Behavioral and neural foundations of multisensory face-voice perception in infancy

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Abstract

In this paper we describe behavioral and neurophysiological evidence for infants' multimodal face-voice perception. We argue that the behavioral development of face-voice perception, like multimodal perception more broadly, is consistent with the intersensory redundancy hypothesis (IRH). Furthermore, we highlight that several recently observed features of the neural responses in infants converge with the behavioral predictions of the intersensory redundancy hypothesis. Finally, we discuss the potential benefits of combining brain and behavioral measures to study multisensory processing, as well as some applications of this work for atypical development.

*Behavioral and neural foundations of face-voice perception in infancy**Overview*

Human communication is a multisensory experience. For example, we can see and hear our communicative partners. Often, such cues from these different sense modalities need to be coordinated in order to understand the intent of another person's thoughts and actions. Despite the fact that human communication is a multisensory experience, historically much of the research and theorizing on infant perception, cognition, and learning related to face-voice perception has been done from a unimodal or single sense modality perspective. The purpose of this review article is to summarize and integrate research on the behavioral and neural foundations of face-voice perception in human infants. Specifically, we review selected behavioral studies that examine the development of attention, learning, and memory relevant to infants' multisensory perception of faces and voices. We then review the rapidly emerging literature examining the neural basis of multisensory processing in infants including mention of some relevant findings from the non-human animal and human adult literatures. From the outset, we propose that the intersensory redundancy hypothesis (IRH) provides a useful framework for understanding the perceptual and cognitive processes associated with multisensory communication and may provide insights to the neural foundations of face-voice perception as well. Finally, we briefly review some emerging translational applications of this work.

Unimodal perception of faces and voices

As noted above, our day-to-day interactions, including communicative exchanges, are multimodal or multisensory. While research that examines how auditory and visual information collectively lead to face-voice or person perception has increased in recent years, the majority of research that has examined infants' face-voice perception has done so from either the visual or

auditory sense modality. Therefore, before we describe research on the process and development of infants' multisensory perception of faces and voices, we first briefly summarize findings on infants' perception of faces and voices from a unimodal or unisensory perspective.

Visual Perception of Faces

Over the past several decades a vast literature has accrued demonstrating that infants are excellent perceivers of faces (see Farah, Wilson, Drain, & Tanaka, 1998; Nelson 2001; Pascallis & Kelly, 2009 for reviews). For example, newborns prefer faces compared to other visual stimuli (e.g., Fantz, 1963; Maurer & Barrera, 1981) and 2- to 4-day-old newborns discriminate dynamic images of their mother and a stranger's face (Field, Cohen, Garcia, & Greenberg, 1984; Sai & Bushnell, 1988). Certainly by 3-months of age and possibly from birth, infants can recognize individual faces based on facial features alone and from different orientations (Kelly et al., 2007; Pascalis, De Haan, Nelson, & de Schonen, 1998; Turati, Bulf, & Simon, 2008). Furthermore, the infant brain shows some degree of cortical specialization for face processing. For example, studies using functional near-infrared spectroscopy (fNIRS) have shown that occipital and temporal regions known to respond selectively to faces in adults (e.g., Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997) also respond more to face than to non-face control stimuli in young infants (e.g., Blasi et al., 2007; Csibra et al., 2004; Otsuka et al., 2007). Brain electrophysiology measured from the scalp (using electroencephalography) of infants also shows selectivity in the cortical response to faces compared to non-face stimuli in young infants (e.g., de Haan, Pascalis, & Johnson, 2002). Thus, while infants' face perception is shaped and modified by visual experience throughout the first year of life, even young infants are in fact adept perceivers of faces (see Bar-Haim, Ziv, Lamy, & Hodes, 2006; Pascalis & Kelly, 2009 for reviews). Similarly, while young infants show neural selectivity for faces compared to

non-face stimuli early in development, their neural responses become increasingly specialized for the types of faces (race, species, etc.) experienced in their environment (e.g., Scott, Shannon, & Nelson, 2006; Scott & Monesson, 2010).

Auditory Perception of Voices

Just as infants are excellent perceivers of faces they are also excellent perceivers of voices. Fetuses, for example, are sensitive to auditory stimulation during their last trimester (Querleu, Renard, Versyp, Paris-Delrue, & Crepin, 1988; Querleu, Renard, Boutteville, & Crepin, 1989) and show a preference for their mother's voice compared to a stranger's voice or the voice of their father (DeCasper & Fifer, 1980; DeCasper & Prescott, 1984). Additionally, four-day-old infants discriminate between their "own" language and an unfamiliar language – but not between two unfamiliar languages (Mehler, Jusczyk, Lambertz, Halsted, Bertoncini, & Amiel-Tison, 1988; Moon, Cooper, & Fifer, 1993). Likewise, two-day-old infants, who prenatally heard their mother read a story once a day during their last trimester, showed a preference for their mother reading the familiar story compared to her reading of a novel story (DeCasper & Spence, 1986). Studies using functional magnetic resonance imaging (fMRI) and fNIRS have shown that from the first few months of life the infant brain is specialized for language processing (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; 2010; Pena et al., 2003). More specifically, left-lateralized regions of the frontal and temporal lobe respond selectively to speech and other language-like stimuli compared to backwards speech or non-language sounds within the first few months of life (Dehaene-Lambertz et al., 2002; 2010; Peña et al., 2003). Furthermore, between 6 and 9 months of age both the neural response and looking behavior of infants suggests that language processing becomes increasingly tuned to the particular patterns and sounds of their own language (e.g., Jusczyk, Cutler, & Redanz, 1993 or see

Kuhl, 2010 for a review). Thus, from very early in development, infants discriminate, recognize, preferentially attend to, and engage specialized regions of the brain for processing of faces and voices.

As reviewed above, early in development, infants are adept at perceiving faces and voices. For the most part, however, infants do not encounter faces or voices in isolation, rather infants are typically exposed to coordinated, or temporally and spatially collocated faces and voices. Therefore, just as it is important to understand how infants perceive faces and voices separately (i.e., from a unimodal perspective), it is also important to account for how, when, and under what conditions infants are able to perceive, learn, and remember faces and voices from a multimodal or multisensory perspective.

