

REVIEW ARTICLE

Synchrony in parent-offspring social interactions across development: A cross-species review of rodents and humans

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Abstract

In humans, parent-child neural synchrony has been shown to support early communication, social attunement and learning. Further, some animal species (including rodents and bats) are now known to share neural synchrony during certain forms of social behaviour. However, very little is known about the developmental origins and sequelae of neural synchrony, and whether this neural mechanism might play a causal role in the control of social and communicative behaviour across species. Rodent models are optimal for exploring such questions of causality, with a plethora of tools available for both disruption/induction (optogenetics) and even mechanistic dissection of synchrony-induction pathways (in vivo electrical or optical recording of neural activity). However, before the benefits of rodent models for advancing research on parent-infant synchrony can be realised, it is first important to address a gap in understanding the forms of parent-pup synchrony that occur during rodent development, and how these social relationships evolve over time. Accordingly, this review seeks to identify parent-pup social behaviours that could potentially drive or facilitate synchrony and to discuss key differences or limitations when comparing mouse to human models of parent-infant synchrony. Uniquely, our review will focus on parent-pup dyadic social behaviours that have particular analogies to the human context, including instrumental, social interactive and vocal communicative behaviours. This review is intended to serve as a primer on the study of neurobehavioral synchrony across human and rodent dyadic developmental models.

KEYWORDS

mouse model, optogenetics, parent-offspring, social development, synchrony

1 | INTRODUCTION

Synchrony between parents and their offspring has been studied in various forms across human and non-human species. The majority of these investigations have focussed on behavioural patterns of coordination. However, there is now growing interest in the underpinning neurobiological mechanisms that might subserve synchronous states between parents and offspring. Rodent research represents a unique opportunity to identify and test potential neural mechanisms for parent-offspring synchrony. This review identifies and discusses key parent-offspring social behaviours in rodents that may have specific

parallels and relevance for the study and understanding of parent-offspring neurobehavioural synchrony across both human and rodent species. Here, rodent mothers will be referred to as dams, and rodent offspring will be referred to as pups.

2 | PARENT-OFFSPRING SYNCHRONY ACROSS SPECIES

In humans, attunement between parents and offspring—specifically instantiated as biobehavioural synchrony—is proposed to be a

fundamental mechanism for maintaining healthy homeostasis in the parent-child ecosystem through timely coregulation of the physical, emotional and cognitive needs of the developing infant.¹⁻³ In the human development literature, synchrony is commonly understood as the simultaneous matching of behaviour, emotion or physiological states between parent and infant, such as the temporal mirroring of movements and concurrent increases in oxytocin or changes in heart rate.¹ However, this term is also used more broadly to include non-concurrent (sequential) temporal coordination of behaviour during dyadic parent-child interaction, such as turn-taking and responsive behaviour.^{3,4} Indeed, both forms of temporal contingency may be underpinned by similar neurobiological mechanisms, such as the coupling of (neuro) biological rhythms that drive changes in these states.¹ Therefore, in order not to be overly restrictive, we include exemplars of both concurrent and sequential synchrony in this review.

In humans, increased parent-child synchrony is associated with better socioemotional development of self-regulation skills, empathy and attachment in children, with long term sequelae for individual and social capabilities in later life (see Feldman^{1,2} for reviews). In recent years, the introduction of new hyperscanning techniques for concurrent acquisition of neural activation patterns in two or more interacting individuals has heightened interest in a possible role for parent-child neural synchrony in early development.^{5,6} A growing body of work now suggests that parent-child neural synchrony can arise during various forms of dyadic social interaction including vocal communication,⁷ physical proximity and affectionate touch,^{8,9} emotional referencing,¹⁰ cooperative play,^{11,12} problem solving^{13,14} and book reading.¹⁵ In two-person neuroscience studies, neural synchrony commonly refers to the existence of non-random temporal contingencies between the time series of neural signals that are collected concurrently from two interacting individuals. These time contingencies may be detected either in the oscillatory phase or amplitude of the neural response. Such synchrony is commonly measured using metrics such as the phase-locking value (PLV) or partial directed coherence (PDC) in either simultaneous electroencephalogram (EEG) or functional near-infrared spectroscopy (fNIRS) recordings between parent-child dyads. For a recent review of these methods, please see Czeszumski et al.¹⁶ For example, Santamaria et al.¹⁰ showed lower divisibility and higher strength in the network topography of the mother-child interbrain neural network (where connectivity was measured using both PLV and PDC) during the expression of positive compared to negative affect from mothers, which suggests a role for emotional valence in the generation of parent-child interbrain synchrony. However, the exact neural mechanisms and sensory signals that subserve parent-child synchrony in these studies have yet to be elucidated. Little is also known about the developmental origins and sequelae of neural synchrony, and the role this plays in social and communicative behaviour across species. Although progress has been made to assess causal hypotheses via artificial induction of neural synchrony in adult humans (e.g., Pan et al.,¹⁷), such techniques using non-invasive brain stimulation cannot be used with paediatric populations.

