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Proximate and ultimate mechanisms of human father-child rough-and-tumble play

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ABSTRACT

The aim of this contribution is to attempt to understand the adaptive functions of father-child rough-and-tumble play (RTP) in humans. We first present a synthesis of the known proximate and ultimate mechanisms of peer-peer RTP in mammals and compare human parent-child RTP with peer-peer RTP. Next, we examine the possible biological adaptive functions of father-child RTP in humans, by comparing paternal behavior in humans versus biparental animal species, in light of the activation relationship theory and the neurobiological basis of fathering. Analysis of analogies reveals that the endocrine profile of fathers is highly variable across species, compared to that of mothers. This can be interpreted as fathers' evolutionary adjustment to specific environmental conditions affecting the care of the young. Given the high unpredictability and risk-taking features of RTP, we conclude that human adult-child RTP appears to have a biological adaptive function, one of 'opening to the world'.

Father-child rough-and-tumble play (RTP) has particularly increased in our individualistic and competitive Western industrialized societies over time (Allès-Jardel et al., 2009; Paquette, 2004). Women's entry into the workforce in conjunction with smaller families have led fathers to become more involved with children. Father involvement first emerged as physical play with boys, then gradually devolved into general care-taking of younger and younger children (Bianchi, 2000). Paquette et al. (2020) posited that many decades ago, when families had large numbers of children, it was the older brothers who engaged in RTP with younger boys, so that in more recent times, fathers have replaced brothers in play with boys. The aim of this contribution is to attempt to understand the adaptive functions of father-child RTP in light of biological evolution, even if this type of play with fathers is not universal in humans. A few decades ago, the mother's role was considered to be biological, fulfilling essential functions for the survival of children, and the father's role, at best cultural, playing a variable part in socialization according to the culture. In western societies at least, father-child physical play, including RTP, was not considered to be part of parenting behavior. Such games were seen more as a pleasant distraction without relevance to development of the child. However, research on the neurobiological underpinning of parenting has begun to tease out the brain regions, neural networks and hormones involved in fathering as well as mothering (Abraham and Feldman, 2022; Storey et al., 2020). These findings may begin to explain the biological basis for human father-child RTP. We utilise the 'activation relationship theory' to further explain why human fathers become involved with their children, and specifically in RTP, whereas in the species that are most closely related to us, i.e., chimpanzees and bonobos (with whom we share a common ancestor), fathers do not know their children. We first explain the activation relationship theory, before presenting the evidence for the neurobiological basis of fathering and RTP across animals and humans, positing a view on the biological basis for human father-child RTP.

1. The activation relationship theory

The activation relationship is the child's emotional bond to a parent that fosters his/her opening to the world, with a special focus on parental stimulation and protection through control during the exploration of social and physical environments (Paquette, 2004). More precisely, this parent-child bond is developed to foster regulation of risk-taking in children. The activation relationship theory considers risk-taking to be a basic need that enables children to develop their motor and competitive skills, explore their physical and social environments, and adapt as needed. Men have a universal tendency to take more psychological and physical risks on average than women in all spheres of daily life (Baker and Maner, 2008; Byrnes, Miller and

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Schaffer, 1999; Farthing, 2007; Pawlowski et al., 2008). Men's greater risk-taking is the result of sexual selection, i.e., preservation of the anatomical and behavioral characteristics that provide an individual with a reproductive advantage over others of the same sex (Darwin, 1871). Through risk-taking, men are able to show women their skill as protectors and resource providers, as well as demonstrate to other men that they are adversaries to be reckoned with (Wilke et al., 2006). Studies have shown that women prefer men who take risks, but not when the risks are so high as to cost the man his life—unless in an act of heroism—since they would then be alone in raising their offspring (Farthing, 2007). Therefore, fathers may be better suited than mothers to helping their children, especially boys, learn to control their risk-taking, provided that they have learned to regulate their own risk-taking.

Paquette et al. (2020) suggested that the emergence of the hunter-gatherer lifestyle among our hominid ancestors—and hence the sexual division of labour—led to differentiated maternal and paternal functions. According to the attachment theory (Bowlby, 1969), children regularly seek out contact with attachment figures, principally mothers, when tired, hungry, sick or afraid, or when feeling insecure in the presence of novelty, and this comfort provides them with the necessary confidence to further explore their environment. According to the activation relationship theory (Paquette, 2004), the paternal function is specifically in 'opening the child to the world': children's feelings of confidence result from parents' encouragement of risk-taking during children's exploration of their environment, with parents also protecting their children through discipline (limit-setting, control).

It has been established that both mothers and fathers demonstrate an activation parenting style (Lee et al., 2020; Volling et al., 2019). In our primate ancestors, before the sexual division of labour, probably mothers assumed both attachment and activation functions with their offspring. Simpson et al. (2017) demonstrated that the neonate rhesus macaques who received more tactile stimulation (tickling) from their mother were later less inhibited in their explorative behavior and experienced less fear when approaching novel objects and new social partners. The neonate rhesus who were frequently stimulated by the mother and imitated her facial expressions spent more time in social play with peers one year later (Kaburu et al., 2016). Human mothers, like mothers in many primate species (Palagi, 2018), continue to be the first playmate (activation function) during an infant's first year of life, using tickling and other gentle touch. However, although children develop an attachment relationship and an activation relationship with each parent, generally speaking, in today's occidental societies, women will tend to act as the primary attachment figure (performing maternal functions), while men will tend to serve as the primary activation figure (performing paternal functions about opening the child to the world). Maternal and paternal functions in couples are seen as complementary, whether the couple is composed of same- or different-sex parents.

