

RESEARCH ARTICLES

Intersensory Redundancy Enhances Memory in Bobwhite Quail Embryos

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Information presented concurrently and redundantly to 2 or more senses (intersensory redundancy) has been shown to recruit attention and promote perceptual learning of amodal stimulus properties in animal embryos and human infants. This study examined whether the facilitative effect of intersensory redundancy also extends to the domain of memory. We assessed bobwhite quail chicks' ability to remember and prefer an individual maternal call presented either unimodally or redundantly and synchronously with patterned light during the period prior to hatching. Embryos provided with unimodal auditory exposure failed to prefer the familiar call over a novel maternal call postnatally at 48 hr and 72 hr following exposure. In contrast, embryos provided with redundant, synchronous audiovisual stimulation significantly preferred the familiar call at 48 hr following exposure, but not at 72 hr. A second experiment provided chicks with a single 10-min refamiliarization with the familiar call at either 48 hr or 72 hr following hatching. Chicks given only unimodal auditory exposure prior to hatching did not appear to benefit from this brief postnatal refamiliarization, showing no preference for the familiar call at either 72 or 96 hr. Chicks that received redundant audiovisual stimulation prenatally showed a significant preference for the familiar call (following the brief reexposure 24 hr earlier) at both 72 and 96 hr of age. These results are the first to demonstrate that redundantly

specified information is remembered longer and reactivated more easily than the same information presented unimodally. These findings provide further evidence of the salience of intersensory redundancy in guiding selective attention and perceptual learning during early development.

Amodal information is information that is not specific to one sense but can be detected across two or more sensory modalities. Changes in intensity or the temporal and spatial aspects of sensory stimulation, including such properties as rhythm, tempo, duration, synchrony, and collocation, are examples of information not specific to a single sensory modality. A growing body of research indicates that young infants are capable of intersensory perception, at least in large part, by detecting information that is amodal and invariant across the senses (Bahrick & Lickliter, 2002; Bahrick & Pickens, 1994; Gibson & Pick, 2000; Lewkowicz & Lickliter, 1994; Lickliter & Bahrick, 2000; Walker-Andrews, 1997). Several generalizations have emerged from this body of research, including that infants are remarkably skilled perceivers of amodal information in the first 6 months following birth and that amodal information can guide and constrain perceptual learning in early development (Bahrick, 2001; Gogate & Bahrick, 1998; Hernandez-Reif & Bahrick, 2001; Lewkowicz, 2000, 2002).

Bahrick and Lickliter (2000, 2002) proposed an intersensory redundancy hypothesis to provide a more specific account for how the detection of amodal (redundant) information might organize and guide perceptual learning during early infancy. Intersensory redundancy refers to the spatially coordinated and temporally synchronous presentation of the same information (e.g., rate, rhythm, intensity) across two or more sensory modalities. Thus, the sights and sounds of hands clapping provide intersensory redundancy in that they are synchronous, collocated, and convey the same rhythm, tempo, and intensity patterns across vision and audition. One tenet of the intersensory redundancy hypothesis holds that, in early development, information presented redundantly and in temporal synchrony to two or more senses selectively recruits infant attention and facilitates perceptual differentiation and learning of the redundant information (amodal stimulus properties) more effectively than does the same information presented to one sensory modality at a time. More specifically, the intersensory redundancy hypothesis proposes that this selective attention on the part of the infant will give initial advantage to the perceptual processing, learning, and memory of stimulus properties that are amodal and bimodally specified over modality specific or nonredundantly specified properties of sensory stimulation. Other tenets of the intersensory redundancy hypothesis address the conditions under which detection of nonredundantly specified modality specific and amodal properties of stimulation are facilitated during early development and how detection of redundant and nonredundant stimulus properties changes developmentally (for further discussion, see Bahrick & Lickliter, 2002).

Research with human infants has consistently indicated that different properties of stimuli are highlighted and attended to when redundant multimodal stimulation is made available as compared with unimodal stimulation from the same events (Bahrick & Lickliter, 2002; Lewkowicz, 2000; Walker-Andrews, 1997). For example, Bahrick and Lickliter (2000) assessed the ability of 5-month-old infants to discriminate complex rhythmic patterns in bimodal, redundant stimulation as compared with unimodal stimulation. Infants were habituated to videos of a plastic hammer tapping out a distinctive rhythm under conditions of bimodal, redundant stimulation (they could see and hear the hammer), unimodal visual stimulation (they could only see the hammer), or unimodal auditory stimulation (they could only hear the soundtrack of the hammer tapping). Infants who received the bimodal, redundant stimulation showed a significant visual recovery to a change in rhythm, whereas those who received unimodal visual or auditory stimulation showed no visual recovery to the change in rhythm. Bahrick, Flom, and Lickliter (2002) replicated and extended these findings to younger infants (3 months) and a different amodal property (tempo). Infants who received bimodal, redundant audiovisual stimulation discriminated a change in tempo, whereas infants receiving unimodal visual or auditory stimulation did not.