In this regard, animal models are an invaluable and complementary approach for the study of parent-child neural synchrony. Similar

to humans, parent-offspring interactions are crucial for shaping individual and social capacities in many mammalian species.^{18,19} Rats deprived of parental care, for example, exhibit wide-ranging deficits in social learning of food preferences,²⁰ social recognition,²¹ and fear regulation later in life.²² More specifically, neural synchronisation has now been observed and associated with social behaviour across several animal species. Recent studies show that both bats and mice display inter-brain neural synchrony during close social interactions.^{23,24} In particular, bats show increased levels of interbrain synchrony during vocal communication with members of the same social "clique",²⁵ while mice exhibit increased levels of neural synchrony when competing with conspecifics of higher social status.²³ Further, even pigeons have been shown to be able to synchronise their neural activity for a reward following neuro-feedback training.²⁶ These observations suggest that interbrain neural synchrony may be a fundamental and evolutionarily-conserved mechanism that supports group formation and social behaviour in many animal species. However, to what degree are the neural synchrony mechanisms of human and non-human species comparable, particularly in the context of development?

It is known that humans and rodents follow broadly similar stages of physical and neural development that are marked by transitions during infancy, adolescence and adulthood. Neurodevelopment in mice appears to follow a similar pattern to that of humans, with key neural markers (such as changes in synapse density, myelination and cortical thickness) being achieved in a similar progression (see Semple et al.²⁷ for review). This has permitted relatively straightforward cross-species investigations, particularly in the domain of motor and brain development.^{27,28} This also suggests that basic neuroanatomical and neurophysiological capacities for synchronisation (if present), may emerge in a similar temporal sequence for mice as compared to humans. However, in the domain of social development (specifically, parent-offspring social relationships), less is known about the trajectory of rodents in comparison to humans. More broadly, murine development can be characterised by six stages that parallel human development, and which are identifiable through behavioural and physiological markers.^{29,30} These stages are: neonatal (postnatal day [PD] 0-4), infancy (PD5-11), late infancy (PD12-20), preadolescence (PD21-30), adolescence (PD30-60) and adulthood (PD60 onwards). While behavioural and neural synchrony are already known to occur between adult mice,²³ here we focus our discussion on the early developmental stages of infancy and adolescence, when parent-offspring synchrony is probably of relatively greater importance than peer-to-peer synchrony.

Synchrony mechanisms in non-human animals can be examined with a wide range of methodological tools that possess high spatial and temporal precision. In particular, mouse models can be investigated via a combination of observation (in vivo monitoring of the activity of populations of individual neurons) and perturbation (optogenetics). These tools have already enabled the detailed study of parenting mechanisms,³¹ permitting the selective activation of neuronal circuits that influence motor, motivational, social or neuromodulatory aspects of parenting behaviour.³² New tools for multianimal