Multisensory or Multimodal Communication

Communication between two organisms is the canonical multimodal experience. Within human social-communicative exchanges, visual cues from the face and body of one speaker, along with that speaker's auditory vocal cues, need to be coordinated in order to understand the intent and content of another person's thoughts and actions. In other words, everyday communication involves the coordination of a variety of sensory information. Broadly speaking, communicative exchanges, like various objects and events, provide two types of sensory information: amodal and modality specific information (see Bahrick, Lickliter, & Flom, 2004; Gibson, 1966, Gibson, 1969 for reviews).

Modality specific information is typically defined as that information that is conveyed or tied to one specific sense modality (see Bahrick et al., 2004). For instance, the pitch and timbre (i.e., complexity) of a person's voice is restricted to the auditory system. Likewise, the color of a person's hair or appearance of their face is restricted to the visual system. In contrast, amodal

information is that information that is “without modality”. In other words, the property specified by amodal information is common across two or more sense modalities and is not specific to any one sensory system. Examples of amodal properties include tempo and rhythm of speech, as these properties can be both seen as well as heard. Furthermore, some social information, like affect or emotion, can also be categorized as amodal. That is, the communication of affect is often conveyed in both facial *and* vocal expressions.

Intersensory Redundancy Hypothesis

The fact that everyday objects and events, including communicative exchanges, provide both modality specific and amodal information raises the question of how human infants arrive at a veridical perception of their world. Gibson (1966, 1979) argued that the senses work together to pick up what he termed invariant or amodal information. E. J. Gibson (1969) extended this work to perceptual development and described perceptual development as a process of increasing specificity where more global, invariant, and amodal properties like tempo, rhythm, and intensity, are typically perceived and learned prior to modality specific properties (Gibson, 1969; Gibson & Pick, 2000; Bahrack 2001). More recently, Bahrack and her colleagues proposed an *Intersensory Redundancy Hypothesis (IRH)* that builds from this ecological approach to perception as a framework for understanding how infants arrive at a veridical and unitary perception of our world, including infants’ perception of faces and voices (Bahrack & Lickliter, 2000; 2002; Bahrack, Lickliter, & Flom, 2004). More specifically, the IRH provides an explanation for understanding what properties of an object or event (including faces and voices) infants will attend to, process, and remember based on the information available to the infant (Bahrack & Lickliter, 2000; 2002; Bahrack et al., 2004). One prediction of the IRH is that amodal properties such as tempo, rhythm, and intensity are more perceptually salient and will more

easily capture infants' attention when experienced in multimodal or multisensory contexts compared to a unimodal or unisensory contexts (see Bahrick, Lickliter, & Flom, 2004; Gibson, 1966, Gibson, 1969). Furthermore, the IRH predicts that infants will show an attenuated response to amodal properties when experienced in a unimodal context. In contrast, infants' attention toward and learning of modality specific properties such as color, pitch, or visual orientation will be facilitated in unimodal contexts and are attenuated in multimodal contexts (Bahrick & Lickliter 2002; Bahrick et al., 2004; Flom & Bahrick, 2010). Thus, attentional biases and subsequent learning and memory in infancy depend upon the nature of information available for perceptual exploration. Finally, the Intersensory Redundancy Hypothesis (IRH) also offers a developmental prediction. As perceptual processing becomes more efficient later in infancy, or with increased perceptual experience, both amodal and modality specific properties will be detected, attended to, and learned in contexts of redundant multisensory or non-redundant unimodal stimulation (Bahrick et al., 2004).

Evidence Supporting the Predictions of the Intersensory Redundancy Hypothesis

For nearly two decades, researchers have tested the predictions of the intersensory redundancy hypothesis (see Bahrick, 2010 for a review). Some of the initial experiments investigating the intersensory redundancy hypothesis examined infants' (i.e., 3- to 5-month-olds') discrimination of different amodal properties such as rhythm and tempo within unisensory or unimodal contexts as well as multimodal or multisensory contexts (Bahrick & Lickliter, 2000; Bahrick, Flom, & Lickliter, 2002). For example, Bahrick and Lickliter (2000) showed that 5-month-olds discriminate a change in the rhythm of a plastic toy hammer hitting a surface when provided redundant and temporally synchronous bimodal auditory-visual stimulation, but fail to discriminate a change in the event's rhythm when provided unimodal auditory, unimodal visual

stimulation, or temporally asynchronous bimodal stimulation (Bahrick & Lickliter, 2000).

Likewise, Bahrick and colleagues (2002) showed that 3-month-olds discriminate a change in the tempo or rate of the same toy hammer hitting a surface when provided redundant and temporally synchronous bimodal auditory-visual stimulation and not when provided either unimodal auditory or unimodal visual stimulation. These experiments show that the amodal properties of rhythm and tempo are perceived when conveyed in redundant multimodal stimulation and not when conveyed in unimodal auditory or visual stimulation. Evidence from other studies provides support for the developmental prediction of the intersensory redundancy hypothesis which is that infants' attention is initially captured by amodal properties and over the course of development infants perceive and discriminate changes in the same amodal property in multimodal or unimodal stimulation (e.g., Bahrick & Lickliter, 2004; Bahrick et al., 2002). For example, Bahrick and Lickliter (2004) found that 5-month-olds can discriminate a change in tempo when provided either redundant bimodal (audio-visual) stimulation or when provided unimodal (auditory) stimulation, while younger infants (i.e., 3-month-olds) make the same discrimination only within the context of bimodal (audio-visual stimulation) (Bahrick & Lickliter, 2004; Bahrick et al., 2002). Similarly, older infants (8-month-olds) can discriminate a change in rhythm (i.e., the tapping hammer) when provided either bimodal or unimodal stimulation, but younger infants (5-month-olds) show discrimination only when provided bimodal stimulation (see Bahrick & Lickliter, 2000). Thus, older infants show discrimination of tempo and rhythm in either bimodal or unimodal contexts whereas younger infants only did so within the context of bimodal stimulation (Bahrick & Lickliter, 2004). Taken together, early in development infants appear sensitive to changes in amodal properties of tempo and rhythm within the context of synchronous bimodal stimulation. Two- to three-months later, however,

infants can discriminate changes in these same amodal properties when provided either bimodal or unimodal stimulation.

