results. Choice, latency and duration were scored as described in the General Methods section.

Results and Discussion:

No significant preference was noted for either the stuffed model of the bobwhite hen or the stuffed scaled hen at 24, 48, 72 or 96 hrs. after hatching (see Tables 4 and 5). These results clearly indicate that a naive visual preference does not exist for features of the maternal hen, at least up to 96 hrs. following hatching.

In naturalistic environment it would be potentially important for the neonatal bobwhite quail to be able to differentiate between the bobwhite quail hen and the scaled quail hen, since they can be found in the same area. The results of this experiment and Experiment I indicate that neither auditory nor visual stimuli presented alone are sufficient to allow the young chicks to differentiate the maternal bobwhite hen from the other hens after 48 hrs. of age. This suggests that the neonatal chicks must rely on some other form of (or combination of) stimulation. The next experiment was designed to determine if a combination of auditory and visual stimulation might elicite preferential responsiveness at later stages of postnatal development.

TABLE 4. Preference of Subjects in Simultaneous Choice Tests in Experiment IIA.

			Preference		
Experimental Condition	Age (in hrs)	n	Bobwhite Hen	Chicken Hen	No Preference
Naive Visual test between bobwhite hen & scaled hen	24	20	2	3	15
	48	23	6	4	13
	72	20	3	2	15
	96	20	1	2	17

TABLE 5. Latency and Duration of Response by Subjects in Simultaneous Choice Tests in Experiment IIA.

		Latency (in sec)		Duration (in sec)	
Age (in hrs)	n	Bobwhite Hen	Scaled-Hen	Bobwhite Hen	Scaled Hen
24	20	213 (108-300)	196 (98-300)	13 (0-36)	16 (0-33)
48	23	209 (46-300)	237 (255-300)	34 (0-83)	28 (0-32)
72	20	250 (284-300)	233 (142-300)	12 (0-15)	15 (0-19)
96	20	273 (300-300)	261 (300-300)	8 (0-0)	11 (0-0)

Medians and interquartile ranges are given as summaries of group performance only. Significance levels are based on the Wilcoxon test, which compares distribution of scores, not median values.

Experiment IIB:

This experiment assessed whether the naive auditory preference for the maternal call seen at 24 hrs. and 48 hrs. following hatching could be reinstated by the addition of species-specific visual stimulation. Fabricius (1951) was among the first to observe that a combination of auditory and visual stimulation increases the likelihood of eliciting 'following' in young domestic chicks. Since auditory cues appear to lose their salience by 72 hrs. posthatch (Experiment I) and visual cues alone are not sufficient to direct the chick's early social preferences (Experiment IIA), it seemed possible that chicks might require combined audio-visual cues to direct their perceptual preferences in the days following hatching.

Methods :

Taped recordings of the bobwhite and the chicken maternal assembly calls and a stuffed model of the bobwhite maternal hen were used in this experiment. The features of the calls are described in Experiment I and the General Methods section.

Forty-one naive young chicks were tested at 72 hrs. and 96 hrs. after hatching (the time that the naive auditory preference is no longer noted). Chicks were presented with a simultanous choice tests between the chicken maternal assembly call and the bobwhite maternal assembly call paired with the stuffed model of the bobwhite maternal hen. Choice, latency and duration were scored as described in the General Methods section.

Results and Discussion:

Subjects displayed a significant preference for the bobwhite maternal call paired with the stuffed model of the bobwhite hen over the chicken maternal call at both 72 and 96 hrs. of age (see Tables 6 and 7).

These results indicate that the naive auditory preference for the maternal can be reinstated with the addition of visual stimulation. While auditory stimulation alone is insufficient to elicit responsiveness, the addition of the visual components of the hen apparently serves to maintain a preference for the maternal hen.

However, it is possible that the young quail may simply be responding to the fact that the amount of stimuli made available in this experiment were not equivalent. Namely, on one side of the arena combined audio-visual stimuli was presented, and on the other, only auditory simulation was available in the test situation. The question also remains whether the hatchlings continue to favor auditory cues over visual cues when choosing to direct their social preferences at 72 hrs. and 96 hrs .following hatch. These concerns are addressed in the subsequent experiments.

TABLE 6. Preference of Subjects in Simultaneous Choice Tests in Experiment IIB.

