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Using an Animal Model to Explore the Prenatal Origins of Social Development

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Abstract

Prenatal experience is both a formative and regulatory force in the process of development. As a result, birth is not an adequate starting point for explanations of behavioral development. However, little is currently known regarding the role of prenatal experience in the emergence and development of neonatal social orienting, social motivation, or social learning. Our lack of knowledge in this area is due in part to the very restricted experimental manipulations possible with human fetuses. A comparative approach utilizing animal models provides an essential step in addressing this gap in our knowledge of the development of social responsiveness and providing testable predictions for studies with human fetuses and infants. In this chapter we review animal-based research exploring how aspects of prenatal experience can facilitate the development of postnatal social motivation, social recognition, and social learning. We conclude that infant social responsiveness has its roots in prenatal development and that intersensory redundancy present in the prenatal environment promotes the salience of social stimuli during early postnatal development.

Keywords

Prenatal learning • Intersensory redundancy • Origins of social development • Behavioral embryology • Selective attention

Evidence obtained over the last 40 years with human infants indicates that social stimuli such as faces and voices are typically preferred over other stimuli even in the days immediately following birth (e.g., Goren, Sarty, & Wu, 1975; Legerstee, Pomerleau, Malcuit, & Feider, 1987; Maurer & Young, 1983; Valenza, Simion, Cassia, & Umilta, 1996). As a result of the early salience of faces and voices to infants, some developmental psychologists have proposed that neonates' biases or preferences towards social stimuli are

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innate, in that they are present at birth and do not require prior experience (e.g., Balas, 2010; Gergely & Watson, 1999; Meltzoff & Decety, 2003; Muir & Nadel, 1998). However, a growing body of comparative evidence indicates that prenatal experience plays a key role in establishing early postnatal perceptual preferences (Gottlieb, 1997; Harshaw & Lickliter, 2011; Hopkins & Johnson, 2005; Lickliter, 2005; Schaal, Marlier, & Soussignan, 1998). Whether and to what extent prenatal sensory experience influences early social development however remains relatively unexplored (but see DeCasper & Fifer, 1980; Mastropieri & Turkewitz, 1999; Moon, Panneton-Cooper, & Fifer, 1993 for suggestive examples from human neonates).

The use of animal models offers an essential step in addressing this critical gap in our knowledge base. Studies that manipulate human fetuses and infants are necessarily severely constrained and animal based research serves to minimize the amount of exploratory research undertaken with human participants and hone in on issues and directions worthy of further research investment (Gottlieb & Lickliter, 2004; Lickliter & Bahrick, 2000, 2007). In particular, the use of animal models allows the collection of data under more strictly controlled conditions than would be possible with human fetuses and infants and is thus key for eventually connecting theories of early perceptual, cognitive, and social development with biological and neurophysiological mechanisms.

Of course, we cannot answer questions about human development by primarily studying animals, but comparative work can provide new questions, methods, and potentially derive developmental principles that can then be tested with humans. As pointed out by Arnold and Spear (1997), the determinants of early perception and cognition are too basic to consider them solely with tests of humans. The utilization of interdisciplinary, comparative, and convergent research strategies is a critical step in discovering and defining the various conditions, experiences, and events (both internal and external) necessary and sufficient for normal perceptual, cognitive, and social development. This approach can also shed light on the conditions, experiences, and events that contribute to atypical development.

