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Intersensory Redundancy Facilitates Prenatal Perceptual Learning in Bobwhite Quail (*Colinus virginianus*) Embryos

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Information presented redundantly and in temporal synchrony across sensory modalities (*intersensory redundancy*) selectively recruits attention and facilitates perceptual learning in human infants. This comparative study examined whether intersensory redundancy also facilitates perceptual learning prenatally. The authors assessed quail (*Colinus virginianus*) embryos' ability to learn a maternal call when it was (a) unimodal, (b) concurrent but asynchronous with patterned light, or (c) redundant and synchronous with patterned light. Chicks' preference for the familiar over a novel maternal call was assessed 24 hr following hatching. Chicks receiving redundant, synchronous stimulation as embryos learned the call 4 times faster than those who received unimodal exposure. Chicks who received asynchronous bimodal stimulation showed no evidence of learning. These results provide the first evidence that embryos are sensitive to redundant, bimodal information and that it can facilitate learning during the prenatal period.

Young infants perceive coherent, unified multimodal objects and events through different sensory modalities even in the first months of life (Lewkowicz, 2000; Lewkowicz & Lickliter, 1994; Lickliter & Bahrick, 2000; Rose & Ruff, 1987). A growing body of research indicates that infants are capable of intersensory perception, at least in large part, by detecting information that is amodal and invariant across the senses (e.g., Bahrick & Pickens, 1994; Gibson & Pick, 2000; Meltzoff & Kuhl, 1994). Amodal information is information that is not specific to one sense but may be detected across two or more sensory modalities. Examples include spatial and temporal properties of dynamic events such as synchrony, rhythm, tempo, and collocation. A number of studies have demonstrated examples of young infants' detection of amodal properties, including the temporal synchrony, tempo of action, and rhythm uniting the sights and sounds of an object impacting a surface (e.g., Bahrick, 1988, 1992; Bahrick & Lickliter, 2000; Lewkowicz, 1992; Spelke, Bom, & Chu, 1983) and temporal information uniting the face and voice during speech (e.g., Dodd, 1979; Kuhl & Meltzoff, 1984). Infants have also been shown to match faces and voices on the basis of the age and gender of the speaker and the speaker's affective expression (Bahrick, Netto, & Hernandez-Reif, 1998; Walker-Andrews, 1982, 1997; Walker-Andrews, Bahrick, Raglioni, & Diaz, 1991). Several generalizations have emerged from this body of research, including that infants are 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, 1992, in press; Gogate & Bahrick, 1998; Lewkowicz, 2000). However, we know little about what makes amodal information so salient to infants; about the consequences of this salience for later learning, memory, and cognition; or about how the detection of amodal relations relates to and promotes detection of modality-specific stimulus properties.

Bahrick and Lickliter (2000) recently proposed an intersensory redundancy hypothesis to address some of these questions and 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 concurrent presentation of the same information (e.g., rate, rhythm, intensity) across two or more sensory modalities. For the auditory and visual modalities, this also entails the temporally synchronous alignment of the bimodal information. The intersensory redundancy hypothesis proposes that information presented redundantly across two or more sensory modalities selectively recruits infant attention and facilitates perceptual learning of amodal properties more effectively than does the same information presented unimodally. This selective attention on the part of the infant gives initial advantage to the perceptual processing, learning, and memory of stimulus properties that are bimodally specified (amodal) over the processing, learning, or memory of modality-specific properties of sensory stimulation. In other words, when information is simultaneously presented across two or more modalities it is highly salient to infants and can direct attentional selectivity at the expense of information that is not

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redundant (Bahrick & Pickens, 1994; Bahrick, Walker, & Neisser, 1981).

Results from neuroanatomical, physiological, and behavioral studies of both birds and mammals have provided converging evidence in support of this view, demonstrating the salience of multimodal stimulation for the development of attention and perception during early infancy (Bahrick, 1988, 1992; Columbus, Sleigh, Lickliter, & Lewkowicz, 1998; Gogate & Bahrick, 1998; Knudsen & Brainard, 1995; Richards, 2000; Sleigh, Columbus, & Lickliter, 1998; Stein & Meredith, 1993; Walker-Andrews, 1997; Wallace & Stein, 1997). For example, Bahrick and Lickliter (2000) assessed the ability of 5-month-old infants to differentiate between two complex rhythms under bimodal and unimodal presentation conditions. Results indicated that infants can differentiate rhythms following bimodal auditory–visual habituation but not following unimodal visual or auditory habituation. Rhythm becomes "foreground" when an event that has a rhythmic structure is presented across two sensory modalities, whereas rhythm becomes less salient when the same event is perceived in one modality alone. It appears that when infants first learn to differentiate amodal information, differentiation is facilitated by intersensory redundancy and attenuated under conditions of unimodal stimulation. These findings are consistent with those from neurophysiological research suggesting that intersensory stimulation elicits greater neural response than unimodal components of the same events (Stein & Meredith, 1993) and with findings from comparative behavioral research demonstrating the functional distinction between unimodal and multimodal stimulation in early postnatal development (Columbus et al., 1998; Sleigh et al., 1998).

