Developmental Science 9:6 (2006), pp 604–615

PAPER

Intersensory redundancy educates selective attention in bobwhite quail embryos

Robert Lickliter, Lorraine E. Bahrick and Rebecca G. Markham

Infant Development Research Center, Department of Psychology, Florida International University, USA

Abstract

We assessed whether exposure to amodal properties in bimodal stimulation (e.g. rhythm, rate, duration) could educate attention to amodal properties in subsequent unimodal stimulation during prenatal development. Bobwhite quail embryos were exposed to an individual bobwhite maternal call under several experimental and control conditions during the day prior to hatching. Experimental groups received redundant auditory and visual exposure to the temporal features of an individual maternal call followed by unimodal auditory exposure to the same call immediately or after a 2-hr or 4-hr delay. Control groups received (1) the same exposure but in the reverse sequence (unimodal → redundant bimodal), (2) asynchronous bimodal → unimodal, (3) only unimodal exposure, or (4) only bimodal exposure. All experimental groups showed a significant preference for the familiar maternal call over a novel maternal call when tested 2 days after hatching, whereas none of the control groups showed a significant preference for the familiar call. These results indicate that intersensory redundancy can direct attention to amodal properties in bimodal stimulation and educate attention to the same amodal properties in subsequent unimodal stimulation where no intersensory redundancy is available.

Introduction

Attentional selectivity and the processes that underlie it are essential to the ability to detect and differentiate objects and events in the rich array of stimulation available to perceivers at any moment in time (Ruff & Rothbart, 1996). Selective attention thus provides the foundation for what is perceived and learned, and an understanding of what guides this process and how it changes developmentally seems essential for successful theories of learning and memory. An enduring question in developmental science has been what causes some patterns of sensory stimulation to be salient, attended to, and remembered and other patterns of stimulation to be overlooked or ignored during early development?

Research with young infants has consistently indicated that one aspect of stimulation that is highly salient and selectively attended, particularly during early development, is information that is amodal and redundant across two or more senses (Bahrick & Lickliter, 2002; Bahrick & Pickens, 1994; Gibson & Pick, 2000; Lewkowicz, 2000; Lewkowicz & Lickliter, 1994; Lickliter & Bahrick, 2000; Walker-Andrews, 1997). For example, the face and voice of a person speaking share temporal synchrony, common rhythm, tempo, and changing intensity. By selectively attending to these bimodally specified amodal properties, young perceivers can attend to the unitary event, the person speaking, and ignore unrelated sights and sounds nearby. Further, detection of amodal information appears to guide and constrain detection of more specific aspects of stimulation, including information that is specific to a particular sensory modality (Bahrick, 2001; Gogate & Bahrick, 1998). Not surprisingly, a large body of research has demonstrated that young infants are adept perceivers of amodal relations uniting auditory and visual stimulation (e.g. Bahrick, 1992; Bahrick & Pickens, 1994; Lewkowicz, 1996, 2004a; Morrongiello, Fenwick & Nutley, 1998; Spelke, 1979; Walker-Andrews, 1997; Walker-Andrews & Lennon, 1985).

We have proposed an intersensory redundancy hypothesis (IRH) to provide a specific account for how the detection of amodal information might organize and guide selective attention and perceptual learning during early development (Bahrick & Lickliter, 2000, 2002; Bahrick, Lickliter & Flom, 2004). Amodal information is information that can be detected by more than one sense modality. Thus, the sights and sounds of hands clapping provide intersensory redundancy in that they are temporally

Address for correspondence: Robert Lickliter, Department of Psychology, Florida International University, Miami, FL 33199, USA; e-mail: licklite@fiu.edu

synchronous, spatially collocated, and convey the same rhythm, tempo, and intensity patterns across vision and audition. The IRH makes two related testable predictions. According to one prediction, perceptual processing and learning of amodal properties is facilitated in multimodal stimulation, where intersensory redundancy is available, compared with unimodal stimulation, where no redundancy is possible. This prediction has been supported by several studies of human infant perception (Bahrick, Flom & Lickliter, 2002; Bahrick & Lickliter, 2000; Lewkowicz, 2004a, 2004b). For example, Bahrick and Lickliter (2000) assessed the ability of 5-month-old infants to discriminate complex rhythmic patterns in redundant audio-visual stimulation compared to 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), umimodal visual stimulation (they could only see the hammer), or unimodal auditory stimulation (they could only hear the soundtrack of the hammer tapping). Only infants who received the synchronous bimodal stimulation discriminated between the two rhythms, showing a significant visual recovery to a change in rhythm. Infants who received unimodal visual or auditory stimulation or non-synchronous audio-visual 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). Intersensory redundancy available in audio-visual events appears to facilitate detection of amodal properties such as rhythm and tempo during early development.

A second prediction of the IRH holds that when information is presented non-redundantly or unimodally, it selectively recruits attention and facilitates perceptual processing of modality-specific properties (e.g. color, pattern, pitch, timbre) more effectively than when stimulation is multimodal and redundant. Thus, discrimination among individual voices should be enhanced when the voices are presented unimodally, in the absence of intersensory redundancy. For example, when listening to a person speaking on a telephone, the pitch and timbre of their speech are better detected than would be the case in audio-visual stimulation. This prediction has also been supported by recent findings. For example, 3-month-old infants were habituated to the voice of a woman speaking in the context of intersensory redundancy (with a synchronously moving face) or no redundancy (a static face). Test trials played a novel voice with the same woman speaking in synchrony (redundant information) or with a static face (non-redundant). Results demonstrated a significant discrimination of the novel voice in the non-redundant, but not the redundant condition (Bahrick, Lickliter, Shuman, Batista & Grandez, 2003). Similarly, 3- and 5-month-old infants have been shown to detect a change in orientation of a hammer tapping (a property available visually but not acoustically) following unimodal visual habituation, but not following redundant audio-visual habituation (Bahrick, Lickliter & Flom, 2006).

