40 Perceptual Development and the Origins of Multisensory Responsiveness

ROBERT LICKLITER AND LORRAINE E. BAHRICK

Introduction

Most objects and events present a mix of visual, auditory, tactile, and olfactory stimulation simultaneously. How do young infants come to perceive and derive meaning from this array of multimodal stimulation? How do young infants determine which sights and sounds constitute unitary objects and events and which patterns of stimulation are unrelated to one another?

Historically, two prevailing theoretical views, known as the integration view and the differentiation view, have dominated attempts to address these important questions regarding the development of intersensory perception (see Bahrick & Pickens, 1994; Gibson & Pick, 2000; Lewkowicz, 1994). Generally speaking, the *integration view* proposes that the different sensory modalities function as separate sensory systems during the initial stages of postnatal development and gradually become integrated during the course of development through the infant's activity and repeated experience with concurrent information provided to the different sensory modalities (Birch & Lefford, 1963; Friedes, 1974; Piaget, 1952). According to this view, young organisms must learn to coordinate and integrate the separate senses during early development. The *differentiation view* holds that the different senses form a primitive unity early in development, and as the infant develops, the sensory modalities differentiate from one another. In this view, the senses are initially unified, and infants differentiate finer and more complex multimodal relationships through their experience over the course of development (Bower, 1974; Gibson, 1969; Marks, 1978).

As a result of these opposing views, the most prominent question guiding behavioral research on early intersensory development over the past several decades has focused on whether intersensory development proceeds from initially separate senses that become increasingly integrated through the infant's ongoing experience, eventually resulting in coordinated multimodal perception, or whether the development of intersensory perception is a process of differentiation and increasing specificity (Kellman & Arterberry, 1998; Lewkowicz & Lickliter, 1994a; Rose & Ruff, 1987).

In recent years the discussion has become less polarized, due in large part to the adoption of a more systems-based approach to the development of perception, according to which any given perceptual skill or ability is generated by a network of multiple, cocontributing neural, physiological, and behavioral factors (Gottlieb, Wahlsten, & Lickliter, 1998; Lewkowicz, 2000; Lickliter & Bahrick, 2000; Thelen & Smith, 1994). Although some controversy remains as to whether perceptual development proceeds from a wholistic unity to differentiated sensory modalities or from separated senses to coordinated multimodal experience (i.e., Bushnell, 1994; Maurer, 1993), the dominant view at present argues against an all-or-none dichotomy between integration and differentiation views of perceptual development. The increasing research focus on the processes and mechanisms underlying human and animal infant intersensory perception over the past several decades has provided mounting evidence that the separate senses are not so separate, highlighting the importance of differentiation in early development. Moreover, both differentiation and integration processes appear to be involved in perceptual development and function in an intercoordinated manner. In this chapter, we briefly review converging evidence across species, developmental periods, and properties of objects and events suggesting a general developmental trajectory in which differentiation of amodal and modality-specific stimulus properties emerges in a coordinated and interdependent manner, with the detection of more global, amodal stimulus properties leading and constraining perceptual responsiveness to more specific properties of objects and events.

Infant perception of multimodal information

There is now compelling neural, electrophysiological, and behavioral evidence of strong intermodal linkages in newborns and young of a variety of avian and mammalian species, including humans (e.g., Carlsen & Lickliter, 1999; Frost, 1990; King & Carlile, 1993; Knudsen & Brainard, 1991, 1995; Lewkowicz & Turkewitz, 1981; Lickliter & Banker, 1994; Mellon, Kraemer, & Spear, 1991; Stein & Meredith, 1993; Withington-Wray, Binns, & Keating, 1990). For example, infant animals have been shown to be more sensitive to intersensory correspondences than older animals in a classical conditioning learning paradigm (Spear & McKinzie, 1994). Animal and human infants also demonstrate an array of intermodal perceptual skills in the weeks and months following birth, including the detection of temporal and spatial contiguity between auditory and visual stimulation, the detection of multimodal information specifying the self and body motion, and intersensory facilitation, in which stimulation in one modality enhances responsiveness to stimuli in other modalities (Lickliter & Stoumbos, 1991; Lyons-Ruth, 1977; Morrongiello, Fenwick, & Chance, 1998; Rochat, 1995; Spelke, 1979; Turkewitz & Mellon, 1989).

Of particular interest is the fact that human infants have been shown to be skilled perceivers of *amodal* stimulus properties in the first several months following birth (Bahrick, 1988, 1992; Bahrick, Flom, & Lickliter, 2002; Bahrick & Lickliter, 2000; Bahrick & Pickens, 1994; Lewkowicz, 2000; Walker-Andrews, 1986, 1997). Amodal stimulus properties are those that can be conveyed by more than one sensory modality, whereas modality-specific properties can only be conveyed by one particular sensory modality. Thus, temporal synchrony, spatial collocation, intensity, rate, duration, and rhythm are all examples of amodal stimulus properties that can be specified simultaneously by several sensory modalities. They stand in contrast to modality-specific stimulus properties, which can only be conveyed by one particular sensory modality, such as color, pitch, or sweetness. As a case in point, the sights and sounds of hands clapping share temporal synchrony, a common tempo of action, and a common rhythm. The amodal properties of synchrony, tempo, and rhythm are thus concurrently available both visually and acoustically. Detection of this information enables the infant to perceive sights and sounds that belong together. Given that the role of integration has often been seen to link together separate sensations to form a unified percept (Piaget, 1952; von Helmholtz, 1968), infants' ready detection of amodal stimulus properties makes the need for intersensory integration unnecessary and unlikely.

A large body of developmental research utilizing infant habituation techniques has demonstrated that infants are adept at perceiving and responding to a host of amodal relations uniting stimulation across visual, auditory, vestibular, tactile, and proprioceptive stimulation in the first months following birth (see Gibson & Pick, 2000; Lewkowicz & Lickliter, 1994a, for reviews). This early detection of amodal information provides support for the view that development proceeds from a global unity of the senses to increasing differentiation of finer levels of stimulation (see Bahrick, 2001; Lickliter & Bahrick, 2000, for further discussion).