It should be emphasized that the importance of redundant stimulation for directing attentional selectivity is expected to be most pronounced during early perceptual learning in a given domain and that we are not implying that young infants are unable to detect amodal stimulus properties in unimodal stimulation. In fact, a number of studies have demonstrated that infants are adept perceivers of amodal information such as rhythm or tempo in unimodal stimulation (Chang & Trehub, 1977; Demany, McKenzie, & Vurpillot, 1977; Mendelson, 1986; Morrongiello, 1984, 1988; Rose & Ruff, 1987). Rather, the intersensory redundancy hypothesis proposes that amodal stimulus properties such as rhythm, tempo, or intensity are most salient and easiest to detect when they are bimodally presented. From this view, infants are more likely to selectively attend to amodal properties in bimodal, temporally coordinated stimulation and attend to other stimulus properties in conditions of asynchronous or unimodal stimulation (Bahrick, Lickliter, & Flom, 2000a, 2000b). Further, once infants detect an amodal property in bimodal stimulation, attention to that property can carry over to conditions of unimodal stimulation as well. For example, Bahrick and Lickliter (2000) found that once intersensory redundancy had recruited infant attention to the amodal property of rhythm during habituation, 5-month-old infants were then able to detect a new rhythm in unimodal test trials. Thus, amodal stimulus properties such as rate or rhythm may be more difficult but are not impossible to detect in unimodal stimulation. Rather, it is a matter of attentional focus. Infant attention is likely to be selectively focused on amodal properties under conditions of redundant bimodal stimulation and more focused on other features (modality-specific properties such as color or pitch) under conditions of unimodal stimulation.

Recent findings from 3- and 5-month-old infants have provided converging evidence for this shift in selective attention to stimulus properties as a function of bimodal versus unimodal exploration. Three-month-old infants were found to discriminate a change in tempo following bimodal but not unimodal habituation (Bahrick et al., 2000a). Similarly, 5-month-old infants discriminated a change in complex rhythm following bimodal but not unimodal habituation (Bahrick & Lickliter, 2000). In contrast, 5-month-old infants detected a change in the orientation of a moving object (unimodal visual property) following unimodal habituation and failed to detect a change in orientation following bimodal habituation (Bahrick et al., 2000b). In other words, unimodal exploration facilitated detection of modality-specific properties. Taken together, these results support the view that information presented redundantly across two sensory modalities is more likely to recruit attention to the redundantly specified (amodal) properties of events, whereas the same event presented to one sensory modality selectively recruits attention to modality-specific aspects of the event and facilitates perceptual learning of those properties at the expense of others. This scenario would suggest that in a world where dynamic events provide predominantly multimodal stimulation, bimodally specified stimulus properties are more likely to be selectively attended during early development, thereby fostering perception, learning, and memory of those aspects of stimulation prior to other modality-specific aspects within a given domain.

At present, most research on the role of intersensory redundancy in perceptual development has been conducted with human infants 3–7 months of age (but see Bahrick, 2001, and Slater, Quinn, Brown, & Hayes, 1999, for recent examples with 3-week-olds and newborns), who have already had a wealth of perceptual experience in a multimodal world. If the intersensory redundancy hypothesis reflects a general developmental principle, then redundancy should potentially be a potent contributor to perceptual responsiveness and learning at earlier stages of development and in other animal species as well. Results from rat pups (Kraebel, Vizvary, & Spear, 1998; Mellon, Kraemer, & Spear, 1991; Spear & McKinzie, 1994) and quail chicks (Lickliter, Lewkowicz, & Columbus, 1996) suggest the importance of temporally and spatially coordinated multimodal information to nonhuman animal infants' perceptual responsiveness. However, further research assessing attention and discrimination of amodal properties such as rate, duration, tempo, and rhythm under both unimodal and bimodal presentation conditions and at different periods of development is needed to extend these initial findings and further test the intersensory redundancy hypothesis.