Related comparative research has also demonstrated the facilitative effect of intersensory redundancy on perceptual learning of amodal stimulus properties, even during the prenatal period. Lickliter, Bahrick and Honeycutt (2002) assessed bobwhite quail embryos' learning of an individual maternal call in the period prior to hatching. Quail embryos were exposed to an individual bobwhite maternal call for 10 min/hr for 6, 12, or 24 hr, under conditions of unimodal auditory stimulation, concurrent but non-redundant auditory and visual stimulation, or redundant and temporally synchronous auditory and visual stimulation. Redundant stimulation was provided by presenting a 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 (one day after hatching) to determine whether they would prefer the familiar maternal call over an unfamiliar variant of the maternal call. Only chicks that received redundant audio-visual exposure demonstrated perceptual learning under all exposure periods. They preferred the familiar maternal call following 6, 12, and 24 hr of exposure, whereas chicks that received non-redundant audio-visual exposure prenatally showed no preference for the familiar call following any exposure duration. Chicks receiving the unimodal auditory familiarization prior to hatching showed perceptual learning only following the longest period of prenatal exposure (24 hr). Thus, synchronous and bimodally specified information (intersensory redundancy) promoted auditory learning at a rate that was four times that of unimodal auditory exposure and temporal synchrony was necessary for this rapid learning to take place.

A subsequent study assessing memory for the familiar call (Lickliter, Bahrick & Honeycutt, 2004) found that chicks receiving redundant, bimodally specified information about the temporal features of the maternal call as embryos remembered the call four times longer than did chicks receiving unimodal exposure prior to hatching. Importantly, this dramatic facilitation of perceptual learning and memory cannot be explained by a simple increase in overall amount of prenatal stimulation. Chicks that received concurrent but non-redundant audio-visual stimulation as embryos had the same overall amount of stimulation and showed no preference for the familiar call following any exposure period. Similar to the results from human infants reviewed above, 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 non-redundantly or unimodally.

Of course, after some months of perceptual experience infants readily detect amodal properties in unimodal as well as bimodal stimulation (Bahrick & Lickliter, 2002, 2004). Given that detection of amodal properties in early development is evident in bimodal, redundant stimulation and attenuated or absent in non-redundant unimodal stimulation, how do infants eventually learn to detect amodal properties in unimodal stimulation? Might intersensory redundancy play a role in this developmental shift in the deployment of selective attention? One possibility is that once young infants detect an amodal property of an event (e.g. rhythm or tempo) in bimodal stimulation, attention to that property might be facilitated during subsequent exposure to the same property in unimodal stimulation (education of attention). The results of a study with human infants (Bahrick & Lickliter, 2000) indicated that this might be the case. In this study, once redundant bimodal stimulation recruited attention to the amodal properties of rhythm in an habituation procedure, 5-month-old infants were subsequently able to detect rhythm changes in unimodal test trials, whereas following non-redundant unimodal stimulation infants were unable to detect rhythm changes in the unimodal test trial. This finding suggests that detection of amodal stimulus properties in redundant bimodal stimulation can scaffold or educate selective attention to the same stimulus properties in unimodal stimulation during early development. The general notion of 'educating attention' was proposed by J. Gibson (1979) and developed by Zukow-Goldring (1997) in her work on the role of amodal information in guiding gestural and speech perception (see also Ingold, 2001). Here we empirically test this notion as it applies to perceptual learning and memory during perinatal development, using quail embryos and neonates.

Given that systematic manipulation of sensory experience is not possible with human fetuses or infants, comparative work with animal subjects provides a useful step in defining the various conditions, experiences, and events involved in the emergence and maintenance of normal perceptual development (Lickliter & Bahrick, 2000). One important advantage of the use of animal subjects to study perceptual learning is the ability to alter the type, timing, and amount of particular sensory experience available to the embryo or infant. Importantly, studies of both avian and mammalian 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). For example, laboratory reared nightingales learned more songs when the tutor songs were paired with a synchronized flashing light than when the songs were presented without the redundant visual stimulus (Hultsch *et al.*, 1999). As reviewed above, we found that bobwhite quail are remarkably sensitive to bimodally specified amodal information even during the prenatal period (Lickliter *et al.*, 2002, 2004). Precocial birds such as domestic chicks, ducks, and quail are particularly well suited for this type of research, as they develop in an egg, thereby allowing ready access to the developing embryo during the prenatal period. In addition, chicks can respond in behavioral tests almost immediately after hatching.

The present study assessed whether intersensory redundancy available in bimodal stimulation can educate attention to amodal temporal properties in unimodal stimulation during early development. Given that exposure to redundant bimodal stimulation can direct embryos' attention to amodal stimulus properties (Lickliter *et al.*, 2002), we predicted that embryos receiving redundant bimodal and subsequent unimodal stimulation from the same event should benefit from the initial bimodal exposure period by continuing to detect the amodal stimulus properties in the unimodal stimulation. This would in effect create a longer period of familiarization to the amodal features of the call such as rhythm, rate, and duration, allowing subjects to successfully remember and prefer the familiar maternal call several days following hatching. In contrast, we predicted that control embryos receiving initial exposure to unimodal stimulation followed by bimodal stimulation would not selectively attend to the amodal temporal properties of the maternal call; rather, embryos in this condition would attend to the modality-specific features of the call during the initial unimodal exposure. These embryos would thus have less familiarization with the temporal features of the call and be poorer at remembering and preferring the familiar call in postnatal testing, despite receiving identical amounts of prenatal exposure to the familiar call.

General methods

Subjects

Subjects were incubator-reared bobwhite quail (*Colinus virginianus*) embryos. Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Grumbach BSS 160 incubator (Munich, Germany) that maintained a temperature of 37.5°C and a relative humidity of 75%–80%. The only sounds available to the embryos were their own vocalizations and those of their broodmates and the background low frequency noise emitted by the fan of the incubator. On Day 22 of incubation, embryos were transferred to a Model 1602N Hova-Bator portable incubator (Savannah, GA) in a light- and sound-attenuated room, which permitted systematic delivery of supplemental acoustic and visual stimulation prior to hatching. To control for developmental age, only those chicks that hatched on Day 23 of incubation were used in this study. To control for possible between-hatch variation, subjects for each experimental condition were selected from at least three different hatches of eggs.