If the intersensory redundancy hypothesis reflects a general developmental principle, then redundancy should potentially be a strong contributor to perceptual responsiveness and learning at earlier stages of development and in other animal species. Studies of nonhuman animal infants have shown sensitivity to amodal stimulus properties in the days, weeks, and months following birth (e.g., Hultsch, Schleuss, & Todt, 1999; Kraebel & Spear, 2000; Mellon, Kraemer, & Spear, 1991; Spear & McKinzie, 1994), but little is known about whether animal embryos or fetuses are sensitive to redundantly specified amodal information during the prenatal period. Recently, Lickliter, Bahrick, and Honeycutt (2002) assessed whether bimodal redundantly specified information can guide attentional selectivity and facilitate perceptual learning prior to hatching in a precocial avian species. Precocial birds (e.g., domestic chicks, ducks, and quail) are particularly well suited for this type of research, as they develop in an egg (allowing ready access to the developing embryo during the prenatal period) and can respond in behavioral tests almost immediately after hatching.

Previous research with precocial birds has indicated that concurrent (but nonredundant) bimodal stimulation can interfere with prenatal perceptual learning. Typically, precocial avian embryos learn an individual maternal call when it is presented unimodally during the last 24 hr prior to hatching (e.g., Gottlieb, 1988; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). In contrast, a number of studies have demonstrated that avian embryos fail to learn an individual maternal call when it is presented concurrently with visual stimulation in the period prior to hatching (Gottlieb, Tomlinson, & Radell, 1989; Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). This intersensory interference occurred only when

the two sensory systems (auditory and visual) were stimulated concurrently. It was thought that the embryo was not capable of adequately attending to simultaneous bimodal stimulation in that the overall amount of prenatal stimulation appeared to effectively overwhelm the young organism's attentional or learning capabilities (Radell & Gottlieb, 1992). However, Lickliter et al. (2002) found that it was not the amount of bimodal stimulation that contributed to the observed intersensory interference effect but rather how the bimodal stimulation was presented.

In the Lickliter et al. (2002) study, bobwhite quail embryos were exposed to an individual bobwhite maternal call for 10 min per hour for 6, 12, or 24 hr, under conditions of unimodal auditory stimulation, concurrent but nonredundant auditory and visual stimulation, or redundant and temporally synchronous auditory and visual stimulation. Redundant stimulation was provided by presenting a pulsing light that flashed in synchrony and with the temporal patterning (rhythm, rate, duration) of the notes of the maternal call. All chicks were then tested 24 hr later (1 day after hatching) to determine whether they would prefer the familiar maternal call over an unfamiliar variant of the maternal call. Chicks that received redundant audiovisual exposure preferred the familiar maternal call following all prenatal exposure periods, whereas chicks that received nonredundant audiovisual exposure prenatally showed no preference for the familiar call following any exposure duration. Chicks receiving the unimodal auditory familiarization prior to hatching preferred the familiar call only following the longest period (24 hr) of prenatal exposure. Thus, synchronous and bimodally specified information (intersensory redundancy) promoted auditory learning at a rate that was four times that of unimodal auditory exposure. Importantly, this dramatic facilitation of perceptual learning in embryos receiving redundant, bimodal information cannot be explained by a simple increase in overall amount of prenatal stimulation. Chicks that received concurrent but nonredundant audiovisual stimulation as embryos showed no preference for the familiar call following any exposure period. Similar to results from studies of human infants, avian embryos showed enhanced perceptual learning when amodal information (tempo, rhythm, duration) was presented redundantly and in a temporally coordinated manner, but not when the same information was presented nonredundantly or unimodally.

This study examined whether the facilitative effect of intersensory redundancy would extend to the domain of memory. To address this issue, we assessed memory for a familiar maternal call in quail chicks prenatally exposed to redundant, synchronous audiovisual information versus chicks exposed to unimodal (auditory) information in the period prior to hatching. In keeping with our intersensory redundancy hypothesis and with the findings of previous studies with both animal and human infants, we predicted that quail embryos provided with redundant audiovisual exposure to a maternal call would display enhanced postnatal memory for that call relative to embryos provided with only unimodal auditory exposure during the period prior to hatching.

GENERAL METHOD

Certain features of the experimental design were common to both experiments and are described before presenting the details of each individual experiment. Additional details of procedures and testing are available in Lickliter et al. (2002).

Subjects

Subjects were incubator-reared bobwhite quail (*Colinus virginianus*) embryos. Fertile, unincubated eggs were received weekly from a commercial supplier and were incubated communally in a Petersime Model I incubator (Petersime, Inc., Zutte, Belgium) under conditions described in detail elsewhere (Banker & Lickliter, 1993; Lickliter & Virkar, 1989). To control for possible effects of variations in developmental age, only those chicks that hatched on Day 23 were used in this study. The possible influence of between-batch variation in behavior was controlled by selecting subjects for each experimental group from at least three different hatches (i.e., weeks) of eggs. Given their incubator rearing, the only sounds to which embryos were exposed prior to our experimental manipulations were their own embryonic vocalizations, those of their broodmates, and the low-frequency background noise of the incubator's fan and motor. Following hatching, chicks were group-reared in large plastic tubs containing seven to nine same-age chicks to mimic naturally occurring brood conditions. Food and water were continuously available throughout the duration of each experiment, except during the testing trials.

