

Shaping the development of complex social behavior

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Abstract

Early life experiences can have an enduring impact on the brain and behavior, with implications for stress reactivity, cognition, and social behavior. In particular, the neural systems that contribute to the expression of social behavior are altered by early life social environments. However, paradigms that have been used to alter the social environment during development have typically focused on exposure to stress, adversity, and deprivation of species-typical social stimulation. Here, we explore whether complex social environments can shape the development of complex social behavior. We describe lab-based paradigms for studying early life social complexity in rodents that are generally focused on enriching the social and sensory experiences of the neonatal and juvenile periods of development. The impact of these experiences on social behavior and neuroplasticity is highlighted. Finally, we discuss the degree to which our current approaches for studying social behavior outcomes give insight into “complex” social behavior and how social complexity can be better integrated into lab-based methodologies.

KEYWORDS

development, neuroplasticity, parental, peer, postnatal, social complexity

INTRODUCTION

The neural systems that contribute to social behavior are shaped by genetic variation, environmental influences that occur throughout the lifespan, and the interplay between these factors.¹ Consequently, there exists both within-species and between-species variation in social behavior that can shift in response to broad environmental cues.^{2–5} Similar to sensory/perception systems, which are fine-tuned by the experience of visual, auditory, gustatory, olfactory, and tactile stimuli,^{6–8} the social brain and behavior is shaped by social experiences, many of which include these primary sensory stimuli. For most species, development occurs within the context of parent–offspring interactions which vary in duration, frequency, and complexity and illustrate how variation within the early social environment can impact brain development and behavioral phenotypes. This phenomenon is illustrated by studies in rodents of the impact of natural variations

in maternal care during the postnatal period on offspring social and reproductive behavior.^{9,10} Caregiving behavior in humans is similarly implicated in the process of scaffolding the development of neural systems that regulate emotional responses and social competence.¹¹ Thus, given the plasticity in neural systems during early life, this period is a window of development during which the social environment can exert lasting effects on social behavior.

Exploration of the impact of early social experiences on the social brain has relied on experimental manipulation or detailed characterization of these experiences. Though human neuroimaging approaches are increasingly being applied to further identify brain regions and circuits that are shaped by the social environment, these studies are primarily correlational. Experimental analyses of these systems have relied heavily on the study of lab-based social species, particularly rodents, in which cellular/molecular analyses of the brain are combined with behavioral phenotyping.⁵ However, the experimental study of the

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influence of early life social environments has focused primarily on deprivation/adversity rather than on enhancement of the social environment. Moreover, the definition of social behavior within studies of the impact of the social environment is very broad, ranging from tests of dyadic approach–avoidance (“simple”) to dynamic changes in social interactions in group-living animals that consider temporal, relational, and contextual factors (“complex”). A critical question that emerges from this literature is whether complex social environments can shape the development of complex social behavior. To answer this question and highlight future directions of research in the field, this review will explore the lab-based paradigms for studying early life social complexity, the methodological approaches to assessing social behavior and whether these methods give insight into complex social behavior, and describe the neural systems that likely mediate the relationship between early life social environments and social behavior.

PARADIGMS FOR STUDYING EARLY LIFE SOCIAL COMPLEXITY

While there is an extensive literature on the impact of early life environments on developmental and adult neurobehavioral outcomes, these studies have primarily focused on the deprivation of social interactions (e.g., isolation) or exposure to a broad range of stressors that impact the quality of those social interactions. In laboratory rodents, these approaches include maternal separation, maternal exposure to stress (e.g., restraint, chronic variable stress, and predator odor), limited bedding and nesting, and social isolation at weaning.^{12–15} These manipulations of the social environment typically result in increased stress reactivity, impaired cognitive functioning, and decreased social behavior. There are parallels between these outcomes and the impact of peer-rearing compared to mother-rearing in lab-reared rhesus macaques.¹⁶ In humans, these models may approximate the experience of institutionalized rearing, where basic physical needs are met but social interactions during infancy are low in frequency and consistency.¹⁷ Overall, studies using these paradigms suggest that in the absence of social interactions during development, there are global impairments in functioning that include disruption to the formation of social bonds that support later life social behavior. However, these approaches do not explore the impact of early life social complexity.

A critical feature of socially complex environments is the shift from a standard environmental experience to one that more readily captures the ecological features of the environments in which development would typically occur for the species being studied.^{18,19} The rearing conditions of laboratory animals are designed to standardize the experience of animals and facilitate monitoring by facility staff. This is achieved by the utilization of cage sizes that limit exploratory behavior, the use of bedding material that maintains cage cleanliness and the ability to monitor animals, and housing conditions in which a single dam and litter are present during the postnatal period and/or weaning with a small group of same-sex individuals. Thus, complexity involves adding sources of variation in the experience of lab animals that mimic

the highly stimulating environments that might occur in the natural world. It should be noted that implementation of this complexity may require careful consideration of the dynamics of welfare monitoring by animal facility staff. Here, we will consider several lab-based, early life environmental manipulations that are designed to capture some elements of social complexity, including (1) neonatal handling, (2) fostering, (3) communal rearing, (4) biparental rearing, (5) environmental enrichment (EE), and (6) postweaning social exposure.