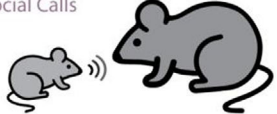
	Instrumental/Survival	Social Interactive	Vocal Communication
Humans	<p>Maternal stroking and carrying during breastfeeding aids feeding.</p> 	<p>Gentle stroking exerts calming effects on infants.</p> <p>Gaze and vocalizations during maternal play can regulate attention.</p> 	<p>Infants' cries elicit maternal responses. Mothers are sensitive to their own infant's cries.</p> <p>Mothers use infant-directed speech and singing as ostensive cues.</p> 
Mice	<p>Maternal licking/grooming occurs during nursing.</p> <p>Maternal licking/grooming maintains pup hygiene.</p> <ul style="list-style-type: none"> • Nursing • Nest Building • Pup Solicitations 	<p>Licking/grooming by dams calm pups and regulates future social behaviour.</p> <p>No documented maternal play with pups.</p> <ul style="list-style-type: none"> • Maternal Licking/grooming • Allogrooming • Social Play • Social Rearing • Sniffing 	<p>Unique pup calls elicit specific maternal responses. Dams recognise their own pups' call signatures.</p> <p>No documented pup-directed maternal vocalizations.</p> <ul style="list-style-type: none"> • Pup Isolation Calls • Wriggling Calls • Social Calls 
References	Kaye ₃₈ ; Feldman ₂ Hart & Powell ₄₀ ; Weaver et al. ₃₉	Bridges ₄₁ ; Fujita et al., 2019 Wolff ₄₃ ; Gross & Hen ₄₂ ; Burenkova et al., 2019	Morsbach & Bunting ₄₆ ; Leerkes et al. ₄₅ ; Kaplan et al. ₄₄ D'Amato et al. ₃₆ ; Mogi et al. ₃₇

FIGURE 1 Table illustrating parallels between human and rodent parent-offspring social behaviour in three main categories: Instrumental/survival, social interactive and vocal communicative behaviours. Differences between species are highlighted in pink. Bullet points list specific murine behaviours discussed further in this review.^{36,37}

tracking,³³ recording²³ and perturbation³⁴ now allow rodent models to be used for the investigation of social interactive behaviour under naturalistic conditions.³⁵ However, to fully leverage the benefits of rodent models for advancing research on parent-offspring synchrony, the cross-species translational gap must first be narrowed to better understand parallels and differences in the specific social behaviours that are associated with biobehavioural synchrony in human and mouse parent-offspring dyads.

Drawing from human parent-child research, we focus on three broad categories of social behaviours: instrumental/survival, social interactive, and vocal communicative behaviours (see Figure 1). Instrumental behaviours are defined here as maternal behaviours that are essential for a pup's survival, such as nursing, hygiene maintenance and nest-building.

By contrast, social interactive behaviours are defined as behaviours that do not directly contribute to survival but may improve developmental outcomes. These include maternal licking/grooming (LG) (outside of the nursing context), allogrooming and social play. Finally, vocal communicative behaviours include all classes of vocalisation produced by either dam or pup. Whilst non-exhaustive, these categories of behaviour were selected because they are expressed

during early life in both human and murine species, and may afford (to a lesser or greater extent) parent-offspring behavioural coordination and synchrony.^{29,30,38–40} The following sections will map parallels and differences in parent-offspring social behaviour between human and rodent models, highlighting implications for the design and interpretation of cross-species experiments.

3 | PARENT-OFFSPRING SOCIAL BEHAVIOURS ACROSS RODENT AND HUMAN DEVELOPMENT

3.1 | Instrumental behaviours

Instrumental behaviours between a mother and her child are the most basal dyadic interactions necessary for survival. These mother-child interactions are crucial during early development, when the child is fully reliant on their mother for basic needs. One such behaviour is nursing, where young feed on their mother's milk for sustenance. In both human and rodents, feeding is typically initiated by the infant—through infant cries in humans⁴¹ and pup solicitations such as

