

Intersensory Experience and Early Perceptual Development: The Role of Spatial Contiguity in Bobwhite Quail Chicks' Responsiveness to Multimodal Maternal Cues

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In contrast to the large body of work on young infants' capacity to perceive temporally based intersensory relations, little research has been done on the role of spatial contiguity in the development of audio-visual integration. This study examined the effects of early postnatal sensory experience on an avian neonate's responsiveness to the spatial contiguity between maternal auditory and visual cues. Specifically, we assessed whether a bobwhite quail chick's ability to respond to the correspondence between the location of auditory and visual events is affected by its sensory-stimulation history. Results revealed that chicks denied species-typical auditory or visual experience in the period immediately following hatching showed altered patterns of responsiveness to maternal auditory and visual cues. In particular, chicks that received modified postnatal sensory experience demonstrated a higher tolerance for audio-visual spatial discrepancy than did control chicks. These results provide evidence of the important role of sensory experience in the emergence of intersensory integration during the perinatal period and highlight the role of spatial information in early perceptual responsiveness to maternal cues. © 1996 John Wiley & Sons, Inc.

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The perceptual world of the infant is composed primarily of multimodal sensory stimulation. As a result, the infant is provided with a set of sensory inputs that are correlated in space and time. For example, when an infant encounters a caretaker's face, he or she simultaneously sees and hears various amodal cues (e.g., visible and audible features with the same temporal attributes, such as synchrony, duration, or tempo) and modality-specific cues (e.g., visible and audible affective attributes, such as smiling or pitch modulation) emanating from the same spatial location. To date, most research on the development of human audio-visual integration has focused on infants' responsiveness to the temporal contiguity of sensory stimulation (Lewkowicz & Lickliter, 1994a; Rose & Ruff, 1987) and it has become clear that the capacity to detect certain types of temporally based amodal relations is present within the first 6 months following birth (Bahrick, 1987; Bahrick & Pickens, 1994; Lewkowicz, 1991, 1994). In contrast to the relatively large body of work on young infants' capacity to perceive temporally based intersensory relations, relatively little research has been done on the role of spatial contiguity in the development of audio-visual integration (see Field, 1987; Morrongiello, 1994 for reviews).

The few studies that have investigated human infants' responsiveness to intersensory spatial contiguity present a mixed set of results (e.g., Aronson & Rosenbloom, 1971; Condry, Haltom, & Neisser, 1977; McGurk & Lewis, 1974). The one clear finding that emerges from these studies, however, is that young infants have a relatively high tolerance for audio-visual spatial discrepancy (Field, DiFranco, Dodwell, & Muir, 1979; McGurk, Turnure, & Creighton, 1977). In fact, as pointed out by Field (1987), much research on infants' perception of auditory-visual events has relied on this tolerance of spatial disparity to explore other related characteristics of intersensory perception (e.g., Kuhl & Meltzoff, 1982; Lewkowicz, 1992; Spelke, 1979). Despite this tolerance for audio-visual spatial discrepancy, both 4- and 6-month-old infants have been shown to relate auditory and visual information and to perceive sound as an attribute of a specific object when the sound and object are both spatially and temporally congruent (Lawson, 1980; Lyons-Ruth, 1977). It is important to note, however, that neither spatial nor temporal congruence alone appears to be sufficient to support young infants' learning about sight-sound correspondences (but see Spelke, 1981 for an alternative view).

More recently, Morrongiello and her colleagues (Morrongiello, 1994; Morrongiello, Fenwick, & Nutley, 1994) have suggested that spatial and temporal contiguity are likely to interact to influence infants' early intersensory perception. In addition, they provide evidence that spatial contiguity becomes increasingly important over the course of development, with older infants exhibiting a lower tolerance for audio-visual disparity when compared to younger infants. Specifically, Morrongiello et al. (1994) reported age-related changes between 4 and 8 months of age on the impact that spatial co-location has on infants' successful formation of sight-sound associations. Although not yet examined systematically, this developmental trend of a greater demand for spatial co-location is likely the result of infants' increasing experience with multimodal objects and events over the course of the months following birth.