Neonatal handling

Neonatal handling of rodent pups was developed as a form of early life tactile stimulation that involves brief separations of pups from the dam.²⁰ Though there is variability in the duration of separation (typically less than 15 min) as well as the conditions experienced during separation (e.g., use of heating, litter vs. individual pup housing), neonatal handling is generally considered a robust strategy for increasing the levels of dam–pup interactions.^{21,22} In particular, levels of pup-directed licking/grooming (LG) increase following neonatal handling. This increase is not compensating for any loss of LG experienced by pups as the short period of absence from the nest during handling is quite typical of normative dam–pup interactions. For the neonatal pup, LG serves immediate developmental needs, including the promotion of urination and defecation.²³ Natural variations in maternal LG have been observed within lab-reared mice and rats that occur even in the absence of genetic variation.^{10,24} Cross-fostering studies support the conclusion that the experience of low versus high levels of postnatal maternal LG has broad developmental programming effects through epigenetic changes within genes that regulate neuroendocrine functioning.^{25,26} Though high levels of LG can occur within litters that are unmanipulated, the shift toward high LG can be observed within handled litters as well as other models of early life social complexity.^{21,27} Moreover, female rodents that experience EE during adolescence exhibit elevated LG toward pups suggesting that increased tactile stimulation may be a critical mechanism driving the effects of socially complex environments.²⁸ Other manipulations have also been used to elevate levels of LG by rat dams, including applying palatable food stuffs to individual pups.²⁹

Fostering

Though laboratory rodents can differentiate between pups within a litter and between their own and other litters, in most cases, postpartum females will display caregiving behaviors toward any neonate that they are cohoused with during the postnatal period.^{30–32} Fostering manipulations involve transferring litters or individual pups from their biological dam to another dam immediately following parturition, though delayed fostering may also be used to explore sensitive periods during development.³³ Dams engage in increased maternal LG in the period immediately following cohousing with fostered pups, and studies in rats suggest that this response to fostering is limited to the

first week postpartum and corresponds with a decrease in ultrasonic vocalizations by fostered pups.³⁴ Fostering has been used to examine how strain or species differences in maternal care such as nursing and LG shape offspring outcomes, typically by fostering pups to dams that exhibit robust differences in the frequency of maternal behavior compared to the biological mother of the pups.^{35,36} Fostering has also been used to study whether postnatal maternal care can shift behavioral phenotypes in rodents with genetic, pharmacological, or virally induced social behavior deficits.^{37,38} A cross-fostering design, in which there is an exchange of litters/pups between dams, is also a typically used paradigm to dissociate the impact of the postnatal rearing environment from prenatal or genetic influences on developmental outcomes.³⁸ Litter sizes are often standardized during cross-fostering as variations in litter size are known to affect developmental outcomes in rodents through shifting parental behaviors and interactions between littermates.³⁹ Though cross-fostering has been used to investigate the role of maternal behavior in shaping offspring development, it should be noted that fostering can lead to unintended outcomes on offspring physiology, including shifts in body weight, metabolism, and cardiovascular outcomes.^{38,40}

Communal rearing

The communal care of young is a common rearing strategy for many species.⁴¹ In the laboratory, inbred and outbred female rodent dams will readily form communal nests.^{27,42} Lab-based communal nests typically include three dams placed into a new cage with three litters on the day of parturition.²⁷ These litters are typically nonbiological offspring of the dams, with the comparison group being fostered offspring reared by a single dam. Similar to fostering, increases in LG are typically observed during the period of nest formation, during which time the dams form a single nest within the cage.²⁷ In addition to elevated levels of maternal stimulation of pups, this early life manipulation allows for higher levels of social interaction with peers throughout development until weaning. Pups reared in communal nests also experience enhanced thermoregulation due to a large number of pups, and concomitantly, communal dams exhibit reduced nestbuilding compared to dams rearing litters under standard environmental conditions.²⁷ A variant of the communal rearing paradigm is to have three dams rearing pups that differ in age by a few days. Using this approach, it has been shown that the youngest litters tend to receive the highest levels of LG from dams, while the oldest litters receive higher nursing by dams.⁴³ Communal rearing paradigms using just two lactating dams rather than three have also been used within laboratory studies.⁴⁴

Biparental rearing

Approximately 6% of rodent genera exhibit some form of biparental care where both parents (mother and father) contribute to the rearing of offspring.⁴⁵ These species tend to be monogamous with strong mate bonds. In the laboratory, several studies have examined the

consequences of rearing offspring biparentally compared to rearing conditions where the father is absent. Variation in overall parental care can also be observed in biparental rearing conditions. Lab-based studies of biparental rearing have typically used the following species: prairie vole (*Microtus ochrogaster*), mandarin vole (*Microtus mandarinus*), California mouse (*Peromyscus californicus*), Campbell's dwarf hamster (*Phodopus campbelli*), Mongolian gerbil (*Meriones unguiculatus*), and Common degu (*Octodon degus*). The importance of social stimulation provided by fathers is most commonly examined by comparing biparentally reared offspring to those reared by single females without the male present. Among biparental species, the absence of the father results in significantly less social stimulation of the litter.⁴⁵ Fathers may also stimulate contact between offspring and both parents indicating that the presence of both parents is more than additive.⁴⁶ Biparental rearing has also been observed in laboratory mice that are not generally considered a biparental species. In these paradigms, pups are born to dams who have cohabited with the father since copulation. In such cases, fathers contribute additional caregiving and pup social stimulation, and may even be stimulated to do so through communication with the dam.^{47,48}

Environmental enrichment

EE encompasses a variety of sensory, physical, social, and cognitive stimulations relative to standard housing conditions. Enrichment has commonly been applied to adult laboratory animals to improve welfare and promote naturalistic species-typical behavior.⁴⁹ It is also utilized following exposure of individuals to stressors or in animal models of disease to foster recovery of impaired phenotypes.⁵⁰ There is a long history of housing rodents of many species in EE to investigate neural and behavioral plasticity in adult and aged animals.^{51,52} EE has also been used to examine developmental plasticity, with enrichment typically occurring during the postweaning adolescent period.⁵³ Most frequently, animals reared in EE are compared to standard-housed animals and/or socially isolated animals. There exists a great variety of different EE approaches, although it appears that environmental complexity and novelty are two key features that induce maximal plasticity.⁵⁴

