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The influence of prenatal experience on behavioral and social development: The benefits and limitations of an animal model

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Abstract

Prenatal experience is both a formative and a regulatory force in the process of development. As a result, birth is not an adequate starting point for explanations of behavioral development. However, surprisingly little is currently known regarding the role of prenatal experience in the emergence and facilitation of perceptual, cognitive, or social development. 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 and providing testable predictions for studies with human fetuses, infants, and children. Further, animal-based comparative research serves to minimize the amount of exploratory research undertaken with human subjects and hone in on issues and research directions worthy of further research investment. In this article, I review selected animal-based research exploring how developmental influences during the prenatal period can guide and constrain subsequent behavioral and social development. I then discuss the importance of linking the prenatal environment to postnatal outcomes in terms of how psychologists conceptualize "innate" biases, preferences, and skills in the study of human development.

Although most psychologists likely appreciate the significant role of animal models in advancing knowledge in biology, physiology, neuroscience, and medicine, fewer may appreciate the value of animal-based research to the study of human behavioral development. 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) a couple of decades ago, 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 prenatal conditions, experiences, and events that contribute to atypical development, a major focus of this Special Issue.

Decades ago, Ambrose (1968) noted several specific contributions that animal-based research can make to the study of human development. These include (a) development of new research techniques and methods, (b) clarification of concepts or frameworks used in the study of human development, (c) identification of special or unique features of human development, and (d) identification of issues in human development that need additional research investment. All of these contributions continue to be evident within developmental science today. Animal-based developmental research also allows for (e) the use of longitudinal and transgenerational research designs, (f) the articulation of more precise links from behavior to underlying neurophysiology, and (g) more direct tests of the biological plausibility of current theories of human development. For example, some developmental psychologists have proposed that human neonates' bias toward social stimuli such as faces and voices are innate, present at birth, and independent of prior experience (e.g., Balas, 2010; Meltzoff & Decety, 2003). Streri, Coulen, and Guellai (2013) recently argued for an "innate predisposition to social interaction in newborns." However, animal-based studies have consistently shown that prenatal experience plays a key role in establishing early postnatal perceptual and social preferences, biases, and predispositions (Gottlieb, 1997). As a case in point, prenatal exposure of quail embryos to non-conspecific maternal vocalizations redirects their species-typical auditory preferences following hatching (Harshaw & Lickliter, 2011).

A compelling example of the multiple dividends of animal-based developmental research comes from the rapidly growing field of epigenetics, which focuses on modifications to gene activity arising from environmental effects in the absence of any alteration to DNA sequence. Epigenetic processes are increasingly recognized as a key means by which early life events can have long-lasting effects on neurobiology and

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behavior (Moore, 2015). Recent work utilizing a range of different animal species has shown that the specifics of life experience, such as quality of maternal care, diet, exposure to stress, and levels of social interaction, can result in epigenetic modifications of gene expression and influence multiple behavioral outcomes, including stress tolerance, learning, memory, and cognition (e.g., Sultan & Day, 2011; Sweatt, 2010). For example, evidence from rodent studies indicates that epigenetic regulation and modification of gene expression plays an important role in the development of the nervous system, synaptic plasticity, and the maintenance and survival of neurons (see Graff, Kim, Dobbin, & Tsai, 2011).

Animal-based evidence has also linked epigenetic mechanisms to events and experience in the prenatal environment. For example, Mueller and Bale (2008) reported that adult male rats that had been born to mothers who experienced gestational stress showed changes in the expression of corticotropin-releasing factor and glucocorticoid receptor genes, as well as increased hypothalamic–pituitary–adrenal axis responsivity. Prenatal stress exposure resulted in changes in gene expression in both the hypothalamus and amygdala, elevating stress sensitivity in adults. Human-based research has reported similar results. Oberlander et al. (2008) have shown that newborns of mothers who experience depression during the last trimester of pregnancy show increased methylation of the glucorticoid receptor gene when compared to infants born to symptom-free mothers. Further, this increase in methylation was positively correlated with elevated salivary cortisol levels in response to stress at 3 months following birth. How these patterns of stress sensitivity play out across the life span is not yet known, but animal-based studies are making considerable inroads into unpacking these complex relations, as they allow experimentally tractable studies of the impact of prenatal experience on development using genetic, physiologic, immune, neurological, and behavioral levels of analysis (see Curley, Jensen, Mashoodh, & Champagne, 2011), which can then be translated into hypothesis driven studies of human development.

