The basis of behavioral change in new fathers

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Abstract

Human paternal behavior has only been studied for the last 20 years. Before that, research was focused on mothers. Since fathers play an important role in the development of a child, paternal behavior should also be studied to get a better understanding of the underlying mechanisms that are involved. When fathers enter fatherhood, changes in testosterone, cortisol, prolactin, oxytocin, and vasopressin that promote father-child interactions and bonding are observed. Besides hormone changes, neuronal activation changes are also seen in the paternal brain comparable to the maternal brain. However, the cortical areas are more activated in the paternal brain in response to infant stimuli than in the maternal brain.
Hormones possibly interact with each other and with different brain areas, resulting in the displayed paternal behavior. How physiological changes result in paternal behavior or paternal behavior results in physiological changes, needs to be further investigated.

Table of contents

Introduction

Parental care is a strategy that some animals adopted to increase the fitness of their offspring. In many species, parental care is very important for the survival of the infants (Storey et al., 2000). However, parental care is very differently expressed among species. This difference is seen in the parent that provides the parental care. In 95% of mammals, only the female provides the young with parental care (Clutton-Brock, 1991). The other 5% of mammals also show care provided by the father (Moller, 2003). Humans belong to this 5% and display paternal behaviors.

Human maternal behavior has been wildly studied over the years. It has been linked to several hormones that play a role in mammalian maternal behavior. For example, prolactin, oxytocin, vasopressin, and cortisol increased maternal behavior in humans (Storey et al., 2000; Bosch et al., 2008; Grodon et al., 2010; Storey et al., 2020).
Besides the hormonal changes related to maternal behavior, neuronal changes were also observed (Mascaro et la., 2014). These changes result in more activation of empathy networks in the brain towards infants (Mascaro et al., 2014).
It is believed that parental behavior is caused by similar changes in mothers and fathers (Feldman et al., 2019). Still, the number of studies focused on human paternal behavior are limited.

The behavioral changes in fathers were often overlooked, because the mother and infant were the center of attention when it came to parental behavior studies. Over the last 2 decades, interest in the human paternal behavior emerged and for the last 10 years, it became a more popular topic.

Understanding of the basis of paternal behavior is very important for both parents and infants. Disrupted paternal behavior has very negative effects on the development of infants (Barker et al., 2017; Bruno et al., 2020).

This essay will discuss the hormonal and neuronal changes that cause paternal behavior. How do hormones and neuronal networks change in fathers before and after childbirth and how could these changes influence paternal behavior?

I hypothesize that there will be hormonal and neuronal changes in fathers. These changes are probably like the changes seen in mothers. Since testosterone is mainly a male hormone, this hormone could explain paternal behaviors only seen in fathers.

Changes in behavior after childbirth

Paternal behavior

Fathering behavior in humans is commonly described as caregiving (Gettler et al., 2011). The amount of caregiving is often assessed by the time the fathers physically spend with his child. Other studies also included reaction time to infant cries, affectionate touch and use of high-pitched, rhythmic speech directed towards the infant (Fleming et al., 2002; Mascaro et al., 2014; Nicholas et al., 2019). These types of behavior correspond with the caring role the father has adopted.

Paternal responsiveness and feelings have also been assessed in terms of father's response to infant cries (Storey et al., 2000; Fleming et al., 2002). In the study of Fleming, two types of cries were used: pain and hunger. The feelings of fathers and non-fathers in response to the cries were very different. Fathers reported significantly more feelings of sympathy and alertness compared to non-fathers. The fathers also reported a difference between the two types of cries. In response to the pain cries, fathers felt a higher need to response than to the hunger cries. Experienced fathers felt this need to respond to pain cries even more (Fleming et al., 2002). These results clearly show that fathers adapt to their caring role and feel the need to nurture and protect their children.

These caring behaviors are possibly related to neuroendocrine developments in fathers during and after pregnancy.

Disrupted paternal behavior

While normal paternal behavior leads to positive effects for his offspring, disrupted paternal behavior has the opposite effect. Some fathers fail to adapt to their new role as caregiver. Becoming parents is a stressful event for both mothers and fathers. Every individual reacts differently to such a tremendous change. In some individuals, the stress becomes too much and results in depression (Bruno et al., 2020). Both mothers and fathers have reported these depressive mental changes (Sundstrom Poromaa et al., 2017; Bruno et al., 2020).

It is often thought that fathers do not experience postpartum depression to the extent that mothers do. Nevertheless, this might be due to the limited research that has been conducted on the mental health, after birth, on fathers (Sundstrom Poromaa et al., 2017). Mental health of fathers is often overlooked because the focus lies on the mother during and after pregnancy. Symptoms of depression and mood alterations in fathers are usually less severe or completely different compared to mothers, but this does not make it less important (Bruno et al., 2020). To get a better understanding of postpartum depression in fathers, different screening methods need to be used (Baldoni et al., 2020). Screening methods that are not based on postpartum depression symptoms of mothers, but on the symptoms of fathers (Baldoni et al., 2020).