Social exposure

Though increased social interactions are typically included in EE, there are paradigms that focus exclusively on examining the developmental effects of increased opportunities to form social relationships. These paradigms generally involve increasing group size or cohousing animals with individuals who vary in their social behavior.⁵⁵ For example, in mice, "cross-housing" is a procedure where individuals are housed from weaning either with their own or other strains of mice that differ in social behavior.^{56,57} This procedure enables the study of how variations in postweaning social dynamics shape behavioral development. This procedure differs from cross-fostering in that the housing

with other strains occurs postweaning rather than during housing with dams. Animals may be singly or repeatedly provided with access to other conspecifics. These experiences may involve increased opportunities for engaging in social play, a common behavioral feature of all developing mammals, as well as increasing olfactory and other sensory exposures to social stimuli.⁵⁸ Play interactions during this period are largely rewarding for the young of most species.⁵⁹ Another approach to social exposure is to focus on olfactory enrichment, where animals have extended duration of exposure to olfactory stimuli from social conspecifics, providing animals from birth with access to a variety of novel social odors.⁶⁰

MEASURES OF SOCIAL BEHAVIOR: FROM SIMPLE TO COMPLEX

Social behavior encompasses a broad range of behaviors that change over developmental time and include affiliative, agonistic, associative, sexual, parental, and juvenile interactions between individuals. These behaviors are highly dependent on sensory/perception systems, emotion regulation, and cognitive abilities, particularly those involved in sensory discrimination and memory. Table 1 provides an overview of the tests typically used in lab-based studies of rodent social behavior. It should be noted that though these tests are typical within the social behavior literature, the degree to which these tests assess “complex” social behavior is debatable.^{61,62} Social behavior tests are often very short-term examinations of social behavior with brief durations of assessment that provide a snapshot of behavior that lacks analyses of trajectories over developmental time. In addition, standard social behavior tests investigate the behavior of individual animals toward a social stimulus or two animals interacting in dyads. This approach limits the capacity to understand the social behavior of individuals within larger social contexts.¹⁸ Social behavioral tests are often conducted with animals who are experimentally naive to each other and, therefore, do not have a relationship history. Thus, there may be confounds with these social assessments and general response to novelty. Moreover, these tests do not provide insights into the formation and maintenance of social relationships over time, which serve as a critical feature of social functioning.^{63,64} Finally, standard tests of social behavior typically rely on the comparison of mean differences in the frequency or latency of behavior rather than the temporal patterns of behavior that are a feature of complex social responses.⁶⁵

Efforts to shift social behavior analyses of laboratory rodents to capture the dynamic and complex features of social functioning have utilized several approaches that focus on technological advances in the tracking and quantification of behavior. There has been increasing emphasis within the social behavior literature on detailed observations of behavior in large groups across longer periods of time for a wider variety of species.^{18,66} These approaches have largely been facilitated through the utilization of more complex housing systems to improve ethological validity and the ability to track the movement and behavior of individual animals over long periods through Radio Frequency Identification (RFID) tracking, video tracking, and

pose estimation. For example, housing rats and mice in large groups in enriched environments with detailed behavioral observations have shown that both male and female animals will form highly linear dominance hierarchies.^{63,67} Within these hierarchies, individuals have unique social ranks and show flexible patterns of dominant and subordinate behavior toward other individuals. Similarly, housing naked mole-rats in large laboratory housing systems allows this species to recapitulate social features of the subterranean colonies inhabited in the wild, including a high degree of social role specialization.^{68,69} Methods that combine RFID and computer vision tracking with pose estimation and machine learning enable a much higher resolution of behavioral assessment across multiple animals.⁷⁰ These approaches can determine social configuration events (e.g., the number of animals in nests or groups, or trains of moving animals), events in dyads (e.g., how animals approach, investigate, and break contact from each other), or group dynamics (e.g., how animals form or dissolve groups). Data acquired from these approaches enable the characterization of group-level differences in social behavior and the assessment of how social relationships (agonistic and affiliative) develop over time.

Though transitioning to strategies for assessing complex social behavior may ultimately lead to a more nuanced understanding of the social brain and behavior, there are significant obstacles to this transition. Housing laboratory animals in large complex environments may not be feasible in all animal facilities. Also, automated video tracking methods may impose constraints such as (i) type of caging system used, (ii) need to mark animals, (iii) total number of animals that can be tracked, (iv) computational power required to collect data, and (v) which specific behavioral parameters can be extracted. Moreover, a growing issue with high-throughput, long-term studies is how to interpret the vast quantities of social data that can be collected. There is a need to develop statistical approaches and methodologies that facilitate an understanding of typical or atypical patterns of social dynamics over time.⁶⁴ Although there have been several attempts to identify specific social behavioral phenotypes from such data (e.g., simBA⁷¹), this is an ongoing challenge for social behavior researchers. The approaches that have been developed are typically focused on adult social behavior and so there is also a need to develop tools that can be used at earlier developmental timepoints. Despite these constraints, there is a growing community of researchers who are developing tools to enable complex social behavior to be better represented in the literature.