This developmental trend toward greater reliance on spatial concordance reaches its mature form in adults, who exhibit a strong propensity for unifying the auditory and visual attributes of a stimulus when they are spatially displaced with respect to one another (see Welch & Warren, 1986 for a review). Perhaps the best known demonstration of the adult's propensity to unify spatially discrepant audio-visual sources of information is the so-called "ventriloquism" effect (Jack & Thurlow, 1973), in which adults

tend to hear the voice of the ventriloquist as emanating from the mouth of the puppet. Experimental investigations of this phenomenon have shown that in most cases the location of a visual stimulus will readily modify the perceived location of an auditory stimulus (Warren, Welch, & McCarthy, 1981).

The adult's strong propensity to unify spatially disparate auditory and visual sources of stimulation and the finding of infants' increasing use of spatial cues for forming object-sound relations raises an important developmental question. Namely, what experiences during early development contribute to the emergence of audio-visual integration of spatial information? Although a large literature on adults' adaptation to rearrangement of sensory inputs has provided some clues to the role of experience in the perception of intersensory unity (Welch, 1978; Welch & Warren, 1986), the applicability of this literature to early development is open to question because nearly all this work is derived from adult subjects. Additional studies of the spatial rearrangement of sensory inputs during early development are sorely needed to advance our understanding of the role of experience in the emergence of intersensory integration. These types of studies are, however, difficult to undertake with human infants and the use of comparative approach offers a useful and potentially powerful step in experimentally examining these issues. In particular, the use of animal species with relatively rapid rates of sensory system development allows the systematic manipulation of the intra- and extra-organismic factors thought to be involved in the development of audio-visual integration early in life. Lewkowicz and Lickliter (1994b) have recently argued that this kind of convergent-operations approach is a particularly effective method for discovering the developmental processes underlying the development of intersensory integration.

Evidence derived from both behavioral and neurophysiological studies of different altricial animal species suggests that spatial contiguity plays a key role in intersensory perception. Behavioral studies with both young birds and adult mammals have shown that the spatial contiguity of auditory and visual information is critical for the organism's veridical perception of its immediate environment (Knudsen, 1985; Stein & Meredith, 1993). On the neurophysiological level, studies have shown that this behavioral requirement for spatial contiguity goes hand in hand with the alignment of neural receptive field maps in the different sensory modalities (Knudsen & Knudsen, 1985; Stein & Meredith, 1993, Stein, Meredith, & Wallace, 1994). Of particular interest for the present study are the results from Knudsen's work with young altricial barn owls, showing activity-dependent neural processes involved in responsiveness to multimodal information. For example, Knudsen (1983) raised developing barn owls that had one ear plugged, changing the relative timing and intensity of inputs to the two ears and thereby altering the bird's auditory receptive fields in the optic tectum, the brain region involved in the localization of sensory events. Despite the fact that these ear-occluded birds had to function on the basis of abnormal binaural cues, they nonetheless developed an auditory map in surprisingly good register with their visual map (Knudsen, 1983). However, when the ear plug was removed after the owls became adults, the input from the previously deprived ear was far stronger than when the auditory map was first formed, resulting in misaligned auditory and visual spatiotopic maps. Correction of this misalignment was found to be dependent on the availability and use of visual spatial cues. If no visual information was provided the birds (i.e., the owl was reared in the dark), no corrective reorganization was observed (Knudsen, 1985). Presumably, under normally occurring conditions, the owl's map alignment reflects ongoing experience with auditory and visual stimuli that are concurrently produced by the same object or event and are thus reliably linked in time and space.