On the other hand, infants can also detect perceptual information that is not amodal in the months following birth. Infants clearly become more skilled at detecting intersensory relations that are modality-specific or arbitrary in their co-occurrence over the course of the first year of life (Bahrick, 1994, 2001; Bushnell, 1994; Lewkowicz, 1994). Many relations between stimulus properties conveyed concurrently to different modalities are arbitrary in the sense that they are not united by redundant information common across the different sensory modalities and thus can vary as a function of context or stimulus domain. For example, the relation between the appearance of an object and the verbal label we give it, or that between a person's appearance and the specific sound of his or her voice, or that between the type of sound a particular toy produces and its color and shape are cases of arbitrary pairings of concurrent stimulation across two or more sensory modalities. Given that there is no common information that links the specific characteristics of stimulation presented to the two or more modalities, arbitrary relations must be learned by experiencing the information in the modalities together, and may thus be characterized as depending on some process of association or integration. Research findings indicate that this process is likely initially guided by the detection of amodal relations, including temporal synchrony, temporal microstructure, and spatial colocation (Bahrick, 2001; Gogate & Bahrick, 1998; Hernandez-Reif & Bahrick, 2001; Lewkowicz, 2002). For example, young infants can learn to relate specific sounds with objects of a particular appearance, but only when temporal synchrony unites the motion of the object and sound (Bahrick, 1994; Gogate & Bahrick, 1998). The detection of global, amodal information appears to guide and constrain the detection of more specific information, both ontogenetically and within a given episode of exploration, so that unitary multimodal objects and events are explored first and modality-specific details are perceived in the context of more general principles that organize these details.

In sum, it appears that both integration and differentiation processes are involved in the emergence and maintenance of various types of intersensory functioning. The recognition of the important role of these processes and their interaction has led several investigators, including Bahrick (1994), Botuck and Turkewitz (1990), Lewkowicz and Lickliter (1994b), Smith (1994), Thelen and Smith (1994), and Werner (1957), to suggest that integration and differentiation processes are best considered as complementary rather than competitive or mutually exclusive processes. Recent work in developmental psychology and psychobiology is providing a clearer picture of how differentiating amodal relations *and* integrating arbitrary or modality-specific information across the senses can interact with one another in the development of early percpetual and cognitive skills. A brief review of this body of work provides a forum for exploring its implications for a more fully realized understanding of the origins and development of intersensory perception.

The salience of amodal stimulus properties during early development

What causes some patterns of sensory stimulation to be salient, attended to, and remembered by young organisms, and other patterns of stimulation to be ignored? Although we are not yet able to conclusively answer this important question regarding selective attention, a growing body of evidence from developmental psychology and psychobiology suggests that infants' adept detection of amodal relations is a fundamental component of selective attention during early development (Bahrick, 1992, 1994, 2001; Lickliter, Bahrick, & Honeycutt, 2002; Slater, Guinn, Brown, & Hayes, 1999). In particular, the detection of amodal relations appears to specify the unity of multimodal stimulation, capture and direct infant attention, and facilitate the further differentiation of a coordinated multimodal object or event (Bahrick & Lickliter, 2000; Bahrick & Pickens, 1994; Lickliter & Bahrick, 2001). Such detection of amodal relations can guide and constrain the detection of other nested intersensory relations, including modality-specific and arbitrary stimulus relations.

As a case in point, 7-month-old infants have been shown to be capable of learning the arbitrary relation between an object and a speech sound, but only when the object is moved in temporal synchrony with the sound. When the object is still or moved asynchronously with the speech sound, 7-month-olds show no evidence of linking the speech sound and the object (Gogate & Bahrick, 1998). In this example, learning of arbitrary relations appeared to be (at least initially) guided and facilitated by the detection of amodal relations present in multimodal stimulation. Hernandez-Reif and Bahrick (2001) have likewise shown that 6-month-old infants can detect the arbitrary relation between the tactually perceived shape of an object and a specific color or pattern, but only under conditions when amodal information for object shape unites their visual and tactile exploration. In other words, the relation between an object's color or pattern and its shape appears to be learned by young infants only in the presence of amodal shape information made concurrently available to vision and touch.

Related research has also found a developmental lag between the detection of amodal and arbitrary relations provided by a given event during early development. By 3 months of age, infants viewing objects striking a surface are capable of detecting the amodal audiovisual relations of temporal synchrony and the temporal microstructure specifying an object's composition. However, not until 7 months of age do infants detect the arbitrary relation between the pitch of the impact sound and the color and shape of the objects (Bahrick, 1992, 1994). Further, it was found that even when modality-specific properties (the pitch of a sound and the color of moving objects) were made more readily discriminable, amodal relations were nevertheless perceived developmentally prior to these modality-specific relations. Such findings suggest that the redundant, amodal properties of objects and events are typically more salient and perceived earlier than modality-specific or arbitrary multimodal relations.

This developmental sequence, whereby perceptual learning progresses from detection of amodal to arbitrary and modality-specific relations, promotes learning about consistencies and regularities across the senses during early development. For example, detection of amodal stimulus properties such as temporal synchrony and spatial collocation can foster appropriate, veridical generalizations on the part of the young organism and can minimize inappropriate generalizations about arbitrary stimulus relations that vary widely across contexts or are specific to only certain objects or events. In this scenario, detection of amodal relations are thought to guide and constrain perceptual learning about modality-specific relations such that general perceptual principles (e.g., voices go with faces, single objects make single impact sounds) are well established prior to learning more specific details of these events (e.g., Mary's face goes with a soft, high-pitched voice; the blue rattle makes a jingling sound when dropped). Bahrick's (1992, 1994) findings that 3-month-old infants were able to detect temporal synchrony and amodal information specifying object composition in single and multiple objects striking a surface, but not until 7 months of age could infants could detect the arbitrary, modality-specific relation between the pitch of the sound and the color and shape of the moving objects, provides support for the view that detection of amodal relations can guide and constrain early perceptual learning.

Although these results and those from other investigations of infants' capabilities for perceiving amodal relations (for reviews, see Lewkowicz, 2000; Walker-Andrews, 1997) indicate that young infants are remarkably skilled at perceiving coherent multimodal objects and events from the flow of sensory stimulation, the origins of this capacity and its implications for perceptual and cognitive development remain poorly understood. Recent evidence from comparative psychology and developmental psychobiology utilizing animal embryos and infants has, however, provided some insight into the emergence and maintenance of intersensory functioning (Lickliter, 2000a; Lickliter & Bahrick, 2000; Lewkowicz & Lickliter, 1994a). This body of work, along with parallel findings from the neural and electrophysiological literature, indicates a strong link between sensory systems and a functional distinction between unimodal and multimodal stimulation during early development (see Stein & Meredith, 1993; Stein, Meredith, & Wallace, 1994; Stein, Wallace, & Stanford, 2000). In particular, research with both animal and human infants indicates that different properties of stimuli are highlighted and attended to when concurrent multimodal stimuli rather than unimodal stimuli are made available to young organisms.