			Preference		
Experimental Condition	Age (in hrs)	n	Bobwhite A-V	Chicken Call	No Preference
Simultaneous test between bobwhite -AV & chicken call	72	20	17*	0	3
	96	21	16*	1	4

* $p < 0.001$ (binomial test)

TABLE 7. Latency and Duration of Response by Subjects in Simultaneous Choice Tests in Experiment IIB.

		Latency (in sec)		Duration (in sec)	
Age (in hrs)	n	Bobwhite A-V	Chicken Call	Bobwhite A-V	Chicken Call
72	20	114** (22-230)	284 (300-300)	156** (80-271)	0 (0-0)
96	21	117* (23-300)	287 (300-300)	139** (17-248)	8 (0-0)

Medians and interquartile ranges are given as summaries of group performance only. Significance levels are based on the Wilcoxon test, which compares distribution of scores, not median values.

* $p < 0.01$
** $p < 0.001$

(Wilcoxon tests; shorter latency and longer durations are indicated.)

Chapter 5
Experiment III

While the previous experiment was designed to assess the importance of visual stimulation to early auditory preferences, it does not specifically test the cue hierarchy hypothesis proposed by Johnston and Gottlieb (1985). Thus, in this experiment chicks were presented with both visual and auditory maternal cues in the simultanous choice test, but the situation was arranged in such a way that the available auditory cues did not permit a choice to be made. In other words, auditory cues were ambiguous in the testing situation. Under these conditions, the "cue hierarchy" hypothesis would predict that a choice based on available visual cues should be made (i.e., if the auditory cues are available, use them; if not available, use visual cues.).

Methods:

The recording of the bobwhite maternal assembly call, as well as the stuffed models of the bobwhite maternal hen and the scaled quail, were used in this experiment. Forty-two naive young chicks were tested at 72 hrs. and 96 hrs. after hatching (the time that the auditory preference is no longer noted). Chicks were presented with a simultanous choice between the bobwhite maternal assembly call paired with the stuffed model of the bobwhite hen and the bobwhite maternal assembly call paired with the stuffed model of the scaled quail (that is, both hens emitting the same call). Presentation of the stimuli were counterbalanced

across subjects to prevent a possible side bias from affecting the results. The choice, duration and latency of response by the chicks were scored as described in the General Methods section.

Results and Discussion

As illustrated in Tables 8 and 9, subjects displayed a significant preference for the stuffed model of the bobwhite hen paired with the bobwhite call over the stuffed model of the scaled hen paired with the bobwhite call at both 72 and 96 hrs. of age following hatching.

These results serve to support the cue hierarchy hypothesis as originally proposed by Johnston and Gottlieb (1985), in that when auditory cues were ambiguous or not reliable, the young chicks depended on visual cues to direct their social preference. However, the results of this experiment do not provide any evidence as to which, if any, of the two forms of sensory stimulation were dominant at 72 and 96 hours of age. The next experiment was designed to assess this question.

TABLE 8. Preference of Subjects in Simultaneous Choice Tests in Experiment III.

			Preference		
Experimental Condition	Age (in hrs)	n	Bobwhite Call & Hen	BWhite Call & ScaledHen	No Preference
Simultaneous choice test between BSBC & SSBC	72	22	19*	1	2
	96	20	17*	0	3

* $p < 0.001$ (binomial test)

TABLE 9. Latency and Duration of Response by Subjects in Simultaneous Choice Tests in Experiment III.

		Latency (in sec)		Duration (in sec)	
Age (in hrs)	n	Bobwhite Call & Bobwhite Hen	Bobwhite Call and Scaled-Hen	Bobwhite Call & Bobwhite Hen	Bobwhite Call & Scaled Hen
72	22	123* (44-202)	216 (70-300)	74** (28-107)	6 (0-12)
96	20	139** (85-233)	277 (300-300)	49** (16-101)	3 (0-0)

Medians and interquartile ranges are given as summaries of group performance only. Significance levels are based on the Wilcoxon test, which compares distribution of scores, not median values.

* $p < 0.01$
** $p < 0.001$

(Wilcoxon tests; shorter latency and longer durations are indicated.)

Chapter 6

Experiment IV

This experiment was designed to assess the dominance of auditory cues and visual cues in directing the early social preferences of hatchlings. The importance of the auditory modality during the earlier stages of development has been shown in Experiments I and II. This experiment attempts to assess which sensory modality is dominant when stimuli from both modalities are required to elicit a preferential response from the young quail neonate. Specifically, chicks were presented with both auditory and visual cues, but in such a manner that they were forced to choose one cue over the other in order to register a species-specific preference.