The present study is a further application of a convergent-operations approach to the investigation of the effects of early experience on the development of spatial intersensory integration. We studied a highly precocial avian species, the bobwhite quail, to determine how early experience can affect the neonate's behavioral responsiveness to the spatial contiguity of maternal audio-visual cues. Specifically, we rearranged the spatial relation between the species-specific auditory and visual cues normally present in hatchlings' postnatal environment and assessed chicks' subsequent pattern of responsiveness to maternal multimodal cues. Various aspects of the normal or species-typical pattern of bobwhite chicks' responsiveness to maternal audio-visual cues are already known and have been described in some detail (e.g., Lickliter, 1993, 1994; Lickliter & Banker, 1994; Lickliter & Virkar, 1989). Thus, it is clear that newly hatched chicks initially rely on maternal auditory vocalizations to direct their early filial responsiveness, but by several days following hatching chicks require combined maternal auditory and visual cues to direct their social preferences. What is currently unknown, however, is what role spatial contiguity plays in the bobwhite chick's early intermodal responsiveness.

General Methods

Certain features of our experimental design were common to all experiments, so we describe these first before presenting the particular details of each experiment.

Subjects

The subjects were 240 incubator-reared bobwhite quail chicks (*Colinus virginianus*). Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Petersime Model I incubator, maintained at 37.5°C and 85–90% relative humidity. After 20 days of incubation, the eggs were transferred to a hatching tray located at the bottom of the incubator. To control for possible effects of variations in developmental age, only those birds that hatched between the last half of Day 22 and the first half of Day 23 of incubation were used as subjects. The embryo's age is calculated on the basis of the first day of incubation as Day 0, the second 24 hr of incubation as Day 1, and so on. The possible influence of between-batch variation in behavior was controlled by drawing subjects for each experimental group from three or more different batches (weeks) of eggs. As a result of their incubator rearing, the only sounds to which the hatchlings had been exposed prior to the time of experimental manipulation or the time of testing were their own embryonic and postnatal vocalizations (and those of their broodmates) and the low-frequency background noises emanating from the incubator fan and motor. Following hatching, subjects were group-reared in large plastic tubs (45 × 25 × 15 cm) containing 10–12 same-aged chicks to mimic naturally occurring brood conditions (Stokes, 1967). All chicks were thus maternally naive prior to testing. The sound-attenuated room in which the hatchlings were reared was illuminated by a 100-W brooder lamp suspended above the plastic rearing tubs, which maintained an ambient air temperature of approximately 30°C. Food and water were continuously available throughout the duration of each experiment.

Testing

Testing was conducted postnatally at 48, 72, or 96 hr (± 3 hr) of age in a test apparatus described in detail in previous studies (Banker & Lickliter, 1993; Lickliter & Virkar, 1989). In brief, each chick was tested once in a 5-min simultaneous-choice

test in a large, circular arena, 160 cm in diameter, surrounded by a black curtain which shielded the observer from the subject's view. In these trials, each quail chick was placed in the test apparatus equidistant from opposing approach areas. These rectangular approach areas comprised less than 10% of the total area of the arena and were delineated by green lines painted on the floor of the arena. Each approach area contained a dome-radiator speaker which was hidden by the curtain and connected to a Tascam model 122-B cassette tape recorder (to allow for auditory stimulation) and a taxidermically prepared model of an adult quail hen (to provide visual stimulation). The location of the particular auditory and visual stimuli presented during testing in each experiment was alternated between chicks to prevent any possible side bias from influencing results. During testing, the latency and duration of each chick's response to the opposing stimuli were recorded by trained observers blind to the experimental design of the particular experiment. Latency of response was scored as the amount of time (in seconds) elapsed from the onset of the trial until the subject entered an approach area. Duration of response was scored as the cumulative amount of time (in seconds) the bird remained in an approach area during the 5-min test. When, over the course of the 5-min trial, a chick stayed in one approach area for more than twice the time it spent in an opposing approach area, a preference for that stimulus array was recorded. Some birds entered and spent time in both approach areas during a test without showing a preference for either one. This behavior was scored as *No Preference* in the tables showing test results. The subject had to remain in an approach area for at least 10 consecutive s for a score to be counted; this criterion prevented any random movements from being counted as a response to the presented stimuli. If a subject did not enter either approach area or did not accumulate a duration score of 10 consecutive s for at least one approach area over the course of the trial, it was considered a nonresponder and received a score of 300 s for latency (the length of the trial) and 0 s for duration for both test stimuli.