Differential effects of unimodal and multimodal stimulation

Functioning tactile, vestibular, chemical, and auditory modalities are likely interacting during the late stages of prenatal development in precocial animal species, and the onset of visual experience at birth or hatching significantly increases opportunities for multimodal stimulation during the postnatal period (Gottlieb, 1971a; Lickliter 2000b). Relatively little is known about the nature of perinatal intersensory interactions and the possible contributions of different types of sensory experience to newborns' perceptual preferences and abilities (but see Lickliter, 1995; Tees & Symons, 1987; Turkewitz, 1994; Turkewitz, Gilbert, & Birch, 1974). Converging research from both neural and behavioral levels of analyses has, however, consistently indicated differential effects of unimodal versus multimodal sensory stimulation on young and mature organisms' perceptual responsiveness.

For example, a number of neurophysiological studies of the adult cat have indicated that the temporal and spatial pairing of stimuli from different sensory modalities can elicit a neural response that is greater than the sum of the neural responses to the unimodal components of stimulation considered separately (Stein & Meredith, 1993; Stein et al., 1994). Spatially coordinated multimodal stimulus combinations produce significant increases over unimodal responses in an array of extracellular measures of neural activity in adult animals, including response reliability, number of impulses evoked, peak impulse frequency, and duration of the discharge train. This superadditive effect of bimodal stimulation, in which the magnitude of neural effects resulting from bimodal stimulation exceeds the level predicted by adding together responsiveness to each single-modality stimulus alone, has also been reported in behavioral investigations. Stein, Meredith, Honeycutt, and McDade (1989) have also demonstrated that the effectiveness of a visual stimulus in eliciting attentive and orientation behaviors in cats is dramatically affected by the presence of a temporally congruent and spatially collocated stimulus in the auditory modality. Responses made by cats to spatially coincident audiovisual stimuli were more accurate than those made to either form of unimodal stimulation.

In a similar vein, communicative displays like the threat expressions of macaque monkeys and the recruitment signals of ants have been shown to have different consequences on the behavior of conspecifics, depending on their unimodal or multimodal presentation (see Partan & Marler, 1999). Taken together, these various findings provide converging support for the notion that unimodal and multimodal stimulation elicit differential responsiveness across different species, different developmental stages, and different tasks.

Research with precocial avian embryos and hatchlings has consistently demonstrated the importance of multimodal sensory stimulation in the emergence and maintenance of normal or species-typical patterns of perceptual organization. Beginning with the pioneering work of Gottlieb (1971b) on the development of species identification in precocial birds, a large body of work has accumulated indicating that multimodal experience in the period following hatching is a key component in the development and maintenance of the early perceptual and social preferences underlying species identification (e.g., Gottlieb, 1993; Johnston & Gottlieb, 1981; Lickliter, Dyer, & McBride, 1993). More recently, studies of precocial bird embryos and hatchlings have demonstrated that subjects denied normal levels of multimodal stimulation during the early postnatal period show impaired perceptual responsiveness to both unimodal and multimodal maternal information

(Columbus & Lickliter, 1998; Columbus, Sleigh, Lickliter, & Lewkowicz, 1998; Gottlieb, 1993; Sleigh, Columbus, & Lickliter, 1998). As a case in point, quail chicks receiving enhanced exposure to unimodal (either auditory or visual) maternal stimulation following hatching showed altered patterns of responsiveness to both unimodal and bimodal maternal information. Regardless of whether their unimodal maternal experience was auditory or visual, chicks demonstrated enhanced unimodal and delayed bimodal responsiveness when compared with control chicks receiving typical levels of multimodal stimulation (Sleigh et al., 1998).

Related work with both quail chicks and ducklings on the effects of reducing available multimodal stimulation following hatching has also demonstrated altered patterns of auditory learning (Gottlieb, 1993; Lickliter & Hellewell, 1992) and attenuated intersensory functioning (Columbus & Lickliter, 1998), further highlighting the importance of multimodal stimulation to the normal emergence of intra- and intersensory functioning in early development. Similar findings from several other species of birds and mammals examined at the neural level of analysis also indicate that the uncoupling of multimodal experience can lead to significant changes in the young organism's normal developmental trajectory (King, Hutchings, Moore, & Blakemore, 1988; Knudsen & Brainard, 1991, 1995; Withington-Wray et al., 1990).

Recent evidence also indicates that experiential modifications of prenatal unimodal or bimodal sensory experience can alter neuroanatomical structure, physiological regulation, and perceptual learning during the period prior to birth or hatching. For example, Carlsen (1999) examined the effects of differing amounts of unusually early visual stimulation of quail embryos in the period prior to hatching on the dendritic morphology of neurons in the area of the telencephalon known as the visual Wulst, a structure similar to the mammalian visual cortex. The Wulst has a layered organization and response properties very similar to mammalian striate cortex (Pettigrew & Konishi, 1976). Quail embryos exposed to prenatal visual stimulation showed altered patterns of intersensory responsiveness to maternal auditory and visual cues and were also shown to have significant changes in the number of spines and degree of branching of dendrites in the Wulst when compared with control chicks not receiving prenatal visual stimulation. Embryos receiving relatively small amounts (10 min/h) of prenatal visual stimulation in the days prior to hatching showed enhanced audiovisual responsiveness to maternal cues and had significantly fewer dendritic spines than controls following hatching. In contrast, embryos receiving relatively large amounts (40 min/h) of prenatal visual experience showed delayed intersensory responsiveness following hatching and had a significantly greater number of spines and more branching than control chicks. These results suggest that providing embryos with unusually early visual experience can modify emerging patterns of neural pruning and resulting architecture. How modifications in prenatal auditory experience would affect neuronal structure in the visual Wulst remains to be explored, but existing behavioral evidence demonstrating effects of prenatal auditory stimulation on subsequent visual responsiveness (Lickliter & Stoumbos, 1991; Sleigh & Lickliter, 1997) suggests that similar patterns of neuronal change in visual areas (in addition to the auditory region of the telencephalon) are plausible following augmented prenatal auditory stimulation.

