

Annual Review of Developmental Psychology The Origins of Social Knowledge in Altricial Species

## Katerina M. Faust, Samantha Carouso-Peck, Mary R. Elson, and Michael H. Goldstein

Department of Psychology, Cornell University, Ithaca, New York 14853, USA; email: michael.goldstein@cornell.edu

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### Keywords

altriciality, developmental niche, social learning, comparative development, exogenetic inheritance

#### Abstract

Human infants are altricial, born relatively helpless and dependent on parental care for an extended period of time. This protracted time to maturity is typically regarded as a necessary epiphenomenon of evolving and developing large brains. We argue that extended altriciality is itself adaptive, as a prolonged necessity for parental care allows extensive social learning to take place. Human adults possess a suite of complex social skills, such as language, empathy, morality, and theory of mind. Rather than requiring hardwired, innate knowledge of social abilities, evolution has outsourced the necessary information to parents. Critical information for species-typical development, such as species recognition, may originate from adults rather than from genes, aided by underlying perceptual biases for attending to social stimuli and capacities for statistical learning of social actions. We draw on extensive comparative findings to illustrate that, across species, altriciality functions as an adaptation for social learning from caregivers.

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## 1. INTRODUCTION

Humans begin life relatively helpless, with limited motor control, poor visual acuity, and the inability to effectively thermoregulate or feed ourselves. We cannot sit up until 6 months, or take our first steps for a year. In contrast to animals such as horses or giraffes, which can run from their first day of life, humans are motorically incompetent. This makes infants entirely reliant on the care and protection of their parents. Children are weaned and no longer dependent on their mother for food by about 3 years of age, but unlike other mammalian species, including other primates, they continue to depend on adults for care and provisioning for many years after weaning (Bogin & Varea 2017). With a modern time to independence of 18 years, or 23% of our average life span, humans have the most protracted time to maturity of any animal. This leisurely developmental pace is puzzling because it comes with high costs, requiring considerable parental investment and rendering helpless offspring at high risk of dying before reaching reproductive age. Natural selection must have favored immature, altricial infants because of some benefit that outweighs these costs. Yet most researchers have concluded that immaturity has no inherent advantages; it must be an unfortunate by-product of selection for some other trait, such as large brains, a response to an unstable ecological niche requiring behavioral plasticity, or the result of the limits of a bipedaladapted birth canal or maternal metabolism (Dunsworth et al. 2012).

Despite infants' immaturity in many physical domains, they excel at a number of skills in the social domain. Babies under 1 week old can visually distinguish human faces from other stimuli, and by 4 months of age they preferentially look at faces (Fantz 1961, Johnson et al. 1991, Morton & Johnson 1991, Easterbrooks et al. 1999). Newborns can even discriminate among individual faces, and will vary their rate of sucking more to see a picture of their mother's face (Walton et al. 1992) or hear the sound of their mother's voice over that of another woman (DeCasper & Fifer 1980). Infants appear to have a bias for looking at faces or facelike stimuli, as well as the ability to learn a preference for the face of their mother shortly after birth (Morton & Johnson 1991,

Easterbrooks et al. 1999). Infants also prefer faces with open eyes (Batki et al. 2000) and are more attentive to faces that are gazing at them than to those with averted eyes (Farroni et al. 2002). These tendencies result in babies preferentially attending to social stimuli, particularly from caregivers, and engaging with social cues such as mutual gaze.

Recognition of conspecifics and caretakers is only one way in which the organization of infant attention aids in social development. Infants are also remarkably attuned to language, preferring at birth to listen to language over similarly complex nonlanguage sounds (Vouloumanos & Werker 2007). The strength of this preference predicts expressive vocabulary at 18 months (Vouloumanos & Curtin 2014). By 5 months of age, infants can associate lip movements with corresponding sounds (Spelke & Cortelyou 1981) and specific phonemes (Kuhl & Meltzoff 1982).

These capacities allow infants to recognize conspecifics and organize their attention to identify relevant social cues. By the age of 9–18 months, human babies become efficient social learners— experts at seeking and soliciting information about the environment from social agents. Furthermore, young children are selective in which social partners they model or learn from. Eighteenmonth-olds discriminate between reliable and unreliable agents who previously provided helpful or false information, and are subsequently more likely to learn a novel word from the reliable speaker (Koenig et al. 2004, Crivello et al. 2018).

It remains unclear how this remarkable suite of adaptive social abilities originates. A debate has raged for decades between developmental researchers about whether these abilities are innate or learned. Nativist approaches suggest infants are endowed at birth with several systems of core knowledge, including social knowledge (Spelke & Kinzler 2007). Core knowledge theory posits that infants possess considerable cognitive competence that they cannot demonstrate in performance because of their immature language skills, attentional capacity, or functional memory. For example, the core system representing agents and their actions is thought to enable an infant to predict and attempt to mirror the goals of intentional agents (Spelke & Kinzler 2007). Researchers have also suggested that social imitation is an innate process, as neonates as young as 12 days old are capable of imitating the facial expression of adults, specifically tongue protrusions (Meltzoff & Moore 1977).

We argue that human social capacities often do not fall neatly into either category of fully innate or fully learned but rather exist on a spectrum between the two (Figure 1). The information guiding the development of most social abilities lies somewhere in between, needing to be learned over the course of development but bolstered or enabled by innate (i.e., constructed with information primarily from the genetic level of organization) perceptual biases. For example, infant social abilities may arise from their ability to perceive patterns of information in the environment. One way to extract such structured information is through statistical learning. This domain-general process allows individuals to detect and acquire patterns in incoming sensory information by tracking recurrent regularities (transitional and co-occurrence probabilities, nonadjacent dependencies, etc.) and enables the generalization of learned structure (Santolin & Saffran 2018). Statistical learning is integral to communicative development, and human infants are able to use statistical learning to segment words from continuous speech (Saffran et al. 1996, Graf Estes et al. 2007). After exposure to the statistics of adult behavior during daily caregiving, young animals might start to generate predictions about the probabilities of subsequent behaviors. For example, 10- to 11-month-old human infants familiarized with videos of everyday action sequences (e.g., picking up a dropped towel) display heightened interest in sequences interrupted midaction (as a woman reaches toward the towel) compared with sequences interrupted at a boundary point (as the woman grasps the towel; Baldwin et al. 2001). We argue that the ability to pick up on statistical regularities of action patterns may translate into the generation of predictions about future actions from their