Data Analysis

The primary data of interest in each experiment were the measures of preference (derived from latency and duration of response) for the auditory and visual stimuli presented during the trials. Three such measures of preference were utilized: (a) differences in the latency and (b) differences in the duration of time spent in proximity to each stimulus array by a subject in a group was evaluated by the Wilcoxon matched-pairs signed-ranks test, and (c) an individual preference, assigned to any subject that stayed in one approach area for more than twice as long as the other, was evaluated by the chi-square test. As it turned out, the results of the experiments were so clear using this preference measure that in order to conserve space, the latency and duration measures are not presented in any detail. In all cases, preference was perfectly correlated with differences (or no differences) in the latency and duration scores. Significance levels of $p < .05$ were used to evaluate results and all reported p values were two-tailed.

Experiment 1: Effects of Spatial Disparity on Chicks' Intermodal Responsiveness to Maternal Cues

Previous studies utilizing bobwhite quail chicks have demonstrated that neonates reliably direct their social preferences on the basis of available maternal auditory cues at 24 and 48 hr following hatching (Heaton, Miller, & Goodwin, 1978; Lickliter, 1994; Lickliter & Virkar, 1989). In contrast, by 72 hr of age bobwhite chicks no longer

reliably respond to auditory cues presented alone and instead require combined maternal auditory and visual cues to direct their filial responsiveness (Lickliter, 1994; Lickliter & Virkar, 1989). Furthermore, when chicks are presented with a choice test in which identical maternal auditory cues (the same bobwhite maternal call) are paired with a species-typical bobwhite hen versus a nonconspecific scaled quail hen, they show a significant preference for the species-typical bobwhite hen by 72 hr following hatching (but not at earlier ages, see Lickliter & Virkar, 1989). Importantly, this pattern of species-specific visual responsiveness does not appear to depend on chicks' previous exposure to an adult bobwhite hen, but rather has been shown to depend on chicks' ongoing physical interaction with siblings (broodmates) in the days following hatching (McBride & Lickliter, 1993).

The purpose of this initial experiment was to investigate the importance of spatial contiguity in the bobwhite chick's postnatal responsiveness to maternal audio-visual cues. Specifically, we assessed the effects of spatially separating the bobwhite maternal call from the bobwhite hen on chicks' patterns of preferential responsiveness in the days following hatching. If spatial contiguity between maternal auditory and visual cues is important to chicks' early patterns of perceptual responsiveness, then chicks receiving spatially disparate maternal cues should respond differently from chicks receiving congruent auditory and visual information.

Methods

The subjects were 120 bobwhite quail chicks, drawn from eight separate hatches. All chicks were reared in social groups of 10–14 same-aged chicks and were individually tested in a simultaneous choice test at either 48, 72, or 96 hr (± 3 hr) following hatching. Chicks were divided into two groups for testing purposes. Subjects in the control group ($n = 60$) were presented with a stuffed model of an adult bobwhite quail (*Colinus virginianus*) hen paired with the bobwhite maternal call versus a stuffed model of an adult scaled quail (*Callipepla squamata*) hen paired with the bobwhite maternal call. In other words, both hen models were emitting the same maternal call and these visual and auditory maternal cues were co-located on each side of the test arena. The side of presentation of the two hens was counterbalanced across subjects to prevent a possible side bias from affecting results. Chicks in the experimental group ($n = 60$) were presented the same stuffed hens and identical maternal calls during testing, but the bobwhite hen was separated from the bobwhite maternal call by 60 cm. The scaled quail hen and maternal call remained co-located. Thus, experimental chicks could respond to (a) the silent bobwhite hen, (b) the bobwhite maternal call, or (c) the nonconspecific scaled hen paired with the bobwhite maternal call. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