Following hatching, chicks were reared in groups of 10–15 same-aged chicks to mimic natural brood conditions (Stokes, 1967). Chicks were housed in large plastic tubs in a Nuaire Model NU-605-500 Animal Isolator (Plymouth, MN), which filtered the air and provided background fan noise that served to mask sounds originating from outside the rearing room. Ambient air temperature was maintained at approximately 35°C in both the rearing room and the behavioral testing room. Food and water were continuously available to chicks throughout each experiment except during testing.

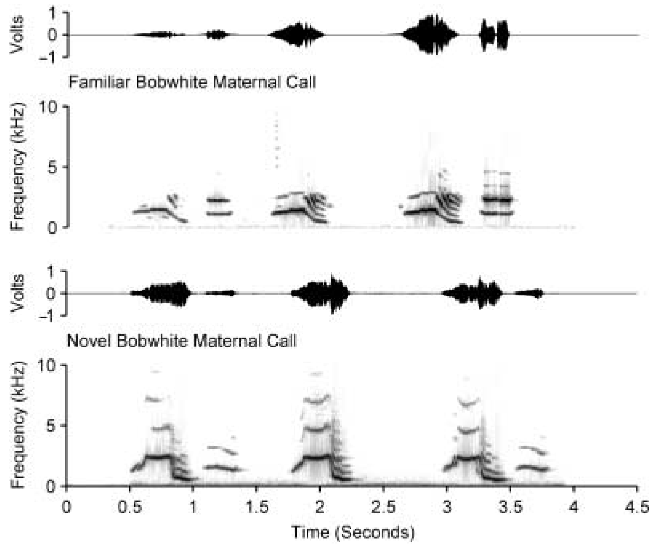

Figure 1 *Spectograms of the two bobwhite maternal calls (familiar and novel) presented during testing. The two calls are similar in phrasing, repetition rate, and the major peak of dominant frequency. They vary in the minor peaks of dominant frequency and in temporal microstructure (note-internote intervals).*

Procedure

The bobwhite quail embryo's bill normally moves into the air space at the large end of the egg approximately 24–36 hr prior to hatching, producing a visible indentation 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 a portable incubator in a darkened room. During the 24-hr period prior to hatching, embryos received intermittent exposure (10 min/hr) to various sensory stimulation regimes. The auditory stimulus used in all conditions was an individual variant of the species-typical bobwhite quail maternal assembly call (hereafter referred to as Call B or the familiar call; see Heaton, Miller & Goodwin, 1978, for acoustical details). 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 maternal call was broadcast from a portable compact disk player at a peak intensity of 65 dB, measured by a Bruel & Kjaer Model 2232 sound-level meter (Marlborough, MA). 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 approximately 3.5 s (notes occurred at an average rate of 1.7 note/s) and was followed by an 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 (see Figure 1). The audiovisual redundancy available in some of the conditions was achieved by recreating the temporal patterning of the maternal call notes in a pulsed light. The flashing light was temporally synchronized to the notes of the call, matching the duration of each note and the spacing between notes. Thus, the amodal temporal properties of rhythm, rate, and duration were redundantly specified to both the visual and auditory modalities. The patterned light was delivered by a Proxima 2810 desktop projector (InFocus Corp., Wilsonville, OR) situated directly above the portable incubator containing the embryos and connected to a computer running an audio-visual redundancy program (see Lickliter *et al.*, 2002 for a description of the program). The asynchronous bimodal condition was achieved by playing the maternal call and patterned light 0.5 s out of phase with each other, resulting in a total duration of 4.0 s and an interburst interval of 0.5 s.

Testing

Testing occurred at 48 hr (± 2 hr) after prenatal stimulation offset. The testing procedure took place in a circular arena 130 cm in diameter, surrounded by a wall 60 cm in height. The walls of the apparatus were lined with foam to attenuate echoes and were covered by an opaque black curtain to shield speakers and other irregularities that could serve as visual cues to subjects. The floor of the arena was painted black. A video camera suspended near the ceiling in the center of the room allowed for remote observation of behavioral testing. The video camera sent a signal to a TV monitor located in an adjoining room. Two rectangles drawn only on the TV monitor demarcated approach areas on opposite sides of the arena, each 30×15 cm in size. These two approach areas together represented less than 10% of the total area of the arena. Mid-range dome-radiator speakers were located behind the curtain in each of the approach areas. Each speaker received input from a separate compact disc player.

Testing involved placing an individual chick in a start-box equidistant from the two approach areas. All chicks received a 1-min settling period followed by a 5-min simultaneous choice test between two variants of the bobwhite maternal assembly call, one played from each speaker. One of these calls was unfamiliar (hereafter referred to as Call A or the novel call) and one of the calls was familiar in that embryos had received exposure to this call prior to hatching (Call B). These two maternal calls were recorded in the field and are similar in phrasing, repetition rate, and frequency modulation. They vary primarily in minor peaks of dominant frequency and in the temporal microstructure of rhythm and duration (Figure 1; see also Heaton *et al.*, 1978). Previous studies have revealed that chicks do not show a naïve preference for either of these two variants of the bobwhite maternal call (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992). The sound intensity of each call was adjusted to peak at 65 dB, measured from the start box where chicks were introduced into the arena. The locations of the two maternal calls presented during testing were counterbalanced across trials within groups to prevent a possible side bias from affecting results.

