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BRIEF REPORT

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The intersensory redundancy hypothesis: Extending the principle of unimodal facilitation to prenatal development

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Abstract

Selective attention to different properties of stimulation provides the foundation for perception, learning, and memory. The Intersensory Redundancy Hypothesis (IRH) proposes that early in development information presented redundantly across two or more modalities (multimodal) selectively recruits attention to and enhances perceptual learning of *amodal* properties, whereas information presented to a single sense modality (unimodal) enhances perceptual learning of *modality-specific* properties. The present study is the first to assess this principle of unimodal facilitation in non-human animals in prenatal development. We assessed bobwhite quail embryos' prenatal detection of pitch, a modality-specific property, under conditions of unimodal and bimodal (synchronous or asynchronous) exposure. Chicks exposed to prenatal unimodal auditory stimulation or asynchronous bimodal (audiovisual) stimulation preferred the familiarized maternal call over a novel pitch-modified maternal call following hatching, whereas chicks exposed to redundant (synchronous) audiovisual stimulation failed to prefer the familiar call over the pitch-modified call. These results provide further evidence that selective attention is recruited to specific stimulus properties of events in early development and that these biases are evident even during the prenatal period.

KEYWORDS

development of perception, intersensory redundancy, prenatal auditory discrimination, selective attention, unimodal facilitation

1 | INTRODUCTION

In recent years investigators working at the neural, physiological, and behavioral levels of analysis have provided new insights into the nature and processes that guide attentional allocation to both unimodal and multimodal stimulation during early development (e.g., Bahrick & Lickliter, 2000, 2012; Colombo, 2002; Hollich, Newman, & Juscyzk, 2005; Lickliter, Bahrick, & Markham, 2006; Reynolds, Bahrick, Lickliter, & Guy, 2014; Richards, Reynolds, & Courage, 2010). Infants have been shown to quickly establish efficient patterns for selectively attending to relevant and coherent aspects of their environment. These patterns become increasingly efficient with experience, eventually evolving into the expert patterns that characterize adult selective attention. Given the obvious importance of selective attention for perceptual, cognitive, social, and linguistic development, a central issue for developmental science is to identify what principles govern this process.

Bahrick and Lickliter (2000, 2002, 2014) have proposed a model of selective attention, the Intersensory Redundancy Hypothesis (IRH), to explain how and under what conditions attention and perceptual processing are promoted to different aspects or properties of events (amodal vs. modality specific) during early development. Intersensory redundancy refers to the temporally synchronous and spatially collocated occurrence of the same information (e.g., rate, rhythm, duration, intensity shifts) across two or more senses. For example, when the rhythm and tempo of speech can be perceived by looking and by listening, the rhythm and tempo are redundantly specified. Most naturalistic, multimodal events provide intersensory redundancy for multiple amodal properties. By definition, only amodal properties (as opposed to modality specific properties) can be redundantly specified across the senses.

A growing body of research has demonstrated that infants are adept perceivers of intersensory redundancy and that the salience of redundancy can guide early attentional selectivity in both human and nonhuman animal infants (e.g., Bahrick & Lickliter, 2000; Bahrick, Flom & Lickliter, 2002; Farzin, Charles, & Rivara, 2009; Flom & Bahrick, 2007; Jordan, Suanda, & Brannon, 2008; Kraebel, 2012; Lewkowicz, 2004, 2010; Lickliter, Bahrick, & Honeycutt, 2002, 2004). However, most objects and events also provide non-redundant modality specific information, such as the appearance of a face, the color of clothing, or the specific acoustic qualities of a voice. What guides selective attention to these various properties of events during bouts of exploration? Relatively little is known about how perception of amodal information (i.e., tempo, rhythm) is coordinated with perception of modality-specific information (i.e., color, pitch) and how this coordination influences the deployment of selective attention during early development.

The IRH has proposed and generated evidence for two principles of early event perception—intersensory and unimodal facilitation. *Intersensory facilitation* refers to the principle that redundantly specified amodal properties (such as rhythm, tempo, and intensity) are detected more easily and earlier in development when they are perceived in bimodal (or multimodal) synchronous stimulation than when the same amodal properties are non-redundantly specified in unimodal stimulation. Perception of amodal properties such as temporal synchrony (Bahrick, 1992; Lewkowicz, 2000), tempo (Bahrick et al., 2002), rhythm (Bahrick & Lickliter, 2000), and affect (Flom & Bahrick, 2007) is enhanced in young infants receiving bimodal audiovisual as compared to unimodal stimulation. For example, rhythm and tempo are detected more readily by young infants when they are perceived redundantly through two sense modalities rather than a single sense modality (Bahrick & Lickliter, 2000; Bahrick et al., 2002).