The Avian Model for Studying the Role of Experience in Prenatal Development

The embryonic bird develops entirely within the egg, externalized from the mother, thereby providing a well-controlled "laboratory" for introducing experimental manipulations into the prenatal environment. Precocial birds (e.g., chickens, ducks, quail) allow easy access to the embryo for prenatal observation and manipulation. Further, their developmental age and experiential history can be precisely controlled since they can be incubated in the laboratory, and they have several important similarities to human sensory organization. Like humans, in precocial birds all five sensory modalities are functional in the late stages of prenatal development. Further, like humans, avian embryos can learn the acoustic features of maternal vocalizations prior to hatching (Bailey & Ralph, 1975; Gottlieb, 1971; Heaton, Goodwin, & Miller, 1978). Unlike humans, however, precocial birds have the advantage that they can demonstrate perceptual and social preferences by means of their locomotor behavior in the days immediately following hatching. Leveraging these unique developmental conditions, research has consistently demonstrated that specific features of prenatal sensory experience, particularly the temporal synchrony of multisensory stimulation, can significantly influence embryos' and chicks' arousal, selective attention, perceptual learning, and memory (e.g., Jaime, Bahrick, & Lickliter, 2010; Lickliter, Bahrick, & Honeycutt, 2002, 2004; Lickliter, Bahrick, & Markham, 2006; Reynolds & Lickliter, 2002, 2003). In this chapter, we review this body of research and discuss its implications for the development of social responsiveness during early development. We also explore the usefulness of animal-based research for better integrating the prenatal period into theories of both typical and atypical development.

Exploring the Ecology of Prenatal Sensory Experience

One obvious advantage of the use of animal subjects to study perceptual, cognitive, and social development in the prenatal period is the ability to readily alter both the timing and amount of particular sensory experience available to the developing embryo or fetus. In contrast to mammals where the fetal environment is difficult to access and manipulate, the avian egg environment can be experimentally manipulated independently of the mother and thus provides an accessible means for testing hypotheses about prenatal factors underlying subsequent postnatal development. For example, the avian embryo can be exposed to premature visual stimulation or augmented auditory stimulation by the simple procedure of removing the upper portion of the egg-shell several days prior to hatching, thereby exposing the head of the embryo to external stimulation. As a result, it is possible to readily employ sensory augmentation, sensory deprivation, or sensory substitution techniques during the prenatal period. This approach of modifying typical patterns of prenatal experience has provided a large body of evidence regarding the experiential conditions necessary for the normal development of early sensory organization and perceptual development (e.g., Gottlieb, 1971, 1997; Honeycutt & Lickliter, 2003; Markham, Shimizu, & Lickliter, 2008; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1998). Taken together, this research indicates that the specific effects that prenatal sensory experience can have on early perceptual development and sensory integration depend on a number of interrelated factors, including (a) the *timing* of sensory experience, (b) the *amount* of sensory experience, and (c) the *type* of sensory experience encountered by the avian embryo or mammalian fetus (reviewed in Lickliter, 2000, 2005).

Timing of Prenatal Sensory Stimulation

All the sensory systems begin to develop prenatally in birds and mammals and, in precocial species (including humans), they are capable of functioning before birth. The prenatal environment is thus rich in tactile, vestibular, chemical, and auditory sensory stimulation. However, as first pointed out by Gottlieb (1971), at birth the sensory systems are not on equal footing. This is the case because the onset of function within the various sensory modalities does not occur at the same time in prenatal development. Rather, the sensory systems become functional in a specific and invariant sequence across early development: tactile > vestibular > chemical > auditory > visual (Alberts, 1984; Bradley & Mistretta, 1975; Gottlieb, 1971). Further, the tactile and chemical senses are comprised of many kinds of sense receptors, which have their own timing of development. As a result, because of the timing of their onset of function, the various sensory modalities of birds and mammals have markedly different developmental histories at the time of hatching or birth. For example, at birth the earlier developing tactile and vestibular systems have had much more experience than the later developing auditory system. These temporal dynamics likely have significant consequences for the course of early postnatal perceptual development and much remains to be learned about links between the order and timing of prenatal sensory experience and subsequent postnatal perceptual processing.