Procedure

The bobwhite quail embryo's bill normally penetrates the air space at the large end of the egg approximately 24 to 36 hr prior to hatching, producing a visible indentation (or *pip*) on the outer shell of the egg. Eggs showing these pips during the first half of Day 22 (of the 23-day incubation period) were relocated to Hovi-bator portable incubators (GQF Manufacturing Co., Savannah, GA) located in a darkened room for the last 24 hr of incubation. The portable incubators allowed for the easy delivery of prenatal auditory and visual stimulation, as described later. It is important to note that the top of the eggshell and inner shell membrane were not removed prior to prenatal stimulation, as Carlsen and Lickliter (1999) and Lickliter et al. (2002) demonstrated that quail embryos respond to auditory and visual stimulation presented through the eggshell following movement into the air space in the days prior to hatching.

During the 24 hr prior to hatching, embryos in respective experiments received either (a) no supplemental prenatal sensory stimulation, or intermittent (10 min/hr) exposure to (b) unimodal auditory stimulation, or (c) temporally synchronized audiovisual stimulation. The auditory stimulus used in all experiments was an indi-

vidual variant of the species-typical bobwhite quail maternal assembly call. This maternal call was broadcast from a speaker located at the airhole opening on the top of the portable incubator, directly above the quail embryos within. All the normally occurring acoustic components of the maternal vocalization were present and unaltered. The call consisted of five notes that repeated at a rate of 1.7 notes per sec for a duration of 3.0 sec. The synchronized audiovisual event received by some embryos consisted of the maternal call presented concurrently with a temporally patterned light that was programmed to flash at the same rate and duration as the notes of the maternal call. Thus, the patterned light presented the same temporal pattern as the maternal call, providing embryos bimodally specified intersensory redundancy for rate, rhythm, and duration of the maternal call.

Testing

Testing was conducted postnatally at either 48 hr, 72 hr, or 96 hr (± 2 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 in a circular arena, 160 cm in diameter, surrounded by a wall 24 cm high that was lined with foam to attenuate echoes and covered by an opaque black curtain to shield the observer from the subject's view. Two rectangular approach areas (32×15 cm) located on opposite sides of the arena were marked by green stripes painted on the floor. Each approach area represented less than 5% of the total area of the arena. Mid-range dome-radiator speakers were hidden behind the curtain in each of the two approach areas, and each of these speakers received input from a cassette tape recorder located at a control table. The experimenter sat at this table and observed the subject's activities by means of a large mirror positioned above the testing arena. A system of handheld stopwatches was used to record the latency and duration of response, as described later.

Testing involved placing each chick individually in the arena equidistant from the two approach areas. All birds were given a 5-min simultaneous choice test between two variants of the bobwhite maternal assembly call (hereafter referred to as Call A and Call B) that were broadcast from the speakers located in the two approach areas. These two maternal calls were recorded in the field and are similar in phrasing, call duration, repetition rate, and the major peak of dominant frequency. They varied primarily in the minor peaks of dominant frequency and in temporal macrostructure (burst-pause patterning) and temporal microstructure (note-internote intervals; see Table 1 in Heaton, Miller, & Goodwin, 1978). Previous studies have shown that bobwhite quail chicks do not show a naive preference for either of these variants of the maternal call (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). The locations of Call A and Call B were counterbalanced across individual trials to prevent any possible side bias from influencing results.

Each subject was tested only once. Subjects were scored on both the latency of approach and the duration of time spent in each of the two approach areas. Latency was defined as the amount of time (in seconds) that elapsed from the onset of the trial until the subject entered an approach area. Duration was defined as the cumulative amount of time (in seconds) the subject remained in an approach area during the 5-min trial. A chick that did not enter either approach area during a test trial received a score of 300 sec for latency (i.e., the length of the trial) and 0 sec for duration and was considered a nonresponder. 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 the opposing approach area, a preference for that stimulus was recorded. Occasionally, a chick entered both approach areas during a test trial without showing a preference for either one. This behavior was scored as "no preference" in the tables showing test results.

Data Analyses

The data of interest in each experiment were differences in (a) the latency of approach, (b) the duration of time spent in each approach area, and (c) the number of subjects showing an individual preference (defined as subjects that stayed in one approach area for more than twice as long as the other approach area). The differences in latency and duration of approach were evaluated using the Wilcoxon matched-pairs signed-rank test. Differences in the number of individual preferences were evaluated by the chi-square test. Significance levels of $p < .05$ (two-tailed) were used to evaluate results.