As illustrated in Table 1, control chicks demonstrated a significant preference for the bobwhite hen paired with bobwhite maternal call at both 72 and 96 hr following hatching. Analysis of the latency and duration scores supported this result. Subjects showed shorter latencies and longer durations in their response to the bobwhite hen and call than to the scaled quail hen and bobwhite maternal call. No significant preference was seen for either the bobwhite hen or the scaled hen at 48 hr following hatching, replicating earlier findings in this series (Lickliter, 1994; Lickliter & Lewkowicz, 1995;

Table 1
Preference of Chicks in Simultaneous Choices Tests Between Spatially Co-Located and Spatially Separated Maternal Cues

Control Group					
Age (in hr)	<i>n</i>	<i>n</i> Responding	Bobwhite Call Bobwhite Hen	Bobwhite Call Scaled Quail Hen	No Preference
48	20	17	6	7	4
72	20	19	16*	2	1
96	20	18	14*	4	0

* $p < .01$ (chi-square test).

Experimental Group

Age (in hr)	<i>n</i>	<i>n</i> Responding	Bobwhite Call Scaled Quail Hen	Bobwhite Call Bobwhite Hen	Bobwhite Hen	No Preference
48	20	19	2	16*	0	1
72	20	18	14*	1	0	3
96	20	18	15*	1	0	2

* $p < .01$ (chi-square test).

Lickliter & Virkar, 1989). Experimental chicks showed a significant preference for the spatially separated bobwhite maternal call at 48 hr following hatching, replicating previous results demonstrating that bobwhite chicks prefer maternal auditory cues over visual cues prior to 72 hr of postnatal age (Lickliter, 1994; Lickliter & Virkar, 1989). A significant preference for the co-located scaled quail hen and bobwhite maternal call was seen at both 72 and 96 hr following hatching (Table 1). In other words, chicks provided a choice between the spatially separated bobwhite hen and bobwhite maternal call versus the spatially congruent scaled hen and maternal call preferred the spatially congruent, but species-atypical hen over either the species-specific bobwhite hen or bobwhite call. These results are in contrast to those obtained from control chicks and indicate that by 72 hr following hatching, chicks appear to require spatial contiguity between auditory and visual cues to direct their social responsiveness, even when the spatially contiguous components of the multimodal compound stimulus are mismatched. This finding suggests the existence of a hierarchy of determinants of responsiveness to multimodal maternal cues during early postnatal development, where the spatial contiguity of auditory and visual cues has precedence over the modality-specific nature of the cues.

Experiment 2: Effects of Modified Postnatal Auditory Experience on Chicks' Intermodal Responsiveness to Maternal Cues

The findings of Experiment 1 suggest that chicks' preference for spatial congruity between intermodal maternal cues can effectively override their species-specific visual preferences by several days following hatching. Chicks preferred the species-atypical scaled hen co-located with the maternal call over species-typical but spatially separated bobwhite maternal cues by 72 hr following hatching. From a developmental perspective, this raises the interesting question of what experiences facilitate the emergence of chicks' sensitivity to spatial congruity. For example, is it the case that chicks' ability

Table 2
Preference of Chicks Provided Augmented Postnatal Auditory Experience in Choice Tests Between Spatially Separated and Spatially Co-Located Cues

Age (in hr)	<i>n</i>	<i>n</i> responding	Bobwhite Call Scaled Quail Hen	Bobwhite Call	Bobwhite Hen	No Preference
48	20	18	9	6	0	3
72	20	20	2	8	0	10
96	20	18	3	9	1	5

to respond to the correspondence between the location of visual and auditory events is affected by their postnatal sensory-stimulation history? To begin to assess this question, the present experiment modified chicks' postnatal auditory experience during the period between hatching and testing. Specifically, chicks' received species-specific auditory experience that was not paired with a co-located visual stimulus. If sensitivity to spatial congruity between maternal auditory and visual cues depends on chicks' experience with auditory and visual information being co-located, then altering portions of chicks' early postnatal auditory experience to be "disembodied" should potentially modify their emerging preference for audio/visual spatial congruity.