Animal-based studies have also provided evidence for such intersensory facilitation, even during prenatal development. Quail embryos can learn a maternal call significantly faster when the rate, rhythm, and duration of the call is synchronized with a pulsing light, thus providing intersensory redundancy, than when the call is presented unimodally (auditory only; Lickliter et al., 2002). Lickliter, Bahrick, and Honeycutt (2004) also found that quail chicks receiving redundant bimodal stimulation of the temporal features of the maternal call prenatally remembered the call four times longer into postnatal development than chicks receiving prenatal unimodal exposure.

This remarkable facilitation of selection attention across species is due to redundancy (synchrony across the senses) and not to other factors such as a greater amount of stimulation in two modalities as compared with one. For example, intersensory facilitation is not found in either human infants or quail embryos under conditions of multimodal stimulation where there is no redundancy (e.g., asynchronous but congruent auditory and visual stimulation, see Bahrick & Lickliter, 2000; Bahrick et al., 2002; Flom & Bahrick, 2007; Lickliter et al., 2002).

In some conditions, intersensory redundancy is not available to direct selective attention to amodal properties. For example, in unimodal stimulation (e.g., speaking on the phone; viewing a silent face), information is available to only one sensory modality at a time. In these conditions, the IRH predicts that selective attention and learning should be directed to modality specific properties of stimulation (properties which can be specified only through a particular sensory modality) at the expense of amodal properties (Bahrick & Lickliter, 2002, 2014). We have termed this *unimodal facilitation*. This term refers to the principle that non-redundantly specified modality specific properties such as color, visual pattern, pitch, and timbre, are detected more easily and earlier in development when they are perceived in unimodal stimulation than when they are perceived in the context of redundant bimodal (or multimodal) stimulation, because there is no attentional competition from salient intersensory redundancy. The principles of unimodal and intersensory facilitation should be particularly evident in early development when attentional resources are most limited. Later in development, as infants' attention becomes more flexible and efficient with experience, they are able to discriminate amodal and modality specific properties in both unimodal and multimodal stimulation (Bahrick & Lickliter, 2012).

In contrast with the large body of research on the facilitating role of intersensory redundancy for perceptual processing, only a few studies have focused on unimodal facilitation and the interfering role of intersensory redundancy for early perceptual processing and all studies to date have focused on human infants. These few studies have consistently found that unimodal stimulation facilitates perceptual processing of modality specific properties of events. For example, 3- and 5-month old infants can discriminate and show long-term memory for a change in the orientation of a toy hammer tapping against a surface (upward vs. downward) when they could see the hammer tapping (unimodal visual) but not when they could see and hear the natural synchronous audiovisual stimulation together (Bahrick et al., 2006). The audiovisual condition provided intersensory redundancy, which attracted attention to redundantly specified amodal properties such as rhythm and tempo and interfered with attention to visual information, such as the direction of motion or orientation of the hammer. Performance in an asynchronous control condition (eliminating intersensory redundancy but preserving the overall amount and type of stimulation) confirmed the interfering role of intersensory redundancy. As predicted, instead of impairing perception and memory for orientation, the asynchronous soundtrack enhanced infant perception of orientation when compared with the synchronized soundtrack (Bahrick et al., 2006). Infants also show unimodal facilitation for face perception. A study with 2-month-old infants showed that face discrimination (based on modality-specific properties such as arrangement and shape of visual features) is facilitated when the face is presented unimodally, but not when paired with a synchronous voice (Bahrick, Lickliter, & Castellanos, 2013). Taken together, these findings provide evidence for the principle of unimodal facilitation. They indicate that perception of modality-specific visual properties are enhanced in unimodal visual stimulation and attenuated in audio-visual stimulation, where redundant amodal properties compete for infants' attention.