Exploring the Role of Prenatal Sensory Experience on Perceptual and Behavioral Development

One advantage of the use of animal subjects to study perceptual, cognitive, and social development in the prenatal period is the ability to readily alter the type, timing, and amount of sensory experience available to the developing embryo or fetus (see Lickliter, 2000, 2011). Animal-based research employing sensory deprivation or sensory augmentation during the prenatal period have yielded a useful body of information regarding the experiential conditions necessary for the normal development of early sensory and perceptual organization in animal infants. 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 therefore provides an effective model for testing hypotheses about prenatal factors underlying subsequent postnatal development. The embryonic bird develops entirely within the egg, providing a well-controlled "laboratory" for introducing experimental manipulations into the prenatal environment. In particular, because their prenatal development takes place in ovo rather than in utero, it is possible to provide the avian embryo modified amounts or timing of tactile, vestibular, auditory, and/or visual experience in the egg prior to hatching without surgery or other invasive techniques. Gottlieb (1971a, 1997) pioneered this approach, and over the last several decades other labs have further developed and successfully applied these types of sensory manipulations to extend our knowledge of the prenatal determinants of early perceptual, motor, and social development (e.g., Casey & Sleigh, 2001, 2014; Honeycutt & Lickliter, 2003; Lickliter, 1990, 1994).

Precocial birds (chickens, ducks, and quail) are a particularly useful animal model for this type of research because they allow easy access to the embryo for prenatal observation and manipulation, one can precisely control their developmental age and experiential history as they can be incubated in the lab, and they have several important similarities to human sensory organization. Like humans, precocial birds have all five sensory modalities functional in the late stages of prenatal development. Further, like humans, avian embryos can learn the acoustic features of maternal vocalizations prior to hatching (Gottlieb, 1971a; Heaton, Miller, & Goodwin, 1978). Unlike humans, however, precocial birds can demonstrate perceptual and social preferences by means of their locomotor behavior in the days immediately following hatching. Leveraging these unique developmental conditions, previous behavioral and physiological research has demonstrated that features of prenatal sensory experience, particularly the temporal synchrony of multisensory stimulation, can significantly influence quail embryos' and chicks' arousal, selective attention, perceptual learning, and memory (e.g., Jaime & Lickliter, 2006; Lickliter, Bahrick, & Honeycutt, 2002, 2004; Reynolds & Lickliter, 2002, 2004). More specifically, this research indicates that the specific effects that sensory experience have on early perceptual development and sensory integration depend on several 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 fetus or the newborn (Lickliter, 2005).

It is important to keep in mind that the various sensory systems do not start out at birth on equal footing. This is the case because the sensory systems of birds and mammals, including humans, do not become functional 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 (Gottlieb, 1971b). Because of the timing of their onset of function, the various sensory modalities have markedly different developmental histories at the time of birth. Onset refers to the initial responsivity of each sensory system, not a fully functional system. For example, the earlier developing tactile and vestibular systems have had much more experience during the late stages of prenatal development than has 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 and behavioral and social development.

Turkewitz and Kenny (1982) proposed a novel view of early perceptual development based on their insight that the differential timing of sensory system onset provides a context in which earlier developing sensory systems can develop without competition or interference from later developing sensory systems. They argued that sensory limitations resulting from the immature state of some sensory systems during early development serve to (a) provide a reliable order and structure to prenatal sensory experience, (b) minimize the quantity and complexity of sensory experience during prenatal development, and (c) reduce and regulate the attentional demands placed on the developing embryo or fetus (see Turkewitz & Mellon, 1989). Without the limited sensory functioning associated with prenatal development, a later developing system (e.g., the visual system) could interfere with earlier developing systems (e.g., olfactory or auditory) when they are still undergoing rapid development.

One useful approach to examining the importance and consequences of asynchronous sensory development during prenatal development is to experimentally alter the time when specific types of sensory input would normally be present. 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 did not exhibit a naïve preference for their species-specific maternal call, a reliable phenomenon in chicks not receiving prenatal visual stimulation. Related research demonstrated that increasing the amount of tactile and vestibular stimulation availability prenatally likewise altered postnatal auditory and visual responsiveness in quail chicks (Carlsen & Lickliter, 1999). Differences in the timing of augmented prenatal stimulation led to different patterns of auditory and visual responsiveness following hatching. No effect on normal visual responsiveness to maternal 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 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). Taken together, these findings indicate that augmented stimulation to earlier emerging sensory modalities can either facilitate or interfere with perceptual responsiveness in later developing modalities, depending on *when* the modified prenatal stimulation takes place.