The predictions of the intersensory redundancy hypothesis have also been documented within the context of social perception. For example, Flom and Bahrick (2007) showed that after being familiarized to an unfamiliar adult conveying either a happy, sad, or angry affective facial expression, 4-month olds were able to detect a change in the affective expression, but only when provided redundant bimodal stimulation and not when provided unimodal visual or unimodal auditory stimulation. However, by 5-months of age infants were able to reliably discriminate the different expressions when provided either bimodal or unimodal auditory information (voice alone) and by 7-months of age infants showed reliable discrimination when provided bimodal audio-visual information, unimodal auditory information (voice alone), or unimodal visual information (face alone). These results demonstrate the discrimination of affect in faces emerges first in the context of redundant bimodal stimulation and is later extended to unimodal auditory and then unimodal visual stimulation. Finally, in addition to providing evidence supporting the intersensory redundancy hypothesis, the results of the studies just reviewed also provide a foundation for examining and understanding how infants detect available information and correspondences between faces and voices to form a unitary perception of a person.

Infants' Perception of Auditory and Visual Properties Uniting Faces and Voices

The successful perception of faces and voices in multisensory situations not only involves the uniting of overlapping information (i.e., intensity, rhythm, and tempo), but the integration of modality specific information as well (visual appearance of the face as well the pitch and timbre of the voice). Within the context of early speech perception and language development, 2-month-olds are able to perceive the amodal property of temporal and spatial synchrony uniting

lip movements and the onset/offset of auditory speech (e.g., Dodd, 1979). By 4-months of age, infants match visual speech with the appropriate auditory information (i.e., different vowel sound with the appropriate facial expression; Kuhl & Meltzoff, 1982; 1984; Patterson & Werker, 1999; Werker, 2003). Related research further demonstrates that slightly younger infants (i.e., 3-month-olds compared to 4-month-olds) not only match visible and auditory speech sounds, but also use multisensory auditory-visual speech in imitating the speech of a live actress (Legerstee, 1990). More specifically, they are able to imitate the modeled speech sounds when the face and voice provided a matched or congruent speech sound but not when provided mismatched or incongruent speech sounds (e.g., Legerstee, 1990). Finally, research also demonstrates that older infants (e.g., between 5- and 7-months of age) are able to perceptually recognize, or match, human faces and voices on the basis of a common affective expression, age, and gender (e.g., Bahrick, Netto, Hernandez-Reif, 1998; Walker-Andrews, Bahrick, Raglioni, & Diaz, 1991; Walker, 1982). Infants can also match the vocalizations (e.g., barks) and posture of other species (e.g., canine) on the basis of a common affective expression (Flom, Whipple & Hyde, 2009). In sum, this research demonstrates that within the first 6-months of life, infants are sensitive to and perceive the spatial and temporal coherence of overlapping amodal auditory and visual information within the context of multisensory human speech events and cross-species communication.

Just as infants are sensitive to and perceive synchronized amodal auditory and visual speech events, infants as well as adults, perceptually integrate spatially and temporally incongruent auditory and visual speech events. For example, infants and adults alike are susceptible to the McGurk illusion (e.g., Burnham & Dodd, 2004; McGurk & MacDonald, 1976; Rosenblum, Schmuckler, & Johnson, 1997). Specifically, infants (and adults) commonly

perceive a unique or third speech event when one auditory speech sound is artificially synchronized with different visible speech movements (i.e., lip movements) (Burnham & Dodd, 2004; Rosenblum et al., 1997). In addition to integrating different face and voice speech events, as in the case of the McGurk illusion, infants' also unite auditory and visual speech events in the absence of spatial contiguity (e.g., Pons, Lewkowicz, Soto-Faraco, & Sebastian-Galles, 2009). For instance, younger (6-month old) and older (11-month old) infants can match auditory and visual speech when presented sequentially rather than concurrently (e.g., Pons et al., 2009). Furthermore, younger infants can do so in their native language as well as a foreign language, whereas older infants can only do so in their native language (Pons et al., 2009). Thus, just as infants are able to perceive various amodal properties uniting faces and voices, they are also able to perceive various intersensory relationships necessary for speech perception and language development in the absence of redundant amodal relationships. In addition, infants also perceive these same cues uniting faces and voices when presented in isolation or in conflict with other auditory or visual cues. Finally, infants' intersensory speech perception is shaped by their auditory language experience.

Infants' Learning of Arbitrary Relations between Voices and Objects

In addition to infants' perception of amodal and modality specific properties, the intersensory redundancy hypothesis has also been extended to infants' learning of arbitrary relationships. For example, Gogate and Bahrick (1998) examined whether the presence of the amodal property of temporal synchrony between a moving object and the occurrence of a vowel sound promoted infants learning of an arbitrary object-vowel relation. After familiarizing 7-month-olds to novel object-vowel pairings that occurred in temporal synchrony, asynchronously, or in static or still condition, they observed that infants noticed when the vowel-object pairing

was switched in the synchronous condition, but not in the still or asynchronous condition. The fact that infants did not notice the switch in either the asynchronous or still condition is important as it examines the possibility that it was simply the “motion” that captured infants’ attention and promoted their learning of the arbitrary relationship. Rather, it was the *synchronous* motion of the object and vowel sound pairing that promoted 7-month-olds learning this arbitrary relationship (Gogate & Bahrick, 1998). In addition, 7.5-month-olds have also been shown to use temporally synchronized faces and voices, but not asynchronous faces and voices, to separate, or segment, two speech streams (Hollich, Newman, & Juscyk, 2005). Finally, Gogate, Bahrick, and Watson (2000) have shown that caregivers’ use of temporally synchronous motions decreases as infants develop and increasingly begin to use other strategies in learning object-word pairings. Together, these results provide evidence that the amodal property of temporal synchrony is important in infants’ learning of arbitrary relations between verbal referents and different objects, as well as infants’ segmentation of the speech stream.

Infants’ Learning of Arbitrary Face-Voice Relations

Face-voice pairings also consist of arbitrary associations. For example, the sound (i.e., pitch, timbre, etc.) of a particular voice and the visual appearance of a particular face (i.e., hair color, facial features, etc.) represent such an arbitrary relationship. Until recently, relatively few studies examined whether, and under what conditions, infants are able to match arbitrary features of particular faces and voices. One early study to suggest they may be able to do so reported that 4-month-olds reliably match the faces and voices of their mother and father when the face-voice synchrony was matched (Spelke & Owsley, 1979). However, because this study used faces and voices of males and females (i.e., the infant’s parents) it was not clear whether these infants matched the face and voice on the basis of their arbitrary face-voice relationship or whether they

used the amodal property of gender in making the intersensory match (i.e., males tend to have deeper, more resonate voices and larger, more pronounced facial features compared to females). Walker-Andrews and colleagues (1991) later demonstrated that 4-month-olds do in fact match faces and voices on the basis of gender when the faces and voices are unfamiliar to the infant. While informative, these results do not specify how infants learn the arbitrary aspects of face voice relationships, or whether the amodal relationships are learned prior to or after the arbitrary face-voice relationships.