SOCIAL BEHAVIOR OUTCOMES ASSOCIATED WITH EARLY LIFE SOCIAL COMPLEXITY

The paradigms of early life social complexity that have been described typically induce broad developmental changes that last into adulthood. Though the assessment of complex social behavior has yet to be integrated into most of these studies, there is evidence for the impact of these early life experiences on the expression of a broad range of behavioral outcomes related to social behavior. Here, we will highlight findings suggesting that socially complex environments experienced in early life can shape the emergence of social behavior. The emphasis will

TABLE 1 Typical tests of social behavior in laboratory rodents.

Behavioral domain	Age at testing	Name/description of test	Refs
Social communication	Neonatal	USV production (during isolation or with dam/litter); maternal potentiation of USV calls (increased production of USVs following second isolation from dam)	201, 202
Social preference	Neonatal	Homing social odor preference (orientation toward home-cage vs. unfamiliar odors)	203
Social affiliation	Neonatal	Huddling (proximity during group-housing with littermates)	204
Social memory	Neonatal	Homing social odor discrimination (ability to differentiate home-cage vs. unfamiliar odors)	205
Play behavior	Juvenile	Rough and tumble play (including darts and hops)	173, 206
Social communication	Juvenile and adult	USV production in response to social odors or interaction	207, 208
Social affiliation; social preference	Juvenile and adult	Social preference test; Social approach-avoidance test; Sociability test; Three-chamber test; Social novelty preference test; Partition test (propensity of animals to investigate novel social partners, or preference for familiar vs. unfamiliar social partners, without contact)	209–211
Social affiliation; social aggression	Juvenile and adult	Dyadic social interaction tests with same-age, same-sex conspecifics	212
		Semi-natural or home cage monitoring of affiliative and agonistic interactions in group-housed animals	63, 213, 214
Social avoidance	Juvenile and adult	Social avoidance test (inhibition of investigation of a social partner without contact)	215
Social memory	Juvenile and adult	Social discrimination/recognition of social odors or social partners	216
Social memory; social reward	Juvenile and adult	Conditioned place-preference (conditioning to a context associated with social cues compared to nonsocial cues or opportunities for aggression)	217, 218
Alloparental behavior	Juvenile and adult	Retrieval, licking/grooming, crouching, and time spent in contact with neonatal pups; nestbuilding	219
Social aggression	Adult	Resident-intruder test (territorial aggression; individuals defend their homecage from intruder social stimulus)	220
Social aggression; territoriality	Adult	Scent marking (scent-mark countermarking over other individual's scents)	221
Social dominance	Adult	Dyadic agonistic interactions; Tube test; Warm spot test (competitive abilities in dyadic encounters leading to the formation of dominant–subordinate relationship)	222, 223
Social hierarchy	Adult	Dominance hierarchy formation (assessment of agonistic interactions between group-housed individuals; assess the formation and maintenance of hierarchy)	63, 224
		Social opportunity (ability to socially ascend in a hierarchy following removal of the dominant individual)	225
Social stress	Adult	Social defeat (social avoidance induced by the experience of social aggression/stress)	226
Social bonding	Adult	Partner preference (formation of a selective social affiliation with a mating partner in monogamous rodents)	227
Social learning	Adult	Social transmission of food preference (learning to prefer a novel food from social partners)	228
Social learning; empathy	Adult	Emotional contagion (altering affective state in response to social partner distress); observational fear learning (fear conditioning through observation)	229
Altruism	Adult	Spontaneous helping behavior toward conspecific in the absence of any reward; consolation behaviors to social partners after partner has experienced distress	230, 231

Abbreviation: USV, ultrasonic vocalization.

be on social behavior outcomes that occur outside of the context of reproduction.

Neonatal handling and increased maternal LG

Neonatal handling has been shown to decrease the propensity for social interaction in adult dyadic social tests and increase aggression levels in male but not female rats.⁷² Handling may also enhance social recognition memory in adulthood,⁷³ although other studies suggest no effect of handling on social memory.⁷² Studies of the impact of maternal care on social play can vary depending on the characterization of maternal care and the nature of the play interactions. Within individual litters in rats, higher levels of stimulation of rat pups have been associated with increased social play in males,⁷⁴ and in mouse litters, higher levels of preweaning LG are associated with increased affiliative social play.⁷⁵ Similarly, prairie vole offspring of high-contact dams spend more time socially investigating a novel juvenile partner.⁷⁶ In contrast, low levels of LG experienced by mouse offspring are associated with increased levels of social play,⁷⁵ particularly play dominance behavior, an effect similarly observed in male and female rat offspring.^{77,78} Moreover, experimental manipulations that reduce rat dam LG can also lead to increases in play dominance behavior.^{79,80} Adult offspring of high LG rat dams spend more time in social contact with an unfamiliar individual in a dyadic social interaction test.⁸¹ Finally, male adolescent offspring of highly maternal rat dams have been shown to be more likely to show helping behavior toward conspecifics in a test of empathic behavior.⁸² Prairie voles that experience early handling display higher levels of juvenile alloparental behavior and are more likely to form species-typical partner preferences to sexual partners as adults in contrast to those that do not experience handling.^{83–85} Collectively, these studies suggest a strong modulating influence of early life stimulation and maternal care on the emergence of social behavior.