These comparative results suggest important implications for the care and management of the high-risk preterm human infant. Currently, 1 in 10 infants born in the United States are considered premature (younger than 37 weeks gestational age). A growing number of these infants are critically preterm (younger than 26 weeks gestational age). Under normal conditions, the sequestered environment of the uterus effectively regulates the amount, type, and timing of sensory stimulation available to the fetus during prenatal development. Premature birth results in a dramatic shift in this constraint on the range and type of stimulation the infant receives. For example, preterm infants routinely receive unusually early visual experience, augmented auditory experience, and reduced vestibular experience during their extended stay in the neonatal intensive care unit (NICU). Further, the preterm infant is relatively unable to turn toward or away from visual stimuli or to coordinate motor behavior with auditory stimulation in the weeks following birth. The range of perceptual, social, and cognitive consequences of these altered patterns of sensory experience is only beginning to be explored. We do know that exposure to stressors in the NICU is associated with regional alteration in brain structure and function, including abnormalities in motor behavior (Smith et al., 2011). Further, 30%–60% of very preterm children experience perceptual and cognitive impairments as well as social and emotional difficulties (e.g., Emberson, Boldin, Riccio, Guillet, & Aslin, 2017; Taylor, Minich, Klein, & Hack, 2004). Comparative work with animal subjects can provide useful insights and guidelines for advancing our understanding of these varied consequences of preterm birth, as well as identifying potentially important interventions in the care and management of the high-risk preterm infant.

The precocial avian embryo can be exposed to premature visual stimulation or augmented auditory stimulation by the simple procedure of removing the upper portion of the eggshell several days prior to hatching, thereby exposing the head of the embryo to external stimulation. As a result, it is possible to easily provide sensory augmentation, sensory deprivation, or sensory substitution techniques during the period prior to hatching. This approach of modifying typical patterns of prenatal experience has provided a body of evidence regarding the experiential conditions necessary for the normal development of early sensory organization and perceptual development (e.g., Gottlieb, 1997; Honeycutt & Lickliter, 2001, 2003; Lickliter, 2005; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1998). Related animal-based research has also begun to explore the prenatal factors that can contribute to atypical developmental outcomes.

For example, research demonstrates significant differences in learning abilities in preterm infants when compared to full-term infants (e.g., Haley, Grunau, Oberlander, & Weinberg, 2008; Haley, Weinberg, & Grunu, 2006), suggesting that exposure to an atypical sensory environment may lead to impairment in basic learning skills. A study by Haley et al.

(2008) using a conjugate mobile reinforcement paradigm (where the overhead mobile movement is contingent on the infant's foot kicking response) demonstrated that preterm infants differed from the full terms. Specifically, they showed less evidence of learning, spent less time looking at the mobile, had lower cortisol levels, showed greater heart rate responses to contingency, and dampened heart rate responses to non-reinforcement. Detecting contingencies can be considered as a primary skill on which other skills develop, including perceptual, behavioral, and cognitive skills. Tarabulsy, Tessier, and Kappas (1996) have argued that the ability to detect contingencies allows predicting events and organizing behaviors in coherent ways, both to attain desirable outcomes and to avoid aversive consequences. Moreover, learning about cause and effect and discovering that one's own actions can influence events provides an important basis for early social responsiveness (e.g., Rochat, 2001).

If normal patterns of prenatal sensory experience foster contingency detection and learning, then avian embryos that receive modified prenatal sensory experience should show deficits in contingency learning when compared to controls. We tested this prediction and found that modifying typically occurring amounts of prenatal sensory experience, particularly auditory stimulation, can interfere with early postnatal social contingency detection and learning (Raju, 2014). Quail embryos that received augmented levels of auditory stimulation during the week prior to hatching showed impaired contingency detection and learning when compared to unmanipulated control chicks in the days following hatching. We have also found that modifying species-typical prenatal auditory experience can affect postnatal perceptual narrowing for species-typical vocalizations (O'Dowd, 2014). Quail embryos receiving exposure to a range of species-atypical auditory stimuli in the week prior to hatching showed reduced species-specific perceptual (auditory) narrowing when compared to control chicks in the week following hatching. In addition, we found that quail embryos exposed to acoustically modified maternal vocalizations prenatally could generalize this familiarization experience and show modified postnatal auditory preferences for maternal vocalizations (Lickliter, Bahrick, & Vaillant-Mekras, 2017). Taken together, these findings underscore the sensitivity of the bird embryo to variations in prenatal experience and point to the range of postnatal consequences of modified prenatal experience.