#### Nonhuman animal capacities

•		Migration in birds	Song in songbird	as Ref	erential alarm ca	liis in Jays
	Imprinting in ducks	Species recognition in rapt	ors		Tool use in c	ows and apes
Fixed a	action patterns	Parental behavior in mamn	nals Empa	thy in rats	Signature wh	istles in dolphins
Inform from g	aation enes				Infe	ormation from conspecifics
Suc	king/grasping reflexes					
Visual face preference Capacity for statistical learning		Face recognition		Empathy	Morality/ju	istice
		ng Voice recognitio	on	Langu	age C	ultural norms
n social ties	Social pattern recognition	Joint attention	Attachment		Theory of mind	

## capacitie Figure 1

Huma

Spectrum of sources of information for a developing organism. Species-typical behaviors are often regarded as being derived entirely from genes or wholly from learned information gleaned from the environment. For example, at the left side of the spectrum are innate behaviors, determined by genetic information and immutable by experience, such as reflexes. On the far right end of the spectrum are behaviors that cannot be achieved without information from external environmental or social influences, such as learned tool use. However, most behaviors originate through a combination of genetic and learned factors; for example, songbirds instinctually produce song but are unable to achieve a species-typical and reproductively adaptive song without the aid of learning from conspecifics. Similarly, human face recognition is learned but bolstered by an innate perceptual bias for attending to faces. These behaviors fall along the information spectrum according to the known relative degree of influence from genetic and environmental sources. Behaviors are color-coded according to domain: Orange represents reflexes; green, recognition/perceptual ability; and blue, social/communicative ability.

social partners. Our perspective also incorporates findings that social imitation is not innate (as in Meltzoff & Moore 1977), but rather that human infants will protrude their tongue in response to any interesting or arousing stimuli, such as flashing lights or dangling toys (Jones 1996), touches on the palm (Humphrey 1970), or short segments played from the overture of *The Barber of Seville* (Jones 2006).

Humans are born with remarkable innate capacities for gaining knowledge, but we do not require the knowledge itself to be built in. The organization of behavior is influenced by genetic information, but we are also reliably born with an exogenetic inheritance: our parents, our social partners, and our environment (West & King 2008). The prolonged period of social interaction between parents and offspring may foster cognitive skills and facilitate social learning (Uomini et al. 2020). A combination of access to social information in the world around us and an underlying perceptual bias to attend to and organize social information makes us exceptional social learners. Studies of the exogenetic inheritance of nonhuman animals have revealed the surprising learning processes behind many abilities once thought to be innate. Even clearly adaptive and vital skills which are crucial for survival from the first day of life have repeatedly been found to be constructed by information external to the organism. For example, when ducklings are born they follow the sound of their mother's call, a behavior long thought to be innate until it was found that ducklings learn to recognize the call through auditory experience while still in the egg (Johnston & Gottlieb 1981). Evolution selects not for processes but rather for outcomes (Lehrman 1970). Natural selection is indifferent to whether the duckling's behavior is learned or innate; it favors only outcomes that improve the chances of the duckling's survival.

By taking a comparative approach and investigating the development of social competencies in nonhuman animals, we may gain a more biologically and evolutionarily realistic understanding of social learning mechanisms. How have other species solved social challenges similar to those facing human infants? How have social learning and development evolved? We propose that protracted immaturity and dependence on parental care, or altriciality, is not an unfortunate by-product of our evolution but instead a highly adaptive trait of our species, which has enabled human infants to efficiently organize attention to social agents and learn efficiently from social input. The evolutionary goal of altricial species is not to become highly competent as quickly as possible but rather to excel at learning over time.

## 2. THE DEVELOPMENTAL NICHE OF ALTRICIAL YOUNG

#### 2.1. Developmental Niches

The development of young organisms is shaped by their environment. Some environmental factors are physical (e.g., temperature, lighting, gravity), and others are social (e.g., the presence of parents or siblings). These factors will change over time, as a result of the young organism's development. For example, once human infants learn to crawl and walk, they can reach new objects and new locations, and elicit different responses from their caregiver (Kretch et al. 2013, Adolph & Tamis-LeMonda 2014). This idea also applies across species. A young bird, for instance, must fledge and leave the nest. The fledgling's habitat ("address"; Alberts & Cramer 1988) changes from the relatively enclosed nest, which is warm, dark, and filled with kin, to the forest outside, which is brighter, subject to changes in weather, and populated with multiple species. In any given habitat, the niche ("occupation"; Alberts & Cramer 1988) of a young organism is to survive, through learning and adapting to its circumstances. A developmental niche, therefore, encompasses the ways in which an organism interacts with its environment, as well as the challenges that it must overcome.

For humans and other species reliant on parental care, the developmental niche involves recognizing, attending to, and learning from social information. The niche of an infant might involve learning to recognize its caregivers, predicting their behaviors, and behaving in a way that will elicit responses. None of these roles necessarily require built-in social knowledge. For example, humans do not require an innate ability to recognize faces, only a perceptual bias toward facelike objects. The poorly developed perceptual system of human infants makes it easy to attend to facelike objects, with high contrast, bilateral symmetry, and a top-heavy appearance (Simion et al. 2001). Attending to faces allows for later attention to expressions and individuals, and this ability continues to develop as infants mature. Therefore, it is worth examining the developmental niche of humans and other altricial animals in order to understand the kinds of information available and the learning that might take place. Below, we describe the environments of offspring at varying stages of development, as well as the opportunities for social learning that infants encounter.