Each chick was tested individually and only once. Chicks were scored on their latency of approach and the duration of time they spent in each of the two approach areas by an observer blind to the experimental condition. A Visual Basic computer program allowed semi-automated collection of latency and duration of response to the test stimuli. Latency was defined as the amount of time in seconds that elapsed from the onset of the trial until the chick entered an approach area. Duration was defined as the cumulative amount of time in seconds the chick remained in an approach area. Any chick that did not enter either approach area during a test trial was considered a non-responder. These chicks were excluded from subsequent analyses. Preference for a given stimulus was scored if a chick stayed in an approach area for at least twice the time spent in the opposing approach area. No preference for a stimulus was scored if a chick approached both areas during a trial but did not spend at least twice as much time in one approach area as the other. These individual preference scores have been used in a number of prior studies of perceptual discrimination in bobwhite quail (see Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995, for examples). Up to six observers collected data in each experiment. Because of the multiple observers, we used an intraclass correlation coefficient reliability analysis to assess interobserver agreement for total duration of time spent in the approach areas for two videotaped subjects (0.97).

Data analyses

Several measures were analyzed: duration of time spent in each approach area by subjects in a group were compared by the Wilcoxon matched-pairs signed-ranks test to determine whether duration scores for one stimulus differed from that of the other within a condition; individual preference scores were evaluated by the chi-square goodness-of-fit test to determine if subjects in a condition show a significant preference for either auditory test stimulus presented in the two-choice test. Secondary analyses of duration scores were also performed on the interval data using single sample *t*-tests. Significance levels of $p < .05$ (two-tailed) were used to evaluate all results. Latency of initial approach to the familiar and novel calls was also recorded for each subject, but these data were highly variable across individuals and therefore are not discussed further in the individual experiments.

Experiment 1: Prenatal education of selective attention to amodal stimulus properties in unimodal stimulation

This experiment investigated the extent to which intersensory redundancy in bimodal stimulation can 'educate' or scaffold selective attention to amodal stimulus properties in unimodal stimulation. Intersensory redundancy appears to have a powerful impact on the deployment of attention, even during the prenatal period (Lickliter *et al.*, 2002, 2004; Reynolds & Lickliter, 2003), and in multimodal stimulation it can cause amodal properties to become 'foreground' relative to other non-redundant stimulus properties (Bahrick & Lickliter, 2000, 2002). After some months of perceptual experience infants extend detection of amodal properties from redundant bimodal to non-redundant unimodal stimulation (Bahrick & Lickliter, 2004; Lewkowicz, 2004b; Walker-Andrews, 1997). What role does infants' initial detection of redundantly specified amodal information in bimodal stimulation play in this developmental shift? One possibility is that early in development the detection of amodal stimulus properties in redundant bimodal stimulation might scaffold selective attention to the same stimulus properties in unimodal stimulation and promote differentiation, thereby contributing to the development of more flexible attentional skills with increasing perceptual experience. To date there have been no direct tests of this scaffolding notion. The present experiment was designed to explore the educating of attention in prenatal development by providing quail embryos exposure to an individual maternal call under different arrangements of bimodal and unimodal stimulation in the period prior to hatching.

Method

Bobwhite quail embryos were randomly assigned to one of four groups, an experimental (bimodal → unimodal) and four controls (unimodal → bimodal, asynchronous bimodal → unimodal, unimodal only, and bimodal only). The experimental group of embryos (bimodal → unimodal, $n = 33$) received 6 hr of redundant audio-visual exposure to the temporal features (rhythm, rate, duration) of the individual maternal call immediately followed by 18 hr of unimodal auditory exposure to the same features. The sequence control group (unimodal → bimodal, $n = 30$) received the same exposure to the same maternal call, but in the reverse sequence (initial 18 hr unimodal → subsequent 6 hr redundant bimodal), controlling for overall amount and type of stimulation and testing for the importance of sequence of presentation. The asynchronous group ($n = 29$) received 6 hr of non-redundant bimodal exposure (the call and light presented out of phase with one another) followed by 18 hr of unimodal auditory exposure, controlling for the potentially arousing effect of the amount of stimulus input produced by the bimodal stimuli. Additional groups of embryos received only 6 hr of bimodal stimulation ($n = 31$), to test whether the bimodal stimulation alone was sufficient to promote learning of the call, or 18 hr of unimodal stimulation ($n = 33$), to test whether the unimodal stimulation alone was sufficient to promote learning of the call. In all cases, stimulation was presented for 10 consecutive minutes each hour.

Following hatching, chicks were group-reared and tested individually at 48 hr of postnatal age in a simultaneous choice test between the familiar bobwhite maternal call and an unfamiliar variant of the maternal call (Call A, see Figure 1). It is important to note that in prior studies (Lickliter *et al.*, 2002) chicks tested at 48 hr following hatching (2 days following offset of initial stimulus exposure) showed no evidence of preferring the familiar call over a novel maternal call even after receiving 24 hr of redundant bimodal exposure prior to hatching. We predicted that if prior exposure to redundant bimodal stimulation can educate embryos' selective attention to amodal stimulus properties in subsequent unimodal stimulation, then embryos in the experimental group, receiving initial 6 hr of bimodal stimulation followed by 18 hr of unimodal stimulation, should learn and remember the familiar maternal call.

Results and discussion

As illustrated in Figure 2, results of postnatal testing confirmed our predictions. Only chicks in the experimental group (bimodal → unimodal) demonstrated a significant preference for the familiar maternal call at 48 hr following hatching, X^2 (2, $N = 33$) = 12.2, $p = .002$. Chicks from the unimodal → bimodal control group did not show evidence of prenatal auditory learning after hatching, X^2 (2, $N = 30$) = 2.60, $p = .27$, despite receiving the same amount and type of stimulation, but in the reverse order. Chicks from the asynchronous bimodal → unimodal group also did not show a significant preference for the familiar call, X^2 (2, $N = 25$) = 1.53, $p = .47$. Given that this group also experienced the same overall amount of stimulation, this result suggests that it was the intersensory redundancy that recruited attention to the temporal features of the familiar call and not simply