In this light, there is little if any research concerned with the role of intersensory redundancy in guiding attentional selectivity and perceptual learning during the prenatal period. Of course, systematic manipulation of the human fetus's sensory experience during the prenatal period is generally prohibited, and the use of such experimental methods is possible only with nonhuman animal subjects. One obvious advantage of the use of animal subjects to study perceptual learning in the prenatal period is the ability to readily alter both the timing and amount of particular sensory experience available to the developing embryo or fetus. As a result, comparative studies of birds and mammals have yielded a growing body of information regarding the experiential conditions necessary for the emergence of prenatal perceptual discrimination and learning (Gottlieb, 1971, 1980, 1988; Lickliter, 1993, 1995; Lickliter & Lewkowicz, 1995; Smotherman & Robinson, 1988, 1995). This research has documented that embryos and fetuses are sensitive to a variety of stimulus features in the period prior to birth or hatching, including the timing of sensory stimulation relative to the developmental stage of the organism, the overall amount of sensory stimulation available, and the type (unimodal vs. multimodal) of stimulation provided or denied (see Lickliter, 2000, for a review).

Of particular interest to the intersensory redundancy hypothesis is converging evidence from research with precocial avian embryos suggesting that concurrent bimodal stimulation can interfere with prenatal perceptual learning (Gottlieb, Tomlinson, & Radell, 1989; Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). For example, Gottlieb et al. (1989) found that if duck embryos were exposed to visual stimulation (patterned light) during prenatal exposure to an individual variant of their maternal call, they appeared unable to learn the individually distinctive auditory features of that call. However, when the prenatal visual experience was made to alternate with exposure to the maternal call (i.e., sequential rather than concurrent), the duck embryos were capable of learning the call, as evidenced by their preference for the familiar call over an unfamiliar maternal call in the period following hatching. Similarly, several studies have demonstrated that bobwhite quail embryos fail to exhibit a preference for an individual maternal call when the call is presented concurrently with visual stimulation during the 24-hr period prior to hatching (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). This intersensory interference occurred only when the two sensory systems (auditory and visual; for a parallel example with auditory and vestibular see Radell & Gottlieb, 1992) were stimulated *concurrently* and was not seen when the maternal call was presented unimodally or sequentially with visual stimulation. This pattern of results led Radell & Gottlieb (1992) to suggest that such intersensory interference is likely to occur when immature sensory systems are stimulated simultaneously. They proposed that the embryo is not capable of adequately attending to simultaneous sensory stimulation, in that the overall amount of prenatal stimulation appears to effectively overwhelm the young organism's attentional capabilities.

These findings and their interpretation would appear to challenge the intersensory redundancy hypothesis and its applicability to the prenatal period, in that bimodal stimulation is thought to interfere with rather than facilitate perceptual learning. However, it is important to emphasize that none of the comparative studies of prenatal perceptual learning reviewed above provided subjects redundant, temporally synchronous bimodal stimulation in the period prior to hatching. In all cases, embryos were exposed to concurrent but temporally unrelated (i.e., no common temporal structure) auditory–visual or auditory–vestibular stimulation, thereby eliminating synchrony and potentially obscuring bimodally specified amodal stimulus properties such as rate, duration, or rhythm (Gottlieb et al., 1989; Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). Given that both nonhuman animal infants and human infants have been shown to be highly sensitive to amodal stimulus properties in the weeks and months following birth (e.g., Bahrick, 1988, 1992; Lewkowicz, 2000; Mellon et al., 1991; Spelke, 1979; Spear & McKinzie, 1994), we were interested in whether embryos or fetuses are likewise sensitive to redundantly specified information during the prenatal period. Can redundant bimodally specified information guide attentional selectivity and facilitate perceptual learning prior to birth or hatching, or alternatively, does bimodal information necessarily disrupt the immature attentional capabilities of the embryo or fetus?

To address this issue, in the present study we assessed prenatal auditory learning in bobwhite quail embryos exposed to redundant, synchronous audiovisual information versus embryos exposed to either unrelated, asynchronous (auditory and visual) or unimodal (auditory) information prior to hatching. In keeping with the intersensory redundancy hypothesis, we predicted that amodal rate and duration information presented across the auditory and visual modalities in a temporally coordinated manner would recruit the embryo's attention and foster perceptual learning, whereas the same information presented unimodally or out of synchrony across the auditory and visual modalities would result in attenuated discrimination and learning.