Further, modifications in the *timing* of patterns of prenatal sensory experience have been shown to influence early brain growth and development. Markham, Shimizu, and Lickliter (2008) found that quail embryos receiving augmented auditory stimulation during the middle or late stages of prenatal development showed atypical postnatal visual responsiveness 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 intersensory function. In contrast, embryos receiving augmented auditory stimulation during the earlier stages of prenatal development did not show altered behavioral or neural development. Thus, the effects of modified auditory experience were temporally constrained when the sensory modification occurred mattered. Simply put, *when* prenatal experience or exposure happens can be as important as *what* happens. This principal of prenatal temporal constraints has long been appreciated in the area of teratology, particularly the time-sensitive effects of fetal alcohol exposure.

In addition to altered auditory and visual experience, preterm human infants in the NICU experience dramatically reduced levels of normally occurring tactile and vestibular stimulation, which is typically provided by maternal movements such as walking, running, and climbing stairs prenatally but absent in the confines of the hospital incubator. The perceptual, cognitive, or social consequences of this long-term alteration in tactile/vestibular stimulation during late prenatal development are currently not well understood, and animal-based research can provide an important first step at generating new questions to pursue with this high-risk population. Working with a rodent model, Ronca and Alberts (2016) have quantified the prenatal sensory experience of the rat fetus and documented the extent to which maternal activity provide fetuses sensory experiences of acceleration, pressure, and vibration. This rich flux of ongoing prenatal stimuli has potential implications for sensory, neural, and physiological systems of mammals, including humans (see Previc, 1991).

Under naturally occurring conditions, precocial avian embryos also receive recurrent tactile and vestibular stimulation each time the maternal hen leaves and returns to the nest as well as during intermittent egg turning bouts, which usually occur every several hours over the course of incubation (Freeman & Vince, 1974). In bobwhite quail, field reports indicate that the maternal hen turns the eggs of her clutch with her beak or, more rarely, by kicking them with a rapid leg motion (Stoddard, 1931). This maternal movement and egg turning is required for normal embryonic development, and thus must be mimicked when eggs are artificially incubated. One of the few studies investigating the role of prenatal tactile and vestibular experience was conducted by Carlsen and Lickliter (1999). They showed increasing the amount of normally occurring egg turning during prenatal development can affect patterns of perceptual functioning following hatching, without interfering with hatchability. In particular, chicks that received augmented prenatal tactile and vestibular experience responded to maternal auditory cues presented unimodally into later stages of postnatal development and failed to respond to maternal visual cues at ages normally reared chicks display such species-specific visual responsiveness. While such findings suggest that increasing sensory stimulation during early development can disrupt typical postnatal patterns of perceptual functioning, at present we know relatively little about what are the appropriate ranges of thresholds of prenatal sensory stimulation to support normal perceptual development in birds or mammals.

In this light, there is growing appreciation that modifications in the timing and organization of human fetuses' prenatal sensory stimulation associated with maternal psychopathology can potentially contribute to the development of atypical outcomes following birth. For example, DiPietro (2010) has proposed that increased risk for psychopathology may be transmitted from mother to fetus by means of maternal factors present in the in utero environment. She points out that women who have temperamentally more intense and volatile affect present a different level of daily stimulation to fetuses throughout pregnancy than those who are more eventempered. The rapid acceleration of maternal heart rate that can accompany maternal anxiety or the modified digestive functioning that can accompany maternal depression can provide ongoing changes to the fetus's developmental milieu, leading to as yet unknown postnatal outcomes. As the articles of this Special Issue highlight, the various effects of maternal psychopathology exposure during fetal development are receiving increased research attention and should provide significant dividends in deepening our understanding of the pathways to both typical and atypical developmental trajectories.