nipple-contact or wriggling calls in mice.^{42,43} Successful nursing in both species requires the coordinated actions of mother and offspring—mothers have to avail their nipples, while infants need to latch. In rodents, caring dams often adopt an arched-back position to increase the ease of infant latching. Observations of arched-back nursing within the first few days of life have thus been interpreted as a marker of early life care in rodents.^{22,44} Infants of both species actively identify the location of their mother's nipples using olfactory cues,^{45,46} and often adjust their own positions to enable comfortable latching. In rodents, dam sensitivity to ventrum stimulation through pup latching is necessary to propagate and maintain nursing behaviour by dams,⁴⁷ further illustrating the interdependence of dam-pup behaviours. During breastfeeding in humans, mothers typically respond to their infant's pauses in sucking by stroking or patting their child to resume sucking as a form of "proto-conversation".⁴⁸ These rhythmic interactions are early forms of parent-child behavioural synchrony, which coregulates dyadic behaviour and affiliative bonding.² Similarly in mice, caring dams often lick/groom their pups during nursing. Although the specific timing of licking and suckling rhythms has yet to be explicitly investigated, this behaviour likely contributes to improved bonding in mice as well. Such maternal care is instrumental in the development of stress-reactivity and fear responses in mouse pups.⁴⁹ Hence, in both rodent and human species, the multisensory coordination and synchronisation of maternal and infant behaviour ensures adequate nutrition for the infant and has attendant advantages for affiliative bonding.

In both humans and mice, nursing patterns also evolve over time to adapt to varying energy and nutritional demands of the developing young.⁵⁰ In humans, as infants develop, mothers begin to encourage the transition to solid food,⁵¹ which likely causes a significant fall in nursing across the first year of life. During this transition, dyadic coregulation occurs between the emergent novel behaviours of both mother and child—such as gaze, touch, and rejection, acceptance and indifference of food—which facilitates smoother feeding dialogues and greater behavioural synchrony.^{52,53} Similarly in mice, nursing frequency decreases drastically after infancy.⁴³ The transition to solid food in rodents parallels that of humans, where dams actively avoid nursing during late infancy. This period coincides with a peak in pup solicitations—where pups eagerly seek their dam's nipples outside of the nest. The majority of these out-of-nest pup solicitations are not reciprocated by the dam and may even elicit overt rejection responses (unpublished observations). During this weaning period, pups learn to adapt their behaviour to dam rejections, eventually ceasing solicitations and turning to solid food.^{40,42}

Apart from feeding, maternal LG is essential for the maintenance of pup hygiene, representing an additional instance where dam-pup synchrony may occur. LG of newborns protects them from external pathogens during their most vulnerable stage.⁵⁴ In rats, LG of pup anogenital regions by dams is necessary for the elimination of urine and faeces while allowing lactating dams to recycle these nutrients.⁵⁵ These anogenital LG bouts are typically initiated by dams via an initial licking of the pups' perineum, which causes pups to respond contingently with an elevated rump, allowing further access to their

perineum region.⁵⁶ Similarly in humans, parents play important roles in their infants' waste elimination and hygiene maintenance. While human infants are able to eliminate waste via urination and defaecation, they often express cues to caregivers signalling their intent for excretion.⁵⁷ These cues are met with caregiving behaviours, such as repositioning or cradling the infant, facilitating infants' excretion via elimination communication.⁵⁸ Therefore, mother-infant dyadic coregulation occurs during hygiene maintenance in both species.

3.2 | Social interactive behaviours

One of the earliest forms of non-instrumental social interaction observed in parent-offspring dyads is the use of affectionate touch for comfort. In humans, gentle stroking is an effective way to calm a distressed infant,⁵⁹ and exposure to maternal touch during infancy is known to mediate an infant's physiological and behavioural response to stress⁶⁰ and induce sleep.^{59,61} In addition, touch has also been associated with neural synchrony in human parent-child dyads.⁹ In both humans and mice, affectionate touch during maternal carrying elicits a calming effect on the young.⁶² In mice, maternal LG parallels the effect of affectionate touch in humans. Maternal LG aids in calming down anxious pups⁶³ and encourages future social and environmental exploration.⁶⁴ Rodent maternal LG has also been associated with specific epigenomic changes in pups, which moderates their stress responses.⁴⁹ Similarly, early forms of maternal touch elicit epigenetic changes in humans, altering the infant's hypothalamic-pituitary-adrenal stress reactivity.⁶⁵

Despite its benefits, the frequency of maternal touch decreases across early development in both species.^{43,60} In humans, this decrease is inversely related to the appearance of other forms of social touch—where children begin to interact with their peers during childhood play and subsequent romantic interactions during adulthood.⁶⁰ Similarly in mice, conspecifics begin to allogroom one another reciprocally during preadolescence,⁶⁶ which is a form of prosocial behaviour toward peers.⁶⁷ This shift in comfort seeking from dam-pup interactions to peer-to-peer interactions in mice appears to parallel that in humans (Figure 2). Accordingly, LG-related social synchrony may shift in importance from parent to peer during the adolescent stage.