Differential effects of unimodal versus bimodal stimulation during prenatal development have also been demonstrated at the physiological level of analysis. Reynolds and Lickliter (2002) found that quail embryos' heart rate is significantly affected by the type of prenatal sensory stimulation (unimodal vs. bimodal) provided during the period prior to hatching. Embryos exposed to concurrent but asynchronous bimodal (auditory/visual) stimulation displayed significant increases in heart rate during stimulus exposure, whereas the heart rate of embryos exposed to concurrent intramodal (auditory/auditory) stimulation or unimodal (auditory or unimodal) visual stimulation remained near baseline during stimulus exposure. These results are consistent with behavioral evidence drawn from studies of prenatal perceptual learning in bird embryos. A number of studies have reported that when embryos are unimodally exposed to an individual maternal call in the days prior to hatching, they subsequently prefer this familiar maternal call over an unfamiliar maternal call in postnatal testing (Gottlieb, 1988; Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992). However, when embryos are exposed to an individual maternal call concurrently with noncongruent stimulation to another sensory system (i.e., visual or vestibular), they fail to demonstrate a preference for the familiar call during postnatal testing (Honeycutt & Lickliter, 2001; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). Concurrent (but asynchronous) bimodal stimulation appears to alter both physiological and behavioral arousal (Reynolds & Lickliter, 2002) and can interfere with prenatal perceptual learning. On the other hand, recent evidence indicates that *redundant*, synchronous bimodal stimulation can facilitate perceptual learning, suggesting that different types of multimodal stimulation have different effects on emerging physiological and behavioral organization during early development.

In summary, several related themes can be drawn from recent comparative research on the development of intersensory responsiveness in birds and mammals: (1) There appears to be enhanced behavioral responsiveness to coordinated multisensory stimulation as compared with unimodal stimulation. (2) Multimodal experience appears to lead to different developmental outcomes than unimodal experience. (3) The uncoupling of multimodal experience can lead to abnormal perceptual organization during early development. (4) Modifications in normal types and amounts of prenatal sensory stimulation can lead to altered neural development and increased physiological and behavioral arousal.

The role of intersensory redundancy in early perceptual development

We have proposed an *intersensory redundancy* hypothesis to describe how attention and perceptual processing of different stimulus properties are influenced by unimodal versus multimodal stimulation (Bahrick & Lickliter, 2000, 2002). In light of converging evidence drawn from physiological and behavioral studies highlighting the differential effects of unimodal and multimodal stimulation during early development, the intersensory redundancy hypothesis synthesizes knowledge gained from research on animal and human intersensory development and identifies some of the processes thought to underlie the emergence of intersensory perception. *Intersensory redundancy* refers to the spatially coordinated and concurrent presentation of the same information (e.g., rate, rhythm, intensity) across two or more sensory modalities. For the auditory and visual modalities, this also entails the temporally synchronous alignment of the bimodal information. In our view, intersensory redundancy is a particularly important and salient form of stimulation in early development. The intersensory redundancy hypothesis proposes that information presented redundantly across two or more sensory modalities selectively recruits young organisms' attention during early development, causing amodal (redundant) stimulus properties to become foreground and other stimulus properties to become background during exploration of an object or event. According to the intersensory redundancy hypothesis, selective attention on the part of the infant gives initial advantage to the perceptual processing, learning, and memory of stimulus properties that are redundantly specified over the processing, learning, or memory of nonredundant properties of sensory stimulation. In other words, information that is simultaneously presented across two or more modalities is thought to be highly salient to infants and can direct attentional selectivity at the expense of information that is not redundant (Bahrick & Lickliter, 2000; Bahrick & Pickens, 1994; Bahrick, Walker, & Neisser, 1981; Bahrick et al., 2002; Slater et al., 1999).

More than 20 years ago, Bahrick et al. (1981) demonstrated the salience of intersensory redundancy for directing selective attention during early development. Infants viewed films of two superimposed events (e.g., a toy Slinky moving and a hand-clapping game). For the adult viewer, when the two superimposed events were viewed silently, they appeared to be an amalgamation of ghostly images passing through one another. However, as soon as the sound track to one was turned on, the sound-specified event suddenly stood out from the other event, creating a strong impression of figure and ground. Infants also appeared to be affected this way by the addition of the sound track. By playing the synchronous soundtrack to one of the superimposed events, the investigators were able to direct infants' attentional selectivity to that event, causing them to ignore the silent one. However, once the sound track was turned off and the films were separated (appearing side by side) intersensory redundancy was no longer available, and infants preferred to view the novel, previously silent film. Control studies confirmed this interpretation, in that when infants were presented with only one centrally projected event with sound, followed by silent trials of the two events side by side (familiar vs. novel films), they preferred the previously absent (novel) film. Taken together, these results demonstrate that the intersensory redundancy provided by the natural, synchronous sound track to a visible event can guide infants' visual selectivity, even when another visual event occupies the same spatial location. This behavioral evidence is consistent with findings of heightened neural responsiveness to coordinated multimodal stimulation in adult animals (see Stein & Meredith, 1993).

More recently, intersensory redundancy has also been found to facilitate perceptual learning of amodal properties such as rhythm and tempo in early infancy (Bahrick & Lickliter, 2000; Bahrick et al., 2002). For example, in the Bahrick and Lickliter (2000) study, 5-month-old infants were habituated to films of a hammer tapping out one of two distinct irregular rhythms. The rhythms were presented visually (seeing the hammer) or acoustically (hearing the hammer tapping) or visually and acoustically (bimodal condition). Infants then received test trials depicting either a change in rhythm or no change in rhythm. Results indicated that infants were able to discriminate between the two irregular rhythms when they were presented bimodally (across both the auditory and visual modalities) and therefore redundantly, but not when the rhythms were