Methods:

Taped recordings of the bobwhite and the chicken maternal assembly call, as well as the stuffed models of the bobwhite and scaled quail maternal hens were used in this experiment.

Forty naive chicks were tested at 72 hrs. and 96 hrs. after hatching (the time that the maternal auditory preference is no longer noted). Chicks were presented with a simultanous choice test between the model of the scaled quail hen emitting the bobwhite maternal assembly call and the bobwhite quail hen both emitting the chicken maternal assembly call (that is, the correct hen emitting an incorrect call and the incorrect hen emitting the

correct call). The presentation of the audio-visual stimuli were counter- balanced between subjects to prevent a possible side bias from affecting the results. Choice, latency and duration were scored as described in the General Methods section.

Results and Discussion

Subjects displayed a significant preference for the bobwhite call paired with the scaled hen over the chicken call paired with the bobwhite hen at both 72 and 96 hrs. of age (see Tables 10 and 11). These results indicate that auditory cues remain dominant over visual cues, at least at these stages of postnatal development.

The auditory system has a longer history of use than does the visual system, in that it becomes functional in prenatal development prior to the later maturing visual system. Further, the auditory system appears to have a more extensive history of use, as related work has demonstrated that the precocial avian neonate receives auditory stimulation while still in the egg. These facts may explain why the auditory system remains dominant up to 96 hrs. of age.

TABLE 10. Preference of Subjects in Simultaneous Choice Tests in Experiment IV.

			Preference		
Experimental Condition	Age (in hrs)	n	Scaled Hen BWhite Call	BWhite Hen Chicken Call	No Preference
Simultaneous choice test between BCSS & CCBH	72	20	18*	0	2
	96	20	17*	0	3

* $p < 0.001$ (binomial test)

TABLE 11. Latency and Duration of Response by Subjects in Simultaneous Choice Tests in Experiment IV.

		Latency (in sec)		Duration (in sec)	
Age (in hrs)	n	Bobwhite Call & Scaled Hen	Bobwhite Hen and Chicken Call	Bobwhite Call & Scaled Hen	Bobwhite Hen & Chicken Call
72	20	121* (50-209)	300 (300-300)	50* (15-80)	0 (0-0)
96	20	141* (59-200)	281 (300-300)	58* (23-125)	3 (0-0)

Medians and interquartile ranges are given as summaries of group performance only. Significance levels are based on the Wilcoxon test, which compares distribution of scores, not median values.

* $p < 0.001$ (Wilcoxon tests; shorter latency and longer durations are indicated.)

Chapter 7
General Discussion

Under normal circumstances, a neonatal quail chick receives information in several sensory modalities and must process that information appropriately to control its behavior in an adaptive manner. Two modalities known to be important for the control of filial behavior are the visual and auditory modalities, and in this study I have shown some of the ways in which they interact in the course of early postnatal development.

The sequence of the development of the sensory modalities occurs in a specific order, as shown by Gottlieb (1971). This sequence holds true for both mammals and birds. However, research on this topic has, for the most part, been descriptive in nature. Little work has addressed "why" this sequence exists. At least two explanations may be brought forward for the existence of an invariant sequence of sensory system development. Ontogenically, some sensory systems are more complex than others, and therefore they may require more time and experience to develop fully. A phylogenic or evolutionary explanation can also shed light on the above question. Some systems have a longer evolutionary history, and therefore may develop earlier in the sequence. A complete answer to the question of "why" there is a sequence at all in sensory system development is probably a combination of these two explanations. The same can be said of the question of whether all systems start to develop at the same time or at different times. Since each system is a result of both

maturation and experience, each system relies on interaction with other systems to develop correctly. As each system receives more experience, it develops further and becomes more capable of processing relevant or system-specific information.

The ways in which the sensory systems develop has interesting implications for the study of interaction between phenotype and environment. The sensory systems develop in accordance with the type of environmental experience which they are provided. Yet, the salience of the stimuli vary in accordance with the level of development of the sensory system. This close interaction exemplifies the coactional relationship between phenotype and environment.