Because studies that manipulate sensory experience during prenatal and early postnatal development are difficult to carry out with human participants, animal models can more readily explore the experiential factors contributing to early perceptual development (Lickliter & Bahrick, 2000). For example, studies using precocial birds have shown that modifying sensory experience during the prenatal period can have significant effects on early perceptual development and perceptual learning (reviewed in Lickliter, 2005). In the present study, we assessed Northern bobwhite quail (*Colinus virginianus*) embryos' selective attention to unimodal and multimodal stimulus properties during the late stages of prenatal development. Such attentional biases are thought to emerge in prenatal development as a function of experience with sensory stimulation (Harshaw & Lickliter, 2011; Honeycutt & Lickliter, 2002; Lickliter et al., 2002). Precocial birds such as quail provide a valuable model for this kind of research because they develop in an egg, allowing easy access to the embryo during the late prenatal period. Further, chicks hatch with functioning sensory and motor systems and can respond in behavioral tests in the first days after hatching.

In the current study, bobwhite quail embryos were exposed to an individual bobwhite maternal call either unimodally (auditory only) or bimodally (redundant audio-visual stimulation) on the day prior to hatching. To control for the overall amount of stimulation, an additional bimodal exposure control group received asynchronous audio-visual stimulation (providing no redundancy across the auditory and visual modalities). Following hatching, chicks were tested individually between the familiar version of the maternal call that was presented prenatally versus the same maternal call with an altered pitch range. We were particularly interested in whether prenatal unimodal exposure would facilitate detection and learning of modality-specific properties of stimulation (pitch) and whether prenatal redundant bimodal exposure would interfere with detection and learning of modality-specific properties of stimulation. Although postnatal studies with human infants have supported these predictions for the detection of the orientation of object motion (Bahrick et al., 2006) as well as the discrimination of faces (Bahrick et al., 2013), convergent findings from non-human animals would strengthen the generality of these findings and extend them to the prenatal period.

Two specific hypotheses were examined: (1) prenatal unimodal auditory exposure would facilitate learning of the modality-specific properties of stimulation and (2) prenatal redundant audio-visual exposure would interfere with attention to and learning of modality-specific properties. According to the predictions of the Intersensory Redundancy Hypothesis, this should be the case because only when receiving unimodal exposure to the individual maternal call would embryos focus their selective attention on modality-specific stimulus properties during familiarization and subsequently detect the pitch of the call. In contrast, when receiving redundant bimodal exposure embryos would focus their attention on amodal stimulus properties such as rhythm, rate, or duration of the call, and thus should not detect the acoustic pitch change presented during postnatal testing.

2 | GENERAL METHODS

2.1 | Subjects

Subjects were 132 incubator reared bobwhite quail chicks (*C. virginianus*). Fertilized unincubated eggs were received weekly from a commercial supplier and incubated communally in a BSS-160 Grumbach Incubator maintained at 75–80% relative humidity and 37.5°C. Embryonic age was calculated on the basis of the first day of incubation being Day 0, the second day being Day 01, and so on. To control for potential variations in developmental age, only those birds that hatched on Day 23 were used as subjects. To control for possible differences between batches, subjects for each condition were selected from at least three different batches of eggs. Following hatching, groups of 12–15 same-aged chicks were housed together in a rearing tub until testing. Chicks were given constant access to food and water, except during testing sessions. Ambient air temperature was maintained at approximately 30°C.

2.2 | Auditory stimuli

An individual bobwhite maternal call (recorded in the field, see Heaton, Miller, & Goodwin, 1978, Call A) was acoustically modified by raising or lowering the pitch of the call (comprised of five notes) by one whole step. This pitch alteration was accomplished using the computer multimedia software, MAGIX Audio Studio 10 Deluxe. This resulted in two maternal call variants (one variant with a higher pitch and one variant with a lower pitch) that were used in this experiment. Half of the chicks in each experimental group received the lower pitch variant of the call prenatally, while the other half received the higher pitch variant of the call prenatally. All other acoustic features of the calls were unmodified and thus identical across the two variants of the maternal call. It is important to note that quail embryos not exposed to any supplemental prenatal sensory stimulation (naïve control group, $N = 28$) did not prefer either modified variant of the bobwhite maternal call during testing 24 hr after hatching ($\chi^2 = 1.357$, $p = .507$).