Methods

Sixty bobwhite quail chicks, drawn from five different hatches, served as subjects. Following hatching, chicks were reared in groups of 10–14 same-aged hatchlings and received the same social experience as birds in the previous experiment, with the exception that subjects in this experiment were also exposed to 45 min of recorded bobwhite chick contentment calls for times a day. Thus, chicks received 180 min of augmented, disembodied auditory experience each day prior to testing. The contentment call recordings were obtained from observations of socially reared bobwhite hatchlings in a previous study (see McBride & Lickliter, 1994). The prepared tape loops were played on two Marantz Model PMD 221 portable cassette recorders located 80 cm above the chicks' rearing tub. The tape loops were played concurrently and the recorded calls were presented at a uniform peak intensity of 65 dB, as measured by a Bruel & Kjaer Model 2232 sound-level meter. It is important to note that previous work in this series has shown that postnatal exposure to identical amounts of augmented bobwhite hatchling contentment calls does not alter bobwhite chicks' species-typical responsiveness to spatially congruent maternal auditory and visual cues (McBride & Lickliter, 1994). In this experiment we were interested in whether such altered postnatal auditory experience would alter chicks' responsiveness to spatially disparate maternal cues.

Chicks were individually tested in a simultaneous choice test between the bobwhite maternal call, the spatially separated and silent bobwhite hen, and the spatially co-located squaled quail hen and maternal call at either 48, 72, or 96 hr following hatching, as in the previous experiment. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

The results of testing are shown in Table 2. Chicks exposed to augmented, disembodied auditory experience in the period following hatching failed to show a significant preference for any of the test stimuli at any age tested. In contrast to the results obtained

in Experiment 1, chicks in the present experiment did not prefer the scaled quail hen co-located with the bobwhite maternal call at either 72 or 96 hr following hatching. Rather, chicks demonstrated no reliable preference, as measured by latency and duration scores, at 48, 72, or 96 hr of age, indicating that spatial congruity of auditory and visual cues was not sufficient to guide subjects' social responsiveness. These results suggest that early postnatal experience with disembodied auditory stimulation (i.e., vocalizations not paired with a visual event) can alter chicks sensitivity to spatial information and highlight the role of postnatal sensory experience in the emergence of species-typical intersensory integration. More specifically, hatchlings' normal postnatal sensory experience (i.e., sounds paired with sights) appears to facilitate their ability to detect the spatial concordance of auditory and visual cues.

Experiment 3: Effects of Modified Postnatal Visual Experience on Chick's Intermodal Responsiveness to Maternal Cues

The results of Experiment 2 indicate that ongoing auditory experience decoupled from visual experience can alter quail chicks' intermodal responsiveness to maternal auditory and visual cues. Specifically, chicks receiving disembodied auditory experience following hatching (in addition to their normally occurring postnatal sensory experience) did not show the same pattern of sensitivity to spatial congruity between maternal auditory and visual cues as seen in control chicks in Experiment 1 or in chicks tested to spatially congruent, species-typical maternal cues (McBride & Lickliter, 1994). To explore the generalizability of this effect of modified postnatal sensory experience, the present experiment modified chicks' postnatal visual experience in the period following hatching. Specifically, chicks were deprived of spatially contiguous audio-visual information by denying them the opportunity for patterned visual stimulation from hatching to testing. A previous study in this series (Banker & Lickliter, 1993) found that bobwhite chicks denied postnatal visual experience failed to show a preference for maternal visual cues into later stages of postnatal development than did normally reared birds. It is not known, however, how such deprivation might affect chicks' sensitivity to the spatial congruity of intermodal cues. If visual experience with spatially congruent auditory and visual cues is important to subsequent intermodal responsiveness, then we reasoned that chicks denied normal postnatal visual experience (i.e., sights paired with sounds) should show altered patterns of intermodal integration in the days following hatching.