EXPERIMENT 1: EFFECTS OF PRENATAL UNIMODAL AND BIMODAL EXPOSURE ON CHICK'S POSTNATAL MEMORY FOR A MATERNAL CALL

Previous studies have consistently shown that bobwhite quail embryos are capable of learning an individual variant of a bobwhite maternal call during the late stages of prenatal development (Carlsen & Lickliter, 1999; Honeycutt & Lickliter, 2001, 2002; Lickliter & Hellewell, 1992; Sleigh, Columbus, & Lickliter, 1996). These studies found that embryos familiarized with a particular maternal call (presented unimodally) during the 24 hr prior to hatching significantly preferred that familiar call 1 day later in postnatal testing. The basic procedure in these experiments involved intermittent exposure (10 min/hr) of group-incubated embryos to a recording of a particular individual maternal call over a 24-hr period and then testing hatchlings for their auditory preference between the familiar call and a novel bobwhite maternal call at 24 hr following hatching. This experiment followed this general procedure, but unlike previous studies, manipulated the amount of time that

elapsed from the offset of prenatal stimulation to the postnatal testing trial. We were interested in assessing how long beyond 24 hr following hatching quail chicks prenatally exposed to either unimodal or redundant bimodal stimulation would remember and prefer the familiar call over a novel call.

Methods

One hundred thirty-eight bobwhite quail embryos, divided into three experimental groups, served as subjects. Forty-six embryos received no supplemental prenatal sensory stimulation (control group) prior to hatching, 46 embryos received intermittent exposure to unimodal auditory exposure (10 min/hr) to an individual bobwhite maternal call during the 24 hr prior to hatching (unimodal group), and 46 embryos received intermittent exposure to redundant and synchronous audiovisual stimulation prior to hatching (maternal call + patterned light, redundant group). Under this condition, embryos were exposed to bimodally specified information regarding the rhythmic pattern, rate, and duration of the maternal call during prenatal stimulation periods. Half of the chicks in each of the three groups were assigned to one of the two delay conditions (the amount of time that elapsed between the offset of prenatal stimulation and subsequent postnatal testing). Twenty-three chicks from each group were tested after 48 hr had elapsed since prenatal familiarization to the maternal call, and 23 chicks from each group were tested 72 hr following offset of prenatal stimulation. All subjects were tested individually in a simultaneous choice test (see the General Methods section) that assessed their preference between the familiar call (Call B) and an unfamiliar maternal call (Call A). These maternal calls are known to be equally attractive to unexposed (naive) hatchlings (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992).

Results and Discussion

We considered subjects to have learned and remembered Call B if they exhibited a significant preference for that familiar call over the novel call in the simultaneous choice test and if control subjects showed no preference between the two variants of the call. As illustrated in Table 1, chicks that received no supplemental prenatal sensory stimulation (control group) showed no preference for either maternal call during postnatal testing at 48 and 72 hr delays. Chicks that received unimodal auditory familiarization to an individual maternal call (Call B) prior to hatching (unimodal group) likewise showed no preference for either the familiar call or a novel maternal call (Call A) during testing at 48 or 72 hr following hatching. Analysis of latency and duration of response to the test stimuli by the Wilcoxon test likewise revealed no significant differences in the response to the two maternal calls (Table 2). In contrast, chicks exposed to redundant audiovisual information as embryos showed a significant preference for the familiar call over the unfamiliar

TABLE 1
Individual Preferences of Control and Experimental Groups
in Postnatal Simultaneous Choice Tests in Experiments 1 and 2

Age ^a	Novel Call A	Familiar Call B	No Preference
Control groups			
48 hr (23/23)	5	7	11
72 hr (21/23)	6	7	8
72 hr [R] (19/21)	8	4	7
Unimodal auditory groups			
48 hr (22/23)	5	8	9
72 hr (21/23)	6	7	8
72 hr [R] (17/21)	6	5	6
Bimodal redundancy groups			
48 hr (23/23)	2	14*	7
72 hr (17/21)	4	6	7
72 hr [R] (19/21)	0	13*	6
96 hr [R] (19/21)	1	11*	7

Note. [R] = Refamiliarization with Call B 24 hr prior to testing.

^aNumbers in parentheses indicate *n* responding/total *n*.

**p* < .05.

Call A at 48 hr following hatching, $\chi^2(2, N = 23) = 9.48, p = .009$, but not at 72 hr (Table 1). These chicks also showed significantly longer durations ($z = -3.21, p = .001$), and marginally significant shorter latencies to approach the familiar call ($z = -1.88, p = .059$) at 48 hr following hatching (Table 2).

The results of this experiment indicate that presentation of redundant, bimodally specified information during the late stages of the prenatal period can facilitate memory for a familiar maternal call longer into postnatal development than the same information presented unimodally. Quail embryos exposed to temporally synchronous and redundant auditory and visual information remembered and preferred the familiar call 2 days following prenatal exposure. In contrast, chicks receiving unimodal auditory exposure as embryos failed to prefer the familiar call at this age.

It is important to note that several types of amodal information were available to embryos in the redundant group of this experiment that could have served as the basis for the observed improved memory for the familiar maternal call. For example, the light and maternal call were synchronized both in terms of their temporal macrostructure (burst–pause patterning) and temporal microstructure (note–internote intervals). Thus, synchronization of the call and light made the rhythmic patterning of the auditory and visual information redundant, including the overall duration of the call burst and the duration of individual notes within a burst as well as the pauses between bursts and pauses between individual notes within a burst. Chicks could have detected and remembered any or all of these amodal temporal properties during postnatal testing.