2.3 | Procedure

Approximately 24 hr prior to hatching, embryos were transferred to a sound attenuated stimulation room and placed in a portable hatcher, maintained at approximately 37.5°C and 75–80% relative humidity. This hatcher allowed embryos to receive either auditory or audio-visual stimulation via a transparent plastic window located directly above the embryos. Quail embryos were divided into three experimental conditions: (1) a Unimodal Auditory group ($N = 43$), exposed to an individual variant of the bobwhite maternal call for 10 min/hr during the 24 hr prior to hatching; (2) a Bimodal Audiovisual

TABLE 1 Preference scores for chicks tested at 24 hr following hatching

Stimulus condition	*N*	Familiar call	Unfamiliar call	No preference
Unimodal auditory	43	28*	5	10
Non-redundant audiovisual	30	13*	3	14
Redundant audiovisual	43	13	16	14

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

group ($N = 43$), exposed to an individual variant of the bobwhite maternal call paired with a pulsing light temporally synchronized with the five notes of the call for 10 min/hr for the 24 hr prior to hatching; and (3) a Bimodal Asynchronous group ($N = 30$), exposed to the same maternal call and pulsing light, but presented out of synchrony by 300 ms. The Bimodal Asynchronous group had a somewhat smaller sample size due to incubator failure, resulting in a lack of additional subjects. Unimodal auditory presentations were delivered by means of a computer with a custom designed software program that powered a speaker that broadcast the individual variant of the bobwhite maternal call. The speaker was placed over a small opening located on the top of the hatcher. In the audiovisual synchronous and asynchronous conditions, the computer software program also ran an amplifier connected to an adjustable desk lamp that transmitted a pulsed light presented either in synchrony or out of synchrony with the notes of the maternal call. The lamp was placed directly above the portable hatcher window. The light provided the same amodal information (rhythm, rate, and duration) as the notes of the maternal call in both the synchronous and asynchronous condition.

Chicks in all groups were transferred to rearing tubs immediately after hatching and were housed there in groups of same-aged chicks until testing at 24 hr following hatching.

2.4 | Testing

All chicks from the three prenatal exposure conditions (Unimodal Auditory, Redundant Bimodal, and Asynchronous Bimodal) were tested individually between the familiar version of the maternal call that had been presented prenatally versus the same maternal call altered to a one-step lower or higher pitch range (all other acoustic features held constant). These behavioral tests were conducted in an arena 130 cm in diameter, surrounded by a wall 60 cm in height. The arena surface was painted black and an opaque black curtain covered the wall of the arena. A video camera mounted directly above the arena allowed for remote observation and data collection. Two semi-circular approach areas, each comprising approximately 5% of the total area of the testing arena, were demarcated on a remote video monitor. Both approach areas contained a small speaker recessed in the arena wall and hidden behind the black curtain to allow for the presentation of auditory stimuli during the testing trials. Testing involved placing each chick in the arena midway between the two approach areas (one on the right and one on the left of the chick). The chick was then presented with a 5-min simultaneous choice test between two variants of the bobwhite maternal call, during which its locomotor behavior in the arena was recorded. The sound intensity of each call was adjusted to a peak of 65 dB, measured from the area where each chick was placed in the arena. The locations of the two calls (right or left) presented in the arena during testing were counterbalanced across trials to prevent any possible side bias.

A Visual Basic computer program allowed for semi-automated collection of latency and duration of response to the test stimuli. During testing, the experimenter observed a monitor that displayed live video from the camera located directly above the testing arena. Two semicircular approach areas that contained the hidden speakers were demarcated on the monitor. Each time a chick entered an approach area, the experimenter pressed a button for the duration of time that chick stayed in the approach area. The program then provided the total duration of time spent in each approach area for each chick.

2.5 | Data analysis

Nonparametric analyses were used to assess chicks' preference for the auditory stimuli presented during the testing trials. The variable of interest was the total duration of time spent within familiar versus novel call approach areas. Chicks failing to spend at least 30 s in any approach area were scored as non-responders. There were six non-responders in the Unimodal Auditory group, eight non-responders in the Redundant Bimodal group, and two non-responders in the Asynchronous Bimodal group. Chicks that did respond but failed to spend at least twice as long in one approach area than the other were scored as having no

TABLE 2 Means and standard deviations of chicks' duration scores (in seconds)

Stimulus condition	*N*	Pitch-modified familiar call	Pitch-modified novel call
Unimodal auditory	43	83.54* (62.82)	35.47 (47.59)
Non-redundant audiovisual	30	69.87* (55.24)	39.47 (45.78)
Redundant audiovisual	43	54.05 (58.03)	59.42 (53.37)

*$p < .05$ (Wilcoxon signed-ranks test).

preference (see Lickliter et al., 2002 for details). Thus, a chick was scored as showing a preference for a particular maternal call if it spent at least 30 s in an approach area and at least twice as long in that approach area as the other. Duration scores within groups were evaluated using the Wilcoxon matched-pairs, signed-ranks test. Individual preferences were evaluated by the chi-square test. Significance levels of $p < .05$ (two-tailed) were used to evaluate all results.