Postnatal fostering effects on social behavior

Classic studies of fostering between closely related rodent species demonstrate that olfactory and social preferences for the same species as well as aggression levels can be modified via cross-fostering.³⁸ Fostering between mouse strains leads to subtle changes in female olfactory preferences in adulthood and induces changes in the expression of mouse strain-specific chemosignals, suggesting that early environments that have more olfactory complexity can lead to the development of enhanced olfactory processing with implications for social behavior.⁸⁶ Auditory preferences of mice for songs of different strains can also be reversed by cross-fostering, demonstrating that early environments may also shape auditory abilities.⁸⁷ In mice and rats, strain or species-specific patterns of social interaction and aggression can be modified via cross-fostering when these strains differ in maternal care.^{37,88–91} For example, the spontaneously hypertensive rat (SHR) strain exhibits higher social interactions with conspecifics compared to rats of the Wistar-Kyoto (WKY) strain; however, both

strains show social patterns typical of their maternal foster strain when cross-fostered.⁸⁸ These studies illustrate the postnatal plasticity of sensory/perception and behavioral systems involved in social interactions.

Social behavior in communally reared offspring

Studies exploring the impact of communal rearing on social behavior outcomes have primarily focused on laboratory mice, though these effects may be similarly observed in rats.⁹² Outbred mice reared in communal nests appear to have elevated social competencies in adulthood. In social behavior tests where males are paired with the same rearing condition conspecifics, communally reared offspring more rapidly establish dominant–subordinate relationships.^{43,93} Further, communally reared mice engage in higher levels of social investigation and affiliation once a social hierarchy is formed.^{43,93,94} These effects of communal rearing on social competence appear to be a consequence of both enriched maternal and peer interactions.⁴³ Communally reared Balb/c female mice are quicker to retrieve pups and show higher levels of nursing and LG as adults.⁹⁵ In response to an intruder male during a lactational aggression test, these communally reared females display more submissive behavior and reduced offensive behavior, suggesting that they are able to dynamically adjust their aggression levels based on the social context. Social modulation of emotional behavior is also observed in communally reared mice, resulting in reduced anxiety-like behavior when tested with other familiar communally reared mice.⁹⁶ Communally reared mice also display reduced anhedonia and reduced hypothalamic-pituitary-adrenal axis activation in response to a social stress challenge.^{43,94,97} The protective effects of communal rearing are also observed in studies of social behavior in mouse genetic models of autism.⁴⁴

Impact on social behavior of biparental rearing

In many species, the presence or absence of both parents may be an important indicator of the quality of future environments and which reproductive tactics and social behaviors will be most suitable to develop. The importance of biparental care on offspring social development and shifts in reproductive tactics across the life course has been shown in several rodent species through studies that use paternal deprivation (PD) approaches.⁹⁸ A consistent finding in these studies is PD-induced impairments in the ability of offspring to develop a partner preference as adults. This impact of PD has been shown in female offspring in mandarin voles,⁹⁹ and both sexes in prairie voles.^{100,101} In mandarin voles, PD-reared offspring also show reduced affiliation and increased aggression to mating partners.⁹⁹ By using alloparents to substitute for paternal loss in prairie voles, it has been shown that impairments in female partner preference are due to reduced quantity of postnatal care received, while impairments in male partner preference are due to reduced quality of postnatal care received.^{102,103} In mandarin voles, PD is associated with

impairments in social recognition,^{104,105} lower levels of juvenile play behavior,¹⁰⁶ and reduced levels of social interaction in dyadic social interaction tests in adulthood.^{107,108} Similarly, adult California mice that were reared in PD conditions show reduced sociability and increased avoidance and vigilance to a same-sex conspecific.¹⁰⁹ In contrast, PD-reared prairie voles show no changes in social recognition as adults and exhibit higher levels of social affiliation in a social approach test.¹¹⁰

Though this literature focusses on deprivation models, there is evidence that variation in parental behavior and offspring stimulation within biparental rearing conditions shapes social behavior. For example, increased paternal stimulation of California mouse pups can result in increased levels of aggression in adult offspring.¹¹¹ Male and female California mice that experience experimentally induced higher levels of paternal stimulation display higher levels of retrieval behavior as adults.^{112,113} Male prairie voles that experience higher levels of paternal care also exhibit more pup retrievals in an alloparenting test as juveniles.¹¹⁴ Similarly, male offspring of prairie vole mating pairs exhibiting high levels of combined parental contact show greater alloparental care toward infants.^{115,116} Among juvenile voles, the experience of high parental contact is associated with increased affiliative behavior toward novel juveniles but a decreased motivation to disperse from the natal nest.^{76,116}

Environmental and social enrichment effects on social behavior

Developmental exposure to EE typically occurs during the postweaning adolescent period in rodents and has effects on multiple domains of behavior. Among rat offspring exposed to prenatal stress, EE results in increased play behavior and reduced emotionality.^{117,118} Similar enrichment-induced amelioration of the effects of prenatal cocaine exposure and prenatal valproic acid have been observed, including increasing social interaction.^{119–121} In rats, male offspring reared in postweaning enrichment exhibit increased social exploration.¹²² In a comparison of the effects of physical versus social enrichment in rats, social enrichment was observed to increase social communication and approach behaviors.¹²³ One hypothesis regarding the mechanism of social enrichment effects is that these environments allow for increased play behavior that scaffolds further social behavior development. Though there is some evidence to refute this hypothesis,¹²⁴ deprivation of play behavior during this postweaning period has been demonstrated to impact social behavior across a wide range of species. Play deprivation in rats has been associated with a decreased motivation to socially interact and affiliate with same-sex conspecifics.^{125,126} Play deprivation can significantly impair contextually appropriate social behavior, such as agonistic and subordinate behaviors.⁵⁸ For example, play-deprived hamsters and rats are more aggressive as adults when resolving social dominance relationships.^{127–129} Play-deprived hamsters also show increased avoidance behavior toward familiar opponents, indicating an impairment in social relationship development and social stress coping.^{130,131}