Postpartum depression in fathers often leads to disrupted paternal behavior (Sundstrom et al., 2017). As mentioned before, paternal behavior serves the purpose of increasing the survival of the offspring. Depression causes more negative and fewer positive behaviors in fathers towards their children (Sundstrom et al., 2017). Children of fathers that deal with postnatal depression, have an increased risk of emotional en behavioral disorders later in life (Wilson and Durbin, 2010; Stein et al., 2014; Barker et al., 2017). Depressed fathers might also have a larger influence on the mental health of children compared to the influence the mental state of their mother has (Moller et al., 2014). Paternal anxiety was positively correlated with infant anxiety, where maternal anxiety did not show such a correlation with infant anxiety (Moller et al., 2014). These findings express the importance of the understanding of the mental health of fathers and how this influences the behavior towards their children. These paternal behaviors expressed in human fathers are probably connected to hormonal and neuronal changes.

The challenge hypothesis

The challenge hypothesis is the main hypothesis that explains paternal behavior in terms of hormone levels. It has been known for a long time that testosterone plays a role in aggressive behavior in vertebrates (Harding, 1981). It appears that testosterone increase relates to aggression associated with reproduction and a testosterone decrease to social stability (Wingfield et al., 1990).

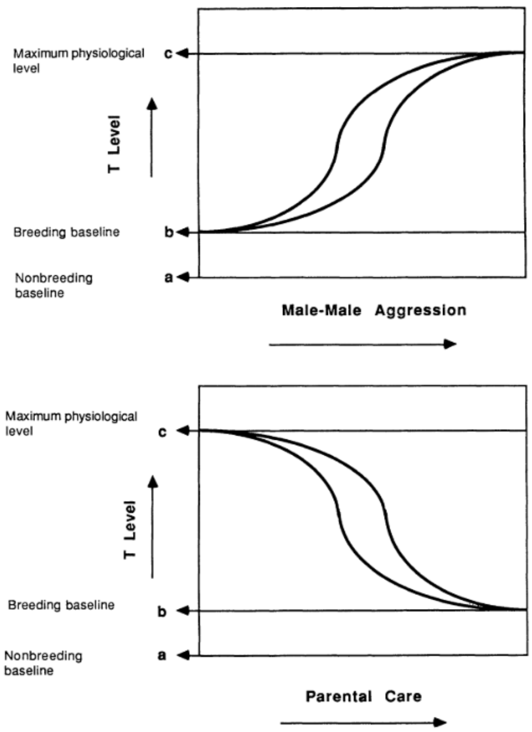

Figure 1. Hypothesized relation between male-male aggression and testosterone(T) (upper graph) and parental (paternal) care and T (lower graph). Male-male aggression increases when testosterone levels increase. On the other hand, parental care increases when testosterone decreases. From: Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "challenge hypothesis'': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies." *American Naturalist*, *136*(6), 829–846. https://doi.org/10.1086/285134

According to the challenge hypothesis high testosterone levels lead to more male-male aggression (Figure 1). This aggression often serves to protect their territory or to fight for a female. At the same time, lower testosterone levels seem to increase paternal behaviors (Figure 1). Testosterone has pleiotropic effects in regulating male-male, male-offspring and male-female interactions.

This challenge hypothesis might also be applicable to human fathers in that reduced testosterone after committing to a long-term relationship and having children results in increased paternal care.

Changes in hormone levels

Testosterone

Since the challenge hypothesis could explain the differences is paternal behavior before and after birth, it might be worth looking into the testosterone levels in fathers around those times.

The connection between hormones and paternal behavior in humans, was first investigated by Storey et al. in 2000. Their goal was to identify a hormonal basis for the paternal behaviors seen in fathers. They found that testosterone, a steroid hormone, dropped in fathers right after the birth of their child (Figure 3; Storey et al., 2000). In addition, men with lower testosterone levels showed more caring behaviors, suggesting that lower testosterone levels enhance paternal responsiveness, possibly by reducing tendencies to engage in non-nurturing behaviors (Storey et al., 2000). Later research showed that testosterone variation in fathers, could predict positive paternal behaviors (Kuo et al., 2016).

As mentioned before, Storey et al. conducted the first study that investigated hormones and paternal behavior. After this first attempt, indicating that paternal behavior could indeed lie at the basis of hormone changes, a follow up study (Berg et al., 2001) was conducted. A control group was added to the study design. The same decline in circulatory testosterone was seen in new fathers in comparison to a control group of non-fathers. To correct for other external environmental stimuli that might influence testosterone levels in men, testosterone levels were also measured during the different time points of the day and on an annual basis (Berg et al., 2001). Important to note is that testosterone levels in the morning were higher compared to the evening measurements (Berg et al., 2001). This outcome was also seen in other studies (Gray et al., 2002) and suggests that levels can change dramatically over short time scales. Men should be able to quickly respond to unpredictable events with high testosterone levels (Wingfield et al., 1990). An explanation for the decrease of testosterone during daytime could be that interactions with the child lower testosterone levels in fathers. Suggesting that behavior can alter hormone levels.