Second, social play—comprising multifaceted interactions involving touch, chasing, and play fighting in mammalian species—has an important role during early development. In humans, social play begins during infancy and occurs throughout life. As such, the mother is usually the first playmate. Maternal play prepares the child for social play with their peers and trains the child to become socially competent (see Palagi⁶⁸ for review).

Play engages multiple ostensive cues from the mother toward her infant, such as gaze, touch and vocalisations. Further, high levels of positive emotion shared during play potentially enhance behavioural and neural synchrony within the dyad.^{9,69} In mice, however, social play is rare and usually occurs after the juvenile period.⁷⁰ Pups have not been documented to play with their dams and are more likely to

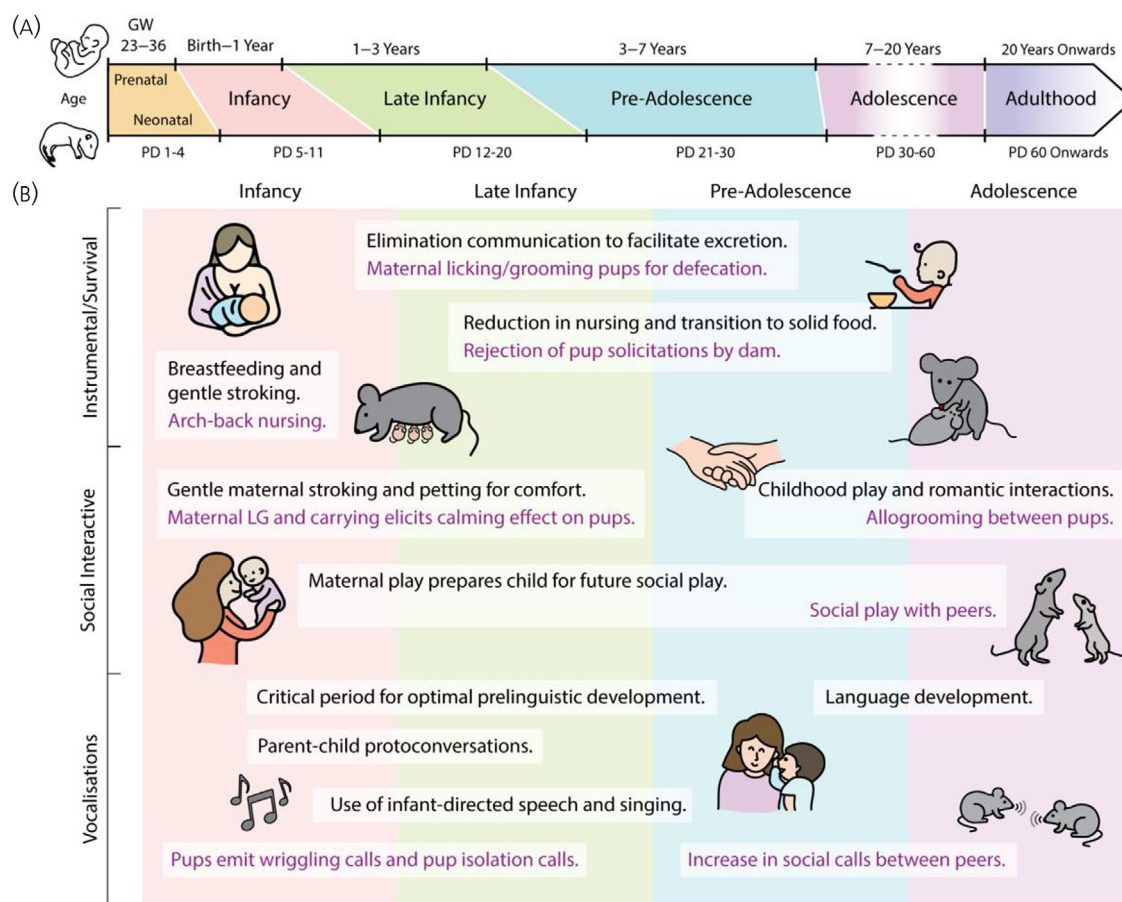


FIGURE 2 Timeline illustrating potential synchrony-related events during early development. Behaviours observed in humans are annotated in black and behaviours observed in mice are annotated in purple. Events with similarities across species are grouped in boxes. GW - gestation week; PD - postnatal day.