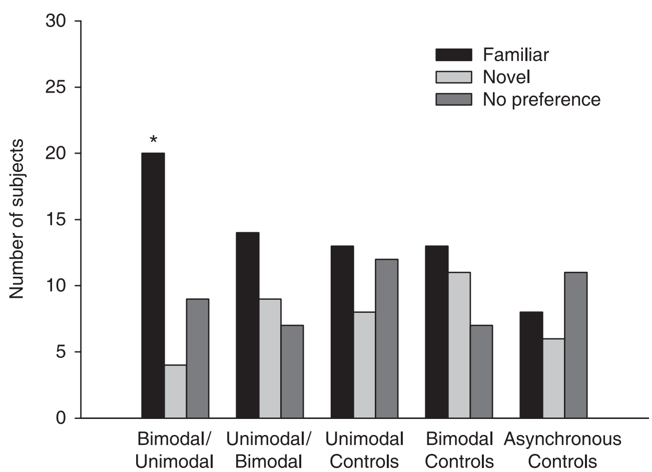

Figure 2 *Number of quail chicks preferring the familiar maternal call over a novel maternal call following bimodal → unimodal, unimodal → bimodal, bimodal only, unimodal only, or asynchronous bimodal → unimodal prenatal exposure in Experiment 1.*

Table 1 *Median duration scores (in seconds) for proximity to the familiar and novel maternal calls in Experiment 1 and Experiment 2*

	Duration	
	Familiar call	Novel call
Experiment 1		
Bimodal/Unimodal	54.8*	18.3
Unimodal/Bimodal	39.8	24.0
Unimodal Control	29.1	22.7
Bimodal Control	26.3	23.5
Asynchronous Control	34.8	31.0
Experiment 2		
No Unimodal Delay	40.1*	9.5
2-hr Unimodal Delay	82.9*	4.4
4-hr Unimodal Delay	62.0*	9.5

* $p < .01$ (Wilcoxon Signed-Ranks Test).

Table 2 *Mean Proportion of Total Duration Time (PTDT) that chicks spent in the approach area with the familiar call relative to the total time spent in both approach areas combined in Experiments 1 and 2*

Experiment 1		
Bimodal/Unimodal Group	$x = .696$	(SD = .28)*
Unimodal/Bimodal Group	$x = .578$	(SD = .32)
Bimodal Control Group	$x = .520$	(SD = .35)
Unimodal Control Group	$x = .563$	(SD = .31)
Asynchronous Control Group	$x = .421$	(SD = .26)
Experiment 2		
No-Delay Group	$x = .719$	(SD = .28)*
2 hr-Delay Group	$x = .860$	(SD = .20)*
4 hr-Delay Group	$x = .794$	(SD = .21)*

* $p < .001$ (single sample t-test).

the arousing effect of increased amounts of stimulation preceding unimodal stimulation. Chicks from the unimodal only and bimodal only control groups likewise did not show a significant preference for the familiar call over the novel maternal call (Call A) during postnatal testing, X^2 (2, N = 33) = 1.27, p = .53 and X^2 (2, N = 31) = 1.20, p = .55, respectively, demonstrating that neither the 6 hr of bimodal exposure nor the 18 hr of unimodal exposure was sufficient to facilitate a preference for the call 2 days after initial exposure.

Additional analyses of duration scores obtained during testing further supported these preference results. There was a significant difference in the duration of response, $z = -2.65$, $p = .008$, to the familiar call in the experimental group (bimodal → unimodal) receiving 6 hr of redundant bimodal exposure followed by 18 hr of unimodal exposure (Table 1). In contrast, none of the control groups showed significant differences in duration scores for either the familiar or novel maternal call during test trials at 48 hr following hatching.

Secondary analyses were also performed on the interval data obtained from the duration measure. We calculated the proportion of total duration time (PTDT) that chicks spent in the approach area with the familiar auditory stimulus relative to the total time they spent in both approach areas combined. According to this measure (similar to that used in human infant research, see Bahrick, 2002; Bahrick & Lickliter, 2004, for examples), a proportion of .50 reflects chance responding, whereas values greater than .50 reflect greater time spent in the approach area with the familiar maternal call. Values less than .50 reflect a greater time spent in the approach area with the novel maternal call (Table 2). To determine whether chicks in a group spent a significant proportion of total duration time in the approach area with the familiar maternal call, single sample t-tests were performed on this measure against the chance value of .50. The results of these analyses paralleled those of the non-parametric analyses and revealed that chicks receiving bimodal followed by unimodal stimulation showed a significant preference for the familiar call, $t(32) = 3.95$, $p < .001$. In contrast, chicks receiving unimodal followed by bimodal stimulation, $t(29) = 1.33$, $p = .195$, asynchronous bimodal followed by unimodal stimulation, $t(24) = 1.50$, $p = .147$, only bimodal stimulation, $t(30) = .312$, $p = .757$, or only unimodal stimulation, $t(32) = 1.15$, $p = .261$, showed no preference for the familiar call during postnatal testing.

These results are consistent with our predictions and taken together with converging evidence from previous studies with quail embryos (Lickliter *et al.*, 2002, 2004) demonstrate that intersensory redundancy can have a powerful impact on the deployment of attention, even during the prenatal period. In addition, the present results indicate that once amodal temporal properties are detected in redundant bimodal stimulation, attention can be educated to the same amodal properties in subsequent unimodal stimulation (where no redundancy is available). Even though embryos in the unimodal → bimodal control condition received the same amount and kind of augmented prenatal stimulation as embryos in the bimodal → unimodal experimental condition, only the experimental group learned and preferred the familiar call in postnatal tests. The order of presentation mattered. Chicks showed evidence of learning the familiar call only when redundant bimodal preceded unimodal exposure, creating the opportunity for educating attention.

One likely explanation for this finding is that initial exposure to redundant bimodal stimulation facilitates attention and therefore selectively promotes perceptual differentiation of amodal properties of stimulation (in this case, the temporal properties of the maternal call). This perceptual differentiation in turn educates attention to the same properties in subsequent stimulation, promoting generalization of learning across contexts. In other words, embryos receiving bimodal → unimodal exposure effectively received a longer familiarization period with the temporal patterning of the call (rhythm, rate, duration) than did embryos receiving the reverse presentation because they were able to detect temporal properties in unimodal stimulation and those in the other conditions were not.