TABLE 2
 Median Latency and Duration Scores (in Seconds) of Control and Experimental Groups
 in Simultaneous Choice Tests in Experiments 1 and 2

Age ^a	Latency						Duration						
	Novel Call A			Familiar Call B			Novel Call A			Familiar Call B			
	M	Interquartile Range	M	Interquartile Range	M	Interquartile Range	M	Interquartile Range	M	Interquartile Range	M	Interquartile Range	
Control groups													
48 hr (23/23)	37	18-68	64	27-108	48	25-80	58	40-63					
72 hr (21/23)	48	22-120	62	32-132	32	15-58	36	12-63					
72 hr [R] (19/21)	42	21.5-112.5	48	26-209	35	15.5-67	22	9.5-57					
Unimodal auditory groups													
48 hr (22/23)	33	12-110	50	16-103	41	16-63	44	17-66					
72 hr (21/23)	41	15-123	62	17-168	35	3-76	38	19-73					
72 hr [R] (17/21)	60	17-155	34	11-80	24	3.5-47	28	10.5-60					
Bimodal redundancy groups													
48 hr (23/23)	51	22-166	37	15-65	23	6-49	95*	49-129					
72 hr (17/21)	33	20-220.5	54	37.5-247.5	19	10.5-64	35	5-55					
72 hr [R] (19/21)	54	27.5-119	25*	11-54.5	12	4.5-32.5	63*	34.5-87					
96 hr [R] (19/21)	63.5	14.25-154	25.5	14-91.25	18	2.75-31.25	49.5*	28.25-83.25					

Note. [R] = Refamiliarization with Call B 24 hr prior to testing.

^aNumbers in parentheses indicate *n* responding/total *n*.

**p* < .05.

The facilitation of memory for a familiar maternal call observed in this experiment stands in contrast to previous studies of quail embryos, which have consistently shown that subjects receiving unimodal auditory exposure to an individual maternal call remember and prefer that familiar call at 24 hr following hatching but not by 48 hr following hatching (e.g., Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). However, chicks receiving redundant, bimodal exposure in this experiment demonstrated a significant preference for the familiar call at 48 hr following hatching. This finding provides further support for the intersensory redundancy hypothesis and indicates that properties of stimulation that are experienced redundantly across two senses are attended, processed, and learned better than when those same properties are experienced in one sensory modality alone.

EXPERIMENT 2: EFFECTS OF A BRIEF REFAMILIARIZATION ON CHICKS' MEMORY FOR AN INDIVIDUAL MATERNAL CALL

To further explore the influence of intersensory redundancy on quail chicks' memory for events that occurred during the prenatal period of development, this experiment repeated the methods of Experiment 1 and also provided chicks a brief postnatal refamiliarization with the same maternal call they were exposed to as embryos. This refamiliarization thus involved exposure to the auditory cues but not the visual cues used in the initial prenatal presentation. In keeping with the intersensory redundancy hypothesis, we predicted that chicks receiving redundant, bimodally specified information as embryos would be more likely to benefit from a postnatal auditory refamiliarization than would chicks that received unimodal exposure to the maternal call prior to hatching. Refamiliarization to previously presented stimulation (once it is no longer remembered) can result in memory savings, the phenomenon whereby prior exposure to information facilitates the relearning of that information (Cornell, 1979; Monk, Gunderson, Grant, & Mechling, 1996; Nelson, 1985; for examples from research with animal and human infants, see Adler, Wilk, & Rovee-Collier, 2000). Would quail chicks briefly reexposed to the familiar maternal call show memory savings when tested at 72 hr, a period when neither the unimodal or redundant group showed evidence of memory for the maternal call (Experiment 1)?

Methods

Eighty-four bobwhite quail embryos, divided into three experimental groups, served as subjects. Following the general procedures used in Experiment 1, 21 embryos received no supplemental prenatal sensory stimulation prior to hatching, 21 embryos received 10 min/hr of unimodal auditory exposure to an individual mater-

nal call (Call B) during the 24 hr prior to hatching, and 42 embryos received redundant and synchronous audiovisual stimulation for 10 min/hr during the day prior to hatching (as described in the General Methods section).

Following hatching, chicks were reared in groups of seven to nine same-age chicks as described in the General Methods section. Twenty-one subjects from each of the three experimental groups were reexposed to the familiar maternal call for one 10-min session at 48 hr following hatching (note that the call was not familiar to the control group, which received no prenatal exposure to the call). An additional 21 subjects from the redundant group received their reexposure to the familiar call for one 10-min session at 72 hr following hatching. Chicks were then tested individually 1 day later (at either 72 hr or 96 hr of age) in a simultaneous choice test that assessed their preference for the familiar maternal call (Call B) versus an unfamiliar variant of the bobwhite maternal call (Call A), as described in Experiment 1.