Turkewitz and Kenny (1985) proposed that the differential timing of sensory system onset provides a restrictive context in which earlier developing sensory systems can develop without competition or interference from later developing sensory systems. If this is the case, it would have important implications for the care and management of preterm human infants (Lickliter, 2000, 2011). The limited sensory capacities of the fetus (as a result of the staggered onset of sensory function across prenatal development) and the constrained and buffered developmental context of the uterus combine to effectively limit and regulate the amount, type, and timing of sensory stimulation available to the fetus during the prenatal period. However, these limited and regulated patterns of sensory stimulation are dramatically disrupted by preterm birth. Infants born weeks or even months before term are routinely exposed to altered amounts, types, and timing of sensory stimulation as compared to full-term infants. For example, the preterm infant housed in the neonatal intensive care unit (NICU) receives substantially decreased amounts of tactile and vestibular stimulation from maternal movement and substantially increased amounts of unfiltered auditory and patterned visual stimulation as compared to full-terms. The perceptual, cognitive, and social consequences of these modifications in movement, sound, and light are not well understood, but studies have suggested that the atypical sensory environment provided in the NICU can have enduring effects on the developing premature brain (e.g., Als et al., 2003; Aylward, 2005; Gressens, Rogido, Paindaveine, & Sola, 2002) and later behavior (Rand & Lahav, 2014).

One approach to examining the importance of asynchronous sensory development is to alter the time when particular sensory input would normally be present during the prenatal period. Using this approach, Lickliter (1990) found that the introduction of unusually early prenatal visual experience interfered with species-typical auditory responsiveness in bobwhite quail chicks following hatching. Chicks that experienced patterned light prior to hatching failed to exhibit the typical naïve preference for their species-specific maternal call, a reliable phenomenon observed in control chicks not receiving prenatal visual stimulation. An important implication of this finding is that prenatal experiential input to one sensory modality cannot be examined in isolation, as the effects of sensory experience not only influence the particular modality in question, but also other developing modalities as well. This finding of intersensory linkages is an important change of emphasis, as the different sensory systems have historically been studied individually. Vision, audition, touch, taste, and smell have been studied as if they operate without significant links to each other. We now know this is not the case, even during prenatal development (Bremner, Lewkowicz, & Spence, 2012; Calvert, Spence, & Stein, 2004).

Findings also indicate that modified prenatal stimulation to earlier-emerging sensory modalities can either facilitate or interfere with species-typical perceptual responsiveness in later-developing sensory modalities, depending on *when* the modified prenatal stimulation takes place. For example, differences in the timing of augmented prenatal stimulation to quail embryos led to different patterns of auditory and visual responsiveness following hatching. No effect on normal responsiveness to maternal visual cues was found when exposure to tactile and vestibular stimulation *coincided* with the emergence of visual function, but when exposure took place *after* the onset of visual functioning chicks displayed enhanced responsiveness to the same maternal visual cues when compared to controls not receiving modified sensory stimulation. When augmented tactile and vestibular stimulation *coincided* with the onset of auditory function, embryos subsequently failed to learn a species-typical maternal call prior to hatching. However, when given exposure to the same type and amount of augmented stimulation *following* the onset of auditory function, embryos did successfully learn the individual maternal call (Honeycutt & Lickliter, 2003). These findings provide evidence of the dynamic nature of sensory experience, as differences in the time of exposure results in differences in subsequent perceptual and cognitive development.

Research also indicates that modifications in the timing of patterns of prenatal sensory experience can have effects on early brain growth and development. For example, Markham et al. (2008) presented augmented amounts of auditory stimulation to bobwhite quail embryos during the early, middle, or late stages of prenatal development and then tested postnatal responsiveness to both maternal auditory and visual stimulation. Embryos receiving auditory stimulation during the *middle* or *late* stages of prenatal development showed atypical postnatal visual responsiveness to a bobwhite hen when compared to controls. These birds also showed a greater number of cells per unit volume of brain tissue in deep optic tectum, a midbrain region implicated in multisensory function. In contrast, embryos receiving modified auditory stimulation in the *early* stages of prenatal development did not show altered behavioral or neural development. These results indicate that modified sensory experience, such as those provided to human preterm infants by the NICU environment, can influence both perception as well as the trajectory of brain growth. These effects were temporally constrained; *when* the sensory modification occurred mattered. This principle of prenatal temporal constraints has likewise been found to be at play in the area of teratology, particularly in the well-known example of the time sensitive effects of fetal alcohol exposure.