Prior to birth, a young organism is immersed in a world of stimulation, tuning its developing senses and circuitry for the postnatal environment. The forms of early learning that take place in utero or in ovo are often those most held up as evidence for innate behaviors (e.g., prior understanding of the response to the duck maternal assembly call as instinctual; Calkins 2015). However, it is the role of experience within a species-typical developmental environment that allows some species-typical early behaviors to manifest. After birth, infants are exposed to more and varied forms of stimulation. The incremental nature of sensory system onset in altricial species (Gottlieb 1971) builds on past experiences, and the presence of adult social partners serves to structure the world and direct infant attention. Together, the developmental influences of prenatal experience

and postnatal environment, shaped and constructed by the parents, provide a wealth of information to the developing infant.

How is this information extracted and organized? Young altricial organisms possess a variety of mechanisms for solving such tasks. The structured nature of sensory input from the world, including adult responses contingent on the actions of infants, allows them to form associations and create predictions, taking an active role in their own development. In the following subsections, we describe comparative research that illustrates the importance of studying altricial species within their developmental niche, as well as examples of studies in human infants.

#### 2.2. Comparative Study of Innate Skills

Studying nonhuman species with similar life history strategies as humans-slowly developing, reliant on an extended period of parental care-can provide insight into our own development and the evolution of communication and social learning. Comparative data indicate that many skills once assumed to be innate due to their necessity for survival may instead develop through the interactions of young organisms with their environment. A predominant example from the animal world involves gulls. Chicks beg for food from their parents by pecking at their bright red bills, encouraging them to regurgitate food. This behavior can be observed only a few days after hatching, leading researchers to conclude that the begging behavior must be innate (Tinbergen & Perdeck 1951). However, further investigation demonstrated that chicks not only need to learn how to beg for food but also need to learn how to eat, an incredibly basic skill. By pecking roughly in the direction of their parent's brightly colored, moving bill, a highly salient cue, the chicks accidentally encounter food. This reward reinforces subsequent pecking at the parent's bill, and gradually leads to the production of stereotypical begging behavior (Hailman 1969). Newborn chicks do not need to hatch with the ability to recognize food, or peck with any degree of accuracy at a bill, or identify their own species from a variety of others. Instead, they quickly learn these critical skills through experience.

In altricial species, instead of requiring hardwired, instinctual knowledge on the part of the infant, evolution has outsourced the information necessary for acting adaptively to the parents, who provide learnable environments. A chick that hatches in a nest without parents to scaffold the development of begging behavior will not survive. All other chicks that eventually reach adulthood are guaranteed to have had parents providing care, from which their own behaviors could develop. Thus, what is innate is not the behavior, but learning.

## 2.3. Immature Perceptual Systems Are an Advantage

Infancy has famously been described as a time of "blooming, buzzing confusion" (James 1890), as the advent of birth plunges the neonate into a world beset by sensory stimulation. However, the incremental nature of sensory system maturation, building on early experiences and the presence of adult social partners, serves to structure the world and direct infant attention. The immature perceptual systems of young altricial species are not a disadvantage but actually facilitate learning.

Evolution has constrained sensory system development to optimize learning for the emergence of adaptive skills. Sensory system development proceeds in a similar order across species: first tactile, then vestibular, olfactory, auditory, and visual sensitivity (Gottlieb 1971). Even though species might be born at different times relative to the onset of sensory function (e.g., ducks hatch with all systems functioning, rats' ears and eyes are sealed for the first few days after birth), there is an invariant, sequential progression in terms of the maturation of function. This developmental heterochronicity confers an advantage, as it allows for scaffolding of early sensory maps onto new stimulation patterns from later-developing senses, resulting in intersensory integration as the various systems mature. If the sequence of sensory development is experimentally altered (e.g., premature exposure), it disrupts species-typical development. Mallard duck embryos learn to follow their mother's assembly call through auditory exposure in ovo prior to any visual input (Lickliter & Gottlieb 1985), but if they are given premature visual exposure through careful removal of the eggshell during development, they do not learn the assembly call (Gottlieb et al. 1989). Moreover, premature opening of rat pups' eyes disrupts species-typical homing behavior, their ability to orient toward the nest (Kenny & Turkewitz 1986). These studies provide evidence that the slow, sequential nature of sensory maturation facilitates learning by limiting the novel stimuli that young organisms encounter. Immature perceptual systems allow for sequential periods of sensory dominance, where new systems inherit the sensory patterns that have been experienced previously. If all sensory systems mature at the same time, as modeled through premature experimental stimulation (e.g., opening rats' eyes early), attention becomes distributed between olfactory and visual input, to the detriment of adaptive behaviors.

Similar sensory maps aid associative learning in human infants. While infants' eyes are not sealed shut at birth, their visual system is still developing, and does not reach an adult level of acuity and color perception for years (reviewed in Kellman & Arterberry 2006). Neonate visual acuity is so poor that newborn infants would be classified as legally blind. This is no detriment, however, as it allows focus on the nearby faces of caregivers. Reducing visual acuity in computational models enables improved learning of basic categories (French et al. 2002) and, when paired with other sensory stimulation, can enhance facial recognition. Pairing maternal odor with face presentation leads to enhanced categorization of human faces in 4-month-old infants (Leleu et al. 2019). Poor-quality visual stimuli may also allow for enhanced attention to auditory cues, such as the mother's voice.

## 2.4. Exploiting Parental Information

Evolution has outsourced critical information for species-typical development, such as feeding and species recognition, to parents. The developmental niche of species with extended periods of parental care is to learn that information.

Species develop at different rates and with different life history strategies. Researchers can compare development across species using a continuum from precocial to altricial strategies. Precocial species have a high degree of sensory and motor control from birth and can function relatively autonomously. Examples of precocial species include ungulates, which can stand and run within hours of birth, and extreme cases such as the brush-turkey, whose chicks hatch, dig themselves out of the composting mound that incubated their eggs, and run off into the forest to live independently without ever encountering their parents (Jones et al. 1995). Many precocial species do not depend on their parents for care.

Altricial species, however, take longer to become independent. Various sensory systems become functional postnatally, and offspring often are unable to thermoregulate, relying on parents for warmth (e.g., incubation, huddling) as well as nutrition. Songbirds, for example, hatch without feathers, do not open their eyes until several days after hatching, and require parents to incubate and feed them. However, parents of altricial species are not only providing nutrition—they are also provisioning information about the social environment.