Results and Discussion

Embryos given no supplemental prenatal stimulation and embryos given unimodal auditory stimulation prior to hatching did not appear to benefit from the brief postnatal refamiliarization to the maternal call. Neither group of chicks preferred the familiar Call B at the 72 hr test (Table 1), and analysis of latency and duration scores further supported this lack of memory savings (Table 2). In contrast, embryos provided redundant audiovisual exposure prenatally showed a significant preference for the familiar call at the 72 hr test following their brief refamiliarization with that call 24 hr earlier, $\chi^2(2, N = 19) = 13.40, p = .001$. They also showed a significant preference for the familiar call at the 96 hr test (following the brief refamiliarization 24 hr earlier), $\chi^2(2, N = 19) = 8.01, p = .018$. Chicks in the 72 hr age group also showed significantly shorter latencies ($z = -2.19, p = .03$) and longer duration scores ($z = -3.68, p = .0002$) for the familiar call, whereas chicks in the 96 hr age group showed significantly longer duration scores for the familiar call ($z = -2.58, p = .01$), but not shorter latencies to approach the familiar call (Table 2).

The fact that chicks receiving prenatal unimodal auditory exposure failed to prefer the familiar maternal call despite the refamiliarization session provides additional evidence that unimodal information is not remembered as well as bimodally specified information during early development. In contrast, chicks receiving redundant audiovisual information as embryos benefited from the brief postnatal refamiliarization, showing a significant preference for the familiar maternal call at both 3 and 4 days following hatching. These chicks thus showed evidence of memory savings. In keeping with previous findings in this series (Lickliter et al., 2002), redundantly specified information appeared to foster both

enhanced learning and enhanced memory for redundantly specified properties as compared to the same information presented unimodally.

GENERAL DISCUSSION

The results of this study are the first to provide evidence that redundant, bimodally specified information is remembered longer and reactivated more readily than the same information presented unimodally. These findings provide further evidence of the salience of intersensory redundancy in guiding selective attention and perceptual learning, even during the prenatal period. Although quail embryos receiving unimodal (auditory only) exposure to a maternal call prenatally failed to remember the familiar maternal call at 48, 72, or 96 hr following hatching, embryos provided with redundant audiovisual exposure prenatally were able to remember and prefer the familiar maternal call at 48 hr following hatching (Experiment 1) and also at 72 and 96 hr following hatching if provided with a brief postnatal refamiliarization with the call (Experiment 2). Taken together, these findings indicate that quail embryos are sensitive to redundant, bimodally specified information during the late stages of the prenatal period and that this information is remembered longer and reactivated more easily than the same information presented unimodally.

Although the salience of intersensory redundancy for guiding and constraining selective attention and perceptual processing is now well documented in studies of behavioral responsiveness in both animal and human infants (Bahrick et al., 2002; Bahrick & Lickliter, 2000, 2002; Lickliter et al., 2002), the underlying factors involved in this salience and facilitation of perceptual processing, learning, and memory is not yet well understood. Intersensory functioning is clearly multidetermined, with diverse internal and external variables interacting in complex ways. Of considerable interest is the finding that a number of neurophysiological studies have reported that the temporal and spatial pairing of stimuli from different sensory modalities can elicit a neural response that is greater than the sum of the neural responses to the unimodal components of stimulation considered separately (a superadditive effect; for a review, see Stein & Meredith, 1993). For example, the activity of a neuron in the cat superior colliculus exposed to simultaneous auditory and visual stimulation differs significantly from the activity of the same cell when exposed to stimulation in any single modality (Meredith & Stein, 1986). Spatially coordinated and synchronous bimodal stimulus combinations produce significant increases (when compared to unimodal stimuli) in several measures of neural activity, including response reliability, number of impulses evoked, and peak impulse frequency. These increases in neural responsiveness to concurrent bimodal stimulation are greater than would be predicted from adding together input to either sensory modality alone and ap-

pears to foster successful orientation and attention in both infant and adult animals (Stein & Meredith, 1993).

Working at the physiological level of analysis, Reynolds and Lickliter (2002, 2003) explored the effects of prenatal unimodal versus bimodal sensory stimulation on heart rate. Measures of heart rate have been successfully used in a number of studies of avian embryonic sensitivity to sensory stimulation (e.g., Gottlieb, 1971; Ockleford & Vince, 1977; Tolhurst & Vince, 1976). Quail embryos exposed to nonredundant (asynchronous) bimodal stimulation prior to hatching exhibited significantly greater increases in heart rate from baseline following stimulus exposure and during stimulus reexposure than embryos exposed to (a) redundant audiovisual stimulation, (b) unimodal auditory or visual stimulation, or (c) no supplemental prenatal sensory stimulation. Thus, not all types of concurrent bimodal stimulation appear similar in terms of the physiological response they elicit. Embryos exposed to nonredundant bimodal stimulation exhibit higher levels of physiological arousal both during and following exposure than embryos provided with redundant bimodal stimulation (Reynolds & Lickliter, 2003). This finding provides further support for the functional distinction between redundant and nonredundant bimodal sensory stimulation during early development.