Animals that are reared from birth in EE exhibit changes in numerous behavioral domains, including increases in social interaction.^{120,122,132} One possible mechanism for these developmental shifts are EE-induced alterations in the quality and efficiency of parental care. For example, environmentally enriched rat dams tend to show less time in passive nursing postures and less time alternating between different nursing postures, suggesting a higher overall efficiency of milk let-down. Environmentally enriched dams have been reported to increase frequencies of high arch nursing posture and LG of offspring, though these findings are inconsistent.^{133–135} Additionally, environmentally enriched dams appear to have increased milk quality, having higher triglyceride levels, and a greater microbiome diversity that contribute to increased lipid, steroid, and glucose metabolism in offspring.¹³⁵ Associated with these changes, offspring of environmentally enriched dams also exhibit higher levels of social investigation of a novel partner as juveniles. It remains to be determined whether EE rearing promotes the development of more complex social behaviors and relationships, and whether this is mediated by changes in parental care or physiology or both.

Postweaning social environments in which rodents are cohoused with individuals who vary significantly in their social behavior provide additional insights into the impact of these social experiences. For example, play-deprived Wistar rats reared during adolescence with the low-playing Fischer rat strain show deficits in social interaction, social memory, and the social transmission of food preferences as adults.¹³⁶ Similarly, male Long Evans rats reared with the Fischer strain are more likely to escalate social interactions into aggressive behavior as adults, whereas female Long Evans rats reared with Fischer rats exhibit fewer reciprocal and prolonged social interactions with novel partners as adults.^{137,138} Among 129S mice that typically do not display high levels of play behavior, cohousing with C57Bl/6J (B6) mice results in reduced huddling and increased time spent playing.⁵⁶ Similar increases in social interaction are observed in BTBR mice housed with B6 mice.¹³⁹ These findings suggest that interaction with other individuals expressing appropriate social behavior during the juvenile phase may support the development of contextually appropriate social behavior.

NEUROBIOLOGICAL SYSTEMS MEDIATING THE LINK BETWEEN EARLY LIFE SOCIAL ENVIRONMENTS AND SOCIAL BEHAVIOR

The social brain encompasses neural systems that can respond to sensory cues; integrate sensory input with neuroendocrine, arousal, and emotional states; regulate motivation and response to rewards; direct behavioral outputs based on this collective information; and retain memories of past social interactions.¹⁴⁰ Thus, social behavior typically involves a broad range of neural systems working interactively. To understand the impact of early social environments on the social brain, it is necessary to examine the overlap between the neurobiological effects of these social experiences and the neural systems that regulate social behavior. Here, we will highlight some of these systems, with a particular focus on neuroplasticity.

Neuropeptides

The oxytocin (OT) and vasopressin (AVP) systems exhibit significant plasticity in response to early life social experiences.^{141,142} The experience of high LG is associated with increased OT receptor density in the central nucleus of the amygdala and bed nucleus of the stria terminalis (BNST) in adult female rats and increased AVP V1a receptor density in the amygdala in adult male rats.¹⁴³ Conversely, neonatal handling has been shown to decrease OT immunoreactive cells in the hypothalamus and amygdala of male rats and is associated with increased AVP immunoreactivity in the paraventricular nucleus (PVN) of the hypothalamus.^{72,144} In prairie voles, neonatal handling is associated with reduced OT receptor binding in the BNST and alterations to OT receptor gene DNA methylation and binding in the nucleus accumbens (NAc), dependent upon sex and duration of handling.^{76,83} Deprivation of biparental care in mandarin and prairie voles leads to decreases in OT neuron and receptor levels in various nuclei of the social brain including the PVN and amygdala, though there does exist significant variation in these effects.^{103,145} Similarly, PD in mandarin voles reduces AVP immunoreactivity in the anterior hypothalamus.¹⁰⁶ Territorial California mice fostered to less territorial white-footed mice show reductions in levels of AVP immunoreactivity in the BNST and supraoptic nucleus associated with reductions in aggression compared to those fostered to California mice dams.⁹¹ Further, California mice experiencing high levels of paternal stimulation show higher levels of AVP innervation of the dorsal BNST but lower levels in the ventral BNST and PVN compared to offspring who received low levels of stimulation.¹¹¹ The experience of communal rearing is associated with increases in OT receptors in multiple hypothalamic brain regions in female offspring, including the lateral septum and BNST, and increases in OT receptor density in several nuclei of the amygdala of communally reared males.^{43,95} Conversely, AVP V1a receptors are decreased within the lateral septum of female offspring reared in communal nests.⁹⁵ Adolescent social enrichment in rats is associated with increases in OT receptor density and increased OT immunoreactivity in the PVN¹⁴⁶ and BNST.²⁸ Moreover, the effects of EE on social behavior can be recapitulated using intranasal OT administration, suggesting a mediating role of this neuropeptide system in linking social experiences to social behavior outcomes,¹⁴⁷ though these effects may differ when there is chronic developmental OT exposure.¹⁴⁸ The link between the OT and AVP systems and the expression of social behavior has been established through comparative, genetic, pharmacologic, and optogenetic approaches that implicate these neuropeptides in social bonding and aggression.^{149,150}

Neurotrophic factors

Neurotrophins, including nerve growth factor (NGF) and brain-derived neurotrophic factor (BDNF), are key facilitators of neuronal proliferation, differentiation, and synapse formation. The impact of early life social experiences on neurotrophin levels can be observed as early as the first week of life. Offspring of high LG dams show elevations of