Multimodal Stimulation During Prenatal Development

Sensory stimulation present in the prenatal environment is typically multisensory in nature. The prenatal environment provides the fetus a variety of concurrent tactile, vestibular, chemical, or auditory sensory information (DeCasper & Fifer, 1980; Hepper, Scott, & Shahidulla, 1993; Kisilevsky & Low, 1998; Smotherman & Robinson, 1986). Although little research has directly focused on this issue, the human fetus likely experiences a great deal of integrated multimodal stimulation across the auditory, vestibular, and tactile senses in utero. For example, when the mother walks, the sounds of her footsteps can be coordinated with tactile feedback as the fetus experiences changing pressure corresponding with the temporal patterning and shifting intensity of her movements, as well as accompanying and coordinated vestibular changes. In addition, the mother's speech sounds, laughter, heart beat, or sounds of breathing may create tactile stimulation that shares the temporal patterning of the sounds as a result of changes in the musculature involved in producing the sounds.

Fetuses also engage in spontaneous motor activity of limbs and body, providing temporally organized, cyclic self stimulation (Robertson & Bacher, 1995). When the fetus moves in the uterus, the movement generates temporally coordinated proprioceptive feedback as well as temporally coordinated tactile consequences of the motion, such as changes in pressure on the skin. The example of fetal thumb sucking well illustrates this coordinated pattern of multisensory self-generated stimulation. Additionally, the mother also responds with temporally coordinated movements to externally generated sounds. She may dance or exercise to music, startle to a loud noise, engage in conversation which has a distinctive turn-taking contingent structure, all of which produce movements that have tactile and/or vestibular correlates that share intensity and temporal patterning with the sounds. Thus, the fetus likely has ample opportunity from self stimulation and environmental stimulation to become familiar with and detect redundant stimulation across the various senses during the late stages of prenatal development. The role of this prenatal intersensory experience in typical perceptual, cognitive, or social development is likely significant but currently not well understood.

We do know that *infant* detection of *amodal* stimulus properties (information that is common across the senses) such as synchrony, intensity, rhythm, and tempo is promoted by multimodal redundancy across sensory systems and is involved in the emergence of normal patterns of perceptual organization (Bahrick & Pickens, 1994; Bremner et al., 2012). Importantly, the temporal and spatial aspects of stimulation are typically conveyed across multiple senses. For example, the rhythm or rate of a ball bouncing can be conveyed visually or acoustically and is completely redundant across the two senses. The sight and sound of hands clapping likewise share temporal synchrony, a common tempo of action, and a common rhythm. Even very young infants are adept perceivers of such amodal stimulation (e.g., Bahrick & Pickens, 1994; Lewkowicz, 2000; Lickliter & Bahrick, 2000). Infants as young as 2 months can detect the temporal aspects of stimulation such as synchrony, rhythm, tempo, and prosody that unite visual and acoustic stimulation from single events, as well as spatial co-location of objects and their sound sources, and changes in intensity across the senses (see Bremner et al., 2012; Lewkowicz & Lickliter, 1994 for reviews). Detection of amodal information in early development does away with the notion of young perceivers having to coordinate and put together separate and distinct sources of information. Our work with quail embryos has established that even when the amount of overall *prenatal* sensory stimulation is controlled, detection and learning of temporal stimulus properties such as tempo and rhythm by embryos are facilitated in redundant bimodal stimulation (which highlights amodal information) as compared to unimodal stimulation (Lickliter et al., 2002, 2004).

Intersensory Redundancy and Social Responsiveness

In particular, we have found that *intersensory redundancy*, the same information simultaneously available and temporally synchronized across two or more sensory systems, facilitates embryos' prenatal learning of an individual maternal call. Lickliter et al. (2002) exposed quail embryos (that can perceive light and sound through the egg shell) to an individual maternal call for 6, 12, or 24 h (10 min/h, for a total of 60, 120, or 240 min of exposure) during the late stages of incubation. The maternal call was presented under conditions of (a) unimodal auditory stimulation, (b) concurrent but asynchronous auditory and visual stimulation (patterned light), or (c) redundant and synchronous auditory and visual stimulation, achieved by presenting the call with a light that flashed in synchrony and had the same temporal pattern (rate, rhythm, duration) as the notes of a maternal call. Following hatching, chicks from all conditions received a simultaneous two-choice preference test for the familiarized vs. a novel maternal call. We found that embryos exposed to the redundantly presented maternal call (auditory and visual) showed dramatic facilitation, learning the call four times faster and remembering it four times longer into postnatal development (4 days) than those exposed to unimodal auditory stimulation (1 day). Further, embryos that received nonredundant asynchronous call and light exposure to control for the overall amount of stimulation showed no evidence of learning the familiarized call following hatching, demonstrating no preference for either maternal call during testing.