Results from behavioral investigations indicate that precocial avian embryos are unable to demonstrate prenatal auditory learning of a maternal call when presentation is paired with concurrent but asynchronous patterned visual stimulation (Gottlieb et al., 1989; Lickliter & Hellewell, 1992), suggesting that the increased physiological arousal elicited by asynchronous bimodal stimulation exceeds some optimal range of arousal and can interfere with perceptual learning. In contrast, the results of this study suggest that redundant bimodal stimulation regulates arousal levels in a range that supports and even facilitates prenatal perceptual learning and memory (see also Lickliter et al., 2002). Given the tight link between arousal and attention during early development (see Gardner & Karmel, 1995; Ruff & Rothbart, 1996), additional research is needed to more directly investigate the neural and physiological processes underlying the observed behavioral effects of intersensory redundancy in guiding selective attention and facilitating perceptual processing, learning, and memory during infancy.

What seems clear at present from converging evidence across different levels of analysis and from several different animal species is that temporally aligned multimodal stimulation (intersensory redundancy) is highly salient during early development. In particular, it appears to initially guide and constrain selective attention and perceptual processing to amodal, redundantly specified properties of stimulation over nonredundantly specified stimulus properties. This salience hierarchy is adaptive in that it provides a framework for initially organizing perceptual processing and learning around patterns of stimulation that constitute unitary objects and events. Such organization is critical to making sense of the continuous

flux of multimodal stimulation available to naive perceivers. Thus, in our view, intersensory redundancy is an important cornerstone in early perceptual and cognitive development (for further discussion, see Bahrick & Lickliter, 2002; Lickliter & Bahrick, 2001, 2004). The results of this study provide additional empirical support for this perspective. Given the strong interconnections observed among the various senses at the neural, physiological, and behavioral levels of analysis (see Calvert, Spence, & Stein, 2004; Knudsen & Brainard, 1995), it seems clear that developmentalists can no longer overlook or undercharacterize the important role of intersensory influences in organizing basic processes of attention, perception, and cognition during early development.

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REFERENCES

- Adler, S. A., Wilk, A., & Rovee-Collier, C. (2000). Reinstatement versus reactivation effects on active memory in infants. *Journal of Experimental Child Psychology, 75*, 93-115.
- Bahrick, L. E. (2001). Increasing specificity in perceptual development: Infants' detection of nested levels of multimodal stimulation. *Journal of Experimental Child Psychology, 79*, 253-270.
- Bahrick, L. E., Flom, R., & Lickliter, R. (2002). Intersensory redundancy facilitates discrimination of tempo in 3-month-old infants. *Developmental Psychobiology, 41*, 352-363.
- Bahrick, L. E., & Lickliter, R. (2000). Intersensory redundancy guides attentional selectivity and perceptual learning in infancy. *Developmental Psychology, 36*, 190-201.
- Bahrick, L. E., & Lickliter, R. (2002). Intersensory redundancy guides early perceptual and cognitive development. In R. Kail (Ed.), *Advances in child development and behavior* (Vol. 30, pp. 153-187). New York: Academic.
- Bahrick, L. E., & Pickens, J. (1994). Amodal relations: The basis for intermodal perception and learning in infancy. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 205-233). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Banker, H., & Lickliter, R. (1993). Effects of early or delayed visual experience on perceptual development in bobwhite quail chicks. *Developmental Psychobiology, 26*, 155-170.
- Calvert, G. A., Spence, C., & Stein, B. E. (Eds.). (2004). *The handbook of multisensory processes*. Cambridge, MA: MIT Press.
- Carlsen, R. M., & Lickliter, R. (1999). Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychobiology, 35*, 215-225.
- Cornell, E. H. (1979). Infants' recognition memory, forgetting, and savings. *Journal of Experimental Child Psychology, 28*, 359-374.