The human species has evolved along a unique and highly complex path that distinguishes it from other primates. Humans live longer than other primates and children are dependent on their parents for a longer time. Large brain size and a prolonged developmental period allow humans to learn the great number of things necessary to adapt to an environment which has become increasingly complex over the course of history (MacDonald, 1993). Because of humans' large brain size, natural selection is believed to have favored women who gave birth prematurely (Fisher, 1983; Shepher, 1978). Thus, the brain of the human baby is not completely developed at birth and continues to develop during the first year of life. Therefore, human babies are less physically developed, more vulnerable, and thus, more dependent on their mothers than other primate babies. This need for a greater maternal investment in caregiving, which would leave the mother less time to find food, would in turn act as a selective pressure for paternal investment, at least with regard to protection from predators and the provision of food (especially game) necessary to the survival of the mother-child dyad (Benshoff and Thornhill, 1979; Ellis, 1992). Indeed, across the planet, fathers generally

assume an important provider role, permitting women to have many young children at the same time (Lancaster and Lancaster, 1987).

Humans live in more extended groups than do other primates, and human beings are distinct from other primates by their ability to cooperate with others (Tomasello, 2014). In our nomadic hunter-gatherer ancestors, males became directly involved with boys by assuming responsibility for opening them to the world so that they could develop the skills necessary for fighting, hunting and exploring the territory for resources, skills that would be vital in adulthood to ensure the survival of their own children (Paquette, 2004). Survival skills include being able to take risks and to regulate aggression. Paquette (2004), primarily interested in the socialization of aggression in children two to five years old, focused more specifically on RTP as a possible mechanism for regulating aggression as risk-taking. Both mother-child and father-child activation relationship are associated with children's injury-risk behaviors in toddlers (Paquette et al., 2022). Father-child RTP frequency at three years of age has been positively associated with the activation score only in boys (Paquette and Dumont, 2013).

The problem with the studies conducted to date on parent-child interactions is that they use risk-free tasks (free play with or without toys, snack time, quiet play, puzzle tasks, problem solving tasks focused on verbal components, etc.). The play context and the dimensions observed are of paramount importance in shedding light on father-mother differences and their differential impact on children's development. It may be supposed that the use of scales based on a definition of parental sensitivity adapted to the exciting physical play concept, and on concepts of competition, intrusiveness, risk-taking and surprising the child, could reveal differences in favour of the fathers. For this reason, the Risky Situation procedure (RS) was developed to provide a measure of the extent to which children explore and take risks and the extent to which parents prohibit or encourage this exploration and risk-taking. The use of the Risky Situation procedure (RS) has shown the existence of three types of activation relationship (Paquette and Bigras, 2010). Underactivated children tend to engage in little exploration, be passive, and withdraw from novelty or stay close to the parent. Activated children are confident and prudent in their exploration and obey when the parent sets a limit. Finally, overactivated children are reckless and non-compliant when the parent sets limits. With small convenience samples, the use of the RS has uncovered negative associations between the score of activation and internalizing problems in toddlers (Dumont and Paquette, 2013) and in preschoolers (Gaumon and Paquette, 2013). Gaumon et al. (2016) found no significant correlation between the activation score and anxiety in a small clinical sample of children being treated for externalizing problems, but the father-child activation score acted as a protective factor in reducing the association between disorganized attachment to mother and preschooler's anxiety. In the same clinical sample, Paquette et al. (2021) showed that overactivated children displayed significantly more externalizing problems than did children with either an activated or an underactivated relationship with their father.

According to life history theory (Aimé et al., 2018; Paquette, 2015), a child's overactivation proves adaptive in a setting fraught with competition over immediate access to unpredictable resources; the child is then inclined to take greater risks to capture as many resources as possible in the short term. In theory, overactivated children will tend to use aggression and other antisocial behaviors regardless of the context, and to strive for high social dominance status in order to maximize immediate access to resources. This profile may be expected to develop mainly in boys living, for example, in situations of poverty and when the parents have a high number of children, to the detriment of their parental involvement with each child. This reproductive strategy is referred to as "quantitative" since it involves having as many children as possible as early as possible (early reproduction). In contrast, the two other profiles bring into play a "qualitative" reproductive strategy that consists in preparing the individual for later reproduction. The activated profile is adaptive in a context of sufficient and stable resources. The

child is able to take calculated risks to acquire resources. Theoretically, activated children develop a varied repertoire of behaviors to cope with diverse competitive situations: they may be expected to use assertiveness, and, if necessary, aggression in confrontational contexts with threatening children, but prefer to use cooperation whenever possible. According to Charlesworth (1988) evolutionary model, cooperation is the best competitive strategy for obtaining more resources in the long term. Child underactivation would be adaptive in a dangerous social or physical environment. This danger can be real or merely perceived by the parents. The underactivated profile could result from parent over-protection, for example due to the interaction between the lower number of children per family in Western societies today and the overrepresentation of various dangers in the media. This profile may be expected to develop mainly in girls, in order to avoid injury or even death, given that their reproductive success strongly depends on their ability to bear children. Underactivated children will tend to avoid conflicts, submit to others and leave resources to those who demand them.

2. Homologies and analogies

Two approaches can theoretically be used to better understand the biological functions of a behavior: comparison of homologies (divergent evolution) and comparison of analogies (convergent evolution). Comparison of homologies consists in tracing phylogenetic steps by comparing the behavior between different related species alive today. Comparison of analogies consists in identifying the conditions which, by way of natural selection, have favored the adoption of the same survival solution in different species, independently of the genetic relationship between them. The homology approach cannot be used either with father-child RTP or with fathering in general, because in the wide majority of mammal species, including primates, only the mothers take care of the children. In chimpanzees, adult males mainly assume a group protection role, even if they occasionally can be found playing with youths, but not necessarily their own offspring, since they are unable to recognize them, their system of reproduction being sexual promiscuity (Paquette, 2004). Young chimpanzees are therefore mainly socialized via contact with the mother, then with peers and adults, especially during RTP (Paquette et al., 2020).