We have also found that providing embryos intersensory redundancy during late prenatal development educates their attention to specific stimulus properties (Lickliter et al., 2006). Quail chicks showed no preference for a familiar maternal call after a brief prenatal unimodal auditory familiarization. In contrast, by first exposing embryos to a redundant audiovisual presentation (call synchronized with flashing light) followed by the unimodal auditory presentation (i.e., bimodal → unimodal), chicks preferred the familiar auditory maternal call 2 days after hatching. Embryos who received the reverse sequence prenatally (unimodal → bimodal) showed no preference for the familiarized call. This education of attention was effective even after delays of 2 or 4 h between initial bimodal exposure and subsequent unimodal exposure, and continued to affect learning and memory days later (Lickliter et al., 2006).

Studies of human infants have found parallel findings. For example, 4 month-old infants detect a change in the tempo of a toy hammer tapping in unimodal visual stimulation, but only if they receive a brief pre-exposure to the tempo in bimodally redundant (synchronous audiovisual) stimulation, thereby educating their attention to the tempo information. Infants fail to detect the tempo change following nonredundant (unimodal visual or asynchronous audiovisual) pre-exposure (Castellanos, Vaillant-Molina, Lickliter, & Bahrick, 2006). By educating their selective attention to amodal properties, both animal and human infants can continue to detect these amodal properties in the same events, even when redundancy is no longer available. This finding suggests that the education of attention can foster flexible processing and may serve as a mechanism for promoting developmental change in attentional selectivity, from detection of amodal properties in multimodal stimulation to detection of the same amodal properties in all types of stimulation.

Promoting Neonatal Social Responsiveness

Given the demonstrations of quail embryos' sensitivity to intersensory redundancy, as well as the documented sensitivity of human infants to intersensory redundancy (see Bahrick & Lickliter, 2002, 2012 for reviews), we are currently exploring the relevance of this sensitivity to early social development. Social events are one of the first and most frequently encountered sources of intersensory redundancy both before and following birth or hatching, and we were interested in whether and to what extent the amount and type of intersensory redundancy available during prenatal development fosters social orienting, social learning, and social memory during early postnatal development. Social events provide high amounts of sensory redundancy relative to most nonsocial events. For example, parents provide social stimulation to their infant that contains a great deal of redundancy across tactile, auditory, and visual sensory systems. Audiovisual speech is rich with intersensory redundancy uniting the tempo, rhythm, and intensity shifts across faces and voices. We have hypothesized that this redundant multimodal stimulation can educate attention and foster the emergence of social orienting in early development by attracting and maintaining selective attention to faces, voices, and audiovisual speech. This could in turn promote early social development, as well as related perceptual and cognitive development (see Bahrick, 2010 for examples in typical and atypical developing infants).

Intersensory Redundancy Responsiveness

Building on our previous animal and human infant research on the role of intersensory redundancy in early perceptual and cognitive development (Bahrick & Lickliter, 2002, 2012; Lickliter & Bahrick, 2004), our working hypothesis is that exposure to multimodal *intersensory redundancy* (the same information simultaneously available and temporally synchronized across two or more senses) provided by the mother prenatally can generate biases or preferences for socially derived intersensory redundancy in the fetus or embryo. This "grabbing" of attention by redundant information would facilitate perceptual processing, learning, and memory for temporal and spatial features of social stimuli, thereby selectively educating attention to important and meaningful aspects of social stimulation during early development (Bahrick & Lickliter, 2012). This selective deployment of attention would in turn support the emergence of neonatal biases or preferences that would in turn further promote the development of early social responsiveness and motivation. These biases or preferences are likely critical for the development of individual recognition, social learning, as well as building the foundation for detecting meaning in speech and affect.