Exploring the Role of Prenatal Sensory Experience on Social Development

Convergent animal–human research has conducted parallel studies of human and avian infants' perceptual development over the last decade and found evidence for several general principles of early perceptual development, including the salience of *intersensory redundancy* (the same information simultaneously available and temporally synchronized across two or more senses) in promoting attention, learning, and memory for amodal stimulus properties (tempo, rhythm, and intensity; e.g., Bahrick & Lickliter, 2000, 2002; Lickliter et al., 2002, 2004; Lickliter, Bahrick, & Markham, 2006). Intersensory redundancy is provided by an event when the same amodal information is temporally synchronized across two or more sense modalities. For example, when the rhythm and tempo of speech can be perceived by looking and by listening, the rhythm and tempo are redundantly specified. Our findings consistently indicate that intersensory redundancy promotes attention and perceptual processing of amodal properties of stimulation in both humans and quail, particularly when attentional resources are most limited, such as during early development (reviewed in Bahrick & Lickliter, 2012). It is not currently known whether and to what extent this sensitivity to redundancy across the senses prenatally contributes to the development of postnatal social responsiveness. Social events provide particularly high amounts of sensory redundancy (e.g., coordinated sounds and movements of speech, affect, and gesture) relative to most nonsocial events, and it is possible that a neonatal bias to redundancy across the senses, established prior to birth or hatching, contributes to the emergence and development of early postnatal social motivation and responsiveness.

The attentional biases and predispositions that lead young chicks to orient and seek proximity to their mother have long been known to be established as a result of prenatal experience (Gottlieb, 1971b). Given our demonstration of quail embryos' and human infants sensitivity to intersensory redundancy (see Bahrick & Lickliter, 2002, 2012) and given that social events are one of the first and most frequently encountered sources of intersensory redundancy both before and following hatching, the question arises as to what extent does intersensory redundancy made available by the mother during the prenatal period foster the development of social orientation, social learning, and social memory during early postnatal development? For both birds and mammals, social companions (particularly the mother and siblings) provide the neonate a rich and regular source of concurrent thermal, tactile, auditory, and visual stimulation. Further, during the late stages of prenatal development mammalian fetuses, including humans, can experience redundancy across auditory, vestibular, and tactile stimulation in utero. In humans, the mother's voice produces vibrations of her spinal column, synchronous movements of her diaphragm, and is often accompanied by movements of her body (Fifer & Moon, 1995). When the mother walks, the sounds of her footsteps are often coordinated with tactile feedback as the fetus experiences changing pressure corresponding with the temporal patterning and shifting intensity of her movements, as well as the accompanying and coordinated vestibular changes. The contribution of this maternally derived redundant prenatal sensory experience to neonates' emerging social orientation and motivation is currently not well understood. In precocial birds like quail, embryos likewise receive coordinated multimodal sensory stimulation in the egg from the mother and from broodmates. For example, when the hen turns the eggs of her clutch or when she leaves and returns to the nest, she typically provides concurrent tactile, vestibular, and auditory stimulation (Stokes, 1967; Tusculescu & Griswald, 1983).

How the effects of such prenatal sensory experience extend to early social development remains relatively unexplored (but see DeCasper & Fifer, 1980, Mastropieri & Turkewitz, 1999; Moon, Panneton-Cooper, & Fifer, 1993, for suggestive examples from human neonates). Use of animal models offers an essential step in addressing this critical gap in our knowledge base, as 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 subjects and hone in on issues and research directions worthy of further research investment (Gottlieb & Lickliter, 2004). Use of animal models also allow us to collect data under more strictly controlled conditions than would be possible with human fetuses and infants and is important for eventually connecting theories of early social development with biological and neurophysiological levels of analysis. In this light, we are currently utilizing quail embryos and neonates to assess whether such temporally synchronized, redundant prenatal sensory stimulation can facilitate the development of neonatal social motivation, social recognition, social learning, and memory. Identifying the critical features of maternally derived prenatal experience that facilitate postnatal social responsiveness and motivation will advance our understanding of the conditions that foster normal social development as well as provide insight into the mechanisms contributing to atypical patterns of social development, a pressing public health issue.