An alternative explanation for the underlying basis of facilitation of learning may be transient, arousal-based effects. That is, perhaps bimodal stimulation is more arousing than unimodal stimulation and there are carry-over effects of this heightened arousal which facilitate learning in subsequent unimodal stimulation. Similarly, it may be that the loss or addition of stimulation to a sensory modality may be arousing to embryos. Thus, in the bimodal → unimodal condition, the loss of visual stimulation in the unimodal exposure period may have resulted in increased arousal, facilitating learning in the unimodal condition when it occurred after bimodal stimulation. This would also provide an effectively longer familiarization period to the call for embryos in the bimodal → unimodal condition than embryos in the unimodal → bimodal condition. Such transient, arousal-based explanations seem less likely, however, for several reasons. First, embryos in the asynchronous condition also experienced the loss of stimulation in one sense modality (asynchronous bimodal → unimodal) but did not show learning. Second, Reynolds and Lickliter (2003) demonstrated that quail embryos show little difference in their levels of behavioral and physiological arousal when exposed to unimodal auditory or visual stimulation vs. redundant bimodal (audio-visual) stimulation in the days prior to hatching. However, embryos do show significantly elevated arousal levels when exposed to asynchronous audio-visual stimulation.

To further assess these alternative explanations, Experiment 2 was conducted to examine whether the effects of educating attention persist across episodes of exploration separated in time. If so, this would help distinguish between explanations based on transient arousal effects from those based on more long-lasting changes due to learning.

Experiment 2: Maintenance of selective attention to amodal stimulus properties during prenatal development

This experiment assessed whether the education of attention effects observed in Experiment 1 were transient or longer lasting. If initial attention to redundant bimodal stimulation fosters perceptual learning of amodal properties and thereby educates attention to those same properties in subsequent unimodal stimulation, then facilitation of learning should likely persist across episodes of exploration. If the effects of educating attention are more transient and/or mediated by changes in arousal due to changes in the amount of stimulation available or the loss of stimulation in one sense modality (from bimodal to unimodal), there should be little or no carry-over across episodes of stimulation separated in time. To address this question of the temporal limits of selective attention during perinatal development, the methods of Experiment 1 were repeated with the exception that instead of sequential presentation with no delay, either a 2-hr or 4-hr temporal delay was introduced between the initial bimodal redundant exposure to the light and maternal call and subsequent unimodal exposure to the maternal call alone.

Methods

Embryos were divided into three exposure conditions: one group (no delay, $n = 27$) received 10 min/hr for 6 hr of redundant audio-visual exposure to the temporal features (rate, rhythm, duration) of an individual maternal call (Call B) followed immediately by 10 min/hr for 18 hr of unimodal auditory exposure to the same maternal call (identical to embryos in Experiment 1). A second group (2-hr delay, $n = 33$) received the 6 hr of redundant bimodal exposure to Call B followed by a 2-hr period of no supplemental stimulation, followed by the 18 hr of unimodal auditory exposure to the call. A third group of embryos (4-hr delay, $n = 34$) received a 4-hr delay between the same sequence of bimodal and unimodal stimulation. Embryos in all groups thus received the same overall amount and type of bimodal and unimodal exposure as embryos in the experimental group of Experiment 1. All chicks were tested at 48 hr following hatching for their preference between the familiar (Call B) and a novel maternal call (Call A), as in Experiment 1.

Results and discussion

As illustrated in Figure 3, chicks receiving no gap between bimodal and unimodal exposure, X^2 (2, $N = 27$) = 20.2, $p = .001$, the 2-hr delay, X^2 (2, $N = 33$) = 44.4, $p = .001$, or the 4-hr delay, X^2 ($N = 34$) = 33.7, $p = .001$, between prenatal bouts of bimodal and unimodal exposure to the maternal call all demonstrated a significant preference for the familiar maternal call at 48 hr following hatching.

Additional analyses of the duration scores further supported these preference results. Chicks in the no-delay, 2-hr delay, and 4-hr delay groups showed significantly longer durations in their proximity response to the familiar

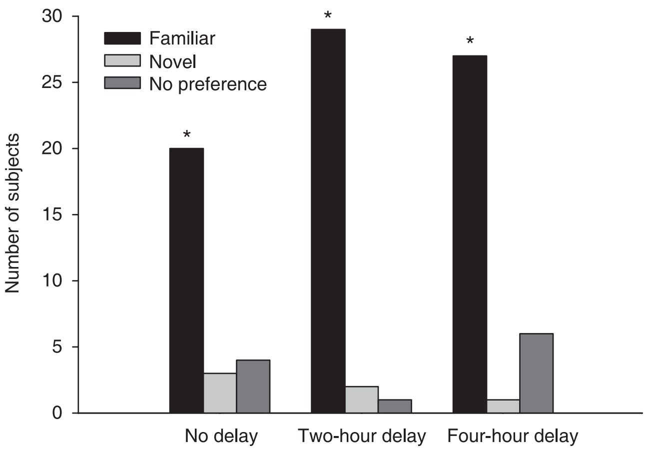

Figure 3 *Number of quail chicks preferring the familiar maternal call over a novel maternal call following no delay, a 2-hr delay, or a 4-hr delay between initial redundant bimodal and subsequent unimodal prenatal exposure in Experiment 2.*

call during testing, $z = -3.003$, $p < .003$, $z = -4.601$, $p < .001$, and $z = -4.471$, $p < .001$, respectively (Table 1). Secondary parametric analyses were also performed on the interval data obtained from the duration measure (Table 2). The results of these analyses paralleled those of the non-parametric analyses and revealed that groups receiving bimodal followed by unimodal stimulation as embryos showed a significant preference for the familiar call, whether they received no delay between the two patterns of stimulation, $t(26) = 4.06$, $p < .001$, a 2-hr delay, $t(33) = 8.07$, $p < .001$, or a 4-hr delay, $t(31) = 10.28$, $p < .001$. Additional analyses by the Mann-Whitney U-test indicated that the duration of response to the familiar call was greater in the 2-hr and 4-hr delay groups than in the no-delay group ($z = -3.99$, $p < .001$ and $z = -2.95$, $p < .003$, respectively), suggesting that a delay between the initial redundant bimodal and subsequent unimodal exposure had a consolidating effect on learning and memory.