The findings of this study, summarized in Figure 3, also have several interesting implications for our understanding of the development of filial behavior and attachments in precocial avian neonates. As demonstrated in Experiments I and IIa, the maternal call is an extremely compelling stimulus for a young quail hatchling, easily outweighing the effects of visual cues during the first 1-2 days of postnatal life. As the hatchling grows older, its visual, motor, and/or social experience supports the progressive maturation of its nervous system, so that by about 3-4 days following hatching, the quail neonate is better able to use visual information to control its filial behavior (Experiments IIb, III). Even at this later age, however, the hatchling will respond to species-typical auditory information in preference to visual information, if the auditory information permits a choice to be made (Experiment IV). On the other hand, if auditory cues are

ambiguous, then the quail chick will respond on the basis of visual cues (Experiment III), as predicted by the cue-hierarchy hypothesis of Johnston and Gottlieb (1985).

Quail embryos receive prenatal auditory stimulation from respiration, self-produced vocalizations, and those of clutchmates during the days preceding hatching. No equivalent visual stimulation is available at this time. Therefore, two conditions exist which apparently serve to foster a naive preference for species-specific auditory stimuli: 1) the earlier development of the auditory system when compared to the visual system, and 2) the longer stimulation history of the auditory system. This prenatal relationship between these sensory modalities appears to continue to influence their relationship following hatching.

Imprinting studies have traditionally stressed the importance of visual features in the formation of postnatal social preferences. The results reported here suggest that previous views of imprinting have been based on potentially incomplete information. Visually presented information is salient, but only if a) species-specific auditory information is not available or is ambiguous, and b) if the visual system has had sufficient time and experience in which to become functional. It is important to note that nearly all research on perceptual development in precocial birds has been and continues to be concerned only with the functional characteristics of single sensory modalities (i.e., Lickliter & Gottlieb, 1985; Kent, 1987). Few, if any, studies before this one have specifically explored the possible existence of sensory dominance and its relationship to intersensory functioning. The

fact that there is a hierarchy in the functional priority of the sensory systems of precocial birds early in postnatal development has important implications for the processing of multisensory information in the immediate postnatal period and in turn, for the way in which the precocial neonate learns about its social and physical environment. Clearly, these findings also force us to reconsider and reevaluate many of the traditional assumptions concerning the imprinting process; in particular, they argue that how the precocial avian neonate learns to differentiate between its maternal hen and other conspecifics during the first days of postnatal life is more complex and dynamic than previously characterized.

In a similar vein, the entire attachment process between the young of any given species and its mother can be characterized as dynamic in nature. In short, the components underlying attachment may change over development as the various sensory systems mature and different sensory cues become salient to the developing young. As a result, what can be considered to mediate attachment at any one given stage of development may not necessarily mediate attachment at a different stage of development.

Turkewitz and Kenny (1982) recently proposed the possible adaptive importance of limitations in sensory function seen in early development. They suggest that limited sensory functioning serves to reduce sensory input, which results in a decrease in competition from other emerging systems at critical ontogenic stages. They cite evidence to suggest that if normally