Our previous work with bobwhite quail has established that even when the amount of overall stimulation is controlled, detection and learning of temporal stimulus properties such as tempo and rhythm is facilitated in redundant bimodal stimulation as compared to nonredundant asynchronous bimodal stimulation and unimodal stimulation during the prenatal period (Lickliter et al., 2002, 2004). For example, we have shown that intersensory redundancy facilitates learning of the temporal features of an individual quail maternal call by presenting a light that flashed in synchrony and had the same temporal pattern (rate, rhythm, and duration) as the notes of a maternal call. During the late stages of incubation, quail embryos (that can detect light and sound through the eggshell) received exposure to an individual call for 6, 12, or 24 hr (10 min/hr for a total of 60, 120, or 240 min of exposure) under conditions of unimodal auditory, concurrent but asynchronous auditory and visual, or redundant and synchronous auditory and visual stimulation, and then received a two-choice preference test for the familiarized versus a novel maternal call after hatching. Embryos exposed to the redundantly presented maternal call (auditory and visual) showed dramatic facilitation, learning the maternal call four times faster and remembering it four times longer into postnatal development than those embryos exposed to unimodal auditory stimulation, and those that received the nonredundant asynchronous call and light exposure. These control chicks showed no evidence of learning the familiarized maternal call following hatching.

Given the importance of intersensory redundancy for guiding early selective attention and perceptual learning, it seems likely that the redundancy made available in social stimulation may facilitate the emergence and development of early social preferences. Because manipulating sensory experience during prenatal and early postnatal development is necessarily constrained for human participants, animal models can be used to more readily explore the experiential factors contributing to early social development, and our current work is leveraging this insight to assess the role of prenatal and postnatal experience with intersensory redundancy on subsequent social motivation. Specifically, we have assessed the role of spatial and temporal audio-visual redundancy on the development of social preferences using two robotic hen models that allowed us to vary the presence or absence of intersensory redundancy available to hatchlings during social choice tests. Our initial results indicate that redundancy can facilitate the development of social motivation and early social preferences (Belnap, Valesquez, & Lickliter, 2018). In particular, hens that moved in temporal synchrony with their maternal vocalizations were preferred over hens that moved asynchronously with their vocalizations. Additional research is currently under way to identify the prenatal experiential factors contributing to this early preference for redundant maternal stimulation.

It is certainly the case that much early human infant perceptual, cognitive, and social development emerges in the context of close face-to-face interaction with caretakers. Adults regularly scaffold infants' attention and provide a rich interplay of concurrent visual, vocal, tactile, vestibular, and kinetic stimulation. The movements and vocal rhythms of infants have also been shown to contain a burst-pause, turn taking pattern that is intercoordinated with the temporal characteristics of adult communication (Jaffe, Beebe, Feldstein, Crown, & Jasnow, 2001). Young infants thus create, participate in, and respond to amodal information in their interaction with adult caretakers in a mutually co-regulated manner, laying the foundation for later milestones of social and communicative functioning. The prenatal origins of these early skills remain to be discovered.

Exploring the Effects of Maternally Regulated Prenatal Hormone Exposure

In addition to the ability to readily modify the prenatal sensory stimulation histories of the embryo, it is possible to readily manipulate hormone levels of maternal origin in the avian egg prior to incubation. Schwabl (1993) was the first to show that the yolk of avian eggs contains quantities of maternally derived hormones, including testosterone, estradiol, and progesterone, and that these hormones can influence offspring development and eventual phenotype. Since then, several studies have assessed this "maternal effect," mostly focusing on physiological factors such as chicks' growth rates, immune response, and stress response (e.g., Gil, 2003, 2008; Groothuis, Muller, von Engelhardt, Carere, & Eising, 2005).

Unlike mammals, birds provide hormones to their offspring only once, prior to laying their eggs. While the avian egg is being formed in the reproductive tract of the female, theca and granulosa cells that surround the oocyte produce hormones that end up in different layers of the egg yolk (Gil, 2003). This constraint means that avian embryos are exposed to maternal hormones from the first day of prenatal development and that the level of specific maternal hormones present in the egg can be experimentally manipulated. Eggs of all avian species that have been analyzed to date contain concentrations of maternally derived steroid hormones, including testosterone and progesterone, as well as corticosterone (Gil, 2003, 2008; Groothuis & von Engelhardt, 2005; Groothuis et al., 2005). As these hormones are detectable before the stage when the embryo begins its own endogenous secretion and these hormones are found even in unfertilized eggs, it seems clear that they are of maternal origin.

The effects of yolk hormones of maternal origin on offspring characteristics have typically been investigated experimentally by comparing the effects of hormone injections into the yolk prior to incubation with the effects of injections of oil vehicle alone (and uninjected controls). These substances can be injected directly into the egg and the circulation of the embryo without mitigation by maternal influences, as would

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happen in placental mammals. It is important that the dose of these hormone injections must be scaled to the natural variation of yolk concentrations for a given species; otherwise, the functional consequences of an experimental treatment would be difficult to interpret (Groothuis & von Engelhardt, 2005).