In a more recent study researchers examined 3-month-olds' learning of arbitrary face-voice pairings (Brookes, Slater, Quinn, Lewkowicz, Hayes, & Brown, 2001). In this experiment, infants were habituated to two temporally synchronous face-voice pairings. Following habituation, infants were presented with a mismatched face and voice. For some of the infants the male face of habituation was now presented in synchrony with the voice of a female (and vice-versa). For others, the mismatched face-voice pairing involved pairing the face of habituation with a different voice, but of the same gender. The results of this study were asymmetrical, as infants showed reliable discrimination when the face-voice pairing was switched to a voice of a different gender and minimal discrimination when the novel face was of the same gender (Brookes, et al., 2001). While important, the results of Brookes and colleagues (2001) did not clarify whether infants used gender or temporal synchrony in detecting the changes in the face-voice relationships or whether amodal properties have perceptual priority in learning arbitrary face-voice relationships.

More recently, Bahrick and colleagues examined 2-, 4-, and 6-month-olds' learning of arbitrary face-voice relations (Bahrick, Hernandez-Reif, & Flom, 2005). In two experiments, Bahrick and colleagues (2005) examined the prediction made by the intersensory redundancy

hypothesis that infants would *initially* focus on amodal properties uniting a face and voice (i.e., temporal synchrony) and then over the course of development infants would focus on the arbitrary features associated with the face-voice pairing. In the first experiment, infants were familiarized (i.e., habituated) to two synchronized male or two female face-voice pairings. It is worth noting in this experiment, unlike previous experiments, infants were exposed to pairings of the same gender to avoid the potential confound of infants learning/matching of faces-voices on the basis of gender (i.e., Spelke & Owsley, 1979; Brookes, et al. 2001). More specifically, half of the infants at each age were habituated to Male A's face and voice as well as Male B's face and voice, while the other half were habituated to Female A's face and voice and Female B's face and voice. Following habituation, infants received two test-trials that depicted a change in the face-voice pairing. Unlike Brookes et al. (2001) and Spelke and Owsley (1979), infants received a change in face-voice pairings for the same gender during the test-trials (e.g., Male A's face would be paired with Male B's voice). Results revealed that 4- and 6-month-olds, but not the 2-month-olds, learned and detected a change in the face-voice pairing. Moreover, this initial learning was not based on gender, as infants were familiarized on two faces-voice pairings of the same gender. Thus, during the first phase of this experiment 4- and 6-month-olds, but not 2-month-olds, showed evidence of learning the arbitrary face-voice pairings.

Following infants' habituation to the two face-voice pairings, and subsequent discrimination or test-trials (i.e., phase 1), infants were given a 10-minute break and were then examined for their memory for the face-voice pairing (i.e., phase 2). During this second or intermodal matching phase, infants were shown, on side-by-side monitors, the two faces they viewed and learned during habituation. For half the trials, infants heard the voice of one of the two faces and on the other half of the trials infants heard the voice that went with the other face.

The results of the intermodal matching phase revealed that only the 6-month-olds looked preferentially longer to the correct face (Bahrick et al., 2005). In other words, while 4- and 6-month-olds learned and noticed when the face-voice pairing was switched, only the 6-month-olds remembered and matched which face went with which voice following a delay.

The results from the study of Bahrick and colleagues (2005) are consistent with and support predictions made by the intersensory redundancy hypothesis. Specifically, younger infants' attention was captured by amodal properties such as temporal synchrony, tempo, and rhythm of speech, as the faces and voices were conveyed in multimodal stimulation. As such, it is not surprising that 2-month-olds, within the context of multimodal stimulation, did not reliably discriminate a change in the modality specific properties of the face-voice relationship. The results of a follow-up experiment, however, revealed that 2-month-olds do notice a change in the face or voice when the events were presented in a unimodal rather than a multimodal or multisensory context (Bahrick et al., 2005). In sum, the results of this series of experiments support the developmental predictions of the intersensory redundancy hypothesis, as infants' attention was shown to become more flexible over the course of development. That is, 4-month-olds were able to attend to the amodal properties as well as the arbitrary face-voice pairing and noticed a change in the arbitrary face-voice relationship. Only the 6-month-olds, however, noticed a change in the arbitrary face-voice relationship *and* remembered this relationship following a delay.

Neural Foundations of Intersensory Perception

As reviewed above, there is ample behavioral support for the intersensory redundancy hypothesis across a variety of contexts with infants, including for perception in communicative contexts involving faces and voices (e.g., Bahrick & Lickliter, 2000; 2002; 2004; Bahrick et al.,

2004; Lickliter, Bahrick, & Markham, 2006; Lickliter, Bahrick, & Honeycutt, 2002). Until recently, however, little was known about the neural foundations for infants' intersensory perception and multimodal processing and, only a fraction of the work that has been done has addressed communication-relevant processing of faces and voices. Instead, our knowledge on the neural basis of multimodal processing and intersensory perception of social and non-social stimuli to date is largely based on evidence from single cell recordings within non-human animals and EEG and fMRI evidence from human adults (e.g., Calvert, Hansen, Iversen, & Brammer, 2001; Giard & Peronnet, 1999; Wallace & Stein, 1997).

From the neuroscience literature with human adults, it is clear that many regions across the cortex are involved in multimodal perception, including primary visual and auditory sensory cortex, and heterogeneous regions of the parietal and superior temporal cortex (see Calvert et al., 2001 or Fairhall & Macaluso, 2009 for reviews). In addition, subcortical regions including the superior colliculus have also been found to be important to multimodal processing in non-human animals and are thought to play similar roles in humans (e.g., Stein, Stanford, Rowland, 2009, 2014). More recently, it has been shown that the particular brain regions involved in intersensory perception in adults depends heavily on the context and type of sensory stimulation (e.g., Talsma, 2015; van Atteveldt, Murray, Thut, & Schroeder, 2014). The questions of which brain regions are involved in multimodal perception in infancy, including multimodal face and voice perception, and whether this changes over development are largely unexplored. This lack of research is arguably due, in part, to the difficulty in applying neuroscience methods with high spatial resolution with infants. However, emerging methods such as fNIRS (e.g., Edwards et al., 2016; Hyde, Boas, Blair, & Carey, 2010; Gervain et al., 2011) and technological developments related to the application of fMRI to infants promise to inform such questions in the future.