The decrease in testosterone after childbirth in fathers was less pronounced in inexperienced fathers compared to experienced fathers (Fleming et al., 2002). Since, testosterone levels decline with age, the data in this research was corrected for age effects on testosterone levels (Fleming et al., 2002). Experienced fathers showed a larger decline in testosterone, suggesting that they are better prepared to care for their newborn and can adapt quickly.

On the other hand, fathers show an increase in testosterone in response the auditory cues of infant cries when they cannot provide care (Storey et al., 2000; Fleming et al., 2002). This increase in testosterone in response to infant cry, was observed more often in inexperienced fathers compared to experienced fathers (Fleming et al., 2002). The need to help their child results in testosterone increase and might lead to protective aggression. However, there are no reports on this. New fathers might show a larger increase in testosterone in response to infant cries, because the situation is still new and unpredictable for them.

While the results presented above are broadly consistent with the conflict hypothesis, it must be noted that these are based only on small groups of American men. Therefore, it is unclear to what extent these findings can be generalized to human beings as a whole.

A longitudinal study in the Philippines found more solid evidence that fatherhood results in decreased testosterone in human males (Gettler et al., 2011). This study took samples from 624 males (single, partnered, or father) from 2005 to 2009. Single men that had high testosterone levels in 2005, were more likely to have found a partner in 2009. Again, supporting the challenge hypothesis that higher testosterone levels are associated with benefits to mating behavior. In the period of 4 years, males that entered a partner relationship and produced a child showed the largest decrease in testosterone. Males that entered a partner relationship, but did not get a child, showed similar testosterone levels to single males. This suggests that becoming a father really causes a decrease in testosterone levels that is independent of the effect of merely living in a monogamous relationship (Gettler et al., 2011). Through father-child interaction and testosterone levels, it was found that direct care of the offspring had a suppressive effect on testosterone levels in fathers (Gettler et al., 2011).

The challenge hypothesis, described by Wingfield in 1990, seems to be applicable to human fathers. Becoming a father reduces testosterone levels, probably due to father-child interactions leading to more paternal behavior in forms of caring behavior (Figure 2; Storey et al., 2000; Berg et al., 2001; Fleming et al., 2002; Gettler et al., 2011; Storey et al., 2020)

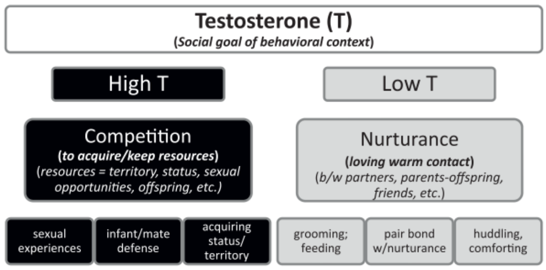

Figure 2. Behaviors resulting from high and low levels in testosterone (T). High testosterone levels go hand in hand with competition behaviors to acquire or keep resources, whereas low testosterone levels are correlated with nurturance behaviors like loving and warm contact. From: Van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The Steroid/Peptide Theory of Social Bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, *36*(9), 1265–1275. https://doi.org/10.1016/j.psyneuen.2011.06.001

Cortisol

Another hormone that changes in males before and after pregnancy is cortisol. This hormone, also known as the stress hormone, has not been studied very well in relation to paternal behavior but may be related to men's parenting effort (Kuo et al., 2018). Short-term increases in cortisol have been associated with better cognitive and behavioral responses to stress (Sapolsky et al., 2000).

Circulatory cortisol declines in males after the birth of their child, were first reported by Berg et al. in 2001. Pleasant and playful father-child interactions were later associated with lower cortisol levels in fathers (Gettler et al., 2011; Saxbe et al., 2014; Kuo et al., 2018). These lower levels of cortisol after birth are sometimes alternated with short increases of cortisol. These short-term increases in cortisol, appeared when fathers switched from direct to indirect care for their child (Kuo et al., 2018).

On the other hand, elevated cortisol levels in males were found around the time of birth (Figure 3; Storey et al., 2000; Berg et al., 2001; Kuo et al., 2018). Labor and becoming a father are stressful events and could explain the increase in cortisol around that time. Increased levels of cortisol could be necessary for fathers to have a better cognitive and behavioral response to this stressful period.

Short-term increases in cortisol were observed in fathers that heard their infant cry (Fleming et al., 2002). Inexperienced fathers showed a greater increase in response to the cry, than experienced fathers (Fleming et al., 2002).