General Method

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

Subjects

Subjects were 234 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). After 20 days of incubation, eggs were transferred to a hatching tray located in the bottom of the incubator. To control for possible effects of variations in developmental age, we used only those chicks that hatched on Day 23. The embryo's age is calculated on the basis of the first day of incubation being Day 0, the second 24 hr of incubation being Day 1, and so on. We controlled the possible influence of between-batch variation in behavior 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 had been 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 10–15 same-age chicks to mimic naturally occurring brood conditions (Stokes, 1967). These rearing tubs were located in a sound-attenuated room illuminated by 100-W heat lamps, which maintained an ambient air temperature of approximately 30 °C. Food and water were continuously available throughout the duration of each experiment.

Procedure

The bobwhite quail embryo's bill normally penetrates the air space at the large end of the egg approximately 24–36 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 Hova-bator portable incubators (GQF Manufacturing, 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 below. It is important to note that unlike in previous studies in this series, the top of the egg shell and inner shell membrane was not removed prior to prenatal stimulation. Carlsen and Lickliter (1999) recently demonstrated that quail embryos respond to auditory and visual stimulation presented through the egg shell following their movement into the air space in the days prior to hatching.

During the 24 hr prior to hatching, embryos received intermittent exposure to unimodal auditory stimulation (Experiment 1), concurrent but unsynchronized bimodal (audiovisual) stimulation (Experiment 1), or temporally synchronized bimodal stimulation (Experiment 2). The auditory stimulus used in all experiments was an individual variant of the species-typical bobwhite quail maternal assembly call. This maternal call was broadcast from a speaker located at the air-hole opening on the top of the portable incubator, directly above the quail embryos within. The recording of the individual maternal call was broadcast from a Sony portable compact disk player at a peak intensity of 65 dB, measured by a Bruel & Kjaer Model 2232 sound-level meter (B & K Instruments, Marlborough, MA) located within the incubator on the substrate supporting the embryos. All the normally occurring acoustic components of the maternal vocalization were present and unaltered. The call consisted of a burst of five notes that displayed a unique and complex rhythmic pattern. The burst had a total duration of 3 s (notes occurred at an average rate of 1.7 notes/s) and was followed by interburst interval of 1 s. The notes of the call burst varied in terms of duration and temporal patterning as well as intensity and fundamental frequency. We achieved audiovisual redundancy by recreating the temporal patterning of the notes in our visual display of a flashing light. In other words, the flashing light was synchronized to the notes of the call, duplicating the duration of each note and the spacing between notes. We achieved this alignment of amodal temporal information by capturing the call's audio track with Apple's QuickTime Movie Player, saving the visual image in waveform, and converting the height of each peak in the waveform into a numerical value, thereby providing time interval and height value for each peak. Final output was a Windows file that would play the call and present a flash from a projector to coincide with the call going above a minimum threshold amplitude. The flash of light persisted until the call's amplitude dropped below this threshold. It is important to note that the intensity of the patterned light remained constant during exposure cycles, whereas the intensity of the call varied during a cycle. Thus, not all available amodal stimulus properties were redundant in this procedure; rather, the amodal properties of temporal patterning (rhythmic structure), rate, and duration were redundantly presented to the visual and auditory modalities, whereas intensity was not. The light was delivered by a Proxima 2810 desktop projector (InFocus Corp., Wilsonville, OR) that was connected to the computer and was situated directly above the portable incubator containing the embryos.

The nonsynchronous bimodal event received by some subjects involved elements from the two previous conditions, such that embryos were concurrently exposed to the maternal call and patterned light from the overhead projector. As in the synchronous condition described above, the auditory and visual stimulation shared common duration and rate information in that the patterned light was made to pulse in the same temporal pattern as the maternal call (a mean of 1.7 bursts/s for 3.0 s duration). However, in this stimulation regime the light was not temporally aligned with the call (i.e., the auditory and visual stimulation were asynchronous) but was presented out of phase with the onset of the call, thereby eliminating intersensory redundancy of temporal information. We accomplished this by delaying the onset of the call relative to the onset of the patterned light by 1–3 s over the course of exposure cycles.

Testing

Testing was conducted postnatally at 24 hr ($\pm$1 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 in height that was lined with foam to attenuate echoes and covered by an opaque black curtain to shield the observer from the subject's view. The floor of the arena was painted flat black. 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 5% of the total area of the arena. Midrange dome-radiator speakers were hidden behind the curtain in each of the two approach areas, and each of these speakers received input from a Tascam Model 122-B 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 hand-held stopwatches was used to record the latency and duration of response, as described below.