- Gardner, J. M., & Karmel, B. Z. (1995). Development of arousal-modulated visual preferences in early infancy. *Developmental Psychology, 31*, 473–482.
- Gibson, E. J., & Pick, A. D. (2000). *An ecological approach to perceptual learning and development*. New York: Oxford University Press.
- Gogate, L. J., & Bahrick, L. E. (1998). Intersensory redundancy facilitates learning of arbitrary relations between vowel sounds and objects in seven-month-old infants. *Journal of Experimental Child Psychology, 69*, 133–149.
- Gottlieb, G. (1971). *Development of species-identification in birds*. Chicago: University of Chicago Press.
- Gottlieb, G. (1988). Development of species identification in ducklings: 15. Individual auditory recognition. *Developmental Psychobiology, 21*, 509–522.
- Gottlieb, G., Tomlinson, W. T., & Radell, P. L. (1989). Developmental intersensory interference: Premature visual experience suppresses auditory learning in ducklings. *Infant Behavior and Development, 12*, 1–12.
- Heaton, M. B., Miller, D. B., & Goodwin, D. G. (1978). Species-specific auditory discrimination in bobwhite quail neonates. *Developmental Psychobiology, 11*, 13–21.
- Hernandez-Reif, M., & Bahrick, L. E. (2001). The development of visual-tactile perception of objects: Amodal relations provide the basis for learning arbitrary relations. *Infancy, 2*, 51–72.
- Honeycutt, H., & Lickliter, R. (2001). Order-dependent timing of unimodal and multimodal stimulation affects prenatal auditory learning in bobwhite quail embryos. *Developmental Psychobiology, 38*, 1–10.
- Honeycutt, H., & Lickliter, R. (2002). Prenatal experience and postnatal perceptual preferences: Evidence for attentional bias in bobwhite quail embryos. *Journal of Comparative Psychology, 116*, 270–276.
- Hultsch, H., Schleuss, F., & Todt, D. (1999). Auditory-visual stimulus pairing enhances perceptual learning in a songbird. *Animal Behaviour, 58*, 143–149.
- Knudsen, E. I., & Brainard, M. S. (1995). Creating a unified representation of visual and auditory space in the brain. *Annual Review of Neuroscience, 18*, 19–43.
- Kraebel, K. S., & Spear, N. E. (2000). Infant rats are more likely than adolescents to orient differentially to amodal (intensity based) features of single-element and compound stimuli. *Developmental Psychobiology, 36*, 49–66.
- Lewkowicz, D. J. (2000). The development of intersensory temporal perception: An epigenetic systems/limitations view. *Psychological Bulletin, 126*, 281–308.
- Lewkowicz, D. J. (2002). Heterogeneity and heterochrony in the development of intersensory perception. *Cognitive Brain Research, 14*, 41–63.
- Lewkowicz, D. J., & Lickliter, R. (1994). *The development of intersensory perception: Comparative perspectives*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Lickliter, R., & Bahrick, L. E. (2000). The development of infant intersensory perception: Advantages of a comparative convergent-operations approach. *Psychological Bulletin, 126*, 260–280.
- Lickliter, R., & Bahrick, L. E. (2001). The salience of multimodal sensory stimulation in early development: Implications for the issue of ecological validity. *Infancy, 2*, 447–463.
- Lickliter, R., & Bahrick, L. E. (2004). Perceptual development and the origins of multisensory responsiveness. In G. A. Calvert, C. Spence, & B. E. Stein (Eds.), *Handbook of multisensory processes* (pp. 643–654). Cambridge, MA: MIT Press.
- Lickliter, R., Bahrick, L. E., & Honeycutt, H. (2002). Intersensory redundancy facilitates prenatal perceptual learning in bobwhite quail embryos. *Developmental Psychology, 38*, 15–23.
- Lickliter, R., & Hellewell, T. B. (1992). Contextual determinants of auditory learning in bobwhite quail embryos and hatchlings. *Developmental Psychobiology, 25*, 17–24.
- Lickliter, R., & Virkar, P. (1989). Intersensory functioning in bobwhite quail chicks: Early sensory dominance. *Developmental Psychobiology, 22*, 651–667.

- Mellon, R. C., Kraemer, P. J., & Spear, N. E. (1991). Intersensory development and Pavlovian conditioning: Stimulus selection and encoding of lights and tones in the preweanling rat. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*, 448–464.
- Meredith, M. A., & Stein, B. E. (1986). Visual, auditory and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, *56*, 640–662.
- Monk, C. S., Gunderson, V. M., Grant, K. S., & Mechling, J. L. (1996). A demonstration of the memory savings effect in infant monkeys. *Developmental Psychology*, *32*, 1051–1055.
- Nelson, T. O. (1985). Ebbinghaus's contribution to the measurement of retention: Savings during re-learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *11*, 472–479.
- Ockleford, E., & Vince, M. A. (1977). Heart rate response to light in the embryos of Japanese quail. *Journal of Experimental Zoology*, *201*, 439–444.
- Radell, P. L., & Gottlieb, G. (1992). Developmental intersensory interference: Augmented prenatal sensory experience interferes with auditory learning in duck embryos. *Developmental Psychology*, *28*, 795–803.
- Reynolds, G. D., & Lickliter, R. (2002). Effects of prenatal sensory stimulation on heart rate and behavioral measures of arousal in bobwhite quail embryos. *Developmental Psychobiology*, *41*, 112–122.
- Reynolds, G. D., & Lickliter, R. (2003). Effects of redundant and non-redundant bimodal stimulation on heart rate in bobwhite quail embryos. *Developmental Psychobiology*, *43*, 304–310.
- Ruff, H. A., & Rothbart, M. K. (1996). *Attention in early development*. New York: Oxford University Press.
- Sleigh, M. J., Columbus, R. F., & Lickliter, R. (1996). Type of prenatal sensory experience affects prenatal auditory learning in bobwhite quail. *Journal of Comparative Psychology*, *110*, 233–242.
- Spear, N. E., & McKinzie, D. L. (1994). Intersensory integration in the infant rat. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 133–161). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.
- Tolhurst, B. E., & Vince, M. A. (1976). Sensitivity to odours in the embryo of the domestic fowl. *Animal Behaviour*, *24*, 772–779.
- Walker-Andrews, A. S. (1997). Infants' perception of expressive behavior: Differentiation of multimodal information. *Psychological Bulletin*, *121*, 437–456.