play with conspecifics of the same litter.⁷¹ Moreover, social play in mice, which includes chasing, pouncing, and crawling over/under the other mouse, are often robust only with environmental enrichment.^{70,72} Therefore, although social play behaviour can be observed in both rodent and human species and is of potential interest for synchrony research, researchers should be aware of differences in the contexts and developmental stages at which these behaviours are expressed (Figure 2).

3.3 | Vocal communicative behaviours

Vocalisations play important roles in social communicative processes across many species—conveying information, emotional state and often signalling danger to conspecifics.⁷³ Humans, in particular, are avid vocal learners—both in the development of speech and the ability to engage in conversational turn-taking. Nathani et al.⁷⁴ posits that vocal development in children can be broken down into five progressive stages—reflexive (0–2 months), control of phonation (3–5 months), expansion (6–8 months), basic canonical syllabus (9–20 months) and advanced forms (16–20 months). Such prelinguistic development is crucial for subsequent language acquisition in children

and occurs within a prepubertal “critical period”, which determines the effectiveness of future learning.⁷⁵ As vocal learning requires auditory feedback and relies heavily on hearing the vocalisations of others as well as sounds emitted by oneself,⁷⁶ the development of vocalisations is dependent on early parent–child interactions.⁷⁷ Greater sensitivity displayed in maternal responses following the infants' prelinguistic mother-directed vocalisations during these interactions has also been found to promote subsequent language development of the child.⁷⁸

On the contrary, it has been suggested that vocalisations in rodents are innate rather than socially learned, with variance in ultrasonic vocalisations (USVs) explained largely by age or genetic differences. Such conclusions have been supported by observations where hearing experience is not required for vocal productions—for example, deaf adult mice are capable of producing normal USVs⁷⁹ and infant mice vocalise before the onset of hearing⁸⁰—as well as by the low vocal plasticity of mice which has been attributed to limited forebrain pathways.⁸¹ On the other hand, due to the complexity and variations in syntax during several social contexts, von Merten et al.⁸² posits that the emission of USVs may include a learning component which has been largely overlooked. Unlike previous studies which focus mainly on quantitative USV features such as fundamental frequency and

number of calls, this study presents convincing evidence for the possibility of vocal learning in mice by considering qualitative differences between the temporal-structural characteristics of different calls. As vocalisations occurring after the onset of hearing are more likely to display components of vocal learning, there is a need for more longitudinal studies focusing on qualitative changes in mouse USVs across development, especially beyond the age of hearing onset when there exists a possibility for vocal learning.

An important form of communicative synchrony in humans is vocal turn-taking—where individuals take turns to speak and listen during a conversation. During conversations, adult dyads that display higher turn-taking often exhibit greater levels of neural synchrony, which is associated with higher conversation quality.⁸³ As such, the timing of turn-taking is thought to index the degree of social connection between communicating individuals.⁸⁴ In humans, early forms of turn-taking are prevalent in rhythmic parent-infant exchanges known as protoconversations, which aid the acquisition of turn-taking abilities in children well before their vocalisations have matured.⁸⁵ Turn-taking is also observed in other mammals during vocal communication and learning. In singing mice (*Scotinomys teguina*), counter-singing occurs in rhythms strikingly similar to human turn-taking conversations.⁸⁶ In marmosets, conversational exchanges between parent-offspring dyads enables the maturation of infant vocalisations.⁸⁷ However, turn-taking has yet to be discovered in laboratory mice. Nonetheless, with more advanced spatial localisation and tracking techniques, future research may yet uncover evidence for rodent parent-offspring protoconversation and related evidence for early communicative synchrony.