Testing involved placing each subject 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 (but not identical) in phrasing, call duration, repetition rate, and the major peak of dominant frequency. They varied primarily in the minor peaks of dominant frequency (see Heaton, Miller, & Goodwin, 1978, Table 1). It is important to note that previous studies have shown that quail chicks do not show a naive preference for either of these variants of the maternal call (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). The sound intensity of each maternal call presented during testing was adjusted to peak at 65 dB (fast response, A scale), measured at the point where the chick was introduced into the arena. We counterbalanced the locations of Call A and Call B 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 s for latency (i.e., the length of the trial) and 0 s 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. The differences in latency and duration of approach were evaluated using the Wilcoxon matched-pairs signed-ranks 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 Unimodal Auditory Exposure on Prenatal Perceptual Learning

Previous studies have shown that maternally naive bobwhite quail embryos are capable of learning an individual variant of a bobwhite maternal call during the late prenatal period (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Sleigh, Columbus, & Lickliter, 1996). These studies have consistently found that embryos exposed to a particular maternal call (presented unimodally) over the course of the day prior to hatching significantly prefer that familiar call in postnatal testing. The basic procedure in these experiments involved intermittently exposing (for 10 min/hr) group-incubated embryos to a recording of a particular maternal call over a 24-hr period and then subsequently testing hatchlings for their auditory preference in a postnatal simultaneous choice test involving the familiar call and a novel maternal call. The present experiment followed this general procedure but, unlike previous studies, manipulated the overall amount of time embryos were exposed to an individual maternal call in the period prior to hatching. We were interested in assessing how much unimodal exposure embryos required to demonstrate a significant preference for the familiar call over a novel call in postnatal testing.

Method

Seventy-eight bobwhite quail embryos, divided into three experimental groups, served as subjects. All embryos in each group were exposed to an individual maternal call (presented without visual stimulation) as described in the General Method, but groups varied in the amount of time they heard the call prior to hatching. Group 1 ($n = 26$) received the same amount of auditory exposure used in previous studies in this series. Specifically, Call B was broadcast for 10 min/hr over the 24 hr prior to hatching (240 total min exposure). Group 2 ($n = 26$) received exposure to Call B for 10 min/hr over the 12 hr prior to hatching (120 total min), and Group 3 ($n = 26$) received 10 min/hr of exposure to Call B over the 6 hr prior to hatching (60 total min). All subjects were tested individually 24 hr following the offset of exposure in a postnatal choice test (see General Method) assessing their preference between the familiar call (Call B) and an unfamiliar maternal call (Call A). Because these maternal calls are equally attractive to unexposed embryos and hatchlings (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992), we considered subjects to have learned Call B if they exhibited a significant preference for that familiar call over the novel call in the simultaneous choice test.

Results and Discussion

As illustrated in Table 1, the two variants of the bobwhite maternal call appeared equally attractive to chicks receiving 60 min or 120 min of prenatal exposure to Call B. Subjects in Groups 2 and 3 who demonstrated a preference during testing were just as likely to prefer Call A as Call B, and an equivalent number of subjects showed no preference for either maternal call. Analysis of latency and duration of response to the test stimuli by the Wilcoxon test likewise revealed no significant differences in response to the two maternal calls (Table 2). In contrast, chicks exposed to Call B for 240 min prior to hatching (Group 1) significantly preferred this familiar call over the unfamiliar Call A in postnatal testing. Analysis of latency and duration scores further supported this result, with subjects showing significantly shorter latencies and longer durations in their response to the familiar maternal call than to the novel maternal call.

These results replicate earlier findings demonstrating prenatal auditory learning in quail embryos receiving unimodal exposure to an individual maternal call (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Sleigh et al., 1996) and extend these findings by showing that a reduction in the amount of prenatal exposure to 2 hr or less is not sufficient to support a subsequent postnatal preference for the familiar maternal call. Embryos appear to require more than 120 min of unimodal auditory exposure to an individual maternal call to prefer that call over a novel call 24 hr after hatching. At this point, it was not known, however, whether bimodal (auditory and visual) prenatal stimulation would result in a similar pattern of response. The next two experiments were designed to examine this question.