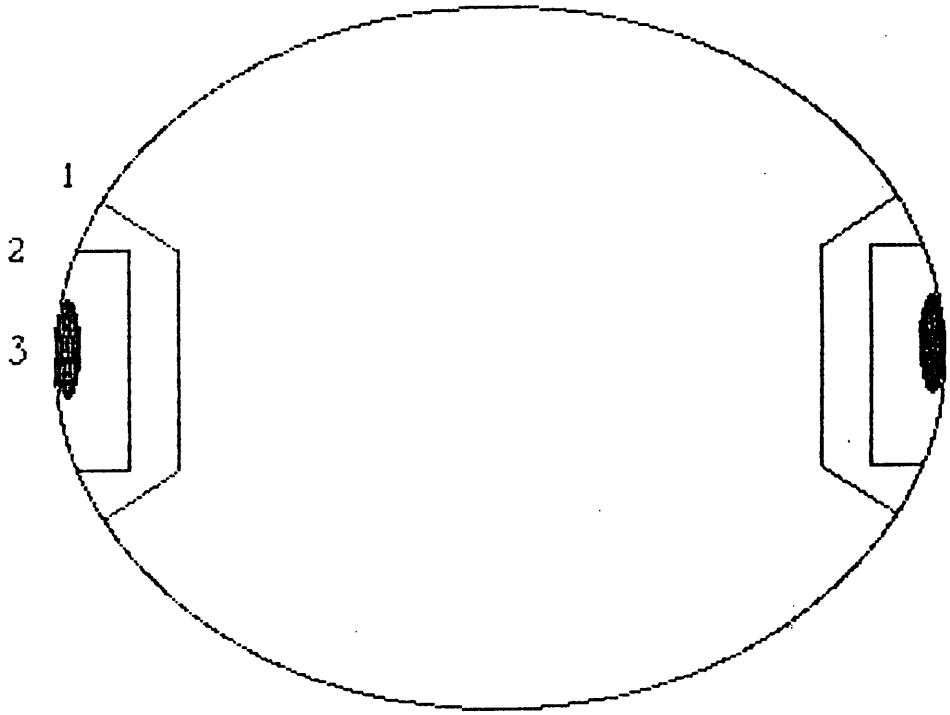
developing sensory functional patterns are altered, neuronal organization may also change. This interdependence of sensory functions is supported by a number of recent studies. For example, Kenny and Turkewitz (1986) studied the effect of early visual stimulation on the development of homing behavior in rat pups. Kenny and Turkewitz concluded that the early increase in visual stimulation during development changed the distribution of attention to various aspects of the environment and in all probability, altered the relationship betweeen sensory systems. These results and the results reported here have potential implications for human research as well. For example, a study by Lewkowicz and Turkewitz (1981) showed that stimulation in one sensory modality influenced the response to stimulation in a second modality by changing the infant's state of arousal. They found that newborn infants attend to quantitative variations in stimulation of both stimulus intensity and organismic factors. More recently, Lewkowicz (1988) has demonstrated dominance of the auditory sensory modality over the visual in 6 month old human infants. This auditory dominance is apparently lost by 10 months of age, suggesting that intersensory relationships are undergoing relatively rapid changes during the first year of life in human infants.

The findings of this study suggest that there is much research to be done in the area of interdependence of sensory functions. Important questions include: What are the prenatal precursors which allow for the proper sequential development of the sensory modalities? What is the order in which these experiential precursors are made available to the young of any

given species? What is the fetus and neonate able to perceive? In addition, this type of research, which lies in the domain of comparative developmental psychology, may provide a potentially important source of comparative data for the growing body of work concerned with sensory dominance in the precocial human infant (e.g., Lewkowicz, 1988).

It is not currently known how the interaction between visual and auditory stimulation changes as the chick matures beyond 4 days of age, nor what other sources of information may come to control its behavior. In any event, the results reported here serve to illustrate the close interaction between maturation and experience that is involved in the early development of behavior. This is a point that was especially emphasized in the theoretical writings of Schneirla (1966) and Kuo (1967). Each of these authors argued that the contributions of maturation and experience to development could not be kept distinct, but must be viewed as coacting in ontogeny to produce behavior.

The Testing Arena



1 : Response Area

2 : Area for Stuffed Hen

3 : Hidden Speaker

* NOTE: ARENA IS ROUND NOT OVAL

Fig. 1

SAMPLE OF A HATCH RECORDING SHEET

GROUP:

N =

DAY 23:00 :

DATE	BIRD #	I.D.	TIME	AGE	REARING CONDITION	COMMENTS

Fig. 2A

SAMPLE OF AN INDIVIDUAL DATA RECORDING SHEET

GROUP: _____ WEEK: _____ SUBJECT: _____

DAY 23: _____ HATCHED: _____ DEV AGE: _____

TEST 1

DATE: _____ TIME: _____ POST AGE: _____

CALL A: _____ LAT 1: _____

DUR 1: _____

CALL B: _____ LAT 1: _____

DUR 1: _____

Fig. 2B

Experiment No.		Age of Testing (hrs.)	Simultaneous Choice	
			Side A	Side B
I	Group 1	24, 48, 72 & 96	▲	
	Group 2	24*, 48*, 72 & 96	▲	■
II A		24, 48, 72 & 96	●	◆
II B		72* & 96*	▲ ●	■
III		72* & 96*	▲ ●	▲ ◆
IV		72* & 96*	▲ ◆	■ ●

▲ - Bobwhite Maternal Assembly Call

● - Stuffed Model of Bobwhite Quail Hen

■ - Chicken Maternal Assembly Call

◆ - Stuffed Model of Scaled Quail Hen

* - Significant Preference Noted

Fig. 3

References

Bateson, P. P. G. (1966). The characteristics and context of imprinting. Biological Review, 41: 177-220.