Studies of human infants, particularly in recent years, portray them as possessing advanced social knowledge or understanding. Infants are variously accorded the ability to understand intentions, mentally represent social dominance (Thomsen et al. 2011), imitate facial expressions—even within days of birth (Meltzoff & Moore 1977)—and make inferences about third-party affiliations (Liberman et al. 2014). While infants do possess a marked capacity for skills in the social domain, research tends to view them as having fully developed sensory systems, essentially placing them on the precocial side of the continuum. However, these assumptions of innateness limit investigation into the development of adaptive social abilities.

We encourage research that views infants in light of their underlying altricial developmental strategy. Like other altricial species, human infants display heterochronicity of sensory systems, a lack of early motor control, and reliance on parents for an extended period of care. To understand the origins of social abilities in infants, and other species, we must examine them within their developmental, inherently social, niche.

#### 2.5. The Prenatal Niche

A developing animal still in the womb is not shielded from the world but rather is exposed to a variety of sensory stimuli that influence critical postnatal behaviors. Fetuses, while constrained in terms of sensory input and motor abilities, are nonetheless actively shaping, and being shaped by, their inherently social in utero or in ovo environment. During this time, developing organisms are exposed to prenatal information that forms the foundations of postnatal knowledge, including vital social adaptations. For example, mother superb fairywrens (*Malurus cyaneus*) call to their eggs during incubation (Colombelli-Negrel et al. 2012). Upon hatching, their chicks produce begging calls containing elements from their mother's incubation call, a "password" that allows mothers to differentiate between their own offspring and those of Horsfield's bronze cuckoo (*Chrysococyx basalis*), which often parasitizes their nests. In this example, not only are fetuses learning to recognize the call of their mother, but also they must learn to produce that call within a few days of hatching in order to receive food.

Prenatal learning is not limited to communicative development, or to the auditory domain. Another comparative example involves species recognition and olfaction in fetal rats. After birth, rat pups must climb up the mother's ventrum and find a nipple in order to suckle. Arousing stimulation from uterine contractions, paired with the scent of amniotic fluid, which the dam subsequently spreads up her ventrum during the birth process, results in the formation of a strong preference for the scent of amniotic fluid (Ronca et al. 1996). The warmth and milk later provided by the mother further strengthen the reward value of proximity to her, and cement thermotactile and olfactory preference for other rats upon maturity (Alberts & May 1984). Species recognition need not be "built into" a fetus, but may be easily constructed given a species-typical developmental environment.

Most recently, and perhaps more unexpectedly, the prenatal environment has been shown to tune postnatal growth, thermal preferences, and reproductive success in zebra finches (Mariette & Buchanan 2016). These small Australian songbirds produce incubation calls when ambient temperatures exceed 26°C, but only during the last 5 days of incubation. If chicks experience incubation calls at this time, in adulthood they are smaller, which can help with hotter environments. In contrast, chicks that do not experience incubation calls grow larger, which is more adaptive for cooler climates. This evidence suggests that parents are able to change the developmental trajectory of their offspring to match the ambient environmental conditions.

Together, these findings emphasize the importance of considering the prenatal environment and suggest ways in which the prenatal environment can structure and support social learning later in life. In addition, they point to ways in which comparative research could enrich our understanding of the prenatal environment of humans, using altricial animal models to show the way forward.

Similar to a young bird, the human fetus possesses a mature auditory system prior to birth, allowing for perception of their auditory environment: the inside of their mother. By the third trimester, fetuses can hear their mothers speaking, and respond with changes in heart rate and motion (reviewed in Moon 2017). Infants are also sensitive to the rhythms of speech. Newborn infants preferred to hear their mother reading a familiar story, one read to them daily during the last 6 weeks of pregnancy, over a novel story (DeCasper & Spence 1986). Neonates can also differentiate between vowels from a native versus nonnative language, results not influenced by time elapsed since birth, indicating that auditory familiarization and learning are occurring prenatally, not postnatally (Moon et al. 2013). Together, these results indicate that early auditory experience can predispose infants to direct attention to sounds that facilitate postnatal communicative development.

## 2.6. The Postnatal Niche

After birth, or hatching, young organisms encounter a world with increased sensory stimulation and the presence of conspecifics. They begin to learn the utility of their behaviors for eliciting responses from those around them, including their parents or other adult caregivers. Through social interactions and social learning, adaptive skills are transmitted down the generations. In the following subsections, we describe the various social challenges that altricial organisms encounter in the postnatal niche: recognizing conspecifics, learning to communicate, and forming predictions about the behaviors of social partners.

**2.6.1. Recognizing conspecifics.** In the course of species-typical development, young animals must learn to recognize conspecifics and demonstrate a preference for social interactions with them. Doing so involves learning the distinct characteristics of their species (e.g., facial characteristics or markings, scent cues, auditory cues). Recognition of these specific cues can be built up through more general perceptual learning processes.

The development of species recognition in rat pups serves as a useful illustration. Young pups are born blind and deaf, using olfactory cues learned in the womb to navigate to the mother's nipples after birth (Ronca et al. 1996). During the first postnatal days, pups are unable to thermoregulate, and huddle with their siblings to maintain optimal body temperature. Over time, their preferences narrow from any source of heat and tactile stimulation (regardless of whether this source is another rat, a different species, or a heated water bottle) to a strong preference for other rats (Alberts & Brunjes 1978). As they huddle with their siblings and mother, rat pups are learning the olfactory cues of their species (Alberts & May 1984). Early perceptual biases toward thermotactile stimulation therefore shape the emergence of species recognition.