Experiment 2: Effects of Nonredundant Bimodal Exposure on Prenatal Perceptual Learning

This experiment provided quail embryos with concurrent visual stimulation during their exposure to an individual maternal call in the period prior to hatching. Specifically, subjects receiving exposure to maternal Call B were also exposed to a patterned light matching the rate and duration of the notes of the maternal call. However, the visual and auditory stimulation was temporally misaligned, in that the pulses of patterned light were out of synchrony with the notes of the maternal call. As a result of this temporal displacement, embryos were not provided redundant, bimodally specified information regarding rate or duration. Several previous studies of avian embryos have indicated that concurrent (but asynchronous) bimodal stimulation during the prenatal period can interfere with auditory learning (Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). However, these studies did not match rate and duration information across sensory modalities and also did not systematically vary the overall amount of bimodal stimulation embryos received prior to hatching. The present experiment provided embryos the same rate and duration information across concurrent (but asynchronous) auditory and visual stimulation to further probe the potentially facilitating or interfering effects of prenatal bimodal sensory stimulation on perceptual learning.

Table 1
Preference Scores for Subjects Tested 24 Hr Following Hatching

Experiment and condition	n	n responding	Preference: Call A	Preference: Call B	Preference: No preference
Experiment 1					
240-min Call B	26	25	2	18*	5
120-min Call B	26	25	10	10	5
60-min Call B	26	26	6	10	10
Experiment 2					
240-min asynchrony	26	26	10	11	5
120-min asynchrony	26	26	9	6	11
60-min asynchrony	26	26	6	10	6
Experiment 3					
240-min synchrony	26	26	2	16*	8
120-min synchrony	26	26	4	16*	6
60-min synchrony	26	20	4	16*	6

* $p < .05$ (chi-square test).

Table 2
Median Latency and Duration Scores for Subjects 24 Hr Following Hatching

Experiment and condition	Latency		Duration	
	Call A	Call B	Call A	Call B
Experiment 1				
240-min Call B	76.0	13.5	30.5	69.0*
120-min Call B	30.5	52.5	39.0	42.0
60-min Call B	32.0	43.0	47.0	63.0
Experiment 2				
240-min asynchrony	25.5	49.0	44.5	52.0
120-min asynchrony	38.0	45.5	57.0	41.0
60-min asynchrony	32.0	49.5	43.0	63.0
Experiment 3				
240-min synchrony	85.0	26.5*	28.0	71.5*
120-min synchrony	63.0	44.5	20.5	76.5*
60-min synchrony	33.0	27.0	26.5	66.0*

* $p < .05$ (Wilcoxon test).

Method

Seventy-eight bobwhite quail embryos served as subjects. Embryos were divided into three experimental groups, all of which received concurrent exposure to maternal Call B (consisting of notes presented at an average of 1.7 notes/s) and a light pulsed at an average of 1.7 flashes/s (see General Method for details). The onset of the light was, however, initiated out of phase with the onset of the call. We accomplished this by allowing a 1–3 s delay between the onset of the repeating 3-s cycles of patterned light and the onset of the repeating 3-s cycles of the maternal call. Embryos were thus exposed to the same temporal pattern (rate and duration) from the maternal call and the patterned light, but asynchronously and nonredundantly. As in the previous experiment, Group 1 ($n = 26$) received 240 min of prenatal exposure to the bimodal event, Group 2 ($n = 26$) received 120 min of exposure, and Group 3 ($n = 26$) received 60 min of total exposure to Call B and the patterned light.

Results and Discussion

Results are shown in Tables 1 and 2. Embryos exposed to the maternal call paired with visual stimulation failed to demonstrate a significant preference for either the familiar maternal call (Call B) or the novel maternal call (Call A) during postnatal testing, regardless of the amount of prenatal exposure. Correspondingly, there were no significant differences in the subjects' latency and duration for either of the calls presented during testing (Table 2).

The results of this experiment converge with those of previous studies (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992) in demonstrating that bimodal presentation of auditory and visual information interferes with quail embryos' prenatal auditory learning. Even though the visual stimulation made available in this experiment provided embryos additional exposure to the rate and duration of the call, it nonetheless appeared to interfere with auditory learning, paralleling the results of prior studies concerned with concurrent (but nonredundant) prenatal bimodal stimulation (see also Gottlieb et al., 1989; Radell & Gottlieb, 1992, for examples from ducklings). Whereas embryos exposed to a maternal call presented unimodally (for a total of 240 min) demonstrated a significant preference for that familiar call in postnatal testing (Group 1, Experiment 1), embryos exposed to the concurrent presentation of the maternal call and patterned light in this experiment failed to demonstrate a preference for the familiar call following hatching regardless of overall exposure time (Table 1). Because the auditory and visual information was presented in an asynchronous manner, embryos were denied experience with temporally aligned and bimodally specified information regarding rate and duration during the prenatal exposure periods. It is possible that the availability of such amodal information could facilitate perceptual learning during the prenatal period, given that nonhuman animal infants and human infants have been shown to be highly sensitive to amodal stimulus properties during early development (Bahrick & Pickens, 1994; Spear & McKinzie, 1994). To examine this issue, we designed the next experiment to assess the effect of redundant, bimodally specified audiovisual information on prenatal auditory learning.