In both mice and humans, unique vocalisations exist in the context of parent-offspring communications. In humans, early mother-child interactions often involve unique maternal vocalisations such as infant-directed speech (IDS) and infant-directed singing.^{88–90} These serve as important communicative cues for a child's learning and development.⁹¹ IDS is commonly characterised by exaggerated changes in pitch, slower rate of speaking and additional emphasis on vowels.⁴⁴ In a study by Schachner and Hannon,⁹² IDS was shown to be more effective in driving social preference of infants, whereby infants prefer individuals speaking in IDS as compared to individuals using normal speech. Similarly, infant-directed singing has also been found to engage infants as effectively as books or toys, and is significantly better at capturing an infant's attention compared to other forms of recorded music.⁹³ Similar observations have been made in non-human primates, where infant-directed vocalisations such as grunts and girneys are used by female rhesus macaques to attract infant attention and encourage handling,⁹⁴ while improving learning and long-term memory retention.⁹⁵ IDS equivalents have not been discovered in mice, and most calls documented during early development appear to be exclusively emitted by pups.

Mouse pups emit unique cries to communicate with their parents, many of which have been well documented in the literature. While USVs have traditionally been studied using quantitative measurements, such as fundamental frequency and call durations, the focus of recent studies has started shifting towards the qualitative features of

these calls.^{96,97} These spectro-temporal characteristics allow the distinction of similar frequency calls made in different contexts, providing deeper insights into the function of USV communication in mice. One major category of pup vocalisation is pup isolation calls. These calls range from 40–90 kHz, and are emitted when pups are separated from their dam or siblings during their first 2 weeks of life.⁹⁸ Spectrograms from various pup isolation studies have shown that pup isolation calls consist of mainly downward and flat calls, with occasional two-syllable calls and frequency steps.^{98–100} These calls possibly act as distinctive signatures for dams to recognise their pups,³⁷ functioning as auditory cues for maternal retrieval.¹⁰¹ With growing motor and visual abilities, pups become capable of returning to their nest without requiring maternal retrieval. In humans, mothers are able to recognise the cries of their own infants,¹⁰² and the extent of maternal sensitivity to infants' cries predicts the child's subsequent attachment security.¹⁰³ Similarly in mice, greater maternal responsiveness to pup calls results in a decrease in pup isolation calls and reduced anxiety levels in later life.³⁶ These results support the importance of parent-offspring communicative synchrony in ensuring optimal early development in both humans and mice.

Juvenile calls emitted by rodent pups can function to communicate their affective state to peers during social interaction.⁷⁷ Short calls are commonly emitted by juvenile mice during social interaction,¹⁰⁴ while long modulated USVs, such as frequency steps, complex and two syllable calls, function as social calls in later development.¹⁰⁵ The rise in long modulated USVs may reflect greater interest towards their peers approaching the onset of sexual maturity, possibly occurring in conjunction with social interactive behaviours. Such call variability in different social contexts and in the presence of different audiences¹⁰⁶ parallels the wide spectrum of human prosody in different social contexts.¹⁰⁷ However, most USV studies record young mice in isolation or examine social interaction in adult mice,⁷⁷ which may elicit different types and proportions of calls as compared to naturalistic settings. There remains a gap in our understanding of the natural changes in vocalisation patterns across mouse development and how these changes occur in conjunction with emerging social interactive behaviours. Hence, USV recordings in naturalistic set-ups where pups are able to freely interact with the dam and their peers throughout development may be more ethologically relevant.