Methods

Sixty bobwhite quail chicks, drawn from five separate hatches, served as subjects. Following hatching, chicks were reared in a portable brooder with 12–15 same-aged siblings. The brooder was placed in a darkened room and covered with black paper and black fabric to eliminate the opportunity for postnatal experience with patterned light. While we could not be sure that this manipulation eliminated all visual experience for each subject, the dark rearing condition certainly served to drastically attenuate normal visual experience. Chicks could, however, physically contact and hear their siblings present in the brooder. Food and water were continuously available to the chicks throughout the experiment, and the air temperature in the brooder was maintained at 30°C to match the rearing conditions of subjects in Experiments 1 and 2.

Table 3
Preference of Chicks Denied Patterned Postnatal Visual Experience in Choice Tests Between Spatially Separated and Spatially Co-Located Maternal Cues

Age (in hr)	<i>n</i>	<i>n</i> responding	Bobwhite Call Scaled Quail Hen	Bobwhite Call	Bobwhite Hen	No Preference
48	20	17	4	4	1	8
72	20	16	5	8	0	3
96	20	17	7	5	1	4

Prior to testing, each subject was removed from the dark-rearing brooder for a period of 2 min to allow its eyes to adjust to the light of the testing room. All subjects were then tested individually at either 48, 72, or 96 hr following hatching as described in Experiment 2. Thus, chicks could respond to (a) the spatially co-located, nonconspicuous scaled quail hen and bobwhite maternal call, or (b) the silent bobwhite hen, or (c) the bobwhite maternal call. Choice, latency, and duration of response were scored as described in the General Methods section.

Results and Discussion

As seen in Table 3, dark-reared chicks did not display a significant preference for any of the three stimuli presented in the simultaneous choice tests at either 48, 72, or 96 hr of postnatal age. These results stand in contrast to those obtained from both control and experimental chicks in Experiment 1 and parallel the results obtained from chicks receiving altered auditory experience in Experiment 2. These results indicate that denying chicks normal, ongoing experience with co-located auditory and visual information can lead to a reduced responsiveness to spatial congruity in the days following hatching. While chicks' responsiveness to the spatially separated bobwhite hen was low, it is important to note that some chicks did respond to each of the three categories of stimuli (auditory only, visual only, audio/visual) in the testing situation, implying that subjects were capable of responding to visual information despite their lack of postnatal visual experience (Table 3).

General Discussion

The results from the present set of experiments provide evidence that the socially directed perceptual responsiveness of bobwhite chicks is dependent, at least in part, on the spatial contiguity between the audible and visible attributes of maternal cues. By way of brief review, the findings from Experiment 1 showed that normally reared hatchlings exhibit a significant preference for spatially contiguous over spatially noncontiguous auditory and visual maternal cues, even though the spatially contiguous cues included species-atypical visual cues. Experiments 2 and 3 demonstrated that this reliance on spatial congruity is dependent on the chick's postnatal sensory experience. Specifically, Experiment 2 showed that chicks do not exhibit a preference for spatially contiguous auditory and visual cues following ongoing postnatal exposure to hatchling contentment calls presented without their normally available visual counterpart (i.e., live hatchlings). This interference was seen despite the fact that subjects were reared

with same-aged siblings that were providing contiguous auditory and visual stimulation. Experiment 3 showed that postnatal visual deprivation during the same postnatal period also resulted in hatchlings showing no significant preference for spatially contiguous or spatially noncontiguous maternal cues.