Studies of both altricial and precocial avian species manipulating yolk hormone levels within the upper limit of naturally occurring levels indicate that maternal steroid hormones can influence the physiological and behavioral traits of offspring, including growth rate, stress sensitivity, and emotional reactivity (Gil, 2003, 2008; Gil & Faure, 2007; Groothuis et al., 2005). For example, Japanese quail chicks hatched from eggs receiving elevated levels of testosterone prior to incubation showed shorter latencies to approach a novel object and to stand up after a tonic immobility test, as well as less vocalizations in an open field test (Daisley, Bromundt, Mostl, & Kotrschal, 2005). Bertin, Arnould, Mousu, Meurisse, and Calandreau (2015) found that elevated yolk testosterone, progesterone, and estradiol resulted in less emotional reactivity and object neophobia in domestic chickens, suggesting that enhanced hormone levels during prenatal development might be related to a reduced fear response and better coping strategies in novel environments. Environmental factors present during egg formation such as maternal stress, social instability, and availability of food resources can modify yolk steroid concentrations (Bertin et al., 2015); this finding highlights the dividends of this line of research for improving our understanding of the links between maternally derived prenatal factors and postnatal developmental outcomes.

Studies from our lab have shown that bobwhite quail chicks hatched from eggs with elevated yolk testosterone show improved prenatal auditory learning when compared to control chicks (Bertin, Richard-Yris, Mostl, & Lickliter, 2009). In contrast, chicks hatched from eggs with elevated yolk progesterone levels showed impaired prenatal auditory learning when compared to controls (Herrington, Vallin, & Lickliter, 2015). Further, we found that mean duration in tonic immobility (a classic test for emotional reactivity in birds) was significantly longer in testosterone-treated chicks when compared to sham injected and control chicks (Bertin et al., 2009). Perhaps most intriguing is our preliminary finding that increased levels of testosterone during prenatal development interfered with chicks' postnatal ability to track and avoid human gaze (Salazar & Lickliter, 2018). Previous work from our lab has shown that unmanipulated chicks show effective gaze tracking in the days following hatching, actively avoiding areas that humans direct their gaze toward (Jaime, Lopez, & Lickliter, 2009). Taken together, these results suggest that elevated levels of testosterone may interfere with or attenuate emerging social orientation, and additional research is currently under way to assess this intriguing possibility.

Limitations of Animal Models for the Study of Human Development

An important issue at play when comparing nonhuman animal and human research findings is the temptation to assume that animal models are actually mimicking their human counterparts in psychological, social, or behavioral function. The idea of the utility of using animal models to directly understand human psychological or behavioral development is simply not tenable (Gottlieb & Lickliter, 2004). In contrast, it is certainly the case that the results of programmatic experiments with animals can provide interesting and significant hypotheses (not facts) about human development. Whether these propositions turn out to be relevant to human development and behavior can only be determined by human-based studies.

Caution is also needed when interpreting the findings from animal models in terms of identifying underlying processes and mechanisms at play in behavioral and social development. Experimental animals are not exposed to the range of competing and often interacting experiences that humans receive. Laboratory animals are typically reared in highly controlled physical and social environments, precluding naturally occurring variations in daily experience. This can lead to misinterpretations and overgeneralizations of research findings. For example, Hood and Cairns (1989) changed the typical regimen of *isolation rearing* of mice selectively bred for four generations for high levels of aggression to *social rearing* and found the mice no longer exhibited their usual high level of aggressive behavior. In this case, when the developmental experience of selectively bred mice was altered, the selectively bred behavior was no longer evident; such behavioral plasticity highlights the importance of not overgeneralizing our interpretations of research findings generated in specific rearing conditions. As Kalueff and Tuohimaa (2004) point out, measures of animal behavior that are resistant to even subtle variations in experimental conditions, including housing, testing equipment, and general laboratory procedures are hard to come by.

A number of authors have argued that adult animal models of psychiatric disorders should fulfill a multidimensional set of criteria of validity to be considered relevant for human pathology. These include predictive validity, face validity, construct validity, and species validity, among others (see Willner, 1984). Belzung and Lemoine (2011) have proposed that adult animal models used to study anxiety disorders or depression should not simply resemble such human disorders, but rather the processes by which both animals and humans come to be in these atypical states should also be similar. This standard of external validity seems appropriate for the use of animal embryos and fetuses to study the prenatal transmission of risk for psychiatric disorders, with the caveat that our knowledge of the influence of prenatal experience on animal or human infant psychosocial development is currently meager at best.