4 | WIDER CONTEXTUAL CONSIDERATIONS ACROSS SPECIES

We have highlighted several parallels in parent-offspring synchrony-related social behaviours in mice and humans, which exist in the context of feeding, comforting touch and vocal solicitation. We have also highlighted species-specific effects in the context of play and vocal turn-taking. However, other caveats remain in the interpretation and extrapolation of findings across species. The first consideration is litter size. Mammals typically follow the one-half teat rule,¹⁰⁸ where litter size usually equates to half the number of teats, and maximum litter size equates to the total number of teats. This evolutionary adaptation

is important to ensure sufficient nutrition for each individual offspring. Following this rule, humans average at one baby per mother, while mice average at five pups per dam (although the typical litter size for laboratory mice is 6–8). This allows the human mother to allocate proportionately more attention and resources per child as compared to the rodent dam. Indeed, although dams often engage in communal nesting in natural settings to cope with litter demands,¹⁰⁹ they still struggle to ensure that each pup is adequately cared for. In extreme cases, dams commit infanticide to cope with environmental demands (although the existence of infanticide in laboratory mice has been debated).^{110–112} This difference in litter size also fundamentally alters parent-offspring social dynamics.

Although communication between human mothers and infants is bi-directional, human mothers frequently initiate bouts of communicative synchrony, during which they lead conversational rhythms whilst their infants follow.^{113–115} By contrast, mouse parent-offspring communications are most frequently pup-initiated, with dams playing a more reactive role. Large litter sizes drive pups to vie for attention (primarily through pup vocalisations), while dams allocate sparse attentional resources based on need. Physiological constraints also limit the directionality of vocal communication in mice. Unlike humans who are able to hear from birth, pups are not able to hear until PD10.¹¹⁶ Therefore, rodent vocal communication during infancy is completely unidirectional—from pup to dam. Accordingly, when conducting cross-species investigations, the likely directionality of social and synchronous behaviour needs to be carefully considered.

A further important difference is the duration of infancy in humans and rodents. Although there are structural similarities in their developmental trajectories (Figure 2),^{27,28} in real time, infancy spans years for a human but only a week for the mouse. The prolonged infancy of humans renders them helpless and immature for a longer time, permitting (and requiring) stronger mother-infant affiliative bonding, which is supported through synchronicity. For the faster maturing mouse species, establishing and maintaining a synchronous parent-offspring bond is of lower importance. Instead, pups learn to explore the world together with their littermates and social learning is often directed towards strangers (evidenced by indiscriminate social transmission of food preference—Kitchenham et al.¹¹⁷ and preference reversal from dam to stranger mice past P14¹¹⁸). Accordingly, opportunities for studying parent-offspring synchrony are more transient in rodent models and may be of comparative lower importance than peer-to-peer synchrony particularly in later developmental stages.

5 | CONCLUDING REMARKS

Parent-offspring synchrony is essential for healthy development of young in both mice and humans. In particular, neural synchrony appears to be a potential mechanism where the long-lasting effects of behavioural parent-offspring synchrony may be implemented. Although human and mouse parent-offspring relationships are fundamentally different, due to evolutionary deviations, many behavioural and developmental parallels may still be harnessed to investigate mechanisms

involved in human parent-child neural synchrony though rodent models. For instance, maternal responsiveness towards her own infant's cries remain a conserved form of interactional synchrony between mother-infant dyads, where specific maternal responses are elicited in both humans and mice. The role of touch in parent-offspring interactions is also consistent in humans and mice, despite some differences in mechanism and function. Despite differences afforded by litter size, rodent models of early social development may prove to be particularly relevant for understanding parent-child dynamics in larger families, where parental attention on children may be more divided. Like humans, individual female mice also exhibit varying propensities for reactivity to their pup's cries for attention. Caring dams react with shorter latencies to pup calls, while others may continue strolling about—ignoring pups in turmoil. These natural differences can also be exploited to map different types of parenting styles in humans to the behaviour and type of synchrony observed in mice. Finally, mouse models are particularly valuable assets for parent-offspring neural synchrony research as they allow in-depth study and manipulation of the neural circuitry underpinning synchrony phenomena and their social behavioural outcomes. This review represents a first step to harnessing the power of cross-species models for dissecting the mechanisms involved in parent-child biobehavioural synchrony.

AUTHOR CONTRIBUTIONS

Gao Xiang Ham: Formal analysis; methodology; writing – original draft; writing – review and editing. **Kai En Lim:** Formal analysis; methodology; writing – original draft; writing – review and editing. **George Augustine:** Conceptualization; funding acquisition; writing – review and editing. **Victoria Leong:** Conceptualization; funding acquisition; project administration; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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