Human infants are born with perceptual biases which enable them to organize their attention toward social stimuli. Through experience with their environment, they become increasingly specialized at attending to species- or culture-specific stimuli, a phenomenon known as perceptual narrowing (e.g., Lewkowicz & Ghazanfar 2009, Xiao et al. 2014, Krasotkina et al. 2018). This phenomenon is characterized by improvements in the ability to discriminate between stimuli of familiar types, such as the tones of their native language or different faces of their own race, with a corresponding decline in the ability to discriminate among stimuli with which they have little experience (Kelly et al. 2007, 2009). For example, only over time do infants learn to process upright faces more efficiently than inverted faces (Bhatt et al. 2005) and to prefer human faces over monkey faces (Pascalis et al. 2002). This perceptual narrowing is not universal but rather modulated by experience, as 9-month-old babies who were consistently exposed to monkey faces beginning at 6 months retained the ability to discriminate between them (Pascalis et al. 2005). Similarly, newborns show no preference for human speech sounds over rhesus monkey vocalizations, but develop this preference over the first 3 months (Vouloumanos et al. 2010). Infants also gradually

sharpen their ability to make fine discriminations between the phonemes of their native language (Kuhl et al. 2006), recognize typical phoneme combinations, determine word boundaries, and recognize their language's stress patterns (Saffran et al. 2006), while multilingual children maintain the ability to distinguish between a broader range of phonemes than do monolingual children (e.g., MacWhinney 2015). Such perceptual narrowing of faces and speech may serve to facilitate social communication.

As highly social animals, human infants must learn to effectively communicate with members of their particular social group. Through social interaction early in life, infants gradually learn to recognize familiar social stimuli (such as same-race faces and native language sounds), while losing the ability to interpret those of other social groups (Xiao et al. 2014). Immature perceptual systems, in combination with a socially situated niche, can thus give rise to species recognition and foster further social interactions.

**2.6.2.** Learning to communicate. Contingency is a crucial mechanism for the development of species-typical communication. Over the course of development, juveniles of many species produce immature-sounding vocalizations that may nonetheless elicit responses from conspecifics, such as parents or unrelated adult caregivers. In this context, contingency refers to a behavioral response from adults within a short time window (i.e., seconds) after a juvenile has vocalized. Parental contingency significantly improves juveniles' vocal learning outcomes.

The role of contingent responses in vocal learning was previously established in cowbirds (*Molothrus ater*) (King & West 1983). In this species, males use song to court a mate—therefore, learning a species-typical song is key for reproduction. Females contingently respond to especially potent song elements with small, rapid wing movements called wing strokes (West & King 1988). These responses are rewarding to the juvenile because they indicate female arousal, and are correlated with copulatory postures in the breeding season. Therefore, wing strokes reinforce production of the juvenile song type that elicited a wing stroke.

Recent findings indicate that contingent nonvocal responses also shape communicative development in the zebra finch (Carouso-Peck & Goldstein 2019). As the juvenile sings, the mother's arousal behaviors in response to more mature vocalizations shape song production in the direction of the father's song. Zebra finches share many life history traits with humans, including monogamy, biparental care of offspring, and the importance of learned vocalizations for social interactions (Goldstein & Schwade 2008), and may thus provide a tractable model for studying the communicative development of human infants.

Marmosets (*Callitbrix jacchus*) also possess social structures similar to those of humans, unlike other primate species, and display vocal learning abilities (Ghazanfar & Liao 2017). Vocal exchanges between marmosets, primarily to maintain contact while visually isolated in dense vegetation, exhibit coupled oscillator dynamics (i.e., turn-taking properties) similar to the conversation of humans (Takahashi et al. 2013). Turn-taking provides multiple opportunities for parents to contingently respond to the immature vocalizations of infants. Infants that receive a greater proportion of contingent parental responses to their vocalizations begin to produce mature-sounding contact calls much more rapidly than those with reduced contingent feedback, in both naturalistic (Takahashi et al. 2015) and experimental studies (Gultekin & Hage 2017). Parental responsiveness is therefore crucial for species-typical communicative development, to the extent that marmosets that experienced limited parental contact during early development continue to produce infantlike vocalizations as subadults (Gultekin & Hage 2017).

Contingency is also crucial for early social learning in humans. Infants who were given contingent vocal responses upon babbling incorporated the phonological patterns of their parents, while infants who received the same number of noncontingent responses did not (Goldstein & Schwade 2008). Moreover, efficacious contingent behaviors are not limited to vocal responses. After only 10 minutes of receiving nonvocal contingent responses upon babbling, such as smiling or being touched, infants increased the number and quality of their vocalizations, producing more mature-sounding syllables (Goldstein et al. 2003). These findings indicate that contingency is key in the early communicative development of infants as well as a variety of other species that share similar social structures.

**2.6.3. Predicting actions and intentions.** Why is contingency so effective for learning? The answer may lie in the predictability of the parent response to infant vocalizations. After exposure to the patterns of adult behavior during daily caregiving, young organisms might start to generate predictions about the probabilities of subsequent behaviors. For example, 10- to 11-month-old human infants can detect interrupted actions (Baldwin et al. 2001), as discussed above. This ability to pick up on statistical regularities of action patterns may thus translate into the generation of predictions about future actions from their social partners. However, only some infant predictions will be correct, and prediction errors may serve to guide attention and learning.

In nonsocial domains, discrepancies between prediction and observation can attract infant attention in an inverted-U-shaped pattern, with attention peaking at moderate levels of discrepancy (Kinney & Kagan 1976). Internally generated predictions about events may therefore direct infant attention toward stimuli that are neither too predictable nor too unpredictable. Correct predictions, which lessen the discrepancy between prediction and observation, reduce the learner's uncertainty about the world. These correct predictions are intrinsically rewarding, driving further exploration and generation of predictions, in a process known as curiosity-driven learning (CDL) (Oudeyer et al. 2007). An intermediate level of complexity is a moving target: Situations that seem impossibly complex at first may become learnable, and then overly simplistic as learning proceeds. Over time, the young learner monitors its own rate of incorrect predictions and strives to minimize them, maximizing learning progress. The neural mechanisms underpinning this intrinsic motivation to learn have been linked to the dopaminergic system, which encodes reward prediction errors (Bayer & Glimcher 2005). Intrinsic motivation stems from correct, rewarding predictions, as well as the desire to reduce uncertainty.

CDL serves as another mechanism of early information acquisition. Moreover, CDL may facilitate statistical learning, and vice versa. Infants preferentially attend to visual and auditory stimuli with intermediate levels of complexity (Kidd et al. 2012, 2014), which result in more rapid learning of visual sequences (Tummeltshammer & Kirkham 2013). In addition, objects labeled during predictable events, as opposed to events that violated predictions, are better recalled at test (Benitez & Saffran 2018). The interaction between predictable events and structured auditory input may thus enhance communicative development.