These results replicate and extend those of Experiment 1 and indicate that once amodal temporal properties are detected in redundant bimodal stimulation, selective attention can be educated to the same amodal properties in subsequent unimodal stimulation. This unimodal exposure to the same event does not have to immediately follow initial redundant bimodal exposure (i.e. sequential presentation). Rather, quail embryos can maintain selective attention for specific stimulus properties in bimodal and unimodal stimulation, even over different bouts of exploration several hours apart. This finding supports the view that perceptual learning underlies the 'education of attention' found in Experiment 1 and that selective attention and learning can persist across a delay of at least 4 hours. This finding casts doubt on the view that transient changes in arousal resulting from bimodal stimulation or from the loss of stimulation to one sense modality (bimodal to unimodal) were important factors in the facilitation of learning observed in Experiment 1. If changes in arousal were a key factor one would not expect facilitation of learning following a 2-hr or 4-hr delay, nor would one expect greater evidence of learning after a 2-hr or 4-hr delay than in the no-delay condition.

Intersensory redundancy appears to recruit the young organism's attention in such a way that redundant, bimodally specified amodal information becomes 'foreground' and other information becomes 'background' (see Bahrick & Lickliter, 2002, for discussion). The results of the present experiment suggest that this 'pop-out' effect for amodal stimulus properties appears to continue across a period of hours when the same objects or events are experienced unimodally. This scaffolding of the embryo's attention can play an important role in what is perceived and learned in the period prior to hatching and could serve to foster the emergence of attentional flexibility during early development by allowing young organisms' sensitivity to amodal properties to transfer from bimodal to unimodal stimulation with increasing perceptual experience.

General discussion

Converging evidence from comparative and developmental psychology has shown that animal and human infants are adept perceivers of amodal information present in multimodal stimulation (Lewkowicz, 2000; Lewkowicz & Lickliter, 1994; Lickliter & Bahrick, 2000). Further, research in this area has demonstrated that different properties of stimuli are highlighted and attended when redundant multimodal stimulation is made available to young organisms as compared with unimodal stimulation from the same events (see Bahrick, 2004; Lewkowicz, 2004a; Lickliter & Bahrick, 2004). The results of this study provide the first evidence that intersensory redundancy in bimodal stimulation can educate or scaffold attention to certain properties of stimulation in unimodal events, even during the prenatal period. The synchronous alignment of audible and visible stimulation appears to highlight available amodal information (rhythmic pattern, rate, and duration) and appears to guide selective attention to these same stimulus properties in subsequent unimodal exposure where no redundancy is available.

In Experiment 1, only bobwhite quail embryos receiving redundant bimodal exposure to an individual variant of the bobwhite maternal call followed by unimodal (auditory) exposure to the same call showed evidence of learning and preferring the call 48 hr later in postnatal testing. Embryos receiving the same amount and kind of prenatal exposure to the individual maternal call, but in the reverse order (unimodal → bimodal), showed no preference for the familiar call, nor did embryos receiving unimodal alone, bimodal alone, or asynchronous bimodal exposure followed by unimodal exposure. Thus, only when redundant bimodal stimulation preceded the unimodal stimulation did embryos learn the call and subsequently prefer it in postnatal choice tests. Redundant bimodal stimulation appears to focus selective attention on amodal temporal features of the call, allowing embryos to continue to detect and learn these features during subsequent episodes of unimodal stimulation. This effectively resulted in a longer period of familiarization for the temporal features of the individual maternal call and chicks were able to remember and prefer this familiar call 2 days following hatching. Further, Experiment 2 demonstrated that the education of attention could occur even with a 2-hr or 4-hr delay between the initial bimodal and subsequent unimodal prenatal exposure to the maternal call. This finding suggests that once embryos selectively attend to specific stimulus properties such attention can foster differentiation and learning which persists across different periods of time and bouts of exploration. This finding also indicates that enhanced learning resulting from education of attention is neither transient nor primarily arousal-based. Chicks that received a 2-hr or 4-hr delay between bimodal and unimodal prenatal exposure to an individual maternal call were just as adept at remembering and preferring the familiar call following hatching as were chicks receiving no delay between bimodal and unimodal exposure as embryos. In fact, they showed significantly better performance than those with no delay. This finding suggests that the delay could have had a consolidating effect on memory.

The results of the present study indicate that detection of amodal relations in bimodal stimulation can quickly lead to detection of these properties of events in unimodal stimulation during the prenatal period. Later in development, as infant attention becomes more flexible and perceptual processing becomes more efficient with experience, infants come to detect both amodal, redundantly specified properties and non-redundantly specified amodal and modality specific properties in stimulation of various types. Detection of amodal temporal information emerges in bimodal, redundant stimulation (e.g. Bahrick & Lickliter, 2000; Bahrick *et al.*, 2002; Lickliter *et al.*, 2002, 2004) and is later extended to unimodal stimulation (Bahrick & Lickliter, 2004). Education of attention is one avenue for promoting this developmental shift.

What processes underlie this developmental shift? E.J. Gibson (1969) and J.J. Gibson (1979) argued that perceptual learning is best conceived of as a fine-tuning or sensitization of the perceptual systems to specific features of the environment (see Bahrick, 2001; Gibson & Pick, 2000; Ingold, 2001, for further discussion). The present results are consistent with this differentiation view of perceptual development, in that quail embryos originally exposed to bimodally specified amodal stimulus properties (i.e. rhythm, rate, duration of a maternal call) later detected these amodal temporal properties in subsequent unimodal stimulation. Differentiation of amodal properties in bimodal stimulation generalized to subsequent unimodal stimulation. These initial conditions likely set in motion a cascading set of influences on attention that can continue to effect perception, learning and memory into later stages of development (see Bahrick & Lickliter, 2002, 2004; Lickliter & Bahrick, 2001, for further discussions).