In addition to answering questions about which brain regions are involved, neuroscience methods also have the potential to inform our understanding of the nature and timing of multimodal processing in the brain. Research to date has begun to map out when and how multimodal face and voice stimulation is integrated, perceived, and remembered in the adult brain (e.g., Talsma, 2015; van Atteveldt et al., 2014). A comprehensive review of the adult work on multimodal processing and perception is beyond the scope and focus of this article. Instead, we discuss several functional neural signatures of multimodal processing and perception that have emerged in adults and have begun to be studied in infants.

One such neural signature that has been routinely observed in human adults (and non-human animals) is that bimodal stimulation elicits greater neural responses than unimodal stimulation alone (e.g., Giard & Peronnet, 1999; Brefczynski-Lewis, Lowitzsch, Parsons, Lemieux, & Puce, 2009). Single cells within the deep layers of the superior colliculus in non-human animals reveal an exponentially greater or superadditive response to synchronous bimodal audio-visual stimulus compared to unimodal auditory, unimodal visual, or to the summation of these two unimodal responses (e.g., Wallace & Stein, 1997; Wallace, Wilkinson, & Stein 1996). Likewise, when adults are asked to identify an object based on bimodal auditory-visual stimulation, unimodal auditory, or unimodal visual stimulation, event-related potentials (ERPs) are greater in amplitude to the bimodal stimulation compared to the sum of the unimodal auditory and unimodal visual responses (e.g., Giard & Peronnet, 1999; Santangelo, Van der Lubbe, Olivetti-Berlardinelli, & Postma, 2008). Increased neural responses to bimodal stimulation are not restricted to basic auditory and visual sensory regions of the cortex, but evident in higher-level association areas such as the right fronto-temporal cortex as well (Fort, Delpuech, Pernier, & Giard, 2002a, 2002b). Importantly, these superadditive-like effects in

humans are not restricted to object-sound pairings but observed for face-voice pairings as well (e.g., Brefczynski-Lewis et al., 2009).

Some initial evidence of greater neural responses to bimodal compared to unimodal stimulation has also been observed in infants (Hyde, Jones, Porter, & Flom, 2010; Reynolds, Bahrick, Lickliter, & Guy, 2014). In one experiment, Hyde and colleagues (2010) compared event-related potentials to bimodal stimulation (i.e., a large colored circle paired with a “bong” sound and a small circle paired with a “ping” sound), unimodal auditory stimulation (i.e., the lower pitched “bong” and higher pitched “ping” sounds), and unimodal visual stimulation (i.e., the large and small colored circles) in 3-month-old infants and adults. Following previous work, Hyde and colleagues used a subtraction technique to compare the auditory response during the bimodal audio-visual stimulation (subtracting the response to the unimodal visual condition from the response to the audio-visual condition, AV-V) to the unimodal auditory response (A) (see Besle, Fort, Delpuech, & Giard, 2004; Giard & Peronnet, 1999 for similar analyses with adults). Analyses revealed more negative going mid-latency potentials over fronto-temporal scalp sites (N450) to bimodal stimulation compared to unimodal auditory stimulation (see Figure 1, panel B). Greater fronto-temporal negativities were also observed in adults to the same stimuli, albeit earlier and stronger over the left hemisphere (N2)(Figure 1, panel D). Thus, even 3-month-old infants, like adults (e.g., Fort et al., 2002b; Giard & Peronnet, 1999), show greater neural responses for bimodal compared to unimodal stimulation (also see Reynolds et al., 2014).

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A second neural signature of intersensory perception found in adults is integration of redundant multimodal information early in the time course of sensory processing (Braidia, 1991; Green 1998). As discussed earlier, temporal face-voice synchrony provides redundant information across multiple senses. When adults are presented with synchronous audio-visual speech, early auditory evoked components (N1-P2) are attenuated compared to unimodal auditory speech but not to asynchronous audio-visual speech (Pilling, 2009, Besle et al., 2004; Besle, Fort, and Giard, 2005). In other words, early auditory attenuation occurs in the presence of synchronous, but not asynchronous bimodal speech with adults. In addition to early sensory integration, these results also highlight a third neural signature of intersensory perception found in adults: neural attenuation for synchronously presented stimuli compared to asynchronously presented stimuli.

From the few studies that have been conducted, it appears that infants, like adults, can integrate redundant multisensory information early in sensory processing (Bristow et al., 2009; Hyde, Jones, Flom, & Porter, 2011; Knop, 2014). For example, Hyde and colleagues (2011) presented 5-month-olds with static images of face paired with a voice saying “hi” in perfect temporal synchrony or asynchronously. Similar to findings with adults (see Besle, Bertrand, & Giard, 2009 for a review), Hyde and colleagues (2011) observed evidence of early auditory-visual integration on the auditory P2 in 5-month-old infants (see Figure 2, panels B). The observed infant auditory response was greater for the *synchronous* condition, which contrasts with findings in adults showing that *asynchronous* stimuli typically evokes a greater early sensory response (see Figure 2, Panel B). However, Hyde and colleagues (2011) did observe a

greater response (more negative) for the asynchronous condition compared to the synchronous condition on the later-going Nc component, known to index attentional orienting in infants (see Reynolds & Richards, 2005).