Experiment 3: Effects of Redundant Bimodal Exposure on Prenatal Perceptual Learning

Method

Seventy-eight bobwhite quail embryos served as subjects. All embryos received temporally aligned auditory and visual stimulation during the period prior to hatching. Specifically, the maternal call and flashing light were presented concurrently and redundantly, such that the temporal pattern, rate, and duration of the light were synchronized with the pattern, rate, and duration of the individual notes of the maternal call (see General Method for details). Under this condition, the embryos were exposed to bimodally specified information regarding rhythmic pattern, rate, and duration during prenatal exposure periods. As in the previous experiment, subjects were divided into three experimental groups that varied in the total amount of time they were exposed to the maternal call paired with patterned light prior to hatching (240 min, 120 min, or 60 min of exposure).

Results and Discussion

Chicks exposed to redundant auditory and visual information as embryos demonstrated prenatal perceptual learning, regardless of their overall amount of prenatal exposure. Chicks receiving 60, 120, or 240 min of exposure to Call B prior to hatching all showed a significant preference for the familiar maternal call in postnatal testing (Table 1). Correspondingly, analyses of latency and duration scores supported these results: Chicks showed significantly shorter latencies and longer durations in their response to the familiar call following 240 min of prenatal exposure and significantly longer durations, but not latency to approach the familiar call following 120 min or 60 min of prenatal exposure (Table 2).

When compared with the results of Experiments 1 and 2, the results of this experiment indicate that intersensory redundancy can facilitate prenatal perceptual learning. In particular, quail embryos exposed to temporally synchronous and redundant auditory and visual information required only 60 min of prenatal exposure to demonstrate a preference for the familiar maternal call in postnatal testing, whereas embryos exposed to unimodal auditory information required 240 min of exposure to show a significant preference. Said another way, embryos receiving unimodal auditory exposure to the maternal call (Experiment 1) required four times the amount of prenatal exposure to demonstrate perceptual learning than did embryos receiving synchronous, bimodally specified information in this experiment.

It is important to note that the present experiment provided several types of amodal information not available in Experiments 1 or 2 that could have served as the basis for rapid perceptual learning. For example, the light and maternal call were synchronized both in terms of their temporal macrostructure (burst–pause patterning) and temporal microstucture (note–internote intervals). Thus, the synchronization of the call and light made the rhythmic patterning of the auditory and visual stimulation 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. Embryos could have detected any or all of these amodal temporal properties.

The striking facilitation of prenatal learning observed in this experiment stands in contrast to earlier studies of avian embryos, which have consistently shown that concurrent, bimodal stimulation interferes with prenatal auditory learning (Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). These reports of intersensory interference prompted Radell and Gottlieb (1992) to suggest that the failure of embryos to process concurrently presented information (which is processed when presented unimodally) was the result of immature attentional processes. Of course, as discussed earlier these studies did not provide subjects intersensory redundancy. The results of the present experiment argue for limiting the bimodal interference conclusion of previous research in this area to conditions in which the concurrent information is asynchronous or temporally misaligned. Providing bimodally specified, redundant information during the late prenatal period resulted in dramatically different outcomes (faciliation rather than interference) from those obtained in these earlier studies. The current results point to the potency of intersensory redundancy in guiding attentional selectivity and perceptual learning during early development.

General Discussion

The results of this study provide the first evidence that intersensory redundancy can guide attentional selectivity and facilitate perceptual learning during the prenatal period. Similar to recent results from human infants (Bahrick & Lickliter, 2000; Gogate & Bahrick, 1998; Lewkowicz, 1996; Slater et al., 1999), avian embryos showed enhanced perceptual learning when amodal information was presented bimodally and in a temporally coordinated manner. This finding highlights the functional significance of the distinction between multimodal and unimodal stimulation for guiding attention and perceptual learning in early development. Multimodal stimulation can make overlapping, temporally coordinated information available to the different senses, and this redundancy appears to have a powerful impact on the deployment of attention, even during the prenatal period.