We will synthesize the literature on the proximate and ultimate mechanisms of RTP in mammals, and then compare human peer-peer RTP (which is universal in our species) and parent-child RTP. We draw on the analogy approach by comparing species in which biparental care is present, describing paternal behaviors and the neurobiological basis of fathering in mammals, in particular the role of hormones.

3. Proximate and ultimate mechanisms of RTP in mammals

RTP is widespread among juvenile mammals (Cenni and Fawcett, 2018; Palagi et al., 2016), but its adaptive functions (ultimate mechanisms) are not yet well understood (Schank et al., 2018). There is limited empirical evidence supporting the hypothesis that juveniles learn specific social and physical skills during play that will be useful during adulthood (Palagi, 2018). Studies in rats demonstrate the importance of RTP for social, cognitive, emotional, and sensorimotor development (Vanderschuren and Trezza, 2014). RTP in the juvenile period enhances the development of executive functions that include impulse control (see Palagi et al., 2016); the monitoring and contextual adjustment of actions influences the development of executive functions of the brain (pre-frontal cortex), which, in turn, leads to the development of more adaptable adults (Pellis and Pellis, 2017).

RTP typically includes elements of both competition and cooperation (Cenni and Fawcett, 2018; Pellis and Pellis, 2017). RTP involves competing for different targets according to the species (for examples, female's nape with male's snout in rats, or licking partner's mouth in Djungarian hamsters)—i.e., targets that differ from those during serious

fighting (Pellis and Pellis, 2017). RTP is also cooperative since it requires that participants coordinate their behaviors both in time and space in order to keep this form of play going (Palagi, 2018) and to reduce the risk of escalation into real aggression (Heesen et al., 2017). The cooperative nature of RTP requires coordination and improvisation: to quote Heesen et al. (2017), "to play together, partners need to recognize each other's playful intentions, anticipate each other's movements, adjust the timing and nature of individual acts, and adapt their moves to the strength and age of their partner". According to these authors, RTP is a joint action that allows for examining cognitive abilities such as shared intentionality and the skill and motivation to share goals and intentions with others. According to Tomasello et al. (2005), shared intentionality is a trait that distinguishes humans from their closest cousin, the chimpanzee. Apes seem to possess some abilities necessary for understanding shared intentionality, like reading others' attention and intentions, but they have difficulty participating in activities involving shared attention directed toward a common goal as opposed to an individual one. Chimpanzees lacked an awareness of joint commitment with a social partner toward a common goal given that only human children, and not chimpanzees, attempted to reengage reluctant human play partners after an interruption (Warneken et al., 2006). However, observations of bonobos or dogs interacting with humans have shown that these two species were very active in their attempts to reengage the play partner (see Heesen et al., 2017).

The features of RTP seem to vary according to the propensity for tolerance in social systems. In socially tolerant species (for examples geladas and Tonkean macaques), where social interactions are highly variable, and few structured or codified according to rank or kin rules, RTP exhibits a high degree of freedom in the combinations of actions, translating into a high degree of unpredictability (see Palagi, 2018). In despotic or intolerant species (for examples rhesus monkeys, Japanese macaques, and sea lions), juvenile individuals tend to refrain from playing with unmatched partners or do so for only short sessions (see Palagi, 2018). Compared to Japanese macaques, Tonkean macaques are less selective in their choice of play partners, including peers and adults, and play more frequently and longer. Cordoni et al. (2018) have shown that play dynamics are different between low-land gorillas (living in polygynic groups) and chimpanzees (living in promiscuous groups). Both adult play and polyadic play (more than two players) were less frequent in gorillas compared to chimpanzees. Play sessions were more unbalanced (and involved more risky play) in chimpanzees than in gorillas, but in the latter, play escalated more frequently into serious aggression. Given that chimpanzees also engaged in higher levels of grooming and contact sitting interactions compared to gorillas, the authors concluded that inter-individual affiliation can account for the differences in play dynamics. These results support the hypothesis that RTP strengthens social bonding between individuals, especially in those species that are cohesive and cooperative such as geladas, chimpanzees and bonobos (Cordoni et al., 2018). Many species of animals, and especially primates, continue to play as adults; indeed, adult social play can have immediate functions such as serving to manipulate social situations (see Palagi, 2018). Bonobos and chimpanzees, both of which live in a fission-fusion society, exhibit strong differences when it comes to adult social play. Known to be more affiliative and to have a wider array of cooperative activities, bonobos are also more playful than chimpanzees, the adults playing with other adults as much as with infants and juvenile of the group, with RTP involving concurrently more than two players, probably to enlarge their social network (see Palagi, 2018). Flanders et al. (2013) proposed the hypothesis that RTP would prepare humans to both compete and cooperate for resources according to their environment.

Emphasizing role reversals and self-handicapping, two important features of RTP that promote reciprocity between players, Schank, Burghardt and Pellis (2018) suggested that fair play in young animals might enable them to acquire skills for behaving equitably as adults. The fair play could evolve in a context of substantial but hard-to-obtain

resources, for example big game hunting in which the spoils are shared collectively within hunter-gatherer societies.

RTP among carnivores and primates exhibits greater complexity in the specific play signals than RTP among rodents (Palagi et al., 2016). Many carnivores display facial signals during RTP, to avoid misunderstanding, cope with a playful interaction successfully, promote social affiliation, and favor cooperation (Palagi et al., 2016). The facial expressions of wolves, coyotes and dogs are more variable and show more degrees of gradation than those of foxes. The same goes for hominoids compared to monkeys (Palagi et al., 2016). Some findings suggest that among macaque species, the tolerant species may use their full play face more frequently than despotic species do (see Palagi et al., 2016). In primates, and probably also in carnivores (such as dogs), the emotional synchronization through facial mimicry accompanies the cooperative side of RTP (Palagi et al., 2016). Experiencing others' emotional states instantly allows an individual to foresee their playmates' intentions and fine-tune their motor sequences accordingly (see (Palagi et al., 2016). Gestural communication plays an important role in RTP in primates, especially in chimpanzees and bonobos, which share a fission-fusion social system, characterized by fluid social interactions. Playful interactions can frequently involve adults in chimpanzees and bonobos, whereas they are more limited to the young in gorillas and orangutans (Palagi et al., 2016).

4. Comparison of peer-peer RTP and parent-child RTP in humans

4.1. Structure

First, it should be noted that RTP is, in both cases, primarily a male activity, just as in many other mammals. There is robust evidence that peer RTP is played most often by boys, and in large boy groups, compared to by girls, or mixed gender groups (Braza et al., 1997; Cordazzo et al., 2012; Lew-Levy et al., 2020; Martin et al., 2011; Storli, 2021). Moreover, girls use fewer and less-rough movements than boys (Harbin, 2016; Tannock, 2011). Similarly, there is robust evidence that fathers engage in more RTP, spend a greater share of their playtime in RTP, and carry out more physically vigorous play than mothers (Amodia-Bidakowska et al., 2020; Fliek et al., 2015; Mellen, 2002), and more with boys than with girls (Jacklin, DiPietro and Maccoby, 1984), although there is variation according to culture (Fry, 2005; Lamb et al., 1982). The peak of father-child RTP is at preschool age (MacDonald and Parke, 1986), when children are 4 years old, while the peak of peer-peer RTP is between the ages of 8 and 10 (Pellegrini and Smith, 1998a).

Father-child RTP differs according to the child's age. Rough play with infants is often labeled RTP, although it lacks any of the chasing or playfight elements, being more specifically boisterous physical play where fathers move their children by bouncing, lifting, manipulating their limbs, and moving their body through space. In contrast, father-child and peer-peer RTP behaviors are very similar in early childhood. Specific to father-child physical play, often described by authors as rough-and tumble play, are the swing, toss, bounce, hug, tickle, horsey and piggyback (Fletcher, StGeorge, and Freeman, 2013; Mellen, 2002; StGeorge et al., 2018). Play chasing is also frequently described as characteristic of peer-peer RTP (Koustourakis et al., 2015). Peer-peer RTP also differs according to the age of the youth: adolescents are more likely to introduce agonistic behaviors or power into their actions (Pellegrini, 1994, 1995).

Moreover, negative emotions such as fear, anger and crying may be fleeting in both father-child and peer-peer play, and if sustained, indicate either the end of the play or the onset of aggression (Paquette et al., 2003). The onset of RTP between father-child and peer-peer is also similar, although more frequently documented in peer-peer play. The onset usually consists of initiations or invitations such as playful poking, chasing or teasing (Bjorklund and Pellegrini, 2002; Smith, 2010). The termination of RTP is also considered to be similar between father-child

and peer-peer play.

Both father-child play and peer-peer play incorporate the characteristics of playfulness, fantasy, restraint, reversal, cooperation and competition (Smith, 2010; StGeorge and Freeman, 2017; Tannock, 2011). What particularly distinguishes father-child RTP from peer-peer RTP is the difference in size, strength, skill and experience in favor of the father. Indeed, the father must engage in significant self-handicapping, and allow role reversal, in order to allow the child to win over an otherwise unbeatable opponent (StGeorge et al., 2018). Fathers are usually sensitively attuned to their child's needs (for stimulation or pause) within the play and provide an optimal balance of arousal and challenge.

4.2. Function

A primary function of peer-peer RTP in early childhood is social affiliation: it allows for the creation of friendships between children (Boulton, 1991). The primary function of father-child RTP is attachment: children who regularly engage in RTP with their fathers quickly develop an emotional bond with them (Paquette, 2004). Moreover, there is robust evidence that both father-child and peer-peer physical play promote the development of social competence such as popularity, peer competence, nonaggressive competitiveness, and social skills (Carson et al., 1993; Kim & Hwang 2017; Luckner, 2007; Mellen, 2002; Parke et al., 1992). The evidence is generally stronger for boys than girls. Although there is more research on emotion regulation in father-child RTP, there is some evidence that both father-child and peer-peer RTP promote the development of emotion regulation. The frequency and quality of father-child RTP are both linked to emotion regulation, expressiveness, or competence (Flanders, Leo, Paquette, Pihl, and Séguin, 2009; Flanders et al., 2010; Hamamcı and Balaban Dagal, 2021; Hong and Han, 2020; Lindsey and Colwell, 2013; StGeorge and Freeman, 2017; StGeorge et al., 2021). Often however, positive associations of RTP with emotion regulation are seen when fathers' leadership or limit setting is higher (Flanders et al., 2010; Hong and Han, 2020). Although there is generally no direct link between RTP and the frequency of aggression (Paquette et al., 2003), some studies have found a positive association between physical aggression in young children and father-child RTP frequency when fathers were less dominant than children (Flanders et al., 2010), and also between physical aggression and peer-peer RTP frequency among adolescent rejected children (Pellegrini, 1994). Veiga et al. (2020) found that preschoolers' RTP with peers at school was related to more physical aggression, and that RTP at home with children and parents was related to more emotion dysregulation and aggression. Moreover, Garcia et al. (2020) found positive associations between adolescent RTP at school and conduct problems and risk-taking behaviors.

As the Garcia et al. (2020) findings suggest, a function of peer-peer RTP amongst children in late childhood and adolescence is to establish and maintain a higher dominance status (Hofstede et al., 2018; Pellegrini, 1995, 2002; Pellegrini and Smith, 1998b). Adolescent boys tend to use various approaches, including physical strength and toughness, to negotiate or to ensure their access to resources or leadership; therefore, RTP becomes a way for them to establish and maintain dominance hierarchies in social groups (Pellegrini, 1993). Paquette (2004) proposed the hypothesis that RTP is a means by which the father can establish his dominance or authority with his child and thus motivate the child's compliance.

RTP is also a means by which fathers teach their children to compete fairly for resources (both currently and in the future) (Palagi, 2018). Thus, fathers who engage in RTP support the development of social and affective competencies that enable children to approach their environment with curiosity and courage, and to compete with others without aggression (Paquette et al., 2003). Evidence from cross-sectional and longitudinal studies shows that executive function, working memory, and attention are positively linked to father-child RTP frequency and or

quality (Anderson, StGeorge, and Roggman, 2019; Freeman and Robinson, 2022).

5. Fathering in non-human animals

Parental behavior is rare in fish and amphibian species because females and males usually synchronize the release of a very large quantity of gametes into the water and then abandon their future offspring. When parental behavior is observed, it is always performed by males (Numan and Insel, 2003). Birds are the champions of biparental care, with over 90% of bird species being monogamous (Ketterson and Nolan, 1994). Generally speaking, testosterone decreases in fathers at the end of the breeding season and prolactin increases with the onset of paternal care (see Numan and Insel, 2003).

Paternal care is relatively rare in mammals (3–5% of species) and includes a broad range of activities where males engage in both indirect care (e.g., nest building, provisioning the female, guarding, defense), and direct care (e.g., feeding, carrying, grooming, playing) (Clutton-Brock, 1991). With few exceptions, paternal care is generally associated with monogamy. Sociobiologically speaking, to maximize its reproductive success, the male mammal has an advantage in making the least possible parental investment and in mating with the highest possible number of partners (sexual promiscuity or polygyny). However, monogamy seems to be the preferred reproductive strategy when maternal behavior alone is no longer sufficient to ensure the survival of offspring, as has been observed in some carnivore species (especially canid species), rodents and primates with altricial young (Kleiman and Malcolm, 1981), i.e., offspring born in a very immature and helpless condition so as to require more care.

6. The neurobiological basis of fathering in mammals: hormones

6.1. Rodents

Among mammals, biparental rodent species (whether monogamous or not) have been the main focus of research on paternity. In general, with the exception of nursing, the same parental behavior is observed in males and females, i.e., nest building, licking, grooming, carrying, etc. The relation of testosterone and prolactin to paternal behavior is less clear in mammals than in birds (Numan and Insel, 2003). Testosterone generally shows a negative relation with paternal care (Saltzman and Ziegler, 2014). Yet the associations are highly variable between rodent species: testosterone is not a factor in prairie voles and California mice, but it increases in male Djungarian hamsters just prior to delivery, and can inhibit paternal care in Mongolian gerbils (Numan and Insel, 2003). Experimental studies with rodents have shown that testosterone increases the likelihood of infanticide (Bales and Saltzman, 2016).

Oxytocin differs between fathers and virgin males in several biparental and facultatively biparental rodent species, but not in a consistent manner. Compared to hormonal changes in mothers, the endocrine profile of fatherhood is quite variable among the handful of biparental mammals that have been studied (Saltzman and Ziegler, 2014). Few experimental studies on rodents have evaluated effects of oxytocin on paternal or allopaternal behavior (Horrell et al., 2019).

Prolactin is higher in rodent fathers living with their mate and pups than in virgin males, newly mated males, and/or expectant fathers (Bales and Saltzman, 2016; Saltzman and Ziegler, 2014). Prolactin does not seem to be essential for paternal care in prairie voles, while it rises postpartum to 20 days in male Mongolian gerbils (Numan and Insel, 2003). However, as yet there is no experimental evidence to support a causal role of prolactin in the onset or maintenance of paternal care (Bales and Saltzman, 2016; Saltzman and Ziegler, 2014).

Few studies have examined the relation between vasopressin and fatherhood. Vasopressin seems to facilitate paternal care in some rodent species (prairie and meadow voles). Prairie vole fathers (as well as mothers) exhibit elevated vasopressin mRNA levels in the hypothalamic paraventricular nucleus and supraoptic nucleus in the postpartum period compared to sexually naïve controls (see (Bales and Saltzman, 2016; Saltzman and Ziegler, 2014). Experimental manipulations in some species of rodents support the existence of a link between vasopressin and paternal or allopaternal behavior (Horrell et al., 2019).

6.2. Non-human primates

The majority of monogamous primates are New World monkeys. Species of marmosets frequently give birth to twins that represent a considerable metabolic demand. Males are as involved in carrying infants from the day of birth as females are. They also engage in extensive grooming. Following the birth of infants, paternal testosterone concentrations drop precipitously in biparental primate fathers (common marmoset, cotton-top tamarin, and humans) (Saltzman and Ziegler, 2014). Testosterone levels do not differ between fathers and other males in marmosets and tamarins (see Numan and Insel, 2003).

In non-human primates, studies showed elevated prolactin levels in fathers during their mate's pregnancy, with mid-gestational elevations and highest levels in the final month of pregnancy (Saltzman and Ziegler, 2014). Once infants are born, fathers maintain significantly higher prolactin levels throughout the period of infant dependency than during the gestational phase (Saltzman and Ziegler, 2014). Prolactin levels in fathers are comparable to those in mothers, but higher than in other males (see Numan and Insel, 2003). Schradin et al. (2003) compared paternal care and prolactin in three species of monogamous New World monkeys: titi monkey, common marmoset and Goeldi's monkey. Fathers of titi monkey and common marmoset always had higher prolactin levels than non fathers and than adult sons. In titi monkeys, the father is the primary caregiver in a small family group of 1–3 young, siblings participate very little, and there is no significant prolactin secretion after birth. In common marmoset and Goeldi's monkey, the father, the mother and older offspring take part in carrying the infants and share food, but the father is the primary carrier whereas the mother is the primary caregiver of twins in common marmoset and of a single infant in Goeldi's monkey. There is a trend toward an increase in prolactin secretion after birth in common marmoset, and a significant increase in Goeldi's monkey. Pharmacological experiments generally do not support a causal role of prolactin in the onset or maintenance of paternal care. In common marmoset, neither of the prolactin manipulations significantly altered fathers' infant-carrying or other parenting behaviors within the family, but both significantly reduced fathers' responsiveness to infant distress calls when fathers were tested away from the family (Saltzman and Ziegler, 2014).

Exogenous vasopressin (but not oxytocin) enhances responsiveness to infant-associated stimuli in caregiver (male and female) marmosets (Taylor et al., 2020). Vasopressin-treated marmosets investigated infant stimuli faster than control group. Vasopressin increased general locomotion in first-time marmoset caregivers that were not actively caring for infants. In both parents and alloparents, oxytocin levels are increased in common marmoset after infant birth and are positively correlated with degree of caretaking behavior exhibited by the individual. Oxytocin and vasopressin enhanced responsiveness to infant stimuli in males and females, respectively, and oxytocin and vasopressin each affected food sharing behavior in male, but not female, caregiver marmosets (see Taylor et al., 2020).

Experience plays a role in rodents and marmoset (Taylor et al., 2020): exposure to and experience caring for young are critical determinants in caregiving behavior. Experience likely causes long-lasting changes in the vasopressin system. Finally, experimental studies provide limited and inconsistent support for the hypothesis that the hormone changes occurring in mammalian fathers are important in the expression of paternal behavior (Saltzman and Ziegler, 2014).

6.3. Humans

Testosterone levels are stable in fathers during the first six months after childbirth and are predictive of levels of father-infant synchrony, but testosterone levels in mothers are neither stable nor predictive (Gordon et al., 2017). The higher fathers' testosterone levels, the lower the frequency of their touch, gaze, positive affect and vocalization (Weisman et al., 2014). The fewer paternal caregiving behaviors, the higher was fathers' testicular volume (Mascaro et al., 2013). A decline of testosterone during the transition to parenthood was related to positive paternal behavior (Fleming et al., 2002). Infant crying has been found to decrease testosterone when coupled with caregiving responses, but increase when caregiving is not possible (cries perceived as a danger signal: see Abraham and Feldman, 2018).

No differences were found in baseline oxytocin and vasopressin between mothers and fathers (Apter-Levi et al., 2014), and no significant differences were present in oxytocin levels between mothers and fathers during the first 4 years after birth (Grumi et al., 2021), but there was more oxytocin in fathers than non-fathers (Grumi et al., 2021). Oxytocin increases during the transition to parenthood in both mothers and fathers, and there is a high individual stability of oxytocin and prolactin across the first months of fatherhood (Abraham and Feldman, 2018). Prolactin increases in new and expectant fathers during pregnancy (Storey et al., 2000), and experienced fathers showed a greater increase of prolactin as compared to first-time fathers (Fleming et al., 2002). Fathers who were most affected by infant cries had higher prolactin (Storey et al., 2000). When parents provide more touch and contact, oxytocin increases after 15 min of play with the infant (Curley and Champagne, 2016). However, there were no significant correlations between paternal oxytocin and fathers' observed interactive behaviors (gaze, vocalization, touch, synchrony, respect for autonomy) during the 5-min play interactions in 1- to 6-month-old infants (Gordon et al., 2017) and 18- to 48-month-old infants (Miura et al., 2015).

Feldman et al. (2010) measured oxytocin levels before and after a 15-minute play-and-touch interaction between fathers/mothers from different families and their respective infants aged between 4 and 6 months. Oxytocin was found to be associated with different types of touch depending on the parent's sex. Oxytocin levels increased in mothers who exhibited significant affectionate contact (proportions of time the parent held the infant in a cradle position and engaged in affectionate touch) with their child, while oxytocin levels increased in fathers who engaged in a great deal of stimulatory contact (proportions of proprioceptive touch, stimulatory touch, and exploratory play). In the experimental study by Naber et al. (2010), the administration of an intranasal dose of oxytocin to 17 fathers before a 15-minute game involving objects with their toddler more greatly stimulated the child's exploration and independence, without altering the sensitivity and non-intrusiveness of the fathers, compared to a control group of fathers. The fathers also tended to show less hostility to the child in the oxytocin condition, by being more patient and showing less discontent. Weisman et al., (2012, 2014) showed that fathers who received oxytocin administration exhibited more infant-directed touch, positive vocalizations, and encouragement of infants' social initiative compared to fathers in the placebo condition.

Gordon et al. (2010) measured prolactin and oxytocin in fathers, averaged across two time points, child age 2 and 6 months. Father-infant play was observed at infant age 6 months. The results showed that prolactin was associated with father-infant coordinated exploratory play, when playing together with toys (presenting, handling, and jointly manipulating the toy when the infant's attention is directed toward the toy). Oxytocin was associated with father-infant affect synchrony when playing together without toys.

Apter-Levi et al. (2014) collected oxytocin and vasopressin from fathers and mothers in different families before observing parents in a 10-minute face-to-face interaction with their 4–6 month-old infants, using objects. Mothers provided more affectionate contact, while fathers

provided more stimulatory contact. Parents with high oxytocin levels displayed significantly more affectionate contact compared to parents with low oxytocin and constructed the interaction towards readiness for social engagement by increasing social salience in response to infant social gaze. In contrast, parents with high vasopressin engaged in stimulatory contact and tended to increase object-salience when infants showed bids for social engagement. Oxytocin levels were independently predicted by the amount of affectionate contact and the durations of gaze synchrony, whereas vasopressin levels were predicted by stimulatory contact, joint attention to objects, and the parent increasing object salience following infant social gaze. The results further specify how synchronous bio-behavioral processes with the mother and father support the human infant's entry into the family unit and prepare the child for joining the larger social world.

Li et al. (2017) found intranasal oxytocin to increase the caudate nucleus, dACC and visual cortex response in fathers viewing pictures of their toddlers, suggesting that intranasal oxytocin augments activation in brain regions involved in reward, empathy and attention in human fathers. In contrast, vasopressin had no effect on paternal neural responses to viewing pictures of their toddlers. Neither oxytocin nor vasopressin significantly modulated the neural response of fathers to infant cries.

Recently, Morris et al. (2021) made a study of father-to-infant physical touch during a triadic parent-infant free play task during four minutes including father, mother, and infant (6 months-old). The results showed that fathers who engaged in more playful proprioceptive touch (i.e., tossing the child in the air or bounding playfully) showed higher levels of both unextracted and extracted oxytocin. Gentle affectionate touch (i.e., patting or stroking the infant; loving touch with the sole purpose of expressing affection) and functional proprioceptive touch (i. e., moving the child from one spot to another) predicted higher unextracted but not extracted oxytocin levels. Fathers who did not engage in physical touch showed lower levels of both unextracted and extracted oxytocin.

7. The neurobiological basis of fathering and RTP in mammals: the neural circuitry

The neural circuitry underlying paternal behavior remains relatively unexplored and the existing studies have mainly been conducted on rodents (Horrell et al., 2019, 2021). The neural substrates of parental care overlap substantially between males and females (Numan, 2020). The prefrontal cortex (PFC), the medial preoptic area of the hypothalamus (MPOA), the medial amygdala (MeA), and the Mesolimbic Reward Pathway are involved in parental care in both males and females. MPOA expresses receptors for prolactin, oxytocin, estrogen, and progesterone; in biparental rodents, the MPOA is highly responsive to stimuli from pups given that it inhibits nuclei in the aggression/fear circuitry and excites the reward circuitry (Horrell et al., 2019).

In humans, despite the lack of difference in plasma concentrations of oxytocin and vasopressin in mothers and fathers, there are differences in brain activation areas that may support the observed sex differences in parent-infant behavioral interactions (Storey and Ziegler, 2016). Atzil et al. (2012) showed a significant positive correlation between activation of the amygdala and vasopressin concentrations in fathers, and a correlation between amygdala activation and oxytocin concentrations in mothers. In general, mothers' oxytocin concentrations were more closely related to emotional areas (amygdala and nucleus accumbens) and fathers' oxytocin more related to socio-cognitive areas (superior-occipital and temporal gyri and the left medial prefrontal cortex).

Our knowledge of the neural circuitry of RTP is mainly based on studies with rats. RTP engages large and diverse regions of the brain, including those involved in motivation, reward, sensory, and motor processing (in VanRyzin et al., 2020). Early in life, hormones trigger the process of sexual differentiation in the brain, in particular two nodes related to the propensity for males to engage in RTP more frequently and

with higher physical intensity: the medial amygdala (MeA), involved in processing social information, and the lateral septum (LS), characterized by more vasopressin-expressing neurons in males. A third node, the prefrontal cortex (PFC), contributes generally to the structure of RTP and ability to respond to play initiations, and correlates with activity in other connected regions within the striatum and amygdala.

8. Discussion

Even without conducting a systematic analysis of homologies, one can immediately observe a degree of specialization in paternal behavior in the course of evolution when comparing biparental species of rodents and primates. In rodents, with the exception of nursing, males adopt the same parental behavior as females. In non-human primates, males appear to be primarily involved in transporting the young. Finally, in humans, adult males play a greater role than females in the function of opening to the world, by encouraging children to take initiatives in unfamiliar situations, to explore, to take risks, to overcome obstacles, to be braver in the presence of strangers, and to stand up for themselves in order to discover and adapt to their physical and social environment (see Paquette et al., 2020).

Analysis of analogies in biparental species of mammals uncovers that the endocrine profile of fathers is highly variable across species, compared to that of mothers. This can be interpreted according to the father's evolutionary adjustment to specific environmental conditions that are responsible for the young requiring more care. This hypothesis could ideally be tested by comparing the hormonal profile of fathers between humans and wolves, both of which have the same ecological niche, i.e., collective big-game hunting. As with humans, life is a balance between cohesive and conflictive behaviors in wolves, as is evidenced by the presence of leadership, not just dominance. One might expect to find the same endocrine profile in the fathers of these two species. Fathers in biparental canid species (gray wolf, coyote, African wild dog) play with, babysit and defend their pups, and provision them with food (Horrell et al., 2019). Compared to other canids, wolves should be the most playful and the least aggressive. RTP among adult wolves has not been systematically described, but it appears to involve all of the play behaviors shown by dogs (see Palagi et al., 2016). The basic social unit of a wolf population is the breeding dominant pair and its offspring including members of more than one litter, i.e., a large nuclear family (Mech and Boitani, 2003). There is a prolonged maturation, given that wolves only reach full maturity at 5 years of age, thus increasing the opportunity for offspring to learn the more subtle components of hunting and foraging behavior that are not innate. Grouping in wolves does not necessarily yield greater hunting efficiency, but appears to more strongly facilitate the subsistence of young wolves through the sharing of large prey (Mech and Boitani, 2003). Wolves cooperate in caring for the young. During the first month after birth, father contributes indirectly in the form of defense of homesites, hunting, and provisioning the lactating female. From the second year of life, when the pups can ingest solid food, biparental care becomes more symmetrical between the mother and the father. When the pups are out of the den, the father and any other adults regurgitate food to the pups. As in the case of humans, in wolves, monogamy does not appear to be obligate, meaning that care by the father is not essential under all conditions (Packard, 2003).