BDNF mRNA in CA1 and dentate gyrus subregions of the hippocampus from postnatal day 8.¹⁵¹ Adult male offspring of highly maternal rat dams have high levels of BDNF mRNA in the amygdala, hippocampus, prefrontal cortex, and striatum, suggesting that early elevations of neurotrophic gene expression may persist until adulthood.⁸² Congruently, adult mice that were reared in communal nests show higher levels of BDNF and NGF protein and mRNA in the frontal cortex, hippocampus, and hypothalamus when compared to standard-reared animals.^{43,96,152} Communally reared mice also have higher levels of hippocampal H3 histone acetylation of the BDNF gene in adulthood. The particular patterning of H3 acetylation observed is associated with more rapid production of BDNF protein following environmental challenge in communally reared adults.¹⁵³ Similarly, biparentally reared female mandarin voles have higher levels of CA1 and CA2/3 hippocampal BDNF compared to singly reared individuals.¹⁵⁴ However, biparentally reared prairie voles have been found to have reduced hippocampal BDNF protein and mRNA and decreases in the BDNF receptor, tropomyosin receptor kinase B (TrkB).¹¹⁰ These findings demonstrate that the relationship between neurotrophins and early life social stimulation may vary depending on species or strain. Social stimulation in the juvenile period can also induce changes in neurotrophin levels, with juvenile rats having higher levels of BDNF mRNA in the amygdala and frontal cortex following social play.¹⁵⁵ Variation in hypothalamic and hippocampal BDNF protein levels also occurs in juvenile prairie voles following their engagement in alloparental care.¹⁵⁶ While the specific role of BDNF in the expression of social behavior has yet to be fully elucidated, neurotrophins are critical for the expression of neural plasticity and BDNF–TrkB signaling may serve an important role in various forms of social learning.¹⁵⁷

Neuroplasticity

Altered neurotrophin levels within the brain have consequences for the variation in neuronal function and plasticity that are observed following exposure to early life social environments. For example, adult offspring of high LG dams exhibit increased hippocampal synaptogenesis and synaptic density from preweaning through adulthood.^{151,158} Within the hippocampus of communally reared offspring, the rates of survival of newly generated neurons are elevated, which is consistent with the established role of BDNF in supporting cell survival.¹⁵⁹ Other forms of enrichment during development also induce dendritic arborization and increases in synapse number and size throughout the cortex.^{160,161} Increased dendritic spine density has been observed in the dentate gyrus of biparentally reared compared to singly reared mandarin voles.¹⁰⁵ Similarly, male, but not female, biparentally reared degu show higher spine frequency on basal dendrites in the ventral medial prefrontal cortex (mPFC) compared to singly reared animals.¹⁶² Indeed, PD in degu has been shown to have widespread effects on the number of neurons throughout the lifespan in many brain regions, including the NAc, amygdala, and hippocampus.^{162–164} In mandarin voles and California mice, PD leads to reductions in the survival of

new cells in the dentate gyrus of females.^{105,165} PD in California mice has also been shown to lead to reductions in the volume of the dentate gyrus in both sexes and the density of microglia cells.¹⁶⁶ How these changes in hippocampal morphology relate to social behavioral changes has yet to be elucidated.

The experience of juvenile play behavior stimulates neuronal activity throughout both limbic and corticostriatal areas that is critical for the development of frontal cortex circuitry.^{58,155} The opportunity to play with peers leads to an increase in plasticity-modulating proteins, such as synaptophysin, spinophilin, and myelin basic protein in the frontal cortex.¹⁶⁷ Male and female rats that have access to increased juvenile play partners or play partners of more playful rat strains have more pruning of dendritic arbors in the mPFC.^{168–170} Some of these play-induced changes to the mPFC may be limited to the juvenile period, whereas the impact of play on dendritic arbors in the orbitofrontal cortex may be maintained over the lifespan and thus responsive to ongoing changes in the social environment,^{168,169,171–173} though this may vary by species.¹³⁰ Activation of the mPFC is evident during social approach behavior and this brain region is critical for the perception and response to social stimuli through connections to the amygdala, which regulate approach and avoidance behaviors.^{174,175} Thus, the impact on neuroplasticity in this brain region will shape fundamental aspects of social behavior.

Motivation–reward

Social behavior is dependent on motivation to engage in interactions with a social stimulus and activation of reward systems to promote sustained social contact. The mesolimbic dopamine (DA) system plays a critical role in the motivation–reward system and is shaped through a broad range of early life experiences.^{176–178} Though adverse experiences have been the typical focus of studies examining the DA system, modulation through increased social complexity in early life may also be evident. Neonatal handling has been found to induce increases in DA D1 receptor levels in the caudate putamen and NAc, which likely contributes to increased activation of dopaminergic neurons and increased incentive learning within social relationships.^{179–181} Density of dopaminergic neurons within the ventral tegmental area are increased among female rats that experience high LG during postnatal development, and expression of DA receptors (D1, D2, and D3) are increased within the NAc in adolescence following this early life experience.¹⁸² Father absence impacts reward sensitivity and decreases the responsiveness of DA neurons in the mPFC in California mice and increases tyrosine hydroxylase levels in several brain regions of degu.^{99,183,184} In mandarin voles, PD leads to reductions in nucleus accumbens D1 and D2 receptor mRNA in adult females, but the opposite pattern is observed in adult male offspring.⁹⁹ The impact of communal rearing or postweaning enrichment on the DA system has been limited or yielded inconsistent findings, suggesting that there may be contextual or genetic factors to consider when exploring the effects of these experiences.^{178,185}