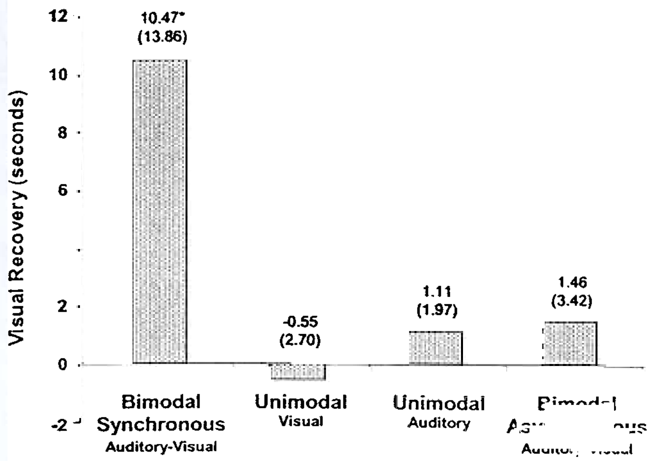


FIGURE 40.1 Five-month-old infants' mean visual recovery to a change in rhythm following bimodal (synchronous vs. asynchronous) or unimodal habituation. Visual recovery is the difference score between visual fixation during the test trials and visual fixation during posthabituation trials. Standard deviations appear in parentheses. $*p < 0.05$.

presented unimodally (only in the auditory or visual modality) or bimodally but out of temporal synchrony (Fig. 40.1). Concurrent and redundant stimulation of the auditory and visual modalities appeared to selectively guide infants' attention to the bimodally specified property of rhythm, fostering successful discrimination, whereas unimodal stimulation did not.

Parallel findings have been obtained demonstrating the importance of intersensory redundancy for detecting the amodal property of tempo in 3-month-old infants (Bahrick et al., 2002). In this study, infants were found to discriminate a change in tempo following bimodal but not unimodal familiarization (Fig. 40.2). Because most objects and events are multimodal,

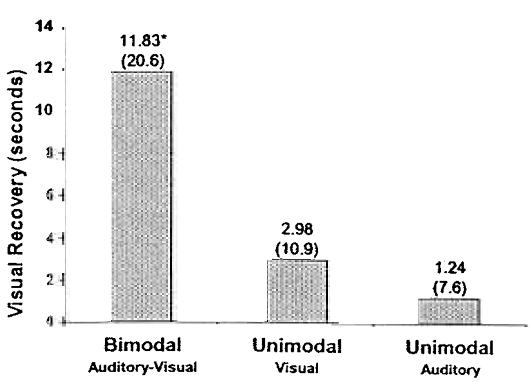


FIGURE 40.2 Three-month-old infants' mean visual recovery to a change in tempo following bimodal or unimodal habituation. Visual recovery is the difference score between visual fixation during test trials and visual fixation during posthabituation trials. Standard deviations appear in parentheses. $*p < 0.05$.

perceptual processing, learning, and memory for stimulus properties specified in more than one sensory modality will be promoted and develop earlier than processing of other properties. Conversely, when multimodal stimulation is not available, attention is likely to be more broadly focused on a variety of stimulus properties, including those that are specific to individual sensory modalities. It is important to note that the salience of redundant stimulation for directing attentional selectivity is expected to be most pronounced during early perceptual learning in a given domain, as infants are clearly capable of detecting amodal stimulus properties in unimodal stimulation within the first months of life (Lewkowicz & Lickliter, 1994a; Rose & Ruff, 1987).

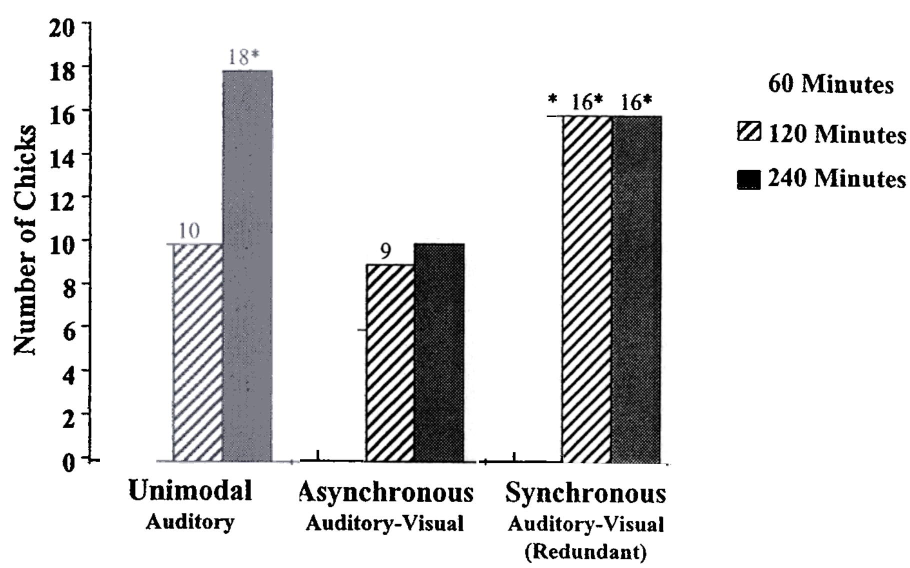
In contrast to the facilitative effects of intersensory redundancy for perceptual learning about amodal stimulus properties, intersensory redundancy can also hinder or constrain learning about modality-specific stimulus properties. Because redundancy selectively focuses attention on the redundant aspects of stimulation and away from other aspects, detection and learning of properties such as pitch, color, or orientation would be attenuated in the presence of redundancy and enhanced in its absence. This attenuation effect was found for the perception of orientation of a moving object in 5-month-old infants (Bahrick, Lickliter, & Flom, 2000). In this study, infants exposed to a hammer tapping out a distinctive rhythm were able to perceive a change in the modality-specific property of orientation (movement upward vs. downward) when the event was experienced unimodally (visual presentation), but not when experienced bimodally (auditory-visual presentation). The addition of redundancy under the bimodal condition appeared to selectively recruit attention to redundantly specified stimulus properties (such as rhythm and tempo) at the expense of the unimodally specified property of orientation.