The results of this study also indicate that the salience of intersensory redundancy during prenatal development depends on the proper temporal alignment of the components of bimodal stimulation (Experiment 3). Asynchronous bimodal presentations did not foster prenatal perceptual learning and in fact appeared to interfere with learning (Experiment 2 vs. Experiment 1). These results parallel those obtained with human infants (Bahrick & Lickliter, 2000; Lewkowicz, 1992) and provide further evidence against the argument that the salience of intersensory redundancy is simply due to increased attention resulting from concurrent stimulation in two sensory modalities. If that were the case, then the subjects in Experiment 2 (who received concurrent auditory and visual stimulation) should have demonstrated prenatal perceptual learning, and as shown in Tables 1 and 2, they did not.

In contrast, the synchronous alignment of audible and visible stimulation appears to highlight amodal information (such as rhythmic pattern, rate, and duration) and can result in increased selective attention to and processing of these amodal properties during a given exposure period. The finding that embryos exposed to temporally aligned auditory and visual information regarding rate and duration of a maternal call learned that call four times faster than embryos exposed to only auditory information (Experiment 3 vs. Experiment 1) strongly argues for this interpretation. It is important to note that the degree to which redundant, bimodally specified information is normally available during the prenatal period for avian (or mammalian) species remains relatively unexplored, and future descriptive work is needed to better document the nature of unimodal and multimodal sensory stimulation typically present during late prenatal and early postnatal development. For example, the prevalence of synchrony, rate, and rhythm information uniting motion, touch, and sound (in ovo or in utero) could be examined. In any case, the present results certainly indicate that precocial avian embryos are sensitive to redundant, bimodally specified information during the late stages of the prenatal period.

Several investigators working with human infants have also reported findings that support the view that multimodal stimulation has greater perceptual salience than unimodal stimulation in early development. In a series of related studies, Lewkowicz (1988a, 1988b, 1992, 1996) has shown that regardless of the specific nature of the information specifying multimodal stimulation (e.g., flashing checkerboards and pure tone, moving objects and punctate sounds, faces and voices), human infants consistently exhibit the capacity to discriminate changes in stimulation when those changes occur in both the auditory and the visual modalities concurrently. In contrast, when changes in stimulative features are unimodal (e.g., a change in the temporal rate of one component or a change in the gender of the speaker), discrimination is not always observed. Bahrick (1988, 1992, 1994) has provided converging lines of evidence for the power of redundant (amodal) information in guiding and constraining early intersensory responsiveness. In these studies, information that was redundant across two or more senses was found to direct infants' perceptual learning and buffer them against learning incongruent or arbitrary intersensory relations. For example, following training, infants were able to learn to pair an object and sound together when they were united by amodal relations (temporal synchrony and composition) but not when the amodal information was incongruent (Bahrick, 1988). Taken together with the current results, this body of work concerned with multimodal stimulation underscores the notion that redundant sensory information can provide the young organism with the potential for enhanced responsiveness during both the prenatal and early postnatal periods. The present study also serves to emphasize that newborns' and young infants' sensitivity to redundant, bimodally specified information (e.g., Bahrick, 2001; Morrongiello, Fenwick, & Chance, 1998; Slater et al., 1999) likely emerges during the prenatal period, a point often overlooked in discussions of perceptual development.

The consistent pattern of findings across different measures of responsiveness, different species, and different stages of development suggests that the concept of intersensory redundancy may be meaningfully investigated as a general principle of early development, potentially applicable across a variety of avian and mammalian species (Lickliter & Bahrick, 2000, 2001). We have recently proposed an intersensory redundancy hypothesis to describe the general nature of this principle and its likely effects on perceptual development (Bahrick & Lickliter, 2000). Specifically, intersensory redundancy is seen to recruit the young organism's attention, causing redundant information to become "foreground" and other information to become "background." This fosters perceptual differentiation, learning, and memory for redundant, amodal properties before other stimulus properties. When the same amodal property (for example, in this study the properties of rate or duration) is presented unimodally, it will not recruit comparable levels of attention and thus will not be perceived, learned, or remembered as well. The results of the present study provide further support for the intersensory redundancy hypothesis and extend its applicability to the prenatal period. Additional research assessing attention and discrimination of other amodal properties, different presentation conditions, and other animal species is needed to assess the generalizablity of intersensory redundancy effects in early perceptual and cognitive development.

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