Beyond merely directing attention to statistical regularities, CDL has been implicated in other information-seeking behaviors. In a robot model of a young vocal learner, the intrinsic motivation to form correct predictions resulted in the self-organization of vocal development (Moulin-Frier et al. 2014). The model progressed from gaining control over its own vocal tract to trying to imitate a partner's vocalizations, demonstrating how CDL might guide the generation of novel vocal and social behaviors.

Despite the importance of CDL for learning in nonsocial domains, it has not yet been applied to social interactions. The social domain contains a high degree of structure, which creates opportunities for infants to generate and test predictions about the behavior of others. Although passive exposure to artificially generated speech is sufficient for learning in many experimental paradigms, infants are situated in a world rich with multimodal cues and social interactions. Thus, theories of early information acquisition must incorporate social learning. To date, at least one study on 9-month-old infants has investigated the interaction between statistical learning and parental responsiveness (M.H. Goldstein, S. Syal & J.A. Schwade, manuscript submitted). Here, infants learned a novel, nonnative syllabic structure only if parent vocalizations (a) contained sufficient phonological exemplars of the new form and (b) were contingent upon infant babbling. Parents may thus scaffold infant communicative development by modifying interactions to adapt to their infants' learning progress. For example, parents might selectively respond to more maturesounding vocalizations, thus promoting usage of these more mature vocal productions in infants, and changing the predictability of adult response (Albert et al. 2017). Given these features, the mechanisms of statistical learning and CDL appear promising for studying learning in the social domain, particularly for altricial species.

Understanding the intentions of others is considered a major developmental milestone in human infants, but is often studied without regard to these lower-level perceptual and learning mechanisms. We propose that statistical learning and CDL, both of which derive from observation of patterns in the environment, could scale up to produce social knowledge and enable the development of adaptive social skills.

Intentionality has been defined in a variety of ways. In general, the signaler has a goal and produces voluntary behaviors directed at a recipient in order to reach that goal, and these signals then change the recipient's behavior in such a way that the goal is realized (Townsend et al. 2016). Schel et al. (2013) outline criteria for intentional communication, including social use (e.g., the signal is produced only in the presence of a recipient), sensitivity to the attentional state of the recipient, manipulation of the attentional state of the recipient, and audience-checking to ensure that the signal is received (e.g., monitoring recipient, gaze alternation). Joint attention skills are not limited to humans. Other species with similar life history strategies as humans (e.g., cooperative breeding) demonstrate similar social abilities. For example, evidence for joint attention between conspecifics has been found in several primates (Whiten & Byrne 1988) and ravens (*Corvus corax*; Pika & Bugnyar 2011). Arabian babblers (*Turdoides squamiceps*), a cooperative breeding species, have recently been found to exhibit joint attention skills when communicating with members of their flock (Ben Mocha et al. 2019).

It may be easier to predict another's intentions after repeated observation of their behaviors. Routine patterns of motion are regularized, and repeated exposure to certain motions might lead infants to form predictions about behavior. For example, infants who are habituated to an actor repeatedly picking up a specific object expect that she will pick up the same object in the future, regardless of object location (Woodward 1998). Infants may not have learned the actor's goal, but instead may have learned the association between the actor's hand and an object. Similar explanations can be applied to more recent research involving anticipatory looking to failed reaches, often taken as an indication of early understanding of intentionality (e.g., Brandone et al. 2020). However, as in Baldwin et al.'s (2001) study, infants look longer at interrupted motions, which may be interpreted either as infants observing that the adult did not complete their goal or as infants demonstrating sensitivity to irregularities in otherwise predictable motions.

Attention allocation while observing social interactions need not rely on understanding of intentionality, but may instead result from low-level mechanisms. In a visual search task, participants were faster to find face-to-face target dyads as opposed to back-to-back dyads. Previous studies suggested that this is a result of perceiving face-to-face images as taking part in a social interaction, which leads to priority in processing (e.g., Papeo et al. 2019). However, reexamination of the effect of the stimuli in these visual search tasks leads to a different conclusion. Face-to-face dyads of entire bodies, faces only, or even arrows pointing at each other all result in comparatively faster localization than dyads composed of back-to-back figures or arrows pointing away from each other (Vestner et al. 2020). Vestner et al. (2020) suggest that salient directional cues influence attention. Two individuals facing each other (or two arrows pointing at each other) create a visual hot spot that attracts attention more efficiently than dyads indicating opposing directions. Rather than requiring the innate ability to recognize social interactions and process them with greater efficiency, we can achieve the same result from low-level sensory input and attentional cues.

Salient directional cues that attract attention can result in differences in learning outcomes, including social learning. Infants observe the probabilistic actions of social partners and from those actions can track statistical regularities, learning their reliability (Tummeltshammer et al. 2014). Once they have learned the reliability of social partners, this leads to differences in attention, as infants prefer reliable informants. Extending the results beyond human social partners, Tummeltshammer et al. (2014) found a similar pattern when infants were cued by reliable or unreliable arrows. Instead of assigning attention and speed of processing to inherently "social" stimuli, infants may instead be attending to information on the basis of their familiarity with the statistical regularities of their interaction partner, which leads to subsequent differences in learning.

## 2.7. Infants Play an Active Role in Their Own Development

Although this review has so far focused on the importance of adult response to juvenile vocalizations in shaping subsequent juvenile behavior, the link between parent and offspring is bidirectional: Infants can alter the behavior of adults. By doing so, offspring can actively influence their own development.

Altricial species might compel parents to pay more attention to the changing needs of their infant, as the requirements of offspring (e.g., provisioning) will change as they mature. Comparative research furnishes evidence that infant vocalizations can shape parental response. Meerkats (*Suricata suricatta*) are sensitive to the acoustic maturity of pup begging calls (Thornton & McAuliffe 2006), and they provision pups with prey items at the appropriate level of difficulty (providing live versus dead scorpions). Infants also play an active role in their own communicative development by changing the behavior and vocalizations of adults around them. The development of alarm calls in vervet monkeys (*Cblorocebus pygerythrus*) is facilitated by adult responses. Infant vervets produce alarm calls in response to a wide variety of stimuli, and only gradually learn to sharpen the association between predator species and alarm call type (Seyfarth & Cheney 1986). When infants correctly produce an alarm call, adults rarely (5% of the time) respond. This selective response from adults appears to serve as a reinforcement of the infant's association between call type and predator identity (Seyfarth & Cheney 1986). Applying these lessons to communicative development in human infants can provide valuable insights.