A focus on the nature of intersensory relationships and the role of intersensory redundancy in early perceptual and cognitive development has also been extended into the prenatal period with studies of animal embryos (see Lickliter, 1995). Given that the prenatal environment of both avian and mammalian species provides a rich array of tactile, vestibular, chemical, and auditory stimulation (Gottlieb, 1971a), it seems plausible that the developing embryo or fetus could be responsive to redundant multisensory information. In this light, we recently explored aspects of the intersensory redundancy hypothesis in precocial quail embryos and found that redundancy across modalities can also facilitate perceptual learning during the prenatal period (Lickliter et al., 2002). Quail embryos were exposed to an individual maternal call for 10 min/h across 6, 12, or 24 hours prior to hatching, under conditions of (1) unimodal auditory stimulation, (2) concurrent but asynchronous auditory and visual stimulation, or (3) redundant and synchronous auditory and visual stimulation. Subjects were then tested one day after hatching to determine if they preferred the familiar maternal call over an unfamiliar variant of the maternal call. Results indicated that for all exposure durations chicks that received the redundant audiovisual familiarization as embryos significantly preferred the familiar call, whereas those that received the nonredundant audiovisual familiarization failed to show a preference for the familiar call. Chicks that received the unimodal auditory familiarization showed eventual perceptual learning, preferring the familiar call following the longest period (24 hours) of prenatal exposure (Fig. 40.3). Thus, embryos receiving redundant information to the auditory and visual modalities about synchrony, tempo, rhythm, and duration required only one-quarter the exposure durations of embryos receiving unimodal information.

These results are the first to show enhanced prenatal perceptual learning when amodal information (tempo, rhythm, duration) is presented redundantly across two sensory modalities. Synchronous bimodal stimulation makes overlapping, temporally coordinated information available to the different senses and can facilitate perceptual learning and memory for redundant, amodal stimulus properties common across sensory modalities, even during the prenatal period (see also Honeycutt & Lickliter, 2002). In contrast, concurrent bimodal stimulation that is not redundant provides the young organism with competing sources of information, potentially interfering with the embryo's ability to successfully attend to either source of information (Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992).

Additional support for this view has recently been provided by Reynolds and Lickliter (2001). Quail embryos exposed to concurrent but asynchronous auditory-visual stimulation had significantly higher baseline heart rates following stimulus exposure and significantly greater changes from baseline during stimulus exposure when compared with embryos that received synchronous (redundant) auditory-visual stimulation or unimodal auditory stimulation. The increased physiological arousal elicited by asynchronous bimodal stimulation may exceed some optimal range of arousal and interfere with perceptual learning, given that precocial avian embryos appear unable to demonstrate prenatal auditory learning of a maternal call when presentation is paired with concurrent but asynchronous patterned visual stimulation (Gottlieb et al., 1989; Lickliter & Hellewell, 1992). In contrast, redundant bimodal stimulation appears to regulate arousal levels in a range that supports and even facilitates prenatal perceptual learning (Lickliter et al., 2002).

Additional studies assessing physiological and behavioral arousal during and following specific types of sensory stimulation should provide further insight into the processes and mechanisms contributing to the origins and development of intersensory perception, learning, and memory. What seems clear at present



all ʼer an unfamiliar matern: all following
s, or redundant, synchr ʼus prenatal

from converging evidence across different levels of analysis and from a variety of animal species is that temporally aligned multimodal stimulation (intersensory redundancy) is particularly salient during early development and is important for initially guiding and constraining selective attention and perceptual learning.

Conclusions

Converging evidence from both the neural (Calvert, 2001; Giard & Peronnet, 1999) and the behavioral sciences (Lewkowicz, 2000; Lickliter & Bahrick, 2000; Massaro, 1998) is providing a new framework for the study of multisensory perception. This framework acknowledges the multimodal nature of both the structure of the organism and the structure of its environment and recognizes that the separate senses interact and influence one another more than has been appreciated until very recently. In particular, we now know that intersensory interactions are present during both the prenatal period and the early postnatal period, raising the interesting question of how such interactions serve to influence subsequent perceptual organization. Although more research with both animal and human subjects is needed to further examine and clarify the role of intersensory responsiveness on perception, learning, and memory during early development, the evidence reviewed in this chapter suggests that overlapping or redundant sensory information can initially guide infants' selective attention and enhance perceptual discrimination and learning of amodal properties of stimulation. The consistent pattern of findings across different measures of responsiveness, different species, and different stages of development suggests that (1) redundant bimodal stimulation is attention getting, (2) redundant bimodal stimulation can lead to enhanced neural and behavioral responsiveness and facilitate adaptive levels of arousal, and (3) redundant bimodal stimulation promotes exploration and learning of global, amodal properties of objects and events. Intersensory redundancy appears to be an important cornerstone of early perceptual development (at least in precocial animal infants; see Wallace & Stein, 1997, for contrasting results with an altricial animal infant) and may be meaningfully investigated as a general principle, potentially applicable across a variety of avian and mammalian species. We propose that differentiation of amodal and modality-specific stimulus properties emerges in a coordinated manner, with the detection of more global, amodal properties leading and constraining perceptual responsiveness to more specific properties of objects and events. Thus, the detection of amodal relations promoted by redundancy across sensory modalites facilitates perceptual organization in young organisms in a manner that can provide an efficient and effective means of acquiring the skills and knowledge of adult perceivers.

REFERENCES

Bahrick, L. E. (1988). Intermodal learning in infancy: Learning on the basis of two kinds of invariant relations in audible and visible events. *Child Development, 59,* 197–209.

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. (1994). The development of infants' sensitivity to arbitrary intermodal relations. *Ecological Psychology, 6,* 111–123.

Bahrick, L. E. (2001). Increasing specificity in perceptual development: Infants' detection of nested levels of multimodal stimulation. *Journal of Experimental Child Psychology, 79,* 253–270.

Bahrick, L. E., Flom, R., & Lickliter, R. (2002). Intersensory redundancy facilitates discrimination of tempo in 3-month-old infants. *Developmental Psychobiology, 41,* 352–363.

Bahrick, L. E., & Lickliter, R. (2000). Intersensory redundancy guides attentional selectivity and perceptual learning in infancy. *Developmental Psychology, 36,* 190–201.

Bahrick, L. E., & Lickliter, R. (2002). Intersensory redundancy guides early perceptual and cognitive development. *Advances in Child Development and Behavior, 30,* 153–187.

Bahrick, L. E., Lickliter, R., & Flom, R. (2000). *Intersensory redundancy: Infants' detection of unimodal properties of events.* Paper presented at a meeting of the International Society for Developmental Psychobiology, New Orleans, LA.

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.

Bahrick, L. E., Walker, A. S., & Neisser, U. (1981). Selective looking by infants. *Cognitive Psychology, 13,* 377–390.

Birch, H., & Lefford, A. (1963). *Intersensory development in children. Monographs of the Society for Research in Child Development, 28.*

Botuck, S., & Turkewitz, G. (1990). Intersensory functioning: Auditory-visual pattern equivalence in younger and older children. *Developmental Psychology, 26,* 115–120.