A second experiment by Hyde and colleagues (2011) using synchronous and asynchronous video clips of a person saying simple phrases found largely similar results, with greater early sensory responses to the synchronous condition and greater mid-latency attentional responses to the asynchronous condition (see Figure 3). Additionally, these authors observed a greater late positive slow wave (PSW) for the synchronous events compared to the asynchronous events (see Figure 3). PSW is typically associated with memory updating in infants (Nelson, 1995, 1996, 1998; Nelson & Collins, 1991, 1992), suggesting that infants in this experiment more effectively retrieved and/or updated dynamic synchronous stimuli in memory compared to asynchronous stimuli. Thus, early sensory responses of 5-month-olds appear to be greater for temporally synchronous faces and voices, likely reflecting early sensory integration but in a different manner than that typically seen in adults (Besle et al., 2004; Pilling, 2009). Greater sensory responses to synchronous stimuli compared to asynchronous stimuli in infants seems to correspond to the attentional bias young infants show behaviorally for amodal properties of bimodal stimuli compared to older infants (and presumably adults) as predicted by the intersensory redundancy hypothesis (Bahrick, 2000; 2001, Bahrick & Lickliter, 2002; Lewkowicz, 2000; 2010 for reviews). In contrast, later attentional responses are greater to temporally asynchronous events. Greater Nc responses to asynchrony may reflect the fact that, after early sensory integration occurs, infants find the asynchronous condition more novel or interesting (Reynolds & Richards, 2005). Alternatively, one might interpret the smaller Nc

response to the synchronous condition as attenuation, similar to that seen in earlier sensory responses of adults but more temporally drawn out.

Similar to the results of Hyde and colleagues (2011), Grossmann, Striano, and Friederici (2006) have shown greater attentional (Nc) responses of 7-month old infants to incongruent face-voice information. More specifically, they showed greater (more negative) Nc responses to emotional voices preceded by a face with incongruent emotion information (e.g. angry face presented before happy voice) compared to instances when the emotion of the voice was presented as consistent, and thus redundant, with the facial emotion presented immediately beforehand (e.g., happy face presented before happy face). Further, consistent with Hyde and colleagues (2011), Grossmann and colleagues also observed enhanced PSW memory responses for the congruently and, thus, emotionally redundant pairings. Although Grossman et al. (2006) did not employ temporally synchronous stimuli, these results provide additional evidence of mid-latency attenuation and later enhanced memory for emotionally congruent stimuli conveying redundant information about an amodal property across multiple senses.

 insert Figure 3 about here

More recently, Reynolds and colleagues (2014) improved on the basic design of Hyde and colleagues (2011), presenting more controlled audio-visual dynamic stimulus videos to 5-month old infants while recording scalp electrophysiology. Specifically, Reynolds and colleagues (2014) presented two different exemplars of the same video clips portraying a female

actress reciting a simple phrase under three conditions: a synchronous audio-visual condition where the audio and visual information matched, an asynchronous condition where the same videos were presented with their soundtracks switched, and a unimodal visual condition where the sound was turned off. This allowed the authors to better isolate effects of intersensory redundancy from differences in sensory stimulation. In this context, Reynolds and colleagues (2014) observed a greater Nc response (more negative) for audio-visual compared to visual presentation alone. These results, which involve the processing of face and voice stimuli, mirror a variety of previous work with adults, infants, and non-human animals showing greater responses for bimodal compared to unimodal stimulation with object stimuli (e.g., Besle et al., 2004; Giard & Peronnet, 1999; Hyde et al., 2010; Pilling, 2009). Reynolds and colleagues (2014) also observed greater attentional responses (indexed by the Nc) for the synchronous compared to asynchronous audio-visual face stimuli, the opposite direction of Nc modulation observed by others (Grossmann et al., 2006; Hyde et al., 2011). Finally, Reynolds and colleagues (2014) showed great efficiency in later memory (indexed by the PSW) for the synchronous audio-visual condition similar to the results of others (Grossmann et al., 2006; Hyde et al., 2011).

Related experiments by Kopp and colleagues have shown that early sensory and later attentional brain responses differentiate in magnitude but not latency between synchronous audio-visual events involving people producing goal-directed actions. Additionally, similar yet subtly asynchronous events do not seem to be distinguished behaviorally by infants, suggesting these events are perceptually fused (Kopp & Dietrich, 2013; Kopp, 2014). For example, results from the most recent of these studies showed greater amplitude early-evoked auditory responses (P2) in 6-month old infants to synchronous audio-visual stimuli of a person clapping compared to an asynchronous yet perceptually fused-version and greater mid-latency Nc attentional

responses to asynchronous version. This contrasts with both amplitude and latency response differences observed between synchronous and asynchronous stimuli that are behaviorally discriminable (Kopp & Dietrich, 2013). Like others studies reviewed, these results provide consistent evidence for early integration of auditory and visual information in sensory processing (see Besle et al, 2009 for a review). The observed pattern of attentional response (Nc) mirrors that observed by some (Grossmann et al., 2006; Hyde et al., 2011), but is the opposite of what others have observed (Reynolds et al., 2014). Uniquely, this study raises interesting questions about how the timing of processing information from different sense modalities may interact to elicit different perceptions in infants.

To our knowledge, only one published study to date has examined the development of the neural signatures of intersensory perception for faces and voices across different ages in infancy (Vogel, Monesson, & Scott, 2012). In this study, Vogel and colleagues (2012) measured ERPs to sequentially presented voice-face pairings in both 5-month-old and 9-month-old infants. In 5-month olds, they observed differential attentional responses (Nc), with a greater response to faces paired with congruent emotional voices compared to faces paired with incongruent emotional voices regardless of the race of the face (African American or Caucasian). Like findings reported on above, the direction of these results is consistent with some previous work (Reynolds et al., 2014) and opposite of what others have found (Knopp, 2014; Grossmann et al., 2006; Hyde et al., 2011). In contrast, 9-month olds did not show attentional response (Nc) differences by congruency in emotion between faces and voices. Instead, they showed latency differences on earlier perceptual processing (P400) of faces by congruency but only for more familiar Caucasian faces. The authors took these results as evidence of narrowing in intersensory perception that mirrors the developmental time course and nature of experience-

dependent narrowing in unimodal auditory and visual perception for voices and faces (see Scott, Pascalis, & Nelson, 2007 or Werker & Hensch, 2015 for reviews). Interestingly, there also appeared to be a shift in the brain systems involved in intersensory processing over development. That is, in both age groups the brain response showed distinctions between the consistency of information between the senses, but at different latencies and scalp locations, indicative of different brain systems. Younger 5-month-old infants showed fronto-central attentional (Nc) response differences, consistent with previous work with similar age groups. Older 9-month-old infants, however, showed similar fronto-central attentional responses across races and only differentiated between congruency in earlier posterior perceptual responses. Although these findings are isolated to a single paradigm to date, they suggest interesting differences in the way older infants may process intersensory information that seem to correspond with notable experience-dependent changes in behavior.