Becoming and being a father often entails various stressful moments. Besides birth, infant cries result in a stress response. This stress response is seen in fathers as an increase in circulatory cortisol (Kuo et al., 2018), probably needed to respond better during these stressful events. Comforting and playful interactions with the child, reduce cortisol levels again (Gettler et al., 2011; Saxbe et al., 2014; Kuo et al., 2018). How cortisol exactly plays a role in paternal behavior remains unclear.

Prolactin

Prolactin is a hormone that plays an important role in reproduction. Especially in the milk production of mothers. Prolactin has also been linked to maternal and paternal behavior in other species (Storey et al., 2020).

The involvement of prolactin in human paternal behavior is until this day poorly understood. First research on prolactin levels during and after pregnancy was conducted on men and women by Storey et al in 2000. This research showed that in both men and women, prolactin levels increased in the period closer to birth (Figure 3; Storey et al., 2000). Fathers with higher prolactin levels after birth, felt more positive and showed greater responsiveness to infant cries (Storey et al., 2000; Fleming et al., 2002). Experienced fathers and fathers that engaged in more playful activities with their children, showed a larger increase in prolactin levels (Fleming et al., 2002; Gordon et al., 2010). Also, fathers of younger children had higher prolactin levels, than fathers of older children (Gettler et al., 2012). From these findings, prolactin levels seem to be related to initiation of contact by fathers.

Prolactin also influences a man's libido. Increased prolactin results in a reduced libido and therefore in more paternal behavior instead of mating behavior (Hashemain, 2016).

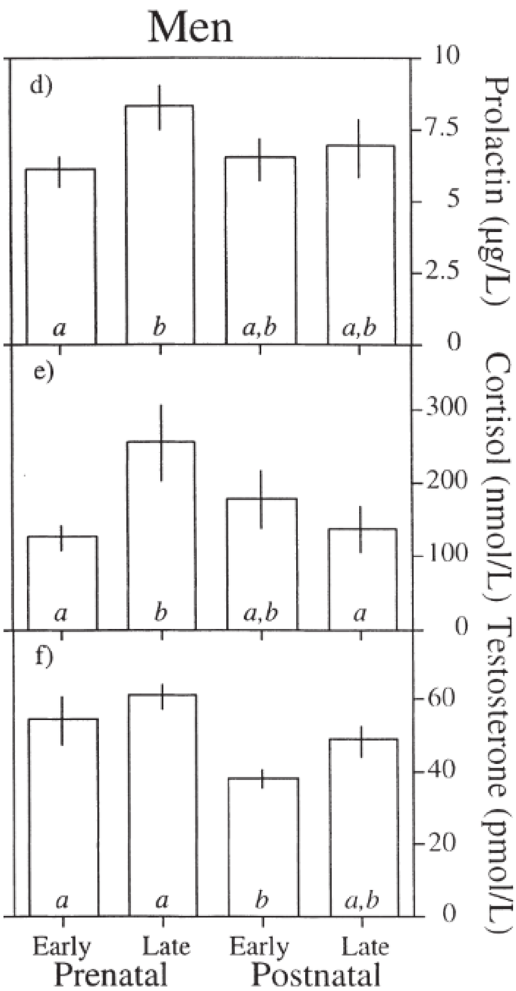

Figure 3. Prolactin (d), Cortisol (e) and Testosterone (f) levels in men before (prenatal) and after (postnatal) birth. Different letters on the bars indicate significant group differences relative to the early prenatal sample. From: Storey, A. E., Walsh, C. J., Quinton, R. L., & Wynne-Edwards, K. E. (2000). Hormonal correlates of paternal responsiveness in men. *Evolution and Human Behavior*, *21*(2), 79–95. http://www.ncbi.nlm.nih.gov/pubmed/10785345

Oxytocin

Oxytocin, a peptide hormone, has been widely studied in different environments and has often been connected to pair-bonding behaviors and reaction to infant stimuli (Grande et al., 2020). Changes in oxytocin during the transition to fatherhood were first examined by Gordon et al (2010). In this study parental behavior was observed from both the mother and father. Also, plasma oxytocin levels were measured. Once during the first week after birth, and once 6 months postpartum. Oxytocin levels increased over this period in both mothers and fathers (Gordon et al., 2010). Differences in oxytocin increase between mothers and fathers were related to the parental care they gave. Fathers had a higher oxytocin increase, when expressing stimulatory parenting behavior like proprioceptive touch, object presentation and tactile stimulation (Gordon et al., 2010). Where mothers showed an oxytocin increase when expressing affectionate parental behaviors (Gordon et al., 2010).

Later research showed that fathers, that were given intranasal oxytocin, had higher quality interactions with their infants (Weisman et al., 2014). Another interesting finding is that genetic variation in oxytