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More than just mothers: The neurobiological and neuroendocrine underpinnings of allomaternal caregiving

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ABSTRACT

In a minority of mammalian species, mothers depend on others to help raise their offspring. New research is investigating the neuroendocrine mechanisms supporting this allomaternal behavior. Several hormones have been implicated in allomaternal caregiving; however, the role of specific hormones is variable across species, perhaps because allomothering independently evolved multiple times. Brain regions involved in maternal behavior in non-human animals, such as the medial preoptic area, are also critically involved in allomaternal behavior. Allomaternal experience modulates hormonal systems, neural plasticity, and behavioral reactivity. In humans, fatherhood-induced decreases in testosterone and increases in oxytocin may support sensitive caregiving. Fathers and mothers activate similar neural systems when exposed to child stimuli, and this can be considered a global "parental caregiving" network. Finally, early work on caregiving by non-kin (e.g., foster parents) suggests reliance on similar mechanisms as biologically-related parents. This article is part of the 'Parental Brain and Behavior' Special Issue.

1. Introduction

In many animal species, offspring survival is dependent on parental caregiving. This drive is accompanied by fluctuations in hormones, as well as modifications in neural structure and function. Given that the primary caregiver in most mammalian species is female, most of our knowledge concerning the neuroendocrine and neurobiological control of parental behavior stems from research on mothers (Bridges, 2016; Kim, 2016; Kim et al., 2016; Pawluski et al., 2016). However, offspring care is not restricted to female mammals, as 6% of mammalian species exhibit paternal care (Kleiman and Malcolm, 1981). Caregiving is also not restricted to biological parents; alloparental caregiving is observed in both human and non-human animal species, however, less is known about the neuroendocrine regulation of this behavior. During a symposium at the 2018 Parental Brain meeting, entitled " Other than mothers – the paternal and alloparental brain", we presented evidence that our understanding of hormone-modulated, parenting-related plasticity should not be limited to the study of mothers.

The neural and endocrine underpinnings of parental behavior have been well studied using many laboratory species, including rats, mice, and voles (Bales and Saltzman, 2016; Kenkel et al., 2017; Kohl et al., 2017; Leuner et al., 2010; Olazábal, 2014; Rilling, 2013; Saltzman et al., 2017; Wynne-Edwards and Timonin, 2007; Ziegler, 2000). This review differs from those because it includes a discussion of parental, alloparental, and unrelated caregivers. First, we reviewed our current understanding of neuroendocrine and neurobiological mediators of paternal care in non-human and human fathers. We selectively highlighted foundational and recent mechanistic work that has advanced our current knowledge of paternal caregiving. Our discussion of human fathers focused on hormonal data as well as neuroimaging data gathered via functional Magnetic Resonance Imaging (fMRI). Second, we reviewed alloparental caregiving exhibited by both human and non-

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human mammalian species, and their neural and endocrine bases. Alloparenting, for the purpose of this review, is defined as care resembling maternal or paternal care; it can involve carrying and/or retrieving, cleaning, protecting, the provisioning of food, teaching, warming, as well as non-direct benefits (Rosenbaum and Gettler, 2018). In rodents, alloparental care is typically measured by assaying pup retrieval as well as licking, grooming, carrying, and huddling over pups. Ultimate, evolutionary explanations for alloparental care might include kin selection when care is delivered to genetic relatives. On the other hand, care directed at non-relatives may provide an opportunity to learn caregiving skills that will later enhance offspring survival.

It is important to mention that methodological differences often preclude direct comparison of results from human and non-human studies, and from studies of laboratory-reared and wild species. Invasive neuroanatomical methods are limited to laboratory species; studies of wild animals are often limited to measures of peripheral hormones and research in humans tends to focus on fMRI.

2. Non-human animal fathers

2.1. Hormonal regulation of paternal care in non-human animals

Jay Rosenblatt, who systematically investigated the psychobiology of mammalian maternal behaviors, described virgin males that cared for pups as maternally behaving males (Rosenblatt, 1967). However, this observation stemmed from the study of species that do not traditionally exhibit paternal care in the wild (e.g., *Rattus*, *Mus;* Table 1). The use of mammalian species that exhibit paternal care in nature has allowed us to better characterize paternal behaviors and identify the underlying endocrine mechanisms contributing to this behavior. Such species include, but are not limited to, California mice (*Peromyscus californicus*; Gubernick and Alberts, 1987), titi monkeys (*Callicebus* spp.; Spence-Aizenberg et al., 2016), prairie voles (*Microtus ochrogaster*; Kenkel et al., 2014), cotton top tamarins (*Saguinus oedipus*; Ziegler et al., 2000; Zahed et al., 2010), common marmosets (*Callithrix jacchus*; Dixson and George, 1982; Ziegler and Sosa, 2016), Djungarian hamsters (*Phodopus campbelli*; Brooks et al., 2005), mandarin voles (*Lasiopodomys mandarinus*; Smorkatcheva, 2003), Mongolian gerbils (*Meriones unguiculatus*; Martínez et al., 2015) and even humans (Delahunty et al., 2007; Fleming et al., 2002; Kim et al., 2014) (Table 1). Research using these paternal species, and others, has demonstrated that mammalian fathers experience fluctuations in peripheral hormone levels in response to offspring, despite not undergoing pregnancy, parturition, and lactation. However, there is little consistency as to what specific hormones are necessary to maintain paternal care in mammalian species. This may be attributed to the independent evolution of mammalian paternal care in varied, specific ecological niches, where evolution realized different proximate solutions to motivating paternal caregiving (Saltzman and Ziegler, 2014; Wynne-Edwards and Timonin, 2007).

2.1.1. Gonadal steroid hormones

The gonadal steroid hormone testosterone (T) and its metabolites, estradiol (E2) and dihydrotestosterone (DHT), have been implicated in the initiation and/or maintenance of paternal behavior. Plasma T levels in Djungarian hamsters (*P. campbelli*) increase prior to the birth of offspring but decrease once pups are born (Wynne-Edwards and Reburn, 2000). Mongolian gerbils with low circulating T engage in more huddling behavior of their own pups, as compared to males with high T concentrations (Clark and Galef, 2000). A post-birth decrease in T is also observed in human males (Alvergne et al., 2009; Berg and Wynne-Edwards, 2001; Gray et al., 2006; Perini et al., 2012b, 2012a). This reduction in T may relate to lowered sexual activity and involvement in male caregiving behavior (Gettler et al., 2013). Interestingly, fatherhood-induced decreases in T are not found among males in societies with polygynous mating systems (Gray, 2003), however, again, paternal involvement in childcare may play a key role in fatherhood-associated changes in T (Muller et al., 2009). In prairie vole fathers, castration impairs caregiving behavior, suggesting that gonadal steroid hormones are important for paternal care in this species (Wang and De Vries, 1993). Using the California mouse, the direct role of T, and more specifically E2, in caregiving has been demonstrated. Castration reduces caregiving behavior in California mice; this behavior is restored following replacement with T (Trainor and Marler, 2001). In fact, both T and E2, but not DHT, restores paternal behavior (i.e., huddling and grooming pups) in California mice males, suggesting that the effects of T on paternal behavior are due to its aromatization to E2. Consistent with this conclusion, T plus fadrazole (an aromatase inhibitor) does not reinstate paternal behavior in California mice (Trainor and Marler, 2002). While Trainor et al. (2003) demonstrated significantly lower T in California mouse fathers compared to males with only mating experiences, no differences in circulating T were observed among virgin males, non-breeding males, and first-time fathers in another study of California mice (Harris and Saltzman, 2013). Methodological differences (e.g., when plasma/serum samples were collected following the birth of pups) may contribute to these disparate outcomes. Taken together, these data suggest that increases in aromatase activity drive paternal behavior in California mice, as has been observed (Trainor et al., 2003).

While the relationship between T and male caregiving behavior is well-defined, the relationship between E2 and male caregiving behavior is less clear. In Djungarian hamsters, while castration reduces E2 concentrations in the periphery, it does not reduce paternal behavior (Hume and Wynne-Edwards, 2006, 2005). E2 levels rise near the time of birth in cotton top tamarins and common marmosets, with levels returning to baseline following the birth of offspring (Nunes et al., 2000; Ziegler et al., 2004). This effect is not observed in Djungarian hamsters (Schum and Wynne-Edwards, 2005). Compared to virgins, new California mouse fathers exhibit elevated peripheral E2 concentrations that slowly return to basal levels by the time of weaning (Hyer et al., 2017).

Evidence supporting a role for progesterone in paternal behavior is limited and mixed among biparental species. Peripheral progesterone levels are lower in California mouse fathers, compared to non-fathers (Trainor et al., 2003). Yet, among Djungarian hamsters, progesterone levels are higher near the birth of offspring, compared to naïve males (Schum and Wynne-Edwards, 2005). Further investigation into the role of progesterone in the regulation of paternal behavior are needed.

2.1.2. Prolactin

Peripheral prolactin (PRL) levels are related to paternal behavior in several biparental species. In Djungarian hamsters, higher PRL levels are associated with paternal behavior during the early neonatal period (i.e., 2-days following birth; Reburn and Wynne-Edwards, 1999). A similar effect was observed in California mouse fathers (Gubernick and Nelson, 1989). Moreover, among mandarin voles, experienced fathers have higher PRL levels than new fathers (Wang et al., 2018). These findings potentially suggest that PRL may be necessary for the initiation of male caregiving behavior in these biparental species and may vary as a result of repeated reproductive experience. Studies using non-human primates also support the case for a role of PRL in fatherhood-related behavior. Common marmoset fathers, who spend the majority of their time carrying their offspring on their backs, exhibit PRL levels five times higher than non-fathers (Dixson and George, 1982). Bromocriptine, a dopamine (DA) agonist that reduces circulating PRL levels, reduces infant retrieval and carrying rate in common marmosets (Roberts et al., 2001) – behaviors that are typically associated with higher levels of PRL. However, not all of the available evidence supports the role of PRL in the modulation of paternal behavior (Wynne-Edwards and Timonin, 2007). For example, either an inconsistent association or no association at all has been observed between peripheral levels of PRL and paternal care in Djungarian hamsters and common marmosets (Brooks et al., 2005; Roberts et al., 2001; Ziegler et al.,

Table 1
Parental behaviors exhibited under natural conditions.

Common Name	Species	Maternal Behavior	Paternal Behaviors	Alloparental Behaviors	Effects of Age?
African striped mouse	*Rhabdomys pumilio*	High levels of direct parental care (nursing, licking, huddling, retrieving)	High levels of direct parental care (huddling, retrieving)	Siblings help with rearing by carrying, grooming, huddling, licking, and retrieving infants	Alloparenting increases with age
Black-tufted marmoset	*Callithrix penicillata*	Considerable parental investment (protecting neonates and weanlings, provisioning of food)	Considerable parental investment (provisioning of food, protecting weanlings)	Juvenile siblings help with rearing by carrying infants	Alloparenting increases with age
California mouse	*Peromyscus californicus*	Considerable parental investment (nest building, nursing, licking, crouching, huddling, grooming, manipulating, retrieving)	Considerable parental investment (nest building, licking, couching, huddling, grooming, manipulating, retrieving)	Uncommon	Alloparental responsiveness declines with age
Common marmoset	*Callithrix jacchus*	Nurse offspring; share carrying with mate	Primary care giver (carrying, grooming, protecting, feeding)	Juvenile siblings help with rearing by carrying infants	Alloparenting increases with age
Cotton top tamarin	*Saguinus oedipus*	Considerable parental investment (protecting neonates and weanlings, provisioning of food)	Considerable parental investment (provisioning of food, protecting weanlings, carrying)	Cooperative rearing of offspring by all group members (carrying, provisioning food)	Alloparenting increases with age
Djungarian hamster	*Phodopus campbelli*	Considerable parental investment (nest building, nursing, licking, crouching, huddling, grooming, manipulating, retrieving)	Considerable parental investment (nest building, licking, couching, grooming, manipulating, retrieving)	Siblings help with rearing by grooming, huddling, licking, retrieving infants	No data
Golden lion tamarin	*Leontopithecus rosalia*	Considerable parental investment (nursing, carrying, protecting offspring, provisioning of food)	Considerable parental investment (carrying, provisioning of food, protecting offspring)	Cooperative rearing of offspring by all group members (carrying, provisioning food)	Alloparenting increases with age
Gray wolf	*Canis lupus*	Considerable, but variable, parental investment (nursing offspring, provisioning of food, protecting weanlings)	Considerable, but variable, parental investment (provisioning of food, protecting weanlings)	Juvenile siblings help with feeding, engaging in play behavior, protecting	No effect of age on alloparenting
Human	*Homo sapien*	Considerable parental investment (nursing, carrying, protecting, provisioning of food, playing)	Considerable parental investment (carrying, protecting, provisioning of food, playing)	Siblings help with rearing (carrying, protecting, provisioning of food, playing)	No effect of age on alloparenting
Laboratory mouse	*Mus musculus*	Considerable parental investment (nursing, licking, huddling, grooming, manipulating, retrieving)	Limited parental care (infanticidal)	Uncommon outside of communal nesting arrangements, then analogous to maternal behavior.	Alloparental responsiveness declines with age
Mandarin vole	*Lasiopodomys mandarinus*	Considerable parental investment (nursing, licking, huddling, grooming, manipulating, retrieving)	Considerable parental investment (licking, huddling, grooming, manipulating, retrieving)	Siblings help with rearing by grooming, huddling, licking infants	Alloparenting more common in young males and older females
Mongolian gerbil	*Meriones unguiculatus*	Considerable parental investment (nursing, licking, crouching, huddling, grooming, retrieving)	Considerable parental investment (licking, couching, grooming, retrieving)	Siblings help with rearing by grooming, huddling, licking, retrieving infants	Alloparental responsiveness declines with age
Naked mole-rat	*Heterocephalus glaber*	Single reproductive female in colony provides care	Biological fathers provide care	Subordinate colony members provide care (retrieving, licking, grooming, provisioning of food)	Alloparental responsiveness declines with age
Norway rat	*Rattus norvegicus*	Considerable parental investment (nest building, nursing, licking, crouching, huddling, grooming, manipulating, retrieving)	No parental behavior (infanticidal)	Uncommon	Alloparental responsiveness declines with age
Prairie vole	*Microtus ochrogaster*	Considerable parental investment (nest building, nursing, licking, crouching, huddling, grooming, manipulating, retrieving)	Considerable parental investment (nest building, licking, couching, grooming, manipulating, retrieving, huddling)	Siblings help with rearing by grooming, huddling, licking, retrieving infants	Alloparental responsiveness declines with age, particularly among females
Siberian dwarf hamster	*Phodopus sungorus*	Considerable parental investment (nest building, nursing, licking, crouching, huddling, grooming, manipulating, retrieving)	Limited parental care	Uncommon	Alloparental responsiveness declines with age
Titi monkey	*Callicebus* spp.	Nurse offspring; limited parental care	Primary care giver (carrying, grooming, protecting, feeding, anogenital licking, play behavior)	Not heavly studied. Uncommon. Behaviors include carrying infants, anogenital licking, face licking	No data

2009). Assessing the role of PRL in initiating, rather than maintaining, male caregiving should be further explored.

2.1.3. Oxytocin and vasopressin

The relationship between fatherhood and peripheral levels of the posterior pituitary hormones oxytocin (OT) and vasopressin (AVP) are less well known. While no direct evidence relates peripheral AVP to paternal behavior, peripheral OT levels increase in California mouse males cohabitating with their pair bonded mate. These levels remain elevated until late gestation, when they plummet and remain low throughout the mate's lactation period (Gubernick et al., 1995). Evidence more strongly supports a relationship between paternal behavior and the central expression of these hormone receptors (see below).

2.1.4. Glucocorticoids

The role of peripheral glucocorticoid (GC) levels on male caregiving behavior is mixed and may be species-specific. In California mice, peripheral corticosterone (CORT) concentrations do not differ among virgin males, non-fathers, and fathers (Harris and Saltzman, 2013). In fact, in California mice, acute treatment with CORT does not alter paternal behaviors (Harris et al., 2011). On the other hand, chronic variable stress transiently disrupts male caregiving in California mice (Harris et al., 2013). This finding suggests that paternal behavior in California mice may be affected by elevations in CORT; however, repeated and prolonged elevations in CORT are required. CORT levels in *Phodopus* differ as a result of caregiving experience. Specifically, compared to CORT levels before pairing with a female, *P. campbelli* and *P. sungorus* males exhibit reduced CORT during their mate's lactation period (Reburn and Wynne-Edwards, 1999). Yet, glucocorticoids (GCs) do not seem to be involved in paternal behavior in prairie voles (Campbell et al., 2009). Overall, the support for GCs in paternal behavior is weak.

2.2. Neurobiology of paternal care

2.2.1. Brain areas and circuit mechanisms

While the neural correlates underlying maternal behavior are well-known, the precise brain regions and neural circuits underlying paternal behavior are less intensively investigated. Numerous techniques and methods (i.e., lesions, neuronal activation, dendritic reconstruction analyses, adult neurogenesis, genetic modulation) have demonstrated several neural regions involved in male caregiving (Table 2), and have revealed the ability of paternal experience to modulate the brain.

2.2.1.1. Neuronal activation and lesion studies. Studies utilizing the immediate early-gene, c-Fos, and lesion studies have played an important role in identifying brain regions and neural circuits that are activated by male caregiving experience. Using male C57BL/6J mice, specific patterns of c-Fos expression have been associated with fatherhood within areas that are also important for the expression of maternal behavior [e.g., MPOA and ventral pallidum (VP)], and social behaviors [e.g., hypothalamus (HYPO) and amygdala (AMYG)]. In Slc:ICR mice, sires exhibiting retrieval behavior display higher c-Fos expression in the MPOA, compared to non-retrieving sires; this c-Fos expression pattern was not observed in the ventral tegmental area (VTA), nucleus accumbens (NAcc), or VP (Zhong et al., 2014). Compared to virgin males, C57BL/6J mouse fathers exposed to pups exhibited more c-Fos expression in the anterior commissural nucleus (ACN), central part of the MPOA anterior (caMPOA), and central part of the MPOA posterior (cpMPOA) (Tsuneoka et al., 2015). Paternal male Trpc2 knockout mice, mice lacking a vomeronasal organ-specific ion channel, express increased c-fos+ cells in the MPOA following exposure to pups, compared to virgin males (Wu et al., 2014). Studies utilizing biparental species, like the California mouse and Mongolian gerbil, have also investigated areas implicated in maternal behaviors along with fear and anxiety-related areas. New California mouse fathers exhibit elevated Fos-like immunoreactivity (ir) following exposure to unfamiliar pups in the MPOA, bed nucleus of the stria terminalis (BNST), and caudal dorsal raphe nucleus (de Jong et al., 2009), as well as in cornu Ammonis (CA)1, CA3, and the dentate gyrus (DG) of the hippocampus (HPC) (Franssen et al., 2011), compared to pup exposed virgins and virgins without pup exposure; similar findings are observed in the MPOA and BNST of Mongolian gerbil fathers (Romero-Morales et al., 2018). These effects may be region specific, as paternal experience reduced c-Fos ir in many fear- and anxiety-related areas of the brain, as well as in the piriform cortex, which is implicated in olfaction (Lambert et al., 2011).

Lesion studies have also added to our knowledge. Lesions to the MPOA and NAcc, and to a lesser extent the basolateral amygdala (BLA), of the biparental California mouse reduced parental behaviors in males (Lee and Brown, 2007). Bilateral cMPOA and/or VP lesions abolish allomaternal behavior (Akther et al., 2014; Tsuneoka et al., 2015) – an effect that also promotes infanticidal behavior in male C57BL/6J mouse fathers (Tsuneoka et al., 2015). Collectively, these studies suggest that the MPOA-VTA-NAcc-VP neural circuit may be involved in paternal behavior.

2.2.1.2. Adult neurogenesis. The addition and survival of new neurons has been observed throughout postnatal development in numerous mammalian species (Gould, 2007). Hence, it is of no surprise that male caregiving experience has been shown to modulate cell proliferation and adult neurogenesis in several brain regions and in numerous species that exhibit paternal care (Leuner et al., 2010). Interactions with pups increases cell proliferation in the olfactory bulb and DG of C57BL/6J male mice – an effect that is mediated by PRL (Mak and Weiss, 2010). Studies utilizing biparental species have added to our understanding of fatherhood-related new cell production and survival. In fact, the findings for these species are opposite those reported in species that are traditionally uniparental in the wild (e.g., *Rattus, Mus*). Fatherhood decreases cell survival in the DG of the HPC in California mice (at weaning) and prairie voles (Glasper et al., 2011; Lieberwirth et al., 2013). A fatherhood-related deficit in adult neurogenesis has also been reported in the AMYG and ventromedial hypothalamus (VMH) of the prairie vole (Lieberwirth et al., 2013). However, the effects of paternal experience on neuronal plasticity are not always negative. In fact, studies using California mice have demonstrated that DG new cell survival is increased fathers during a time of peak pup retrieval (Hyer et al., 2016, 2017) and nestin-ir, a marker for multipotent neural stem cells, is increased in areas CA2 and CA3 of the HPC in paternal males (Lambert et al., 2011). Collectively, these data suggest that fatherhood modulates neural plasticity and that the amount and extent of paternal behavior, at any given point following offspring birth, should be considered when designing such studies.

2.2.1.3. Dendritic morphology. Fatherhood effects on structural plasticity of the brain are not limited to cell survival, as alterations in dendritic morphology have been reported in a few species examined. Around the time of weaning, increased dendritic spine density is observed on DG granule cells and basal dendrites of CA1 pyramidal cells in California mice (Glasper et al., 2015; Hyer and Glasper, 2017). However, fatherhood reduces spine density on apical dendrites in area CA3 of the HPC (Hyer and Glasper, 2017). More recent evidence demonstrates both dendritic spine density as well as total dendritic length is greater on pyramidal neurons in medial prefrontal cortex (mPFC) of new and experienced mandarin vole fathers, compared to newly paired males (Wang et al., 2018).

2.2.1.4. Genetic modulation. The use of genetic tools has allowed us to more directly determine the role of specific neural mechanisms underlying pup-directed behaviors in males. Genetically ablating MPOA galanin neurons impairs paternal behavior in Gal-Cre transgenic mice – an effect also observed in maternal Gal+ mice.

Table 2
Brain regions and major functions.

Brain Region	Abbreviation	Major Function
Amygdala	AMYG	Responsible for the response and memory of emotions
Anterior Insular Cortex	AIC	Visceral somatosensory cortex involved with empathy
Anterior Olfactory Nucleus	AON	Involved in olfaction
Arcuate Nuclei of the Hypothalamus	ARH	Mediates various neuroendocrine and physiological functions
Auditory Cortex	A1	Involved in hearing
Basolateral Amygdala	BLA	Involved in development of conditioned fear
Bed Nucleus of the Stria Terminalis	BNST	Controls autonomic, neuroendocrine, and behavioral responses
Caudal Dorsal Raphe Nucleus	DRC	Responsive to anxiogenic stimuli
Caudate Nucleus	CN	Target of nigrostriatal DA system; involved in reward and motivation
Cerebellum	no abbreviation	Coordinates voluntary movements
Cingulate Cortex	CC	Integral part of limbic system involved with formation of emotions, learning, and memory
Cornu Ammonis 1	CA1	Implicated in memory storage
Cornu Ammonis 2	CA2	Implicated in social memory
Cornu Ammonis 3	CA3	Implicated in associative memories
Dentate Gyrus	DG	Involved in learning, memory, and spatial coding
Dorsal Anterior Cingulate Cortex	dACC	Implicated in empathy
Dorsal Caudate Nucleus	dCN	Involved in habit formation, flexibility, and switching
Dorsal Lateral Septum	LSd	Implicated in emotional processes and stress responses
Dorsomedial Prefrontal Cortex	DMPFC	Involved in complex cognitive processes, like social cognition
Entorhinal Cortex	EC	Hub in a network for memory and navigation
Frontopolar Cortex	FPC	Plays a role in complex, higher order behavior
Hippocampus	HPC	Involved in spatial memory and regulation of emotions
Hypothalamus	HYPO	Involved in regulating pituitary gland function
Inferior Frontal Gyrus	IFG	Implicated in response inhibition
Insular Cortex	no abbreviation	Involved in body representation and subjective emotional experience
Lateral Amygdala	LA	Implicated in regulation of fear and anxiety
Lateral Orbitofrontal Cortex	lOFC	Involved in choice; integrated prior and current information
Lateral Prefrontal Cortex	lPFC	Involved broadly in executive behavioral control
Lateral Septal Nuclei	LS	Implicated in motivated behavior
Medial Amygdaloid Nucleus	MeA	Involved in smell, motivation, and emotional behavior
Medial Orbitofrontal Cortex	mOFC	Target of mesolimbic DA system; involved in reward processing
Medial Prefrontal Cortex	mPFC	Implicated in decision making
Medial Preoptic Area	MPOA	Regulates social behaviors and social reward; critical hub in parental caregiving system
Middle Frontal Gyrus	MFG	Site of convergence of the dorsal and ventral attention networks
Nucleus Accumbens	NAcc	Involved in mediation of reward behavior
Nucleus Reuniens	RE	Reciprocally connected to HPC and MPFC; critical for many working memory tasks
Olfactory Bulb	no abbreviation	Receives input about odors detected by the nasal cavity
Paraventricular Nucleus of the Hypothalamus	PVN	Plays essential roles in control of stress, metabolism growth, and reproduction
Paraventricular Nucleus of the Thalamus	PVNT	Mediates positive and negative emotional behavior
Piriform Cortex	PPA	Involved in olfaction
Prefrontal Cortex	PFC	Implicated in planning, decision making, and social behavior
Preoptic Area	POA	Involved in sleep generation and copulatory behavior
Putamen	no abbreviation	Implicated in movement regulation and many types of learning
Subiculum	SUB	Mediates hippocampal-cortical interaction
Substantia Nigra	SN	Plays a key role in reward and movement
Superior Temporal Sulcus	STS	Involved in social and speech perception
Supraoptic Nucleus of the Hypothalamus	SON	Produces oxytocin and vasopressin
Temporo-parietal Junction	TPJ	Incorporates information from the thalamus and limbic system; implicated in visual, auditory, and somatosensory system regulation
Ventral Anterior Cingulate Cortex	vACC	Part of the default mode network; implicated in social evaluation
Ventral Pallidum	VP	Implicated in hedonic reward
Ventral Striatum	VS	Involved in reward processes and motivation
Ventral Tegmental Area	VTA	Hub of mesolimbic DA system; involved in reward and motivation
Ventromedial Hypothalamus	VMH	Involved in hunger, fear, thermoregulation, and sexual activity
Ventromedial Prefrontal Cortex	vmPFC	Implicated in risk and fear processing

Optogenetically activating these neurons in virgin males suppresses pup-directed aggression and induces pup grooming – a behavior observed in paternal males (Wu et al., 2014). Increasing use of more contemporary techniques may add to our understanding of neural mechanisms underlying allomaternal care.

2.2.2. Paternal behavior and behavioral reactivity

Increasing evidence suggests that fatherhood, specifically interactions with offspring, alters behavioral responsivity. In fact, studies utilizing traditional laboratory mice and biparental rodents suggest that cognition, stress-responsivity, and anxiety-like behaviors are modified with paternal care; however, timing of behavioral testing following the birth of pups is an important variable.

2.2.2.1. Learning and memory. Using a modified version of the Morris Water Maze (i.e., dry land maze), California mouse males with caregiving experience exhibit improved spatial memory, compared to pup-exposed virgins and virgins without pup exposure (Franssen et al., 2011). It is important to note that these paternal California mouse males were not actively caring for offspring, as fathers caring for offspring do not display improved memory around the time of weaning (Glasper et al., 2011). While social memory for offspring is enhanced in C57BL/6J fathers (Mak and Weiss, 2010), social memory for juveniles is reduced in paternal prairie voles (Lieberwirth et al., 2013).

2.2.2.2. Anxiety and behavioral despair. The effects of fatherhood on anxiety-like behavior, while initially appearing contradictory and possibly incongruent, ultimately suggest that offspring interactions at the time of behavioral assessment largely influence behavioral measures of anxiety-like behavior. For example, no difference in

anxiety-like behavior on the elevated plus maze is observed in California mouse first-time fathers days after birth (Chauke et al., 2012; Hyer et al., 2016) or late in the weaning period (Glasper et al., 2011); however, decreased anxiety-like behavior is observed around the time of peak pup retrieval (i.e., PND 16–21; Glasper et al., 2015; Hyer et al., 2016). Similarly, no differences in exploratory behavior during open field testing were observed between virgin males, expectant fathers, or California mouse fathers within the 1st week following offspring birth (Perea-Rodriguez et al., 2018). Additionally, California mouse first-time fathers do not differ behaviorally from virgin males during tail-suspension testing 10 days following the birth of offspring (Zhao et al., 2018, 2017). On the other hand, in experienced California mouse fathers (i.e., sired more than one liter), reduced anxiety-like behavior is observed 3 days post offspring birth during the open field task, compared to virgins or pup-exposed virgins (Bardi et al., 2011). Clearly, reproductive experience and time of assessment are important factors. More evidence supporting a relationship between paternal care and regulation of anxiety-like behavior also exists. Increased anxiety-like behavior (e.g., reduced percent time in the central area of the open field) accompanies a brief separation of mandarin vole fathers from offspring (Kong et al., 2015). While behavioral despair is less explored in relationship to male caregiving experience, data suggest that separation from offspring increases indices of behavioral despair (e.g. passive stress-coping). In both mandarin voles and California mice, repeated and/or prolonged separation of fathers and offspring increases immobility time during the forced swim task, compared to non-fathers (Hyer and Glasper, 2017; Kong et al., 2015).

2.3. Mediation of paternal behavior via neuroendocrine mechanisms

Although males do not undergo pregnancy, parturition, or lactation – reproductive states that are yoked to extensive changes in the neuroendocrine system – similar hormonal mechanisms may underlie fatherhood-related changes in neuroplasticity throughout the brain.

2.3.1. Estradiol

It has long been known that increased estrogen production in the brain may contribute to the onset of male caregiving behavior. For example, in male house mice, prior pup experience results in paternal care and is correlated with estrogen receptor (ER)-ir in the BNST, HPC, subiculum, lateral septal nuclei, entorhinal cortex, PPA, MPOA, and arcuate nuclei of the hypothalamus (ARH) (Ehret et al., 1993). Increased levels of aromatase activity was observed in the MPOA of California mouse fathers 2–3 weeks following the birth of offspring, compared to sexually experienced males without pups (Trainor et al., 2003). Region-specific ER expression may also mediate paternal behavior. In mandarin voles, fathers with high responsivity to pups express more ERα-ir neurons in numerous brain regions that play a key role in caregiving behavior in males, including the BNST, ARH, and medial amygdaloid (MeA) nucleus, compared to low responsivity males (Li et al., 2015). Additionally, ERβ expression is upregulated in the HPC ~ 2 weeks following the birth of offspring in 1st time California mouse fathers, compared to virgins (Hyer et al., 2017; Fig. 1). Further evidence from non-monogamous laboratory ICR mice suggests that aromatization within numerous brain regions [i.e., MPOA, NAcc, VP, VMH, CA3 of the HPC, dorsal lateral septum, AMYG, and prefrontal cortex (PFC)] regulates the initiation, development, and maintenance of paternal behavior, with this effect mediated by communication with the dam (Akther et al., 2015).

2.3.2. Oxytocin and vasopressin

Male caregiving experience modulates region-specific expression of the OT receptor. While hippocampal OT receptor expression is not affected by the duration of paternal experience in first-time California mouse fathers (Hyer et al., 2017; Fig. 1), greater OT receptor binding is observed in the AON, BNST, LS, and lateral amygdala of meadow voles with paternal experience (Parker et al., 2001). Exposure to biological pups increased number of OT-ir cell bodies and fibers in the HPC of California mouse fathers (Lambert et al., 2011), as well as increased the expression of OT in the PVN of paternal mandarin voles (Yuan et al., 2018). Multiparous prairie vole fathers exhibit a greater number of OT-ir neurons in the PVN, compared to virgin males (Kenkel et al., 2014). Likewise, higher levels of OT-ir neurons are observed in the PVN and supraoptic nucleus (SON) of the HYPO of mandarin vole fathers responding highly to pups, compared to low responding counterparts (Li et al., 2015). The role of OT in paternal behavior may be temporally specific, as neither *OT* gene expression or OT receptor binding is altered in prairie vole fathers shortly after the birth of offspring, compared to virgin males (Wang et al., 2000). Similar findings have also been observed in California mouse fathers (~PND3) that express reduced OT mRNA expression in the BNST, but not the MPOA or MeA, compared to virgin males (Perea-Rodriguez et al., 2015). However, by 5–6 days of exposure to their own pups, new mandarin vole fathers exhibit more OT-ir neurons in the NAcc and MeA, compared to virgin males (Wang et al., 2015).

Hypothalamic gene expression of AVP is increased within the 1st week of offspring birth in prairie vole fathers (Wang et al., 2000). California mouse fathers exposed to their own pups display increased numbers of AVP-ir cell bodies and fibers in the HPC (Lambert et al., 2011), with AVP receptor gene expression falling to virgin levels near weaning (Hyer et al., 2017; 1). Together, these data suggest AVP is elevated during fatherhood. These observations are not limited to rodent species, as fatherhood increased the numbers of vasopressin 1a receptors in the PFC of common marmosets (Kozorovitskiy et al., 2006). The expression of AVP in paternal males may be species-specific, as less AVP receptor autoradiography is observed in the anterior olfactory nucleus (AON) of paternal meadow voles compared to that expressed in sexually- and parentally-inexperienced males (Parker et al., 2001). Collectively, these results demonstrate that paternal experience is associated with altered OT and AVP expression in the brain, which may be influenced by the amount of offspring exposure.

2.4. Summary

The use of mammalian species that exhibit paternal care has revealed numerous peripheral hormones (i.e., E2, T, PRL, OT, AVP, CORT) that modulate neural and behavioral responsivity to offspring, even though males do not undergo pregnancy, parturition, or lactation. Given the diverse array of mammalian species exhibiting paternal care, and the lack of consistency regarding the specific hormonal modulators of paternal behavior, it is difficult to make strong generelizations about the neuroendocrine control of non-human mammalian fatherhood-related plasticity. What is clear, however, is that the hormonal changes that accompany fatherhood are temporally specific, suggesting experience with offspring may significantly influence hormone-mediated neuroplasticity.

3. Human fathers

3.1. Endocrinology of fatherhood

3.1.1. Testosterone

Given evidence from non-human animals that T biases males towards investing in mating effort at the expense of parenting effort (Clark and Galef, 1999; Hunt et al., 1999; Wingfield et al., 1990), many studies have examined whether human male T is related to paternal status and/or paternal behavior. Several studies have demonstrated lower levels of T in involved fathers of young children compared with non-fathers (Gray and Anderson, 2010), and one large longitudinal study has convincingly demonstrated decreases in T across the transition to fatherhood (Gettler et al., 2011). On the other hand, T does not

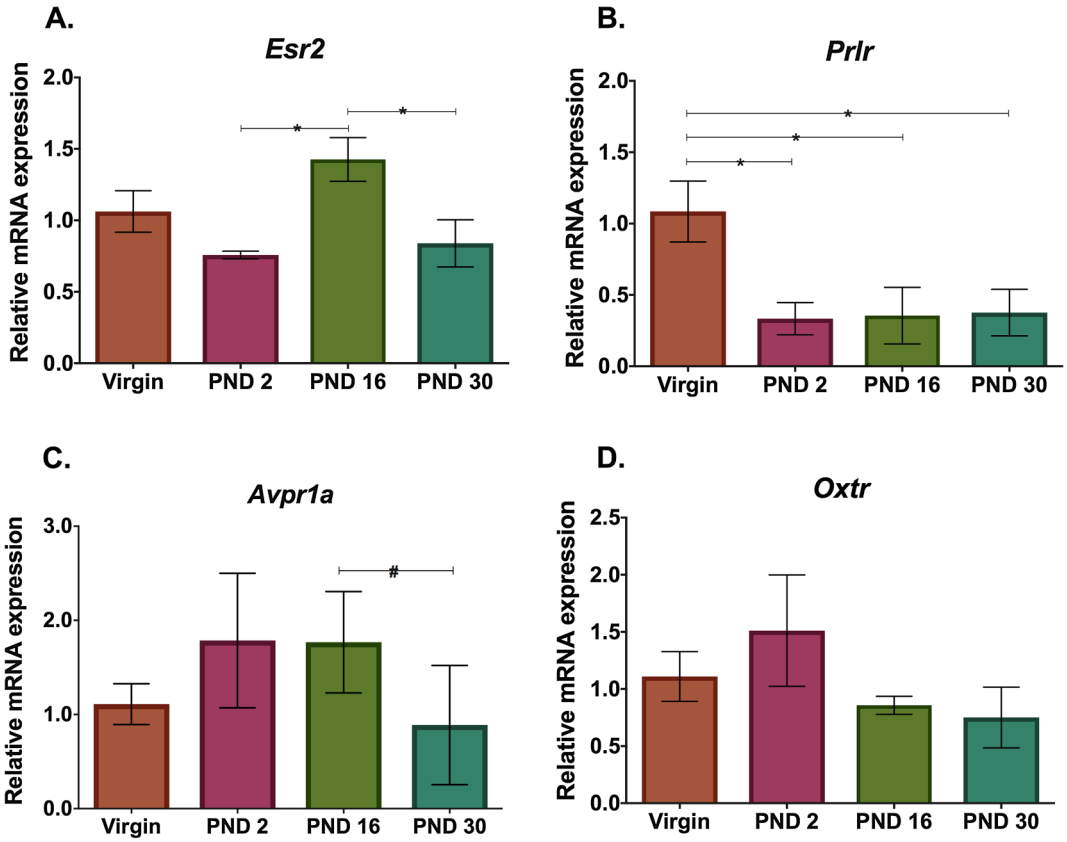

Fig. 1. Fatherhood alters parenting-related hormone expression in the hippocampus of male California mice. (A) More Esr2 mRNA expression is observed in fathers with 16-day old pups, compared to fathers with recent or weaning age offspring. (B) Allomaternal experience decreases Prlr expression. (C) Avpr1a expression is lower in fathers with 30-day old pups compared to fathers with 16-day only pups. (D) Oxtr expression is not differentially expressed as result of allomaternal experience. PND = postnatal day; Esr2 encodes for estradiol beta receptor; Prlr encodes for prolactin receptor; Avpr1a encodes for vasopressin 1a receptor; Oxtr encodes for oxytocin receptor. Bars represent mean ± SEM, *p ≤ 0.05; #p ≤ 0.05 (mean ranks comparison). Data from Hyer MM, Khantsis S, Venezia AC, Madison FN, Hallgarth L, Adekola E, Glasper ER (2017) Estrogen-dependent modifications to hippocampal plasticity in paternal California mice (*Peromyscus californicus*). Hormones and Behavior 96:147–155.

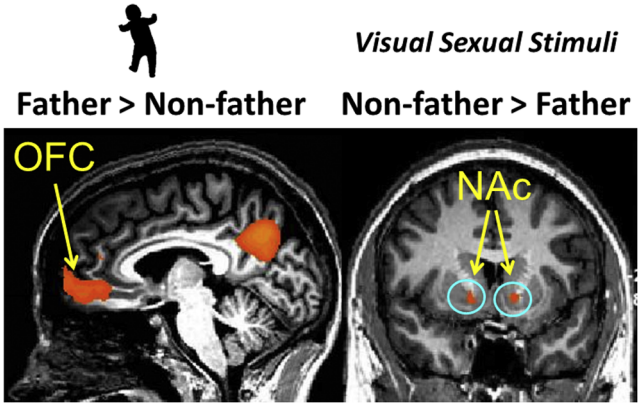

Fig. 2. Neural response to toddlers (left) and to sexually provocative visual stimuli (right) in fathers and non-fathers. Consistent with the life history theory prediction of a trade-off between mating and parenting effort outlined in the main text, fathers show stronger activation than non-fathers in response to pictures of toddlers within brain reward regions (e.g., OFC), whereas non-fathers show stronger activation to visual sexual stimuli in brain reward regions (e.g., ventral and dorsal (not shown) striatum). Images are thresholded at $p < 0.001$ (left) and $p < 0.005$ (right), uncorrected for multiple comparisons. OFC = orbitofrontal cortex, NAcc = nucleus accumbens. Data from: Mascaro, J. S., Hackett, P. D., & Rilling, J. K. (2014). Differential neural responses to child and sexual stimuli in human fathers and non-fathers and their hormonal correlates. Psychoneuroendocrinology, 46, 153–163. https://doi.org/10.1016/j.psyneuen.2014.04.014.

appear to be lower among fathers with little to no involvement in direct caregiving activities (Muller et al., 2009). Fatherhood-induced declines in T seem to support sensitive caregiving. Fathers with lower T spend more time looking at and touching their infants (Weisman et al., 2014), exhibit higher levels of father-infant synchrony (Gordon et al., 2017), report more sympathy in response to infant cries (Fleming et al., 2002), and are more involved in instrumental caregiving activities (Mascaro et al., 2013; Table 3). Fatherhood-induced declines in T may also motivate investment in and sensitivity towards reproductive partners. For example, men whose T decreases more over their partner's pregnancy subsequently report greater postpartum investment in the relationship with the child's mother (Saxbe et al., 2017a). Conversely, higher paternal T at 15 months postpartum predicts intimate partner aggression (Saxbe et al., 2017b).

Although lower T seems to facilitate involved, sensitive caregiving, the relationship between T and caregiving may be non-linear. Low T is also associated with more depressive symptoms in new fathers (Saxbe et al., 2017b), and paternal depression is known to interfere with sensitive caregiving (Davis et al., 2011; Wilson and Durbin, 2010). Thus, moderate, as opposed to low, levels of T may be optimal for sensitive and involved caregiving. This hypothesis is supported by a study that examined the interaction between T and the number of GAG repeats in exon 1 of the androgen receptor (AR) gene, a polymorphism known to affect AR expression. Fathers with either high androgenicity (elevated T and shorter CAGn) or low androgenicity (lower T and longer CAGn) were more likely to be relatively uninvolved with childcare as fathers, leading the authors to conclude that invested fathering is promoted by

Table 3
Ten major findings on the neurobiology of paternal caregiving in humans.

	Finding	Reference
1	Extensive overlap in activation to own child videos among primary caregiving mothers, primary caregiving fathers and secondary caregiving fathers	Abraham et al., 2014
2	Compared with non-fathers, fathers show stronger activation to pictures of unknown toddlers within the medial orbitofrontal cortex (mOFC) and the temporo-parietal junction (TPJ)	Mascaro et al., 2014b
3	Fathers who more strongly activate the ventral tegmental area (VTA) when viewing pictures of their toddler are more involved in caring for the child	Mascaro et al., 2013
4	Anterior insula (AIC) activation in response to infant crying has an inverted-U relationship with paternal caregiving	Mascaro et al., 2014a
5	Older first-time fathers have lower dorsal anterior cingulate cortex (ACC) and anterior insula (AIC) responses to infant cries	Li et al., 2018
6	Compared with fathers of sons, fathers of daughters have a stronger neural response to their toddler's happy facial expressions in areas of the brain important for reward and emotion regulation (mOFC and lateral OFC), whereas fathers of sons had a stronger mOFC response to their son's neutral facial expressions	Mascaro et al., 2017
7	Intranasal oxytocin (INOT) increased activation to own child pictures in both the head of the caudate nucleus and the dorsal anterior cingulate cortex (dACC)	Li et al., 2017
8	Fathers reporting more positive thoughts about their infant have a stronger caudate nucleus response to their infant's cry	Kim et al., 2015
9	Paternal testosterone (T) responses to infant interactions were positively correlated with activation in the left caudate nucleus when viewing videos of their infant	Kuo et al., 2012
10	The number of CAG repeats in the Androgen receptor gene is positively correlated with the anterior insula (AIC) response to unknown infant crying	Mascaro et al., 2014a

intermediate levels of andogenicity (Gettler et al., 2017).

Against this background of lower baseline T levels in involved fathers, paternal T has been found to acutely increase in response to infant crying, perhaps in preparation for aggressive defense of the infant if threatened by predators or enemies (Fleming et al., 2002; van Anders et al., 2012). On the other hand, paternal T actually decreases in response to infant crying when fathers are allowed to nurture and respond to infant distress (van Anders et al., 2012). In fact, the magnitude of paternal T decline in response to infant distress is correlated with paternal sensitivity in a subsequent father-infant interaction (Kuo et al., 2016). Thus, acute decreases in T in response to infant crying may facilitate a nurturing response. On the other hand, acute increases in T could reflect paternal frustration, a known trigger for infant abuse (Barr, 2012).

Finally, although T may interfere with direct caregiving activities, it may facilitate indirect paternal caregiving activities such as provisioning and protection. For example, elevations in T are associated with both hunting and horticultural activity in traditional human societies (Trumble et al., 2014, 2013; Worthman and Konner, 1987).

3.1.2. Oxytocin

If T interferes with sensitive paternal behavior, OT appears to facilitate it. Partnered fathers have higher plasma OT levels than non-partnered non-fathers (Mascaro et al., 2014b; Table 3), and plasma OT levels increase across the first 6 months of fatherhood (Gordon et al., 2010a). Father-infant contact can acutely increase peripheral OT levels. For example, paternal salivary OT is significantly increased by 60 min of skin to skin contact with their preterm infant (Vittner et al., 2018). Plasma OT levels in fathers are correlated with father-infant affect synchrony and with paternal stimulatory touch (Feldman et al., 2010; Gordon et al., 2010a; Vittner et al., 2018). Although central and peripheral OT levels have been considered as largely independent of each other due to the inability of OT to cross the blood-brain barrier (Landgraf and Neumann, 2004), studies in rodents suggest that OT can be synchronously released into both the brain and the periphery (Ross and Young, 2009; Wotjak et al., 1998). Moreover, positive correlations between plasma and cerebrospinal fluid OT concentrations have also been reported in humans (Carson et al., 2015; Wang et al., 2013). Thus, peripheral OT levels may be relevant to paternal behavior.

Intranasal OT (INOT) treatment, now known to elevate OT in both the brain and the periphery (Leng and Ludwig, 2016; Neumann et al., 2013; Striepens et al., 2013), increases paternal play, touch, social reciprocity (Weisman and Feldman, 2013), and even paternal head speed and acceleration during father-infant interactions (Weisman et al., 2013). INOT also increases paternal sensitivity and decreases paternal hostility during interactions with toddlers (Naber et al., 2010, 2013). INOT increases facial mimicry of infants in men (Korb et al., 2016), implying that some of these behavioral effects may be mediated by OT augmentation of paternal empathy.

In contrast to T, OT may also motivate commitment to a reproductive partner, as INOT decreases approach behavior toward an unknown, attractive woman in partnered (but not single) males (Scheele et al., 2012).

3.1.3. Vasopressin

Despite evidence that AVP is involved in paternal behavior in both rodents (Wang et al., 1994) and non-human primates (Kozorovitskiy et al., 2006), the role of AVP in human paternal behavior has been only minimally investigated. One recent study showed that intranasal AVP increased the amount of time that fathers-to-be spent watching baby-related avatars (Cohen-Bendahan et al., 2015). Another study of mothers and fathers combined showed that parents with high plasma AVP provided more stimulatory touch to their 4–6 month old infants during a face-to-face interaction (Apter-Levi et al., 2014).

3.1.4. Prolactin

PRL levels increase in human fathers during the mother's pregnancy (Storey et al., 2000). Fathers with higher PRL levels are more responsive to infant cries (Fleming et al., 2002) and are more engaged in father-infant exploratory play (Gordon et al., 2010b).

3.2. Neurobiology of fatherhood

In humans, the neurobiology of fatherhood has been investigated primarily with (fMRI), which permits measurement of in vivo brain activity while participants are exposed to visual (pictures, videos) or auditory (laughter, cries) stimuli from children. Interpretation of functional neuroimaging results must be done with caution since individual areas often have multiple functions, sometimes rendering multiple interpretations possible (Poldrack, 2011).

3.2.1. Fathers vs. mothers

Research on maternal brain function has outpaced that on paternal brain function. Exposing human mothers to infant stimuli activates neural systems involved in understanding others' facial expressions (the putative mirror neuron system), others' feelings [anterior insula (AIC) and thalamocingulate regions] and others' thoughts [dorsomedial prefrontal cortex (DMPFC)], as well as reward systems involved in approach-related motivation [VTA, substantia nigra, ventral striatum, medial orbitofrontal cortex (mOFC)], and systems involved with emotion regulation (lateral prefrontal cortex) (Rilling, 2013). The smaller body of research on paternal brain function has generally implicated similar neural systems (Rilling and Mascaro, 2017). One recent study tested this idea more systematically. This study compared parental

brain responses among heterosexual primary caregiving mothers, heterosexual secondary caregiving fathers and homosexual primary caregiving fathers as they viewed videos of themselves interacting with their infant compared with videos of an unfamiliar parent-infant interaction. Collapsing across all three parental groups, activation was observed in BLA, ventral anterior cingulate cortex, left inferior frontal gyrus and insular cortex, VTA, bilateral superior temporal sulcus (STS), ventromedial prefrontal cortex, temporal poles and lateral frontopolar cortex. Within these regions, there was a remarkable degree of similarity in activation across the three parental groups. Only two of the eight activated regions showed significant differences across parental groups. Mothers showed greater AMYG activation and less STS activation than did secondary caregiving fathers. Primary caregiving fathers had AMYG activation comparable to mothers and STS activation comparable to secondary caregiving fathers. Remarkably, a behavioral measure of parent-infant synchrony was positively correlated with AMYG activation in mothers and with STS activation in both groups of fathers. Moreover, only primary caregiving fathers showed significant functional connectivity (correlated activation) between the AMYG and STS and this was correlated with the amount of time the fathers spent alone with their child (Abraham et al., 2014; Table 3). Overall, these results suggest a global parental caregiving network that is mainly consistent across parents, but with significant malleability as a function of whether parents adopt a primary or secondary caregiving role.

While the above study compared mothers' and fathers' neural responses to infant visual stimuli, other research has compared their neural response to infant cries. One early study with a limited sample size did not detect differences between mothers (n = 10) and fathers (n = 10) in the neural response to infant crying (Seifritz et al., 2003). Other studies that have been conducted separately in mothers and fathers suggest that first-time mothers and first-time fathers both activate five different neural systems in response to unknown infant cry stimuli: (1) midbrain dopaminergic (approach motivation), (2) thalamocingulate (parental caregiving), (3) fronto-insular (emotional empathy), (4) DMPFC (perspective-taking and theory of mind), and (5) right lateralized auditory cortex extending to the temporal pole (auditory perception) (Li et al., 2018; Lorberbaum et al., 2002; Table 3).

3.2.2. Fathers vs. non-fathers

Life history theory is a branch of evolutionary theory that posits a trade-off between energetic investments in mating and parenting effort (Buss, 2005). This hypothesis has been evaluated by comparing the neural response of fathers and non-fathers to both infant and sexual visual stimuli (Mascaro et al., 2014b; Table 3). Compared with non-fathers, fathers showed stronger activation to pictures of unknown toddlers within the mOFC and the temporo-parietal junction (TPJ), among other areas. Though one must be cautious inferring psychological states from neural activations, mOFC and TPJ are involved in reward and mental state processing, respectively. Thus, fathers may find the child stimuli more rewarding than non-fathers do, and they may make more of an effort to infer the mental states of the children whose picture they are viewing. There were no regions in which non-fathers showed stronger activation than fathers when viewing pictures of unknown children. On the other hand, non-fathers showed stronger activation to visual sexual stimuli than fathers did in brain regions involved with reward (NAcc) and approach motivation (dorsal caudate nucleus). There were no regions in which fathers showed stronger activation than non-fathers when viewing visual sexual stimuli (Mascaro et al., 2014b; Table 3). Collectively, these results support the life history theory prediction of a trade-off between mating and parenting effort by suggesting that fathers find child stimuli more rewarding or motivating than non-fathers, whereas non-fathers find visual sexual stimuli more rewarding or motivating than fathers do.

3.2.3. Variation among fathers

Although paternal involvement is associated with multiple positive developmental outcomes in modern, developed societies (Cabrera et al., 2000; Gaudino et al., 1999; Sarkadi et al., 2008; Weitoft et al., 2003), there is significant variability in the extent to which fathers are involved in caregiving (Hrdy, 2011). Examining variation in paternal brain function may facilitate a better understanding of the proximate explanation for variability in paternal involvement.

One variable that modulates paternal brain function is the degree of paternal involvement. Fathers who more strongly activate the VTA when viewing pictures of their toddler are more involved in caring for the child, as reported by the mother (Mascaro et al., 2013; Table 3). This finding parallels studies implicating the VTA in the motivation to approach and care for offspring in female rats (Numan, 2007). On the other hand, AIC activation in response to infant crying had a non-linear relationship with paternal caregiving, such that fathers with intermediate activation were most involved (Mascaro et al., 2014a; Table 3). The AIC is a visceral somatosensory cortex that is known to track autonomic arousal (Craig, 2003, 2002, Critchley et al., 2004, 2000). While the AIC is important for empathy (Singer and Lamm, 2009), hyperactivity in the AIC has been implicated in anxiety and anxiety disorders (Simmons et al., 2006, 2011). These results therefore suggest that moderate AIC activity reflects an optimal level of arousal that supports engaged fathering.

Paternal age can also modulate paternal brain function. One study of first-time fathers of newborn infants reported that older fathers found infant cries less aversive and had an attenuated response to infant crying in both the dorsal anterior cingulate cortex (dACC) and the AIC. Both the dACC and the AIC are strongly implicated in emotional empathy (Lockwood, 2016; Singer and Lamm, 2009), so less activation in these areas could reflect less parental empathy. Indeed, one study found that more empathic mothers more strongly activate the AIC when viewing pictures of their children (Lenzi et al., 2009). However, dACC activation has also been linked with both physical and psychological pain and the dACC has been proposed to function as a neural alarm signal (Eisenberger and Lieberman, 2004; Panksepp, 2003). This raises the possibility that older fathers find baby cries less aversive or alarming. There is also evidence that empathic over arousal can lead to distress that interferes with compassionate behavior (Eisenberg, 2000; Mascaro, 2011; Millon and Lerner, 2003), which could potentially interfere with sensitive caregiving. For example, in high-risk mothers, stronger AIC responses to own-infant cries were related to more intrusive parenting (Musser et al., 2012). Furthermore, as discussed above, it was fathers with moderate AIC activation that were most involved in instrumental caregiving (Mascaro et al., 2014a; Table 3). Fathers with low and high insula activation may have been less involved due to empathic under and over-arousal to cries, respectively. Thus, lower dACC and AIC activation in older first-time fathers may render fathers better able to avoid the distress associated with empathic over-arousal in response to infant crying.

Infant gender has also been reported to influence paternal brain function. Compared with fathers of sons, fathers of daughters had a stronger neural response to their toddler's happy facial expressions in areas of the brain important for reward and emotion regulation (mOFC and lateral OFC), whereas fathers of sons had a stronger neural response to their son's neutral facial expressions in the mOFC. Furthermore, the mOFC response to happy faces was negatively correlated with the amount of rough and tumble play the father engaged in, while the mOFC response to neutral faces was positively correlated with the amount of rough and tumble play with boys specifically (Mascaro et al., 2017; Table 3).

The identity of the child stimuli, particularly whether the child belongs to the father or not, is also apt to modulate paternal brain function. While fathers activate parental brain systems to a greater extent when viewing pictures of their own compared with unknown infants (Kuo et al., 2012; Li et al., 2017; Table 3), one study found no significant difference in the neural response to own and unknown infant cries and this was paralleled by difficulty distinguishing between them

(Li et al., 2018; Table 3).

Finally, the age of the father's child might also influence paternal brain function. Although this has not yet been investigated systematically in a single study, studies with first-time fathers of newborn infants report more and stronger activation, even to unknown infant crying, than do studies of fathers of toddlers (Li et al., 2018; Table 3). This might be attributable to the novelty of the cry stimulus for new fathers, or to the altered hormonal state of new fathers, including lower T and increased OT as described above.

3.2.4. Hormonal modulation of paternal brain function

Given evidence that hormones like OT and T influence human paternal behavior, studies have evaluated whether these hormones modulate activation in the above neural systems implicated in paternal behavior. One approach involves administering exogenous hormone and examining its effect on brain function. Two recent studies have examined the effect of exogenous (intranasal) OT administration on paternal brain function. One INOT study examined the effect of 24 IU INOT on brain function in human fathers as they viewed pictures of their toddlers. INOT increased activation to child pictures in both the head of the caudate nucleus (CN) and the dACC (Li et al., 2017; Table 3). The caudate is part of the nigrostriatal DA system, which is involved in reward and motivation (Ikemoto et al., 2015) and commonly activated in neuroimaging studies of parental brain function (Rilling, 2013). These results suggest that INOT may increase the reward or motivation to engage with one's child. INOT also increased the dACC response to own child pictures. The cingulate cortex is critically involved in parental caregiving. Damage to the thalamo-cingulate pathway severely disrupts maternal behavior (MacLean, 1990) and the cingulate cortex is commonly activated by child picture and/or cry stimuli in fMRI studies (Rilling, 2013). The anterior cingulate cortex is also central to the vicarious experience of both pain and reward (Lockwood, 2016). These results therefore suggest that OT may enhance paternal empathy. Notably, a recent study in prairie voles showed that consolation of distressed partners is mediated by OT-induced dACC activation (Burkett et al., 2016). These results suggest that this neural mechanism may generalize to human fathers. The second INOT study also found OT to augment fathers' neural response to pictures of their children within the CN, but in its more caudal aspect (caudate body) (Wittfoth-Schardt et al., 2012). These effects of INOT in the CN are of interest given another study that found a positive correlation between new fathers' self-reported positive thoughts about their infant and their CN response to their infant's cries (Kim et al., 2015; Table 3).

Two recent studies also examined the effect of intranasal AVP on paternal brain function. One found no effect of AVP on the neural response to viewing pictures of toddlers or listening to infant cry stimuli (Li et al., 2017; Table 3). The second examined AVP effects on the neural response to infant crying in expectant fathers. Although there was no main effect of AVP, when cry stimuli were accompanied by emotional contextual information (e.g., "this is a sick infant" or "this is a bored infant"), AVP increased activation in the cerebellum, midbrain, posterior medial cortex, HPC, putamen and insula, which the authors speculate reflects increased salience of or empathy for infant crying in AVP-treated to-be fathers (Thijssen et al., 2018).

Another approach to examining whether hormones modulate activation in paternal neural systems is to test for associations between endogenous hormone levels and paternal brain function. Plasma T levels in fathers are negatively correlated with the neural response to viewing pictures of own children within a region of the middle frontal gyrus that is known to be involved in simulating emotional facial expressions (Mascaro et al., 2014b; Table 3), a finding that was interpreted to suggest an inhibitory effect of T on paternal empathy. Despite the negative association between T and paternal empathy and related brain activity, paternal T responses to infant interactions were positively correlated with activation in the left CN when viewing videos of their infant (Kuo et al., 2012; Table 3). Given the caudate's role in approach motivation, these data suggest that T's influence on paternal brain function may not always be negative.

Finally, one study examined the effect of androgen receptor (AR) CAG repeats on paternal brain function, demonstrating a positive correlation between the numbers of CAG repeats and the AIC response to unknown infant crying. This finding suggests that fathers with less sensitivity to androgens (more CAG repeats) have increased neural responses to infant crying in a brain region involved with empathy (Mascaro et al., 2014a; Table 3).

3.3. Summary

In summary, fatherhood-induced decreases in T and increases in OT seem to support sensitive caregiving. Fathers activate mostly the same neural systems that mothers do when exposed to child stimuli, and this can be considered a global parental caregiving network. Compared with non-fathers, fathers activate brain regions involved with reward and approach motivation to a greater extent when viewing child stimuli, but to a lesser extent when viewing visual sexual stimuli. These findings are consistent with a hypothesized trade-off between mating and parenting effort or motivation. Paternal age, child age, child gender, child identity, and degree of paternal involvement have all been found to modulate paternal brain function. Finally, exogenous OT increases paternal neural activity within neural systems involved with empathy and approach motivation and endogenous T seems to also modulate activity within these systems.

4. The study of alloparenting in non-human animals

The study of alloparenting in non-human animals provides us a direct window into the underlying neurobiology of this important aspect of the human social repertoire. Alloparenting has had a major role in recent human evolution and remains a critical subject of study, as a better understanding of its dysfunction may shed light on etiology of child neglect and abuse (Kenkel et al., 2017). These studies have traditionally focused on the "big three" of mammalian taxa: rodents, primates, and social carnivores (Rosenbaum and Gettler, 2018; Table 2). Species differ in terms of whether alloparenting is provided by siblings, other relatives, or even unrelated individuals. Typically, since alloparenting is defined as care resembling maternal or paternal care, it can involve: carrying/retrieving, cleaning, protecting, the provisioning of food, teaching, warming as well as non-direct benefits (Rosenbaum and Gettler, 2018). In rodents, alloparental care is typically measured by assaying pup retrieval as well as: licking, grooming, carrying, and huddling over pups. Several vole species have been instrumental in studying alloparenting because it is not conventionally displayed by lab mice or rats, except under special circumstances. In prairie voles, alloparenting is greater among younger animals and males (though see Kenkel et al., 2017 for a fuller discussion of the ontogeny of alloparenting).

Much of this research has come from an evolutionary perspective and has been chiefly concerned with the impacts of alloparenting on the fitness of caregiver, infant, and relatives. For a more thorough analysis of research that integrates behavior, physiology, and ethology, Rosenbaum and Gettler recently edited a special edition of *Physiology and Behavior* entitled 'Evolutionary perspectives on non-maternal care in mammals: physiology, behavior, and developmental effects' (Gettler, 2018; Rosenbaum and Gettler, 2018). The long-term consequences of alloparenting, as well as its ontogeny, were recently reviewed (Kenkel et al., 2017). Here, we will review the neurobiological and neuroendocrine underpinnings of alloparenting in mammals. One important caveat is that findings are often not directly comparable between humans and non-humans, or between laboratory and wild species due to methodological differences. Only in laboratory species are invasive neuroanatomical methods applicable; studies of wild

animals often rely on measures of peripheral hormones and research in humans tends to focus on fMRI.

Like much of the research into non-maternal caregiving, the overarching theme to the study of alloparenting has traditionally been to frame alloparenting in terms of how the underlying neuroendocrinology relates to that of maternal care. Recently, the endocrine aspect of this underlying hypothesis was explicitly tested by Schradin, Vuarin and Rimbach (2018), who reviewed the extant literature on circulating hormone levels across 10 mammalian, 12 avian, and 1 fish alloparental species (Schradin et al., 2018). Prior to adolescence, many species' alloparents do not show endocrine changes related to caregiving, whereas post-adolescent alloparents often show endocrine changes that match those seen in parents. Specifically, the suite of peripheral hormone fluctuations was defined as an increase in PRL levels, and sex-specific changes in T (decreased in males), estrogen/progesterone (increased in females), and GCs (decreased in males, while increased in females). Two hypotheses were thus supported by this analysis: the *neoteny-helper hypothesis*, which holds that prior to puberty, alloparenting is the default response to conspecific young among cooperative breeders; and the *parent-helper hypothesis*, which holds that alloparents (particularly post-adolescent alloparents) will require a hormonal milieu which resembles that of parents. An example of this latter model can be found in cooperatively breeding carnivores, where alloparents consistently show elevated levels of PRL and OT, along with diminished levels of T and GCs (Montgomery et al., 2018). We will next review the specific evidence for various hormone systems.

4.1. Testosterone

The relationships between non-human alloparenting and androgens have been mixed, leading some to conclude there is no role (Solomon and Hayes, 2012) or no clear role (Rosenbaum and Gettler, 2018) for T in regulating alloparenting. Indeed, T does not appear to be related to alloparental caregiving in mole-rats (Zöttl et al., 2018), African striped mice (Schradin et al., 2013; Schradin and Yuen, 2011), meerkats (Carlson et al., 2006b), African wild dogs (Creel et al., 1997), or red-bellied lemurs (Tecot and Baden, 2018). However, in golden lion tamarins, T levels decline in alloparents, similar to fathers (Bales et al., 2006). Meanwhile, prairie voles rely on the organizational effects of androgens in order to alloparent, as castration in early life inhibits subsequent alloparenting (Kramer et al., 2009; Table 4). In prairie voles, females typically are less alloparental than males, so neonatal castration may divert males onto a female-like developmental trajectory in this regard. Indeed, neonatal castration is one of the few interventions known to suppress the robustly alloparental response of male prairie voles. However, early-life T treatment actually reduces later alloparental behavior in male prairie voles (Roberts et al., 1996), and fails to masculinize alloparental responsiveness in females (Lonstein et al., 2002). The observation that neonatal castration produces effects greater than those of pharmacological inhibition of androgenic and estrogenic activity, has led to the hypothesis that the testes may be contributing other hormones relevant to the development of alloparenting, such as androstenedione, dehydroepiandrosterone, inhibin, or anti-Mullerian hormone (Lonstein et al., 2002). Castration in adulthood does not affect alloparenting in prairie voles (Lonstein and De Vries, 1999; Table 4).

4.2. Estradiol

There is somewhat stronger evidence for a role of E2 in the regulation of alloparenting in animals. Although circulating E2 levels do not change in either black-tufted marmoset (Puffer et al., 2004) or golden lion tamarin (French et al., 2003) alloparents, E2's central actions are important regulators of alloparenting, at least in prairie voles. For instance, there have been several studies in various vole species relating alloparenting to ER expression. Increasing the expression of ERα in the MeA of male prairie voles reduces spontaneous alloparental behavior (Cushing et al., 2008), whereas increasing ERα expression in the BNST has no effect (Lei et al., 2010). Intriguingly, extended alloparenting experience in adult male mandarin voles facilitates subsequent alloparenting while leading to upregulation of ERα in the MeA (Song et al., 2010). Knockdown of ERα in the MeA of male meadow voles (that are typically non-alloparental) was not able to increase alloparenting (Stetzik et al., 2018). Systemic administration of a selective ERα agonist during the juvenile period decreases alloparental responsiveness in prairie voles of both sexes (Perry et al., 2015), whereas blocking ER during this time also decreases alloparental responsiveness in males (Kramer et al., 2009; Table 4). Chronic treatment of adult females with E2 leads to increased alloparental responsiveness (Lonstein and De Vries, 1999; Table 4). However, various perinatal steroid manipulations of either estrogenic or androgenic mechanisms (including both agonists and antagonists) did not alter alloparental responsivity in prairie voles of either sex (Lonstein et al., 2002). We are left with a complex picture where the alloparenting phenotype in prairie voles is generally resilient to manipulations of the gonadal hormones, though alterations of estrogen signaling can affect alloparenting, especially when a targeted manipulation occurs in early life. Recent work in naked mole-rats has shown that E2 signaling is the mechanism by which ingestion of the queen's feces facilitates alloparental responsiveness in subordinates (Watarai et al., 2018; Table 4).

4.3. Prolactin

Owing to its role in lactogenesis and maternal care, the hormone PRL has long been a subject of interest in the study of alloparental care. Indeed, across several mammalian taxa, alloparenting is associated with increased peripheral PRL levels (Schradin et al., 2018). This pattern goes back to an observation in marmoset fathers in 1982 (Dixson and George, 1982) and has since been extended to alloparents (Mota and Sousa, 2000), as well as males of other cooperatively breeding species, such as cotton-top tamarins (Soltis et al., 2005; Ziegler et al., 1996), gray wolves (Asa and Valdespin, 1998), and meerkats (Carlson et al., 2006b; Table 4). Among African striped mice (*Rhabdomys pumilio*), however, philopatric alloparents have levels of circulating PRL similar to non-alloparental roamers, and lower than breeding males (Schradin, 2008; Schradin and Yuen, 2011). More recent work in marmosets failed to find an association between PRL and alloparenting, with the exception of an increase related to the physical effort of infant carrying (da Mota et al., 2006; Table 4). The finding in meerkats is also qualified by the observation that the inclusion of cortisol (CORT) measures reduced the predictive utility of the PRL measure to non-significance (Carlson et al., 2006b; Table 4).

In marmosets, the reduction of circulating PRL by administration of

Table 4
Five major findings on the endocrinology of alloparental care in nonhumans.

	Finding	Reference
1	Testosterone: Neonatal castration is one of the few interventions that will inhibit alloparenting in male prairie voles	Kramer et al., 2009
2	Estrogens: Chronic estradiol treatment facilitates alloparenting in female prairie voles and naked mole rats	Lonstein and De Vries, 1999; Watarai et al., 2018
3	Prolactin: Findings have been mixed	Carlson et al., 2006b; da Mota et al., 2006
4	Oxytocin: Oxytocin receptors in the nucleus accumbens (NAcc) facilitate alloparental care in female prairie voles	Olazábal and Young, 2006a, 2006b
5	Oxytocin: Alloparental species have greater densities of oxytocin receptors in the nucleus accumbens (NAcc)	Kalamatianos et al., 2010

a DA agonist reduces infant carrying by alloparents (Roberts et al., 2001). PRL is also capable of inducing alloparental responsivity to pups in the normally non-alloparental male rat (Sakaguchi et al., 1996). Once male mammals have sufficient experience in carrying out paternal care, however, PRL antagonism fails to block the expression of caregiving (Almond et al., 2006; Brooks et al., 2005).

4.4. Oxytocin

In contrast to the hormone systems discussed above, the study of OT's role in alloparenting has tended to focus on central mechanisms rather than peripheral levels, most likely due to methodological concerns regarding the proper measurement of peripheral OT levels (Brandtzaeg et al., 2016). For instance, there have been a series of studies by Olazabal and colleagues on the role of OT receptors in the nucleus accumbens, a prominent region in the study of reward processes. The density of OT receptors in the NAcc of female prairie voles is positively correlated with alloparental behavior (Olazábal and Young, 2006a, 2006b; Table 4). OT receptor antagonism in the NAcc blocks the expression of alloparenting in female prairie voles (Olazábal and Young, 2006a; Table 4). Likewise, knockdown of OT receptors in the NAcc of female prairie voles in the juvenile period decreases subsequent alloparenting behavior (Keebaugh et al., 2015). Correspondingly, when OT receptors are over-expressed within the NAcc of female prairie voles, alloparenting behavior increases (Keebaugh and Young, 2011), but only if this intervention occurs prior to adulthood (Ross et al., 2009).

Results from adult male prairie voles also implicate a critical role for OT in alloparenting. There is both a surge of peripheral OT and an increase in central oxytocinergic neuronal activity in alloparental male prairie voles (Kenkel et al., 2012). In adult male mandarin voles, there is a report of a single 10 min bout of alloparenting leading to an increase in the number of OT neurons in the HYPO, both in the in supraoptic nucleus and the PVN) one week later (Song et al., 2010). Originally, it was thought necessary to block both OT as well as AVP receptors in male prairie voles to interfere with alloparenting (Bales et al., 2004). However, the selectivity of the AVP antagonist used in that work was later called into question (Manning et al., 2008), and subsequent work was able to inhibit alloparenting using systemic application of a selective OT antagonist (Kenkel et al., 2017).

OT seems to play a similar role in other mammalian species as well. Alloparental species tend to have relatively high densities of OT receptor in the NAcc (Kalamatianos et al., 2010; Olazábal and Young, 2006a; Schorscher-Petcu et al., 2009) (Table 4). Peripheral OT levels are positively associated with alloparental caregiving in marmosets (Finkenwirth et al., 2016). Exogenous OT administration increases the tendency of meerkats to feed and associate with pups (Madden and Clutton-Brock, 2011). Similarly, OT increases the holding and licking of pups by pre-weaning (but not post-weaning) rats (Peterson et al., 1991). In mice and rats, maternal responsiveness to pups can be induced via repeated pup exposures, and in mice, this process involves a gradual increase in oxytocinergic neuron activity, activity in OT receptor expressing neurons, and the concentration of OT, all within the preoptic area (POA), a region well-studied for its role in maternal behavior (Okabe et al., 2017). Furthermore, treatment with an OT antagonist in the POA prevents this acquisition of maternal responsiveness in virgin female mice (Okabe et al., 2017). In contrast to the above findings, a recent report found no changes in alloparenting in male prairie voles in which the OT receptor was genetically ablated using CRISPR gene editing (Horie et al., 2018). Finally, several interventions in early life can influence alloparenting via changes in the OT system (Kenkel et al., 2017), such as early-life stress, alloparenting experience, parenting style, social experience, and single-parent rearing.

4.5. Anxiety and arousal

We have already mentioned how research on the neuroendocrinology of alloparenting resembles that of maternal care; this analogy predicts relatively decreased levels of GC responsivity in alloparents, as maternal behavior is associated with an anxiolytic state (Slattery and Neumann, 2008). We have also discussed above how, across several taxa, alloparenting is indeed associated with diminished peripheral GC levels (Montgomery et al., 2018; Schradin et al., 2018). Most of those studies have focused on peripheral measures taken at baseline. A counter-example to this association between alloparenting and low GC levels can be found in male meerkats, where not only is CORT positively correlated with alloparental care, but playback of pup begging calls elicited increases in CORT levels (Carlson et al., 2006a). More acutely focused studies add further nuance to this relationship and suggest that alloparenting may be anxiolytic – at least in male prairie voles.

In prairie voles, the relationship between hypothalamic-pituitary-adrenal (HPA) axis activity and alloparenting depends on sex and age. Early life CORT treatment leads to a reduction in later alloparenting in female prairie voles (Roberts et al., 1996), while in adulthood, males (but not females) show heightened alloparenting following physical stressors (Bales et al., 2006, 2004). What's more, the amount of pup licking and grooming is positively correlated with CORT levels (Bales et al., 2006). Systemic application of urocortin II, which selectively activates the corticotropin releasing hormone (CRH) type 2 receptor, increases alloparental huddling in prairie voles of both sexes (Samuel et al., 2008). Plasma CORT levels drop following 10 min of exposure to a pup, as does central CRH neuron activity soon after (Kenkel et al., 2012). In the acute phase, male prairie voles exposed to a pup show less anxiety-related behavior when tested immediately afterward in an open field (Kenkel et al., 2017). However, over a chronic scenario, extended alloparenting in the form of voles remaining in the natal nest (and having to contend with the concomitant reproductive suppression) leads to increased indexes of anxiety. Specifically, such alloparental prairie voles experience increased anxiety-like behavior, decreased exploration of novel environments, decreased brain-derived neurotrophic (BDNF) factor in the CA1 region of the HPC, and sex-specific increases in BDNF in the BNST, two important regions for the regulation of anxiety (Greenberg et al., 2012). There are evidently species differences in the effects of chronic alloparenting, however, as in both virgin female rats (Harding and Lonstein, 2016), and African striped mice of both sexes (Pillay and Rymer, 2015), extended alloparenting reduces the expression of anxiety-related behaviors.

The motivations to engage in alloparental care have not been systematically investigated, but may include both positive and negative emotional states. Alloparenting may thus be both induced by states of heightened anxiety and capable of relieving such anxiety. Distressed pups emit aversive stimuli (e.g., cries), the cessation of which may encourage alloparenting via negative reinforcement. Conversely, these same distress stimuli may be so aversive in non-alloparental animals as to trigger an aggressive response towards the pup. One important hurdle in this work is the relative intransigence male prairie voles exhibit regarding alloparenting. Male prairie voles alloparent at high levels and there has not been a simple and reliable way to either reduce this behavior (beyond neonatal castration) or predict which animals will defy expectations and demonstrate a non-alloparental response. Furthermore, given the often-violent nature of non-alloparental animals, repeated testing of these subjects raises serious ethical concerns. Nonetheless, the balance of arousal appears to be an important factor in determining alloparental responsiveness.

In a series of studies by Kenkel et al., the autonomic component of this 'anxiolytic pup' hypothesis was tested using implantable radiotelemetry (Kenkel et al., 2015, 2014, 2012). What followed was an unexpected observation of a robust and dramatic increase in heart rate during alloparenting in prairie voles. Contrary to the bradycardia hypothesized to follow an anxiolytic effect, prairie vole alloparents mount

a sustained tachycardia even while remaining relatively motionless, huddling over the pup. Pharmacological blockade along with analyses of heart rate variability indicated this was being driven primarily by an increase in cardiac sympathetic drive (rather than via a release of the vagal brake). This observation was especially unexpected because previous work has shown similar stress response activity (e.g., HPA axis, sympathetic nervous system) among 60 studies spanning both human and non-human subjects including both physical and psychological stressors. The magnitude of plasma norepinephrine and adrenocorticotropic releasing hormone responses during stress correlate at r = 0.93 (Goldstein and Kopin, 2008). This effect of pup-induced cardioacceleration can be seen in virgin males (Kenkel et al., 2013), virgin females (Kenkel et al., 2015) and sexually experienced fathers (Kenkel et al., 2014).

An explanation for this phenomenon was ultimately found in the realm of thermoregulation (Kenkel et al., 2017, 2015). Maintaining prairie vole pups in a thermoneutral environment reduces the distress calls emitted and abolishes the cardioacceleratory component of alloparenting. This suggests that vole alloparents' high heart rate is part of a response that maintains pup warmth, a critical aspect of care for young rodents. Avoidance or aggression shown towards pups may therefore be consequences of a dysregulated arousal response, related to improper processing of the heightened state of arousal induced by the pup's presence. Although proximately related to thermoregulation, this effect could pose translational relevance to instances of alloparental failure, including abuse and/or neglect, in humans, as child abuse typically occurs within a context of high arousal (Rodriguez and Green, 1997).

4.6. Vasopressin, progesterone, and other neurobiology related to alloparenting

Despite being closely related in both form and function to OT, the neuropeptide AVP has received relatively little attention for its possible role in alloparenting. Beyond the previously mentioned study that had intended to antagonize AVP receptors, it has been shown that alloparenting elicits an increase in the activity of vasopressinergic neurons of the PVN (Kenkel et al., 2012) and that AVP1a receptors in the VP are not related to alloparenting (Barrett et al., 2013).

As was the case with several other hormones discussed above, progesterone has garnered some attention for a possible contribution to alloparenting due to its role in regulating maternal behavior. In virgin male mice, knockout of the progesterone receptor leads to an alloparental phenotype, with more caregiving behavior and reduced aggression directed at infants. Similarly, treatment with the progesterone receptor antagonist RU486 enhances alloparental responsiveness in virgin male wildtype mice (Schneider et al., 2003).

In terms of the brain regions activated during the expression of alloparental care, a pattern is seen that is generally reminiscent of the activation pattern in the maternal brain (Kirkpatrick et al., 1994). Exposure of adult virgin male prairie voles to a pup for 3 h produces increased neuronal activity in: the accessory olfactory bulb, LS, MeA, MPOA, medial portion of the BNST, nucleus reuniens, and PVN of the thalamus; though such exposure does not change activity in the PVN, where the source nuclei of OT and AVP are found (Kirkpatrick et al., 1994). Subsequent work also carried out in adult male prairie voles found activation in the MeA and BNST following 30 min of pup exposure (Northcutt and Lonstein, 2009). In response to exposure to a novel pup, c-fos activation was observed in several areas associated with social behavior and anxiety (the cingulate cortex, LS, MPOA and PVN), as well as areas implicated in reward (the NAcc) in alloparental California mice (Lambert et al., 2011).

Alloparenting seems to promote neurogenesis insofar as exposing prairie voles of either sex to a pup increases cell proliferation in the DG of the HPC, however, this effect is more pronounced in animals that do not respond alloparentally (Ruscio et al., 2008). Before the onset of sexual dimorphism in prairie vole alloparenting (males tend to be more alloparental than females), in sub-adult prairie voles there is already an apparent sexual dimorphism in terms of the underlying neurobiology, as systemic N-methyl-D-aspartate (NMDA) receptor blockade produces differing effects in males and females (Kirkpatrick and Kakoyannis, 2004). Manipulation of the DA system via methamphetamine administration reduces alloparenting in prairie voles of both sexes (Perry et al., 2017). Finally, within the MPOA, there is a population of galanin-expressing neurons that are active during parenting behavior in male mice, the optogenetic activation of which can induce alloparental responsiveness in virgins (Wu et al., 2014).

The question of whether and how the neurobiology of paternal care differs from that of alloparental care remains to be directly explored. In both cases, males of some mammalian species engage in caregiving behavior without experiencing the dramatic hormonal events of pregnancy, birth, and lactation, via utilizing similar neural circuitry and less dramatic hormonal exposures. That said, several factors have contributed to our incomplete knowledge of how these behaviors relate to each other, including differences between species as well as methodological differences between studies (e.g., central vs. peripheral measures, field vs. lab studies). Moreover, direct comparison between the two types of caregiving is made difficult in species such as prairie voles, where the hypothalamic-pituitary-gonadal (HPG) axis is activated by introduction to a novel opposite-sex conspecific, which adds another variable into comparisons of fathers and sexually-naïve alloparents. Conversely, in many species, alloparental helpers are reproductively suppressed. Even in species without an experience-modulated HPG axis, the use of reproductively naïve animals confers little information regarding maternal and/or paternal care. There is also the matter of timescale to consider, as alloparenting is often studied acutely ('What are the immediate early gene reactions to pup presentation?'), while paternal caregiving is often observed more chronically ('How does the father's brain change after a week, month, or year of parenting?'). Fatherhood is studied with regard to the progression of pregnancy and subsequent offspring development, while alloparenting is usually taken to be a static phenomenon. What is common across these various forms of non-maternal caregiving is infant-induced OT release, a reliance on precisely tuned T and E2 signaling, and carefully orchestrated activation in brain regions associated with emotional regulation (in non-humans) and motivation. Beyond that, the similarities and differences between the neurobiology of the three caregiver phenotypes (i.e., mother, father, and alloparent) remain to be directly addressed (Horrell et al., 2018).

4.7. Summary

Studies of non-human alloparenting have implicated an array of brain regions and neurotransmitter systems. Important methodological and species differences make synthesis challenging, so we shall instead highlight several gaps in our understanding that deserve further research. Although oxytocin has received a great deal of attention for its role in alloparenting, there is still much work to be done on the role of vasopressin. Additionally, any effort to reconcile central and/or peripheral hormone measures would be of great value. It is also important to always keep ethological considerations in mind, to wit, prairie voles evidently experience the needs of a pup with more emphasis on thermoregulation than would other, larger species. How alloparenting and paternal caregiving differ deserves further study. If we are to model the dysfunction of human alloparenting that results in child abuse or neglect, we also require a better understanding of the prevention of aggression towards young in non-alloparental adults.

5. Alloparenting in humans

While it is understood that allomaternal behavior refers to the care of offspring by individuals other than biological mothers, it also

includes individuals who share no biological relation to the child but take over partial (as in the case of temporary caregivers or babysitters) or primary (as in the case of adoptive or foster parents) caregiving responsibilities. Alloparenting, or care provided by non-parents, is a common behavior in humans. From an evolutionary perspective, cooperative breeding may have offered critical advantages for human survival and reproductive success. Human infants are altricial and dependent on caregivers at birth. Infant brain maturation occurs in the context of these caregiving relationships and over a prolonged period of development. Access to additional caregivers likely contributed to ongoing social and cognitive development (Hrdy, 2011; Kramer and Veile, 2018). In addition to benefits for offspring, mothers likely benefited from child rearing assistance from non-pregnant or non-lactating individuals, including fathers, relatives, or other members from the community (Feldman, 2015; Geary and Flinn, 2001; Gettler, 2010; Numan and Insel, 2003; Sear, 2016). Support from alloparental caregivers likely enhanced maternal wellbeing (Crognier et al., 2001; Hill and Hurtado, 2009), reduced rates of infant abandonment (Belsky et al., 1991), and shortened birth intervals which allowed for increased reproductive success (Draper and Harpending, 1982). When directed at genetic relatives, allomaternal care likely served to increase individuals inclusive fitness in the community (Hrdy, 2011; Numan and Insel, 2003; Rosenbaum and Gettler, 2018).

Mechanisms that subserve bond formation between a biological parent and infant likely also contribute to all parental bonding and quality, although this has not been investigated systematically. Given recent advances in neuroimaging, it has become possible to non-invasively examine patterns of functional activation in the parental brain. Most of the work has focused on maternal care, with a recent increase in studies involving paternal care. As discussed ea4rlier in this paper, several neural systems have been implicated in parenting behaviors, and together, are theorized as contributing to a large “caregiving network”. Key circuitries include those that support reward, approach behaviors, and motivation (including orbitofrontal and midbrain dopaminergic regions), parental caregiving (thalamocingulate circuitry), emotional empathy (fronto-insular pathways), understanding of others thoughts and intentions (DMPFC) and feelings (AIC), and also emotion learning, vigilance, and anxiety for child safety (AMYG) (Feldman, 2015; Swain, 2011). Comparisons between mothers, fathers, and alloparental caregivers generally show more similarity in activation patterns in these brain regions than differences (despite some differences related to age, primary or secondary caregiver status, and child age), suggesting significant overlap in the neural circuitry that supports caregiving regardless of caregiver type or biological relation. Relatedly, several studies have revealed significant changes in brain organization that take place when parents transition from non-parent to parental status (Kim et al., 2014, 2010). Collectively, these findings highlight that the act of caregiving may lead to cortical reorganization in the adult human brain.

There are very few empirical investigations on the underlying processes that support the formation of alloparenting relationships. We review the limited behavioral and neurobiological research here. Similar to fathers, alloparents differ from mothers in that they do not undergo typical hormonal and neural changes associated with pregnancy and childbirth. Comparisons between alloparental and maternal bonds may elucidate the extent to which human caregiving is influenced by these underlying neuroendocrinological changes. One study investigated this question by comparing natural versus adoptive parental caregivers expression of caregiving behavior. To control for social factors that may influence caregiving, mothers were matched on demographic characteristics including socio-economic status, education level, and age. Natural and adoptive mothers and their infants participated in the Strange Situation Procedure, a standardized set of interactions designed to assess the quality of infant attachment to their mothers, which is presumed to arise from patterns of maternal responsiveness and availability to infants through the first years of life (Ainsworth et al., 1978). Not surprisingly, children cared for by biologically related and adoptive parents developed secure attachments at equal rates, even when accounting for age of adoption and number of previous family placements. These results support the larger notion that humans have the capacity to provide high quality parenting regardless of neural and hormonal influences, biological relatedness, and/or birth status (Singer et al., 1985).

A special case of alloparenting occurs when non-biologically related parents foster or adopt children who are removed from their own families for reasons related to maltreatment. Foster infants are in need of highly invested and responsive foster caregivers to ensure their healthy development after traumatic separation from birth parents (Dozier et al., 2011). Problematically, foster parents differ in their levels of psychological commitment and investment to their foster child (Dozier et al., 2011), and also vary in their levels of sensitive caregiving practices known to support optimal social emotional development (Dozier et al., 2002).

Certain challenges in the foster parent and infant relationship may contribute to caregiving variability. The duration or length of placement in the foster parents’ home is unknown, and relationships are often temporary, potentially weakening foster parents’ motivation to form a long-lasting emotional bond with a child. There is often a shortage of qualified foster parents, which may leave available foster caregivers over-burdened with responsibility of caring for many children at one time. Indeed, prior work has found an inverse association between numbers of children fostered and psychological feelings of commitment to a foster child currently in their care (Dozier et al., 2002).

As observed among biological parents, there may also be neuroendocrinological or neural factors that explain variability in foster parenting behavior. It is possible that the parental brain changes in biological parents may also exist in the alloparental brain, and potentially be affected by experiential factors of foster parenting (i.e., transitioning from non-parental to parental status, characteristics of the child or parent). To our knowledge, only one study has examined this question systematically. This investigation examined foster mothers who recently accepted a foster infant in their home (Bick et al., 2013). Foster mothers were recruited in the early phase of the foster parent relationship and then returned for a follow-up visit when the relationship became more established. At both assessments, foster mothers were asked to participate in a close cuddle interaction with their child for 30 min. Urine samples were taken prior to and after the cuddle interaction and OT production was quantified. In a second task, mothers participated in a play interaction and the quality of maternal behavior was quantified. In a third task, foster mothers’ electrophysiological brain activity was recorded while they viewed an image of their foster infant versus unknown infants. A specific component related to “motivated attention” to visual images was recorded (Schupp et al., 2004). At both assessments, foster mothers’ OT increased significantly after cuddling with the infant. Further, this increase was associated with the extent to which parents showed joy and responsiveness while interacting with their child during the play session. At the first assessment, foster mothers’ OT production predicted the magnitude of neural responses to infant faces in general. At the second assessment, OT levels became specifically associated with neural responses to the foster infant in the foster mothers’ care. These data point to the potential underlying neural and endocrine changes that take place as a foster parent bonds to a foster infant. Collectively, these results also suggest that neuroendocrinological and neural systems that underpin caregiving behavior in biologically-related parents and infants also contribute to behavioral variability in these specific allomaternal contexts. There are important future directions for this study. One question is whether parity or prior foster parenting experience (i.e., the total number of foster children cared for) or kinship status influences these neural and hormonal aspects of bonding. There may also be child characteristics (e.g., age, placement history, social and emotional characteristics) that influence

foster parent behavior. Foster parents' perceptions on whether the relationship is temporary or permanent should also be considered when examining parental brain changes that take place over the course of the relationship.

5.1. Summary

Alloparenting is a common, but understudied, form of human caregiving behavior. Evolutionary advantages of this form of caregiving are numerous, and include increased human infant survival, improved maternal health, and increased inclusive fitness of genetically and non-genetically related society members. Understanding factors that contribute to alloparental caregiving may have critical clinical implications, especially for high-risk populations of infants whose biological caregivers become unavailable. Emerging work shows that both affiliative and reward systems known to support biological parenting in mothers and fathers also support caregiving behavior in non-biological alloparental relationships. Like documented changes in the "parental brain" of biological parents, there is some evidence for neurobiological changes in alloparental neurobiology. It is unclear whether these changes covary with or contribute to bond formation and quality of care. Continued investigation of the underlying neural and social factors (e.g., parity, caregiving experience) that contribute to alloparental caregiving will be an important direction for the field.

6. Conclusions and future perspectives

This review suggests that the neuroendocrine regulation of allomaternal behavior is complex and involves numerous brain regions and circuits. Evidence suggests significant overlap in the neuroendocrine systems and circuitries that subserve parenting in mothers and fathers, as well as alloparents. While many hormones are implicated, their involvement is often both developmentally and species-specific. In humans, fatherhood-induced decreases in T and increases in OT seem to support sensitive caregiving. This pattern is also observed among non-human fathers.

Additionally, fathers activate many of the same neural systems that mothers do when exposed to child stimuli. Thus, a highly conserved caregiving network may be present in human and non-human parents. Compared with non-fathers, human fathers activate brain regions involved with reward and approach motivation to a greater extent when viewing child stimuli, but to a lesser extent when viewing visual sexual stimuli. These findings are consistent with a hypothesized trade-off between mating and parenting effort and motivation – an effect also observed in non-human animals. Paternal age, child age, child gender, child identity, and degree of paternal involvement have all been found to modulate paternal brain function in humans. As previously mentioned, it is difficult to make clear comparisons between human and non-human fathers. However, it is important to note that there is more evidence for cortical involvement and less evidence for MPOA involvement in humans – perhaps because of limited spatial resolution in fMRI. Additionally, most human studies lack the ability to detect the experience-related changes described for rodents (e.g., adult neurogenesis, brain receptor expression). Nevertheless, the clear involvement of OT and the midbrain DA system in human allomaternal caregiving seems largely consistent with the rodent literature.

In general, the alloparental brain utilizes similar neuroendocrine mechanisms to enact alloparental caregiving, as do parents, however, direct comparisons have been lacking to date. There is a need for further work to investigate factors that contribute to alloparenting variability, both in terms of underlying mechanisms that support it and additional individual or social factors that moderate it. A major outstanding question is to what degree fathering behavior differs from an extended bout of alloparenting with regard to the underlying neurobiology of the caregiver. The *neoteny-helper hypothesis*, which predicts a hormonally independent alloparent in pre-adolescence, deserves further testing, as few studies of central alloparenting mechanisms have focused on sub-adults. We can also identify a trend where certain species tend to be studied in terms of only a subset of the hormones known to regulate alloparenting. For instance, there has not been any work on either PRL or progesterone in prairie vole alloparenting. AVP has received scant attention across all alloparental species. In social carnivores and non-human primates, research has tended to focus on peripheral measures due to methodological constraints. The field has also approached alloparenting with a greater emphasis on comparative neuroendocrinology than on translational relevance. Our knowledge of dysfunctional human caregivers is sparse, but if the animal models aim to improve human wellbeing, greater efforts are needed. There is a small but growing literature connecting childhood maltreatment and the OT receptor via genetic polymorphisms conveying susceptibility along with lingering epigenetic consequences (Baker et al., 2017; Zhang et al., 2018). Some of this work has even begun to relate to the development of aggression because of childhood maltreatment. Animal models have established transgenerational effects of adverse caregiving in the context of maternal and even bi-parental care (Perkeybile et al., 2015). The research that comes next could build on these findings to suggest interventions capable of either preventing the entraining of this phenotype in the sensitive young, or remediating it in the adult alloparent. This work will enhance our understanding on the extent to which the human parental brain adapts and responds to caregiving experiences.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yfrne.2019.02.005.

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