In sum, the neural correlates of infant multimodal processing and intersensory perception in infants show many similarities and some differences to those neural signatures observed in the adult literature. There is some evidence that the neural response of infants is greater to bimodal compared to unimodal stimulation, paralleling that observed in adults and non-human animals (e.g., Besle et al., 2004; Giard & Peronnet, 1999; Hyde et al., 2010; Pilling, 2009; Reynolds et al., 2014; Brefczynski-Lewis et al., 2009; Wallace & Stein, 1997; Wallace, Wilkinson, & Stein 1996). Infants also appear to integrate information from different senses early during sensory processing in some contexts, as has also been documented routinely in adults (Hyde et al., 2011; Besle et al., 2009). Further, later attentional responses in adults and infants distinguish between bimodal audio-visual stimulation containing redundant (e.g., synchronous) and non-redundant (e.g., asynchronous) visual face and auditory voice information (Hyde et al., 2011, Grossmann et

al., 2006; Reynolds et al., 2014; Vogel et al., 2012; Besle et al., 2009). However, while adults most often show attenuation of the neural response to synchronous bimodal stimulation (compared to asynchronous; see Besle et al., 2009 for a review), the infant neural response is more inconsistent (Hyde et al., 2011, Grossmann et al., 2006; Reynolds et al., 2014; Vogel et al., 2012). In adults, neural attenuation for bimodal synchrony is thought to reflect more efficient processing and has been documented in both early sensory and later attentional responses (Belse et al., 2004; Pilling, 2009; van Wassenhove, Grant, & Poeppel, 2005), whereas attenuation has only been observed in later going attentional responses in infants (Hyde et al., 2011, Grossmann et al., 2006; Reynolds et al., 2014; Vogel et al., 2012). Inconsistencies in the functional brain response between different experimental contexts in infants should not be taken as a limitation of the work, as most current views of multimodal processing and intersensory perception in adults conclude that context has a large effect on how, when, and where the brain is engaged (e.g., van Atteveldt et al., 2014; Matusz, Retsa, & Murray, 2016; Murray, Lewkowicz, Amedi, & Wallace, 2016). However, the fact that neural attenuation for bimodal synchrony has been documented exclusively in later attentional processing in infants but often appears during earlier sensory processing in adults may reflect a genuine developmental difference between infants and adults in efficiency and time course. That is, the various components of infant multimodal processing, integration, and perception may be more drawn out in infants than in adults.

Several features of the infant brain response to multimodal faces and voices also track behavioral development in face and voice attention, learning, and memory. First, young infants show early sensory responses and later memory responses to bimodal stimulation that favor redundancy (e.g., synchrony) (Hyde et al., 2010, 2011; Reynolds et al., 2014; Grossmann et al., 2006). These aspects of the neural response correspond to some of the attentional preferences

and memory advantages predicted by the intersensory redundancy hypothesis and observed behaviorally in infants of the same age for bimodal redundant face-voice stimuli compared to unimodal face, unimodal voice, or bimodal non-redundant face-voice stimuli (Bahrick, 2000; 2001, Bahrick & Lickliter, 2002; Lewkowicz, 2000; 2010 for reviews). Second, some preliminary results suggest that brain indices of attention, perception, and memory to different race faces and emotion pairings (Vogel et al., 2012) parallel perceptual narrowing effects seen in behavior for race and voice unimodally (see Scott et al., 2007 or Werker & Hensch, 2015).

Conclusions and Future Directions

Here we have reviewed evidence that multimodal processing of, perception of, and learning from faces and voices follow more general principles of the intersensory redundancy hypothesis. First, young infants (around 3- to 5- months of age) attend to various amodal properties such as a common tempo, rhythm, and affective expressions that unite a particular face and voice (e.g., Bahrick & Lickliter, 2000; 2002; Bahrick et al., 2004). Infants of the same age show an enhanced neural response to bimodal compared to unimodal stimulation in both early sensory and later attentional processes. Furthermore, attentional responses distinguish and memory processes are enhanced for situations where amodal properties such as affect are presented redundantly (e.g., synchronously or consistently) compared to situations when they are presented non-redundantly (asynchronously or inconsistently) across the senses (Hyde et al., 2010, 2011; Grossmann et al., 2006; Kopp, 2014; Reynolds et al., 2014). Second, starting around 6-months of age when attention is more flexible for various amodal and modality specific properties, infants can learn various arbitrary features (i.e., the sound of a particular voice and the visual appearance of a particular face) associated with a particular face-voice pairing. Neural and behavioral signatures of multimodal processing comparing younger to older infants suggest

that this development may be coupled with a tuning to the particular combinations of races and species and languages to which they are exposed (Vogel et al., 2012; Scott et al., 2007 or Werker & Hensch, 2015).

With regards to the neural basis and correlates of multimodal processing and perception, many questions remain. The application of neuroimaging technologies with better spatial resolution such as fNIRS and fMRI are needed to resolve which cortical and sub-cortical structures are associated with face-voice perception in infants, how they interact, and how this might change or persist over development. A clearer picture of which contexts elicit which functional patterns of response is needed, particular with relation to mid-latency attentional responses (Nc), given the inconsistencies observed in the few studies published to date (e.g., Reynolds et al., 2014; Hyde et al., 2011). Relatedly, a better understanding of the relationship between sensory and attentional processes as they relate to multisensory perception in infants is needed, especially since the relationship seems to be different in adults. Finally, only a handful of studies have been conducted on multimodal processing and perception in the infant brain and most have been conducted at around 5-6 months. Neuroscience data from more developmental time points in infancy, particularly those where behavioral changes in face and voice perception emerge, are needed to map the trajectory of brain development related to multimodal processing of face and voices during infancy.

It should be noted that the use of brain measures also provides a new arsenal of measures with some advantageous features to better understand behavioral development. For example, behavioral looking measures can indicate whether an infant notices a difference between two types of stimuli or prefers to look at or remembers one type of stimulus over another, allowing inferences regarding face and voice perception, learning, attentional bias, and memory (see

Aslin, 2007 or Oakes, 2010 for reviews). However, brain measures provide the potential to break down the behavioral outcome into component parts such as sensory processing, attention, and memory. For example, combining brain and behavioral measures would allow one to ask how particular sensory, attentional, and memory processes are related to enhanced memory for amodal properties of multisensory face-voice stimulation observed behaviorally in young infants. Thus, brain measures have the potential to provide additional information and may allow us to better understand the culmination of factors that lead to behavioral competencies, how these processes change, and how they may go awry.