3 | RESULTS

A significant number of quail chicks prenatally exposed to either auditory (unimodal) or asynchronous audiovisual presentations of the pitch modified maternal call preferred the familiarized call over the same call with a novel pitch at 24 hr after hatching ($\chi^2 = 20.42$, $p < .001$, and $\chi^2 = 7.4$, $p < .025$, respectively). In contrast, chicks that received redundant prenatal audiovisual exposure to the familiarized call failed to demonstrate a preference for either of the call variants during testing at 24 hr after hatching ($\chi^2 = 0.326$, $p > 0.85$).

Wilcoxon signed-ranks test revealed that the unimodal group showed significantly longer duration ($z = -3.526$, $p = .001$) scores for the familiarized call than the novel call. Chicks from the asynchronous audiovisual condition likewise showed significantly longer duration scores for the familiarized call ($z = -2.221$, $p = .026$). In contrast, chicks that received redundant prenatal audiovisual exposure to the familiarized call failed to demonstrate a preference for either of the call variants during testing at 24 hr after hatching ($\chi^2 = 0.326$, $p > 0.85$). The redundant bimodal group also showed no significant differences in the duration of their proximity to the two calls ($z = -.700$, $p = .484$) during testing. Results are summarized in Tables 1 and 2.

These results indicate that chicks exposed prenatally to either unimodal (auditory only) or asynchronous bimodal (audiovisual) presentations of a pitch modified maternal call were able to discriminate between that familiarized call and a novel pitch variant of that call during postnatal testing. However, chicks that had been exposed prenatally to synchronous audiovisual presentations of a maternal call did not prefer the familiarized call from a novel pitch variant of that call during postnatal testing. These results support our hypotheses and the principle of unimodal facilitation of the Intersensory Redundancy Hypothesis. That is, prenatal unimodal exposure appeared to facilitate learning the modality-specific properties of the maternal call, and prenatal redundant exposure interfered with learning the modality specific properties of the maternal call.

4 | GENERAL DISCUSSION

The present study examined how early perceptual responsiveness can be influenced by exposure to unimodal and multimodal stimulation during the prenatal period. Specifically, we assessed the role of prenatal unimodal versus redundant bimodal exposure on learning and memory for a modality specific stimulus property, pitch. Our results provide the first convergent findings with infant studies demonstrating unimodal facilitation, consistent with the predictions of the Intersensory Redundancy Hypothesis (see Bahrick et al., 2006, 2013). They also provide the first extension of unimodal facilitation to the prenatal period. We found that prenatal unimodal exposure facilitates attention to and learning of the modality-specific property of pitch of an individual maternal call in quail embryos. Conversely, redundant bimodal stimulation appeared to interfere with attention to and learning of the modality-specific property of pitch. This difference in preference between the unimodal and redundant bimodal groups cannot be attributed to the overall amount of stimulation available across these conditions, as chicks prenatally exposed to asynchronous audiovisual stimulation also preferred the familiarized maternal call following hatching. Chicks' preference for the familiar pitch variant of the maternal call following prenatal unimodal or asynchronous bimodal exposure but not following synchronous exposure indicates that they were attending to modality specific features of the call during prenatal stimulus presentations.

Our current findings provide additional evidence that selective attention is recruited toward specific stimulus properties of events in early development, and that these biases can result from experience during the prenatal period. Specifically, our results demonstrate that the principle of *unimodal facilitation*, in which modality-specific properties (e.g., color, pattern, pitch) are detected across species more readily when they are explored through only one sense than when they are detected in synchronous bimodal stimulation. When considered in light of previous studies with bobwhite quail embryos and with human infants (see Bahrick & Lickliter, 2012 for a review), our results support the predictions of the IRH and highlight attentional trade-offs that are at play during early development. Specifically, redundant bimodal events facilitate the detection of amodal properties at the expense of modality-specific properties, whereas unimodal stimulation facilitates detection of modality-specific properties at the expense of amodal properties.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

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