Sensory systems

Though sensory systems are fundamental to the perception, recognition, and response to social cues, there has been limited exploration of the impact of early life social environments on the development of these systems. The literature that does exist is primarily focused on adversity/deprivation experiences. However, studies of cross-fostering and handling in rats suggest that these experiences can alter auditory brain-stem activity and accelerate the development of the middle ear and opening of the ear canal.¹⁸⁶ Preweaning offspring that experience low LG exhibit higher levels of BDNF in the auditory cortex compared to offspring from high LG dams.¹⁸⁷ In terms of visual perception, mice reared from birth in enriched environments exhibit greatly enlarged and coordinated primary visual cortex fields leading to wider visual field coverage.¹⁸⁸ Enriched mice also show accelerated visual acuity and ocular dominance plasticity into adulthood which is in part mediated via elevations in BDNF.^{189,190} Further, EE during the postweaning period is also associated with increased NGF within the adult visual cortex.¹⁹¹

While neonatal odor exposure has been demonstrated to exert a sustained effect on odor processing,¹⁹² the neurobiological impact of social odors has yet to be fully explored. Some evidence suggests that olfactory enrichment can lead to improved olfactory discrimination abilities, possibly via modification of the noradrenergic system, at least in young adult mice.¹⁹³ Genetically ablating mouse olfactory sensory neurons, specifically during the neonatal period, also impairs the ability of individuals to recognize odors in adulthood, demonstrating the importance of neural activity in olfactory sensory neurons during development to scaffold adult sensory abilities.¹⁹⁴ Olfactory discrimination and learning can also be improved by increasing rates of turnover of granule cells in the olfactory bulb as well as increasing levels of neuronal inhibition by these interneurons, suggesting a potential target for developmental effects.¹⁹⁵ Further, neonatal rats that learn to associate odors with foot-shock retain this memory into adulthood and exhibit a proliferation of neural stem/progenitor cells.¹⁹⁶ Despite foundational work indicating that early life socialization can have a profound impact on the dynamics of sensory processing and development,¹⁹⁷ the experimental analyses of the impact of social experiences on the neurobiology and function of these systems require further exploration.

More recently, work in prairie voles has provided strong evidence that variation in early life tactile stimulation of pups can shape connections in the somatosensory cortex leading to changes in cortical organization. Offspring that experience high levels of parental contact have a higher density of connectivity within the primary somatosensory area (S1) compared to offspring who experience less contact.¹⁹⁸ Conversely, offspring reared by low-contact parents have denser connections in the parietal and frontal cortices as well as a wider distribution of callosal connections compared to offspring of high-contact parents. Female offspring of low-contact parents also have reduced size of the primary motor cortex M1 along with reduced myelination of this region.¹⁹⁹ Changes in cortical connectivity may occur very early

in development as shifts between high- and low-contact offspring in the expression of developmentally regulated genes and variation in prelimbic and anterior cingulate cortical thickness emerge as soon as postnatal day 1.²⁰⁰ Although it remains to be determined how these changes relate to alterations in juvenile and adult social behavior, such cortical reorganization in response to early tactile stimulation is likely a critical feature of social development.

SUMMARY AND CONCLUDING REMARKS

Overall, there is support within the literature for the hypothesis that early life environments that are characterized by social complexity can induce changes within the brain that support the development of social behavior. However, the current range of paradigms for modeling social complexity are limited and, in many cases, represent a modest departure from deprivation rather than creating the type of complexity that is characteristic of naturalistic environments. This may be a critical consideration in the design of future studies that explore the biology of social behavior. The dependence of the social brain on complex and stimulating early life environments is evident, yet laboratory rodents are typically deprived of this social and sensory stimulation during development. However, these deficits can be overcome by changes to housing and rearing conditions that increase variability. Beyond the animal welfare benefits of this shift, increasing social and physical complexity of the early life environment is more likely to expand the translational potential of these lab-based approaches when modeling the nuanced and contextually dependent social behavior of humans. Moreover, there is evidence that the impacts of early life social complexity can extend across multiple generations,^{28,95} resulting in the generational transmission of neurobiological and behavioral patterns that better support the ability of individuals to navigate social relationships that vary over time and contexts.

Though there are multiple strategies for assessing social behavior (see Table 1), the degree to which these tests assess complex social behavior varies. In many cases, these tests will be impacted by general aversion or motivation to explore a novel stimulus. Approach versus avoidance in a social context can be difficult to disentangle from similar behavioral responses with nonsocial stimuli. Similarly, aggression in a brief interaction may indicate acute social stress responses but may not provide insights into the way an individual's aggressive behavior changes over time in response to social cues and contexts. These more nuanced and temporally sensitive social behavior changes are an indication of "social competence" rather than any single element of social behavior and depend on the neuroplasticity that can be established during development. The study of social competence can be supported through the use of emerging tracking and behavioral quantification technologies and analytic approaches that enable the study of group-housed individuals over time as they navigate social relationships. However, the challenges to implementing these tools (i.e., housing space limitations, analytical expertise, and infrastructure) must be carefully considered to determine feasibility. Future research exploring the developmental and neurobiological mechanisms sup-

porting the expression of social behavior can make use of these tools that allow for a more naturalistic study of laboratory animals. Finally, most studies have relied on examining social behavior outcomes of early life manipulations at singular or very few timepoints in adulthood. There is a critical need to understand how complex social behavior and competence emerge over time by examining the developmental trajectories of not just behavior but also transcriptional regulation and neural circuit maturation.

AUTHOR CONTRIBUTIONS

J.P.C. and F.A.C. conceived the topic, drafted the manuscript, and revised the manuscript. The manuscript was approved by both authors.

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COMPETING INTERESTS

The authors declare no competing interests.

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