Bower, T. G. R. (1974). *Development in infancy.* San Francisco: Freeman.

Bushnell, E. W. (1994). A dual-processing approach to cross-modal matching: Implications for development. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 19–38). Hillsdale, NJ: Erlbaum.

Calvert, G. A. (2001). Crossmodal processing in the human brain: Insights from functional neuroimaging studies. *Cerebral Cortex, 11,* 1110–1123.

Carlsen, R. M. (1999). *Neural plasticity and the development of intersensory functioning in bobwhite quail.* Unpublished doctoral dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Carlsen, R. M., & Lickliter, R. (1999). Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychobiology, 35,* 215–225.

Columbus, R. F., & Lickliter, R. (1998). Modified sensory features of social stimulation alters the perceptual responsiveness of bobwhite quail chicks. *Journal of Comparative Psychology, 112,* 161–169.

Columbus, R. F., Sleigh, M. J., Lickliter, R., & Lewkowicz, D. J. (1998). Unimodal maternal experience interferes with responsiveness to the spatial contiguity of multimodal maternal cues in bobwhite quail chicks. *Infant Behavior and Development, 21,* 397–409.

Friedes, D. (1974). Human information processing and sensory modality: Cross-modal functions, information complexity, and deficit. *Psychological Bulletin, 81,* 242–310.

Frost, D. O. (1990). Sensory processing by novel, experimentally induced cross-modal circuits. *Annals of the New York Academy of Sciences, 608,* 92–112.

Giard, M. H., & Peronnet, F. (1999). Auditory-visual integration during multimodal object recognition in humans: A behavioral and electrophysiological study. *Journal of Cognitive Neuroscience, 11,* 473–490.

Gibson, E. J. (1969). *Principles of perceptual learning and development.* Englewood Cliffs, NJ: Prentice Hall.

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

Gogate, L. J., & Bahrick, L. E. (1998). Intersensory redundancy facilitates learning of arbitrary relations between vowel sounds and objects in seven-month-old infants. *Journal of Experimental Child Psychology, 69,* 133–149.

Gottlieb, G. (1971a). Ontogenesis of sensory function in birds and mammals. In E. Tobach, L. Aronson, & E. Shaw (Eds.), *The biopsychology of development* (pp. 66–128). New York: Academic Press.

Gottlieb, G. (1971b). *Development of species-identification in birds.* Chicago: University of Chicago Press.

Gottlieb, G. (1988). Development of species identification in ducklings: XV. Individual auditory recognition. *Developmental Psychobiology, 21,* 509–522.

Gottlieb, G. (1993). Social induction of malleability in ducklings: Sensory basis and psychological mechanism. *Animal Behavior, 45,* 707–719.

Gottlieb, G., Tomlinson, W. T., & Radell, P. L. (1989). Developmental intersensory interference: Premature visual experience suppresses auditory learning in ducklings. *Infant Behavior and Development, 12,* 1–12.

Gottlieb, G., Wahlsten, D., & Lickliter, R. (1998). The significance of biology for human development: A developmental psychobiological systems view. In R. Lerner (Ed.), *Handbook of child psychology, Vol. 1: Theoretical models of human development* (pp. 233–273). New York: Wiley.

Hernandez-Reif, M., & Bahrick, L. E. (2001). The development of visual-tactile perception of objects: Amodal relations provide the basis for learning arbitrary relations. *Infancy, 2,* 51–72.

Honeycutt, H., & Lickliter, R. (2001). Order-dependent timing of unimodal and multimodal stimulation affects prenatal auditory learning in bobwhite quail embryos. *Developmental Psychobiology, 38,* 1–10.

Honeycutt, H., & Lickliter, R. (2002). Prenatal experience and postnatal perceptual preferences: Evidence for attentional bias in bobwhite quail embryos. *Journal of Comparative Psychology, 116,* 270–276.

Johnston & Gottlieb (1981). Development of visual species identification in ducklings: What is the role of imprinting? *Animal Behaviour, 29,* 1082–1099.

Kellman, P. J., & Arterberry, M. E. (1998). *The cradle of knowledge: Development of perception in infancy.* Cambridge, MA: MIT Press.

King, A. J., & Carlile, S. (1993). Changes induced in the representation of auditory space in the superior colliculus by rearing ferrets with binocular lid suture. *Experimental Brain Research, 94,* 444–455.

King, A. J., Hutchings, M. E., Moore, D. R., & Blakemore, C. (1988). Developmental plasticity in visual and auditory representation in the mammalian superior colliculus. *Nature, 332,* 73–76.

Knudsen, E. I., & Brainard, M. S. (1991). Visual instruction of the neural map of auditory space in the developing optic tectum. *Science, 253,* 85–87.

Knudsen, E. I., & Brainard, M. S. (1995). Creating a unified representation of visual and auditory space in the brain. *Annual Review of Neuroscience, 18,* 19–43.

Lewkowicz, D. J. (1994). Development of intersensory perception in human infants. In D. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 165–204). Hillsdale, NJ: Erlbaum.

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

Lewkowicz, D. J. (2002). Heterogeneity and heterochrony in the development of Intersensory perception. *Cognitive Brain Research, 14,* 41–63.

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

Lewkowicz, D. J., & Lickliter, R. (1994b). Insights into mechanisms of intersensory development: The value of a comparative, convergent-operations approach. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 403–413). Hillsdale, NJ: Erlbaum.

Lewkowicz, D. J., & Turkewitz, G. (1981). Intersensory interaction in newborns: Modification of visual preferences following exposure to sound. *Child Development, 52,* 827–832.

Lickliter, R. (1990). Premature visual stimulation accelerates intersensory functioning in bobwhite quail neonates. *Developmental Psychobiology, 23,* 15–27.

Lickliter, R. (1995). Embryonic sensory experience and intersensory development in precocial birds. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 281–294). Hillsdale, NJ: Erlbaum.

Lickliter, R. (2000a). An ecological approach to behavioral development: Insights from comparative psychology. *Ecological Psychology, 12,* 319–334.

Lickliter, R. (2000b). The role of sensory stimulation in perinatal development: Insights from comparative research for the care of the high-risk infant. *Journal of Developmental and Behavioral Pediatrics, 21,* 437–447.

Lickliter, R., & Bahrick, L. E. (2000). The development of infant intersensory perception: Advantages of a comparative convergent-operations approach. *Psychological Bulletin, 126,* 260–280.