A fundamental question that motivates research on the development of perception is what causes some properties of sensory stimulation to be salient, attended to, and remembered and other properties to be ignored. Much remains to be learned of the conditions that regulate the development of this selective process. We propose that the ‘grabbing’ of attention by redundant information can facilitate perceptual processing, learning, and memory for amodal features of stimuli, thereby selectively educating attention to specific stimulus properties during prenatal and postnatal development. This selective attention helps prevent young organisms from experiencing what William James famously termed the ‘buzzing booming confusion’ of infancy and simplifies the task of selective learning during early development.

Acknowledgements

This research was supported by NIMH grants RO1 MH26665 and RO1 MH26666 and NICHD grant RO1 HD048432.

References

Bahrick, L.E. (1992). Infants’ perceptual differentiation of amodal and modality specific audio-visual relations. *Journal of Experimental Child Psychology*, **53**, 180–199.

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. (2002). Generalization of learning in three-and-a-half-month-old infants on the basis of amodal relations. *Child Development*, **73**, 667–681.

Bahrick, L.E. (2004). The development of perception in a multimodal environment. In G. Bremmer & A. Slater (Eds.), *Theories of infant development* (pp. 90–120). Malden, MA: Blackwell.

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 Press.

Bahrick, L.E., & Lickliter, R. (2004). Infants' detection of rhythm and tempo in unimodal and multimodal stimulation: a developmental test of the intersensory redundancy hypothesis. *Cognitive, Affective, and Behavioral Neuroscience*, **4**, 141–151.

Bahrick, L.E., Lickliter, R., & Flom, R. (2004). Intersensory redundancy guides infants' selective attention, perceptual, and cognitive development. *Current Directions in Psychological Science*, **13**, 99–102.

Bahrick, L.E., Lickliter, R., & Flom, R. (2006). Up versus down: the role of intersensory redundancy in the development of infants' sensitivity to the orientation of moving objects. *Infancy*, **9**, 73–96.

Bahrick, L.E., Lickliter, R., Shuman, M.A., Batista, L.C., & Grandez, C. (April, 2003). Infant discrimination of voices: predictions from the intersensory redundancy hypothesis. Paper presented at the Society for Research in Child Development biennial meeting, Tampa, FL.

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: Erlbaum.

Gibson, E.J. (1969). *Principles of perceptual learning and development*. New York: Appleton-Century-Crofts.

Gibson, E.J., & Pick, A.D. (2000). *An ecological approach to perceptual learning and development*. New York: Oxford University Press.

Gibson, J.J. (1979). *The ecological approach to visual perception*. Hillsdale, NJ: Erlbaum.

Gogate, L., & 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.

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

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.

Hultsch, H., Schleuss, F., & Todt, D. (1999). Auditory-visual stimulus pairing enhances perceptual learning in a songbird. *Animal Behaviour*, **58**, 143–149.

Ingold, T. (2001). From the transmission of representations to the education of attention. In H. Whitehouse (Ed.), *The debated mind: Evolutionary psychology versus ethnography* (pp. 113–153). Oxford: Berg.

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. (1996). Infants' response to the audible and visible properties of the human face: 1. Role of lexical-syntactic content, temporal synchrony, gender, and manner of speech. *Developmental Psychology*, **32**, 347–366.

Lewkowicz, D.J. (2000). The development of intersensory temporal perception: an epigenetic systems/limitations view. *Psychological Bulletin*, **126**, 281–308.

Lewkowicz, D.J. (2004a). Perception of serial order in infants. *Developmental Science*, **7**, 175–184.

Lewkowicz, D.J. (2004b). Serial order processing in human infants and the role of multisensory redundancy. *Cognitive Process*, **5**, 113–122.

Lewkowicz, D.J., & Lickliter, R. (1994). *The development of intersensory perception: Comparative perspectives*. Hillsdale, NJ: Lawrence Erlbaum.

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**, 451–467.

Lickliter, R., & Bahrick, L.E. (2004). Perceptual development and the origins of multisensory responsiveness. In G. 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., Bahrick, L.E., & Honeycutt, H. (2004). Intersensory redundancy enhances memory in bobwhite quail embryos. *Infancy*, **5**, 253–269.

Lickliter, R., & Hellewell, T.B. (1992). Contextual determinants of auditory learning in bobwhite quail embryos and hatchlings. *Developmental Psychobiology*, **25**, 17–24.

Lickliter, R., & Lewkowicz, D.J. (1995). Intersensory experience and early perceptual development: prenatal physical stimulation affects auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychology*, **31**, 609–618.

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.

Morrongiello, B.A., Fenwick, K., & Nutley, T. (1998). Developmental changes in associations between auditory-visual events. *Infant Behavior and Development*, **21**, 613–626.

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**, 1–11.

Reynolds, G., & Lickliter, R. (2003). Effects of redundant and non-redundant bimodal sensory stimulation on heart rate in bobwhite quail embryos. *Developmental Psychobiology*, **43**, 304–310.
Ruff, H.A., & Rothbart, M.K. (1996). *Attention in early development: Themes and variations*. New York: Oxford University Press.
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: Erlbaum.
Spelke, E.S. (1979). Perceiving bimodally specified events in infancy. *Developmental Psychology*, **15**, 626–636.
Stokes, A.W. (1967). Behavior of the bobwhite, *Colinus virginianus. Auk*, **84**, 1–33.
Walker-Andrews, A.S. (1997). Infants' perception of expressive behaviors: differentiation of multimodal information. *Psychological Bulletin*, **121**, 437–456.
Walker-Andrews, A.S., & Lennon, E. (1985). Auditory-visual perception of changing distance by human infants. *Child Development*, **22**, 373–377.
Zukow-Goldring, P. (1997). A social ecological realist approach to the emergence of the lexicon: educating attention to amodal invariants in gesture and speech. In C. Dent-Read & P. Zukow-Goldring (Eds.), *Evolving explanations of development* (pp. 199–249). Washington, DC: American Psychological Association Press.

Received: 13 June 2005
Accepted: 1 December 2005