Implications of Prenatal Research for Conceptions of Innate or Instinctive Behavior

There is now widespread acknowledgment in developmental science that animal and human infants do not come into the world with ready-made response systems. Rather, behavior emerges and is maintained or transformed over individual development through the interactions of inner and outer events and conditions occurring over the course of the individual's activity and experience (Gottlieb, Wahlsten, & Lickliter, 2006). Although much remains to be learned of the conditions and experiential events occurring during the prenatal period that facilitate this selective process, it is clear that at birth or hatching the avian and mammalian neonate has had a great deal of prenatal experience and the nature and type of this experience must be taken into account when seeking explanations of infant perceptual, social, and cognitive development. Newborns are not sensorally naive at birth, and the sequential onset of functioning of the sensory systems during very early development and the resulting patterns of prenatal intersensory competition and integration across the senses can have a significant influence on how young organisms respond to and learn about their developmental niche in the period before and after birth or hatching (e.g., Alberts, 1984; Gottlieb, 1971b; Lickliter, 1994).

While we are still a long way from understanding the specific pathways and processes of how prenatal experience influences perceptual, behavioral, and cognitive development in birds and mammals, the research findings reviewed above suggests that species-typical and species-atypical behavioral outcomes are generated during individual ontogeny because particular aspects of the temporal and spatial arrangements of organisms and their contexts occur at times when the organism is in particular developmental states, having had a particular developmental past (see Oyama, 2000, for further discussion). Empirical findings from a wide range of species and across disciplines have converged to indicate that development cannot be represented as the unfolding of a fixed or predetermined substrate, independent of the activity, experience, or context of the individual. Development always takes place in some "experiential" context, where experience is defined broadly to include the various stimulative aspects to which individuals are subject during prenatal and postnatal life. Behavior development thus depends on exposure to or interaction with particular features of the organism's developmental ecology; research with precocial avian species has provided multiple examples of how normally occurring prenatal sensory experience can play an important role in the development of behavior before and after hatching. Reliable and repeatable features of sensory stimulation are available prenatally and provide diverse but dependable resources and influences for the developing embryo. Features and properties of available prenatal sensory stimulation (such as amount or intensity, the timing of presentation, and the sources of stimulation) interact with specific organismic characteristics (such as the stage of organization of the sensory systems, previous history with the given properties of stimulation, and the current state of arousal of the embryo) to contribute to the developmental course (both typical and atypical) of young organisms' emerging capacity for perceptual differentiation, perceptual learning, and social responsiveness.

Exploring the specific contributions of prenatal experience to perception and behavior highlights the point that the young organism's context or environment cannot be viewed as merely a permissive or triggering factor in the developmental process; rather, the specific features of the early environment within which the individual organism develops provide essential contributions to the achievement of its varied developmental outcomes. This account of behavioral development represents a radically different view from that assumed by traditional notions of innate, instinctive, or other internally determined characterizations of the regularities of species-typical behavior, as well as traditional notions regarding the sources of atypical behavioral outcomes.

Conclusions

Animal-based research has provided a useful body of evidence in support of the transnatal continuity of neonates' emerging perceptual biases and preferences. Human-based research has likewise documented such transnatal continuity between prenatal and postnatal responsiveness (e.g., DeCasper & Fifer, 1980; Fifer & Moon, 1995). It has become increasingly clear that young infants' biases, predispositions, and preferences are not prespecified; rather, they develop through experience (see Moore, 2009, for discussion). Simply put, animal and human neonatal preferences are shaped by prenatal experience (see Harshaw & Lickliter, 2011; Schaal, Marlier, & Soussignan, 1998). This insight has clear 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 goal, and the use of animal models is an important component of this challenging quest. Comparative developmental psychobiology provides methods, models, and conceptual frameworks for identifying and assessing both organismic and environmental factors contributing to the origins of specific perceptual, cognitive, and social skills. As I have reviewed here, research 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 postnatal perceptual differentiation, social learning, and memory. Extending these insights to the origins of atypical development are sorely needed, and further research with different species, levels of analysis, and methods should be an important priority for developmental science.

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