Perhaps the most striking aspect of the current study is the fact that normally reared chicks chose the spatially contiguous species-specific maternal call paired with a hen from a different species over spatially noncontiguous but species-specific bobwhite maternal cues (Experiment 1). This result demonstrates the important role that hetermodal spatial contiguity plays in chicks' early perceptual responsiveness. In fact, the current findings suggest that spatial-contiguity cues may have developmental priority over modality-specific cues associated with the hen or her maternal call. This is suggested by the finding that chicks preferred a nonconspecific hen as long as it was collocated with the bobwhite maternal call. In other words, chicks appeared to ignore the specific visual attributes of the scaled quail hen and instead attended to the spatial concordance of available auditory and visual cues. Of course, the present findings do not rule out the possibility that learning about modality-specific cues is also taking place during this time. In fact, a number of related studies have shown that young hatchlings can learn about various aspects of the maternal call (Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995; Lickliter & Stoumbos, 1992) and can successfully discriminate the bobwhite hen from the scaled quail hen by 72 hr following hatching (Lickliter, 1994; Lickliter & Virkar, 1989; McBride & Lickliter, 1993). The unique contribution of the present study is that it pitted modality-specific maternal cues in opposition to spatial-contiguity cues, requiring chicks to direct their preferential responsiveness on the basis of one or the other. The results indicated that during early postnatal development chicks responded preferentially to spatial cues when required to choose between spatial and modality-specific cues.

In addition to providing information about the relative importance of spatial and modality-specific cues, the current study showed that certain aspects of chicks' sensory experience during the period between hatching and testing contributed to their ability to respond to spatial contiguity between sights and sounds. The finding that additional auditory stimulation (Experiment 2) or the lack of visual stimulation (Experiment 3) can prevent chicks from responding to the spatial contiguity of auditory and visual stimuli suggests that the spatially concordant, multimodal experience normally available in the posthatch environment is important to chicks' development of integrated intersensory responsiveness. Under normal rearing conditions, the young hatchling is provided with spatially contiguous visual, auditory, and tactile stimulation from its broodmates and this coordinated multisensory experience appears to be essential to the normal emergence of intersensory integration. As the results of Experiment 2 showed, however, the experience of additional disembodied auditory stimulation was sufficient to interfere with the effects of normally available concordant multimodal stimulation. Likewise, Experiment 3 showed that the normal pattern of intersensory integration also can be disrupted by depriving chicks of one component of postnatal multimodal stimulation, namely the visual cues normally provided by other chicks in the rearing environment. It is important to note that Experiments 2 and 3 utilized very different types of experimental manipulations during the early postnatal period and obtained remarkably similar results. Specifically, an "experiential enhancement" technique was employed in Experiment 2 and an "experiential attenuation" technique was used in Experiment 3 (see Miller, 1981). In both cases, however, subjects demonstrated a higher tolerance for audio-visual discrepancy than did normally reared chicks in Experiment 1, suggesting that

ongoing postnatal experience with sight and sound directly influence the young chick's emerging intersensory processes.

In the more general sense, the present results argue that early multisensory integration is best characterized as dynamic and multidimensional. In particular, the capacity for intersensory integration appears to depend on both the physical properties of the stimuli encountered and the experiential history of the developing organism. This idea that control for any given developmental outcome resides in the structure and nature of the relationship between external and internal variables (rather than in any individual factor) has important implications for the study of behavioral development. In particular, this notion of reciprocal interaction highlights the need for an explicit empirical concern with the dynamic relationship between the developing organism and its structured environment. From this perspective, it is not plausible to reduce this complex, dynamic relationship down to solely genetic or neurophysiological levels of analysis. The minimum unit for developmental analysis must be the entire developmental system, comprised of both the organism and the set of physical, biological, and social factors with which it interacts over the course of development.

Notes

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