In general, immature appearance and behavior can elicit specific responses from adults, driving predictable changes in behavior. Infant attention is captured by certain kinds of vocalizations, reinforcing altered vocal production from adults toward their offspring. For example, female greater sac-winged bats (*Saccopteryx bilineata*), a species with vocal production learning, direct vocalizations to their pups that have different timbre and pitch compared with vocalizations directed toward other adults (Fernandez & Knörnschild 2020). Zebra finches also produce pupil-directed song that results in increased juvenile attention (Chen et al. 2016). Juvenile attention to pupil-directed song was positively correlated with their song learning outcomes. Similarly, human infants elicit changes in adult behavior. Infant-directed speech (IDS) is characterized by shorter utterances, slower speaking rate, longer pauses, higher absolute pitch, and increased pitch variability (Fernald et al. 1989). Infants show a robust preference for IDS over adult-directed speech (Cooper & Aslin 1990), and IDS, as opposed to adult-directed speech, serves to maintain infant attention to visual targets (Kaplan et al. 1995). Moreover, IDS enhances infant speech perception (Liu et al. 2003) and word segmentation (Thiessen et al. 2005). By changing the acoustic properties of speech and simplifying its structure, parents capture infant attention and facilitate word learning. The production and quality of IDS are influenced by infant appearance and behavior. Mothers who received positive reinforcement (via the reaction of a simulated infant) to higher-pitched IDS began producing IDS of a significantly higher pitch than did mothers who received positive reinforcement for lower-pitched IDS (Smith & Trainor 2008). Infants thus actively modify their auditory environment through their own behaviors.

In addition to the neotenic appearance of the infant as a driver of adult behavior, immature behaviors, such as babbling, cause parents to change their behavior in structured and predictable ways. The linguistic structure of parents' speech to infants is modified when responding contingently to infant babbling. Contingent speech has shorter utterances and fewer unique utterances than noncontingent speech, with the overall result of simplifying statistical and syntactic structure (Elmlinger et al. 2019). This simplification might make it easier for infants to learn from adult speech.

As infants develop, they begin to gain greater control over their vocal tract. By 9–10 months of age, infant vocalizations that contain more mature-sounding, developmentally advanced vowels receive more frequent responses from caregivers than those that do not (Albert et al. 2017). Early communicative development relies on infants learning the social efficacy of their behaviors—that vocalizations are associated with a response from caregivers. Even 5-month-old infants are aware that their parents react in ways that are contingent on their vocalizations. When parents cease responding to their vocalizations during a still-face paradigm, infants rapidly increase their vocalization rate (Goldstein et al. 2009). This increase in vocalizations suggests that infants have learned the efficacy of their babbling for eliciting parental response.

In summary, infants can leverage mechanisms such as statistical learning and CDL to learn the social structure of their world and generate predictions about the behavior of others. Infant behaviors influence parental responses, while contingent parental responses facilitate subsequent infant learning in a variety of domains, including communicative development. Altriciality, therefore, can be regarded as an evolutionarily developed strategy for social learning. Comparative research, especially on species that have life history strategies similar to those of humans (e.g., slow development, biparental care, and learned vocal communication), can shed light on different aspects of our own social development.

# 3. LESSONS FROM COMPARATIVE RESEARCH FOR STUDYING HUMAN INFANTS

## 3.1. Altriciality, as an Evolutionary Strategy, Outsources Information to the Social Environment

The constraints on sensory, motor, and cognitive systems imposed by altriciality suggest that we should focus on the efficacy of structure in physical and social environments to enable infants to exploit regularities and facilitate learning. Language, for example, has highly predictable regularities, from syllable structure to turn-taking. Many aspects of social interactions are fairly predictable and also highly conducive to learning, such as gaze for directing attention (Ruffman et al. 2011). Such predictability, and the resulting social learning, can also be observed in patterns of parental response to infant behaviors such as crying, gesturing, and vocalizations. Integrating developmental data across many altricial species indicates that evolution has outsourced the information critical for survival to the social environment (e.g., caregivers).

An altricial infant possesses neural and behavioral systems that expect certain experiences (cf. Greenough et al. 1987) and is prepared to learn in a world that has predictable structure. The nervous system relies on ubiquitously available stable environmental information to construct

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itself. A key example from animal behavior is the effect of gravity on rat pup geotaxis (the ability to distinguish up from down). When rat pups underwent gestation in the zero-gravity environment of space, they did not exhibit the self-righting behavior observed in controls just after birth (Ronca et al. 2008). The inability to perform this crucial adaptive behavior was the result of the pups lacking the expected gravitational experience during prenatal development that their system required. Similarly, Gottlieb (1971) found that prenatal exposure in mallard chicks was crucial for appropriate species recognition and call preferences. When the expected information (species-specific calls, and the chick's own vocalizations) was manipulated, the chicks developed maladaptive preferences. Exposure to their own vocalizations was sufficient to block the ambient exposure of non-species-specific calls, but prevented them from forming preferences for their own species vocalizations. The chicks' auditory system requires exposure to their own vocalizations as well as that of conspecifics to form appropriate preferences.

Plasticity is a ubiquitous characteristic of the brain and should be central to how we understand development at a behavioral level. The function of an experience-expectant system is to leverage the environmental structure of the developmental niche, as well as to alleviate the necessity of predetermined capacities or behaviors that could be potentially costly in a dynamically changing environment. Altricial species expect a responsive social environment at the genetic, neural, perceptual, and behavioral levels of organization.