With the exception of testosterone, the levels of the different hormones discussed in this article (oxytocin, prolactin, and vasopressin) are the same in human mothers and fathers. The neural circuitry also appears to be the same in both sexes, at least in rodents. These results support the idea that mothers and fathers have the same basic proximate mechanisms for all types of parenting behavior. Testosterone decreases and other hormones increase in fathers upon contact with children, and a few experiments have shown the intranasal addition of a hormone to alter paternal behavior. Although little studied up to now, vasopressin could be the hormone of parental activation. It has been associated with locomotor activity (transport) in marmoset females and males, and with

stimulatory contact in human mothers and fathers. In humans, although affectionate contact is more characteristic of mothers, and stimulatory contact of fathers (Apter-Levi et al., 2014), associations between hormones and parental behavior are, in our opinion, more dependent on the context of touch than on the parents' sex. To date, oxytocin has been associated with affect synchrony in fathers within a social context (Gordon et al., 2010), with touch affect in mothers within a context of play with toys (Feldman et al., 2010), with mothers and fathers in a context of face-to-face play without toys (Apter-Levi et al., 2014), and with fathers in the context of a free play task (Morris et al., 2021). Oxytocin has also been associated with stimulation contact in fathers within a context of play with toys (Feldman et al., 2010) and a free play task (Morris et al., 2021). Prolactin has been associated with exploratory play in fathers within a context of play with toys (Gordon et al., 2010). Finally, vasopressin has been associated with stimulatory contact in fathers and mothers within a context of face-to-face play without toys (Apter-Levi et al., 2014). Taking into account the activation relationship theory, it would be relevant to conduct a study involving these different hormones within a high-stimulation context (i.e., a context that can trigger intense enjoyment in children), such as tickling play with infants or RTP with toddlers/preschoolers. It may be hypothesized that vasopressin is linked to active play including risk-taking, both with mothers and fathers, whereas oxytocin and prolactin are more involved, respectively, in quiet play (with or without toys) involving affect, and in stimulating exploration.

In this article, we have attempted to provide evidence for the hypothesis pertaining to the biological adaptive functions of father-child RTP in humans. The comparison of the structure and functions of RTP shows a great similarity between on the one hand, father-child RTP and peer-peer RTP in humans, and on the other hand, between peer-peer RTP in humans and peer-peer RTP in other mammals. Moreover, characterized by a high degree of variability and freedom, human RTP, including adults, is similar to observed RTP in tolerant species, the latter being more cohesive and cooperative than despotic or intolerant species (Palagi et al., 2016).

Father-child RTP in humans may be further understood according to the adaptive functions of the immaturity period in human beings (Paquette and Bigras, 2018). According to this model, skills are acquired and iteratively developed across the four stages of infancy (0–3 years), childhood (3–7 years), juvenility (7–11 years), and adolescence (12–18 years). Most mammal species progress from infancy to adulthood without any intervening stages (Bogin, 1990), and the infancy stage ends when breastfeeding stops (Bogin, 1997). Natural selection may have favored the addition of the juvenile period in social mammalian species, with peer-peer RTP acting as a mechanism for learning the motor skills essential for competition and for enabling social affiliation. Findings in both rodents and primates support the hypothesis that the length or degree of postnatal development is related to the prevalence and complexity of the play exhibited (Pellis and Iwaniuk, 2000). Adolescence would then have been established in great apes such as chimpanzees and humans, with peer-peer RTP serving as a mechanism to help establish and maintain dominance status while avoiding the risks of lethal injury normally associated with genuine aggression. A unique developmental stage of humans, childhood would have emerged between infancy and the juvenile period, as an evolutionary strategy to elicit caring from others (Bogin, 1997). Paquette and Bigras (2018) further posit that in childhood, children's interaction with peers and education from adults allows them to learn to manage their emotions and behavior in concrete and social situations and develop the skills needed for cooperation. During the subsequent juvenile period, children organize these skills into flexible structures so as to be able to adapt to the many and varied social contexts found in different human cultures. Experience with multiple carers and playmates in a variety of contexts enables children to develop the behavioral flexibility they need to successfully forge alliances and cooperate in groups. In Western industrialized societies (where monogamy has been culturally established),

among the adults available to the child, it is mainly fathers who take this role of playing with boys and increasingly with girls.

That said, to date, no study has shown a direct association between the frequency/quality of RTP and cooperative skills. The recent increase in fathers' involvement in RTP with their children in individualistic Western industrialized societies is concomitant with their greater involvement in caregiving, a phenomenon related to social context and cultural values (see Ciani et al., 2012). Considering that humans are unique in their scope of cooperation among unrelated individuals, Voorhees et al. (2020) proposed that human cooperation is established by a shared cultural worldview of group identity. It could therefore be that the ancestral mechanism of mammalian RTP is not sufficient to allow the development of cooperation in humans.

However, although not sufficient for a complete explanation, a biological view of human adult-child RTP suggests that it was selected into the fathering repertoire in order for fathers to teach children new skills such as self regulation, prudence in risk taking, and social skills, all of which contribute to survival. The Activation Relationship theory explains that fathers' tendency to excite their children, to engage them in both physical and stimulating play, and to use teasing to destabilize them both emotionally and cognitively, has a function of 'opening the child to the world', that is, fostering children's awareness, exploration and capabilities in the world outside of the dyad (see Lee et al., 2020; Paquette, 2004). Father-child RTP during the childhood and juvenile stages is clearly linked to this function of opening to the world, given its features of high unpredictability and risk-taking, both physical and emotional. Father-child RTP gives the opportunity for children to become skilled not only in motor actions but also in regulating their behavior and emotions when they come across new and unpredictable social and cognitive situations that are difficult to manage yet vital to survival (Palagi, 2018).

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