Translational relevance to studying multisensory processing

As reviewed above, human communication is a multisensory process and often requires coordination of multisensory information. Some forms of atypical development appear to be associated with impairments in this sort of multisensory processing and integration (Leekam, Nieto, Libby, Wing, & Gould, 2007; Iarocci & McDonald, 2006). For example, some evidence suggests that individuals with autism differ from neurotypical peers in the way they process, integrate, and attend to multisensory information (see Bahrack, 2010; Iarocci & McDonald, 2006; Leekam et al., 2007 for reviews). More specifically, individuals with autism have been shown to be less sensitive to amodal properties in contexts of intersensory redundancy compared to typically developing peers, including in the integration of audio-visual speech (e.g., Smith & Bennetto, 2007; Magnee, de Gelder, van Engeland, Kemner, 2008), susceptibility to the McGurk effect (de Gelder, Vroomen, & van der Heide, 1991; Mongillo et al., 2008; Williams, Massaro, Peel, Bosseler, & Suddendorf, 2004), and processing of audio-visual temporal synchrony in some contexts (e.g., Bebko Weiss, Denmark, Gomez, 2006; Mundy & Burnette, 2005). Bahrack (2010) has suggested that autism itself may fundamentally be an impairment in early

intersensory processing, ultimately giving rise to later higher-level social and linguistic impairments, due, in part, to the early different or disrupted attentional biases that reduce attention towards important amodal properties of human social and communicative situations.

It is also suspected that preterm infants have disadvantages when it comes to integrating dynamic, multimodal information from their environment. For example, Pickens and colleagues (1994) showed an atypical pattern of development in integrating synchronous face and voice information among preterm infants (see also Lawson, Ruff, McCarton-Daum, Kurtzberg, and Vaughan, 1984 for example with object-sound integration). More recently, Gogate, Maganti, and Perenyi (2014) showed that preterm infants have difficulty temporally binding changes to synchronous syllable-object pairings and that these difficulties are not solely due to attentional deficits. Furthermore, difficulties appear to persist, to some degree, with only small improvements noted in visual recovery to an auditory syllable, but no improvements for visual object changes after 2 months. Thus, from such results it has been argued that early auditory dominance, which gives way to greater multisensory integration in term infants, persists in preterm infants (Gogate et al., 2014). If this is the case, biases in attention, learning, and memory for multisensory information in early development are likely different for preterm infants compared to term infants.

More work is certainly needed to investigate the existence and extent of differences in multisensory processing and perception in infants and children with developmental differences and/or disorders. The intersensory redundancy hypothesis may provide a useful benchmark to systematically investigate if and how atypical development, such as in those with autism or those who are born prematurely, experience challenges in integrating multimodal information and

whether this gives rise to later developmental deficits, including social and/or language deficits (see Bahrick, 2010).

Closing Statements

The world infants experience is inherently multisensory. It seems William James' (1890) assertion regarding infants' experience of it as “one great blooming and buzzing confusion” is overstated. Instead, the behavioral and neuroscience literature shows that, from very early in development, infants are prepared to attend to and integrate information across different sense modalities and use this convergent information to learn about and from other people.

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Figure Captions

Figure 1. Summary of ERP results for infants and adults reported by Hyde, Jones, Porter, & Flom (2010). A. Difference map of the (AV-visual) minus Auditory for infants at 475 ms. White items represent electrode sites used to calculate the average waveforms. B. Average waveforms for the bimodal (AV-visual) and unimodal conditions over fronto-temporal scalp locations from -200-800 ms for infants. The gray boxes highlight components of interest. The * indicates a significant difference between conditions. C. Difference map of the (AV-visual) – Auditory for adults at 250 ms. White items represent electrode sites used to calculate the average waveforms. D. Average waveforms for the bimodal (AV-visual) and unimodal conditions over fronto-temporal scalp locations from -200-800 ms for adults. The gray boxes highlight components of interest. The * indicates a significant difference between conditions. Reprinted from Hyde, D. C., Jones, B. L., Porter, C. L., & Flom, R. (2010). Visual stimulation enhances auditory processing in 3-month-old infants and adults. *Developmental Psychobiology*, 52(2), 181–189. Reprinted with permission from John Wiley and Sons copyright 2010.

Figure 2. Summary of Experiment 1 results reported by Hyde, Jones, Flom, & Porter (2011). A). Grand average scalp topography at 250 *ms* over left temporal sites for each experimental condition. B). Average waveform from -200-1900 *ms* averaged over left temporal sites characterizing auditory processing. The shaded region represents the statistical comparison of experimental conditions for the auditory *P2*. C). Grand average scalp topography at 700 and 1100 *ms* characterizing the *Nc* for the synchronous and asynchronous conditions over fronto-central sites. D). Average waveform from -200-1900 *ms* averaged over over fronto-central sites. The shaded region represents the comparison of experimental conditions for the *Nc*. . Reprinted from Hyde, D.C., Jones, B.L., Flom, R. & Porter, C.L. (2011). Neural signatures of face-voice synchrony in 5-month-old human infants. *Developmental Psychobiology*. Reprinted with permission from John Wiley and Sons copyright 2011.

Figure 3. Summary of Experiment 2 late processing results reported by Hyde, Jones, Flom, & Porter (2011). A). Grand average scalp topography at 600 *ms* over fronto-central sites (average of all experimental conditions). B). Average waveform from -200-2000 *ms* averaged over fronto-central sites. The shaded region represents the comparison of experimental conditions for the *Nc*. C). Grand average scalp topography at 1200 *ms* characterizing the positive slow wave (*PSW*) over temporal sites. D). Average waveform from -200-2000 *ms* averaged over left and right temporal sites. The shaded region represents the comparison of experimental conditions for the *PSW*. Reprinted from Hyde, D.C., Jones, B.L., Flom, R. & Porter, C.L. (2011). Neural signatures of face-voice synchrony in 5-month-old human infants. *Developmental Psychobiology*. Reprinted with permission from John Wiley and Sons copyright 2011.

Figure 1.

Figure 2.

Figure 3.