Lickliter, R., & Bahrick, L. E. (2001). The salience of multimodal sensory stimulation in early development: Implications for the issue of ecological validity. *Infancy, 2,* 447–463.

Lickliter, R., Bahrick, L. E., & Honeycutt, H. (2002). Intersensory redundancy facilitates prenatal perceptual learning in bobwhite quail embryos. *Developmental Psychology, 38,* 15–23.

Lickliter, R., & Banker, H. (1994). Prenatal components of intersensory development in precocial birds. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 59–80). Hillsdale, NJ: Erlbaum.

Lickliter, R., Dyer, A., & McBride, T. (1993). Perceptual consequences of early social experience in precocial birds. *Behavioural Processes, 30,* 185–200.

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: Attenuated prenatal sensory stimulation affects postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychology, 31,* 609–618.

Lickliter, R., & Stoumbos, J. (1991). Enhanced prenatal auditory experience facilitates postnatal visual responsiveness in bobwhite quail chicks. *Journal of Comparative Psychology, 105,* 89–94.

Lyons-Ruth, K. (1977). Bimodal perception in infancy: Response to auditory-visual incongruity. *Child Development, 48,* 820–827.

Marks, L. E. (1978). *The unity of the senses: Interrelations among the modalities.* New York: Academic Press.

Massaro, D. W. (1998). *Perceiving talking faces: From speech perception to a behavioral principle.* Cambridge, MA: MIT Press.

Maurer, D. (1993). Neonatal synesthesia: Implications for the processing of speech and faces. In B. de Boysson-Bardies, S. de Schonen, P. Jusczyk, P. McNeilage, & J. Morton (Eds.), *Speech and face processing in the first year of life* (pp. 109–124). Boston: Kluwer Academic.

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. D., & Chance, G. (1998). Cross-modal learning in newborn infants: Inferences about properties of auditory-visual events. *Infant Behavior and Development, 21,* 543–554.

Partan, S., & Marler, P. (1999). Communication goes multimodal. *Science, 283,* 1272–1273.

Pettigrew, J. D., & Konishi, M. (1976). Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl. *Science, 193,* 675–678.

Piaget, J. (1952). *The origins of intelligence.* New York: Norton.

Radell, P. L., & Gottlieb, G. (1992). Developmental intersensory interference: Augmented prenatal sensory experience interferes with auditory learning in duck embryos. *Developmental Psychology, 28,* 795–803.

Reynolds, G. D., & Lickliter, R. (2001). *Effects of intersensory redundancy on physiological arousal in bobwhite quail embryos.* Paper presented at the annual meeting of the International Society for Developmental Psychobiology, San Diego, CA.

Reynolds, G. D., & Lickliter, R. (2002). Effects of prenatal sensory stimulation on heart rate and behavioral measures of arousal in bobwhite quail embryos. *Developmental Psychobiology, 41,* 112–122.

Rochat, P. (1995). *The self in infancy: Theory and research.* Amsterdam: Elsevier.

Rose, S. A., & Ruff, H. A. (1987). Cross-modal abilities in human infants. In J. D. Osofsky (Ed.), *Handbook of infant development* (pp. 318–362). New York: Wiley.

Slater, A., Quinn, P. C., Brown, E., & Hayes, R. (1999). Intermodal perception at birth: Intersensory redundancy guides newborns' learning of arbitrary auditory-visual pairings. *Developmental Science, 2,* 333–338.

Sleigh, M. J., Columbus, R. F., & Lickliter, R. (1998). Intersensory experience and early perceptual development: Postnatal experience with multimodal maternal cues affects intersensory responsiveness in bobwhite quail chicks. *Developmental Psychology, 34,* 215–223.

Sleigh, M. J., & Lickliter, R. (1997). Augmented prenatal auditory stimulation alters postnatal perception, arousal, and survival in bobwhite quail chicks. *Developmental Psychobiology, 30,* 201–212.

Smith, L. B. (1994). Forward. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. ix–xix). Hillsdale, NJ: Erlbaum.

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.

Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses.* Cambridge, MA: MIT Press.

Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multisensory integration: Orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience, 1,* 12–24.

Stein, B. E., Meredith, M. A., & Wallace, M. (1994). Development and neural basis of multisensory integration. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 81–105). Hillsdale, NJ: Erlbaum.

Stein, B. E., Wallace, M., & Stanford, T. R. (2000). Merging sensory signals in the brain: The development of multisensory integration in the superior colliculus. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 55–71). Cambridge, MA: MIT Press.

Tees, R. C., & Symons, L. A. (1987). Intersensory coordination and the effect of early sensory deprivation. *Developmental Psychobiology, 23,* 497–507.

Thelen, E., & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action.* Cambridge, MA: MIT Press.

Turkewitz, G. (1994). Sources of order for intersensory functioning. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 3–17). Hillsdale, NJ: Erlbaum.

Turkewitz, G., Gilbert, M., & Birch, H. G. (1974). Early restriction of tactile stimulation and visual functioning in the kitten. *Developmental Psychobiology, 7,* 243–248.

Turkewitz, G., & Mellon, R. C. (1989). Dynamic organization of intersensory function. *Canadian Journal of Psychology, 43,* 286–301.

von Helmholtz, H. (1968). The origin of the correct interpretation of our sensory impressions. In R. M. Warren & R. P. Warren (Eds.), *Helmholtz on perception: Its physiology and development* (pp. 247–266). New York: Wiley.

Walker-Andrews, A. S. (1986). Intermodal perception of expressive behaviors: Relation of eye and voice? *Developmental Psychology, 22,* 373–377.

Walker-Andrews, A. S. (1997). Infants' perception of expressive behavior: Differentiation of multimodal information. *Psychological Bulletin, 121,* 437–456.

Wallace, M. T., & Stein, B. E. (1997). Development of multisensory neurons and multisensory integration in cat superior colliculus. *Journal of Neuroscience, 17,* 2429–2444.

Werner, H. (1957). The concept of development from a comparative and organismic point of view. In D. B. Harris (Ed.), *The concept of development* (pp. 125–148). Minneapolis: University of Minnesota Press.

Withington-Wray, D. J., Binns, K. E., & Keating, M. J. (1990). The maturation of the superior colliculus map of auditory space in the guinea pig is disrupted by developmental visual deprivation. *European Journal of Neuroscience, 2,* 682–692.