## 3.2. Parent-Offspring Systems Can Drive Learning

Provisioning of information by parents is a direct result of selection for altriciality and outsourcing information for survival to the environment. Altricial infants necessarily do not exist in social isolation: They are born with the expectation of experience in an informationally rich social environment. As such, it is crucial to study the parent–offspring system as a unit to reach a complete understanding of development. This lesson has recently revolutionized the study of songbirds, the most ubiquitous model for vocal learning in humans. Zebra finches were typically thought to learn passively from ambient song, as opposed to needing active social feedback. However, recent research has shown that to learn fully formed, high-quality song, zebra finches need information from both the mother and the father (Carouso-Peck & Goldstein 2019).

The parent–offspring system allows for dynamic, bidirectional interactions driven by the needs and responses of both parent and offspring. Parents provide appropriate and predictable feedback to their developing infant, and, in turn, infants use their perceptual biases for statistically reliable events to gather information. As infants grow and develop their needs change, and the flexibility of the bidirectional parent–offspring system facilitates scaffolding of information and social experience. Such a bidirectional feedback system is evident in the explanation of theory of mind put forth by Ruffman et al. (2011). These authors propose that the apparent ability of infants to understand intentionality is not, as previously thought, the result of a preexisting capacity to understand the contents of another person's mind, but instead has its roots in the perceptual ability of infants to extract relevant statistical information and form predictions about their social environment. Discrimination between biological versus nonbiological motion, and between the faces of strangers and those of parents, as well as early language recognition are all part of the infant's developing perceptual biases that enable such rapid learning.

### 3.3. Infants Are Active Social Learners

Traditionally, a reliance on social feedback as a mechanism of learning implied that infants had limited influence on the social forces that shaped them (e.g., Skinner 1981). However, more recent

research on the ability of infants to actively shape their environment indicates that this is not the case. For example, infants' babbling elicits different responses from their caregivers in ways that facilitate learning (Elmlinger et al. 2019). Infants, while constrained by poor motor control, are nonetheless actively engaging with their environment and shaping their own learning.

The perceptual ability to exploit statistical regularities in their environment in ways that guide further attention and learning is not limited to early auditory experience (Kisilevsky et al. 2009) but also characterizes early visual preferences, such as the ability to discriminate between biological and nonbiological motion. Adult cats, chicks, and 2-day-old infants can all discriminate between biological and nonbiological motion (Blake 1993, Vallortigara et al. 2005, Simion et al. 2008), and prefer to observe biological motion. This predisposition for sensitivity to motion patterns may provide infants with expectations that result in apparent understanding of intentionality (Ruffman et al. 2011). Infants can also actively influence their learning opportunities through attending to their caregiver's voice and directing their gaze toward faces, which are a vital source of social information. These attentional redirects by the infant in turn facilitate scaffolding by the parent via contingent speech, gestures, and gaze.

Infant learning is facilitated by information foraging, which is driven by predictable events. For example, infants learn to follow the gaze of their caregivers, since gaze can serve as an indication of interesting or salient items (Deák et al. 2014). In addition to visual information foraging, infants can elicit social information via their vocalizations (Elmlinger et al. 2019). Parents simplify the structure of their speech in response to infant babbling, which may facilitate early language learning. The highly predictable nature of language continues to be leveraged into adulthood. Statistical sensitivity serves as an important part of language processing and results in cognitive entrenchment of regularities in adults (Goldberg 2008). The prevalence of statistical learning in communicative development indicates that it also needs to be investigated in infants.

#### 3.4. The Information Content of Parental Behavior Requires Closer Study

Our comparative perspective, emphasizing the needs of altricial young, requires a deep understanding of parental behavior. How do parents know what information to provision to their infants? How is human parental responsiveness shaped by development and evolution, and what are the implications of cross-cultural variation in parental behavior for infant learning? Mechanisms of human parental behavior have received far less attention than infant development. As a starting point, we propose that the information content of parental behavior is best understood from the infant's perspective. Most assessments of parental behavior, however, rely on global or descriptive ratings, such as Baumrind's (1971) parenting styles, emotional availability scales (Pipp-Siegel & Biringen 1998), and maternal sensitivity scales (Bretherton 2013). These broad ratings have predictive power for broad outcomes (e.g., school achievement). But these global descriptors do not directly inform opportunities for infant learning. Characterizing learning in the parent–offspring system requires that we understand the information content of parental behavior with respect to infant learning mechanisms.

A focus on information requires a microanalytic approach, analyzing small, specific behaviors, such as contingent speech, eye gaze, and gesture, that operate on the same timescale as infant learning. Taking a microanalytic approach to learning has recently revolutionized the study of vocal learning in zebra finches, with the finding that rapid contingent behaviors from mothers change the learned song structure of their sons (Carouso-Peck & Goldstein 2019). Since the ability of infants to perceive and organize social information changes over development, there may be nonlinear relationships between the amount of parental behavior received and infant learning. For example, more contingent responses to infant behavior are not necessarily better for learning.

Higher levels of contingency may be rated as less sensitive (Bornstein & Manian 2013) and may not be conducive to maintaining infant attention if parental behavior becomes too intrusive or too predictable to engage CDL. Useful social feedback may be salient to the learner because of its rarity; female wing stroke feedback to young cowbirds occurs only once per 90–100 immature songs (West & King 1988), and in humans the everyday social interactions that facilitate language learning are punctuated by periods of silence (Tamis-LeMonda et al. 2017) and characterized by visual referential clarity (Suanda et al. 2019) and brief bouts of joint visual attention (Abney et al. 2017). Such peak moments of interaction create salient signal-to-noise ratios of social information. Further investigation of the forms and timing of moment-to-moment interactions is needed to determine the fit between parental behavior and infant learning mechanisms.

In conclusion, a comparative approach to the development of communication and social learning finds that influences from multiple levels of organization are required (**Figure 1**), but predetermined knowledge about the structure of the world is not. In altricial species, social learning and development are grounded in structured and scaffolded social interactions. The highly flexible, bidirectional nature of the parent–offspring system offers valuable insight into the mechanisms by which infants acquire information and solve the challenges of the social niche.

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## Errata

An online log of corrections to *Annual Review of Developmental Psychology* articles may be found at http://www.annualreviews.org/errata/devpsych