Our quail model provides a means to investigate this intriguing possibility. Work is currently underway exploring to what extent the amount and type of intersensory redundancy available during the late stages of prenatal development can facilitate quail neonates' social orientation, social learning, and individual recognition during early postnatal development. For example, we are testing whether the availability of redundant trimodal stimulation, which provides a greater amount and range of redundancy, can increase facilitation of attention, learning, and memory for social stimulation when compared to bimodal or unimodal exposure. Briefly, our paradigm involves providing embryos with various combinations of prenatal vestibular, auditory, and visual stimulation typically provided by the maternal hen as she leaves and returns to the nest and assessing effects on subsequent postnatal social orientation, social learning, and individual recognition of conspecifics (Vaillant, Harshaw, Jaime, Bahrick, & Lickliter, 2010).

Prenatal Roots of Contingency Detection and Contingency Learning

One key aspect of early social responsiveness is neonatal contingency detection and contingency learning. Detecting contingencies can be considered a foundational skill on which other perceptual, cognitive, and social skills develop. Tarabulsy, Tessier, and Kappas (1996) have argued that the ability to detect contingencies allows for predicting events and organizing behaviors in coherent ways, both to attain desirable outcomes and to avoid aversive consequences. Learning about cause and effect and discovering that one's own actions can influence events provides a key basis for infants' emerging sense of social engagement and competence (Rochat, 2001; Watson, 1979). A large body of research has shown that human infants are able to learn contingencies between events that are independent of their actions as well as learn a contingency whose manifestation is dependent on their actions (e.g., Bahrick & Watson, 1985; Millar & Weir, 1992; Rochat, 2001; Rovee-Collier, 1987; Tarabulsy et al., 1996). Importantly, contingency learning relies on the ability to attend to and detect amodal (both temporal and spatial) features of stimulation.

Findings from quail neonates have likewise demonstrated that contingency detection and contingency learning is present during early postnatal development (Harshaw & Lickliter, 2007; Harshaw, Tourgeman, & Lickliter, 2008). For example, we found that postnatal presentation of an individual maternal call contingent on quail neonates' own vocalizations dramatically modifies the acquisition and maintenance of their species-typical auditory preferences in the first days following hatching (Harshaw & Lickliter, 2007). Our previous research had shown that quail embryos and chicks require up to 240 min of passive auditory exposure to an individual maternal call to subsequently remember and show a preference for that familiar call over a novel maternal call (Lickliter et al., 2002; Lickliter & Hellewell, 1992). In sharp contrast, we found that quail chicks receiving exposure to a maternal call contingent on their own vocalizations were able to learn the same maternal call following less than 5 min of total exposure and preferred that familiarized call for at least 24 h following exposure. To put these results in perspective, our previous studies using passive exposure to a maternal call required approximately 3000 repetitions of the call to foster a preference for that call over a novel maternal call. Chicks receiving contingent exposure to a maternal call required less than 45 repetitions. Whether and to what degree such contingency detection and learning skill is present prenatally is not yet known. However, evidence of prenatal interaction between parents and embryos has been documented in a number of avian species (e.g., Norton-Griffiths, 1969; Tusculescu & Griswald, 1983), suggesting the availability of socially based contingent stimulation even prior to hatching.

Interestingly, a number of studies have reported that preterm infants show deficits in contingency detection and learning when compared to full-terms (e.g., Gekoski, Fagen, & Pearlman, 1984; Haley, Grunau, Oberlander, & Weinberg, 2008; Haley, Weinberg, & Grunau, 2006), suggesting that some features of prenatal experience likely contribute to the development of these critical skills. For example, Haley et al. (2008) used a conjugate mobile reinforcement paradigm (where the overhead mobile movement is contingent on the infant's foot kicking response) and found that preterm infants differed from full-terms in their responsiveness to contingency. Preterm infants showed less evidence of learning, spent less time looking at the mobile, had lower cortisol levels, and showed greater heart rate responses to contingency when compared to full-term infants. As suggestive as these findings are, we currently do not know to what extent prenatal sensory experience contributes to the emergence and development of contingency detection and contingency learning. We are currently working with our animal model, the bobwhite quail, to identify the specific prenatal experiences that might foster (or interfere) with neonates' contingency detection and contingency learning during early postnatal development.