Collias, N. E. and Collias, E. C. (1956). Some mechanisms of family integration in ducks. Auk, 73: 378-400.

Evans, R. M. (1973). Differential responsiveness of young ring-billed gulls and herring gulls to adult vocalizations of their own and other species. Canadian Journal of Zoology, 51: 759-770.

Fabricius, E. (1951). The behavior of young Anatide. Acta Zoologica Fennica, 68: 1-178.

Fischer, G. J. (1966). Auditory stimuli in imprinting. Journal of Comparative Physiological Psychology, 61: 271-273.

Gottlieb, G. (1968). Prenatal behavior of birds. Quarterly Review of Biology, 43: 148-174.

Gottlieb, G. (1971a). Development of Species Identification in Birds. Chicago: University of Chicago Press.

Gottlieb, G. (1971b). Ontogenesis of sensory function in birds and mammels. In E. Tobachh, L.R. Aronson, and E. Shaw, The Biopsychology of Development. New York: Academic Press. pp 67-128.

Heaton, M. B., & Galleher, E. (1981) Prenatal auditory discrimination in the bobwhite quail. Behavioral and Neural Biology, 31: 242-246.

Heaton, M. B., Miller, D. B. and Goodwin, D. G. (1978). Species-specific auditory discrimination in bobwhite quail neonates. Developmental Psychobiology, 11: 13-21.

Johnston, T. D. and Gottlieb, G. (1981). Visual preferences of imprinted ducklings are altered by the maternal call, Journal of Comparative Physiological Psychology, 95: 663-675.

Johnston, T. D. and Gottlieb, G. (1985). Development of visually controlled maternal preferences in Peking ducklings. Developmental Psychobiology, 9: 23-36.

Joyner, D. E. (1977). Behavior of ruddy duck broods in Utah. Auk, 94: 378-400.

Kenny,P.A., and Turkewitz, G., 1986, Effects of unusually early visual stimulation on the development of homing behavior in the rat pup, Developmental Psychobiology, 19: 57-66.

Kent, J. P. (1987) Experiments on the relationship between the hen and the chick: The role of the auditory mode in recognition. Behaviour, 102: 1-14.

Kuo, Z. Y. (1967). The Dynamics of Behavioral Development. New York: Plenum Press.

Lewkowicz, D. J. (1988). Sensory dominance in infants: In six-month-old infants' responce to auditory-visual compounds. Developmental Psychobiology, 24(2): 155-171.

Lewkowicz, D.J. and Turkewitz, g., (1981). Intersensory interaction in newborns modification of visual preference following exposure to sound. Child Development, 52:

Lickliter, R. and Gottlieb, G. (1985). Social interaction with siblings is necessary for visual imprinting of species-specific maternal preferences in ducklings (*Anas platyrhynchos*). Journal of Comparative Psychology, 99: 371-379.

Lickliter, R. and Gottlieb, G. (1987). Retroactive excitation: Posttraining social experience with siblings consolidates maternal imprinting in ducklings (*Anas platyrhynchos*). Journal of Comparative Psychology, 101: 40-46.

Lorenz, K. Z. (1937). The companion in a bird's world. Auk, 54: 245-273.

Miller, M. B. & Gottlieb, G. (1981) Maternal vocalizations of mallard ducks (Anas platyrhynchos). Animal Behaviour, 26:

1178-1194.

Porter, R. H. and Stettner, L. J. (1968). Visual and auditory influences on following responses of bobwhite quail. Journal of Comparative and Physiological Psychology, 66: 808-811.

Schneirla, T. C. (1966). Behavioral development and comparative psychology. Quarterly Review of Biology, 41: 283-302.

Storey, A. E. and Shapiro, L. J. (1979). Development of preferences in white Peking ducklings for stimuli in the natural post-hatch environment. Animal Behaviour, 27: 411-416.

Turkewitz,G., and Kenny, P.A., (1982). Limitations on input as a basis for neural organization and perceptual development: A preliminary theoretical statement. Developmental Psychobiology,15: 357-368.

Vince, M. A. (1972). Communication between quail embryos and the synchronization of hatching. Proceedings of the XV International Ornithological Congress. pp. 357-362.

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