If our hypothesis is correct that features of normally occurring prenatal sensory experience, such as multimodal stimulation and intersensory redundancy, are critical to the emergence of contingency detection and learning, then quail embryos receiving modified prenatal sensory experience should benefit less from postnatal contingency exposure when compared to unmanipulated chicks. As a result, they would be likely to fail to remember and prefer a familiarized maternal call in the days following contingent training to that call. As a first step in exploring this research question, we prenatally exposed groups of quail embryos to either augmented prenatal auditory stimulation or unusually early visual stimulation in the days prior to hatching (Raju, Bahrick, & Lickliter, 2013a, 2013b). In the *Auditory* condition, embryos received increased amounts of auditory stimulation (tones with varying pitch) continuously for the last 2 days of prenatal development. In the *Visual* condition, embryos received unusually early visual stimulation (a light suspended 5 in. above the embryos) for 45 min each hour for the last 7 days of prenatal development. Control embryos received no supplemental prenatal sensory experience. Following hatching, all chicks from each of the three groups were individually trained at 24 h of age using a contingency exposure paradigm, in which they were presented a single burst of an individual bobwhite maternal call each time they vocalized over the course of a 5 min session. Auditory preferences for the familiarized maternal call were assessed at 48 h following hatching by means of a simultaneous choice test between the familiar call and a novel variant of the bobwhite maternal call. All chicks were tested only once. Results revealed that chicks that had received either augmented auditory experience or unusually early visual experience prior to hatching failed to benefit from their postnatal contingency training, showing no preference for either the familiar or novel maternal call during testing. In contrast, control chicks showed a significant preference for the familiarized call over the novel maternal call (Raju et al., 2013a, 2013b). These findings, while preliminary, suggest that modified prenatal sensory experience can interfere with contingency learning in quail neonates. Additional research is needed to determine what aspects of the auditory or visual exposure (timing, amount, intensity) contribute to the observed impairment in early contingency learning.

Conclusion

Prenatal experience is both a formative and regulatory force in the process of development. As a result, birth is not an adequate starting point for explanations of perceptual, cognitive, or social development. As we have briefly reviewed in this chapter, animal-based research has provided a body of evidence in support of the trans-natal continuity of neonates' emerging perceptual biases and preferences. Human based research has likewise documented such trans-natal continuity (e.g., DeCasper & Fifer, 1980; Kisilevsky et al., 2003). Simply put, it is becoming increasingly clear that young infants' biases, predispositions, and preferences are not prespecified; rather, they develop through experience (see Moore, 2009 for discussion). Neonatal preferences are shaped by prenatal experience (see Harshaw & Lickliter, 2011; Schaal et al., 1998). This insight has important implications for the study of early perceptual, cognitive, and social development and argues for the value of better integrating the prenatal period into theories of both typical and atypical development.

Shifting the focus of the study of fetal development from *whether* prenatal experience contributes to perceptual, cognitive, or social development to *how* particular experiences at particular times influence the course of early development is a key step in advancing developmental science. We still have a long way to go in realizing this ambitious goal, and the use of animal models is an important component of this challenging quest. Comparative developmental psychobiology can provide useful methods, models, and conceptual frameworks for identifying and assessing both organismic and environmental factors contributing to the emergence of specific perceptual, cognitive, and social skills. Our work with precocial bird embryos and hatchlings has found that the features and properties of available prenatal sensory stimulation (such as amount or intensity, the timing of presentation, and the sources of stimulation) coact with organismic factors (such as the stage of organization of the sensory systems and previous history with properties of stimulation) to guide and constrain perceptual differentiation, social learning, and memory. We are still a long way from fully understanding the specific pathways and processes by which prenatal sensory ecology influences perceptual, cognitive, and social development. Further research on this topic across different species, levels of analysis, and methods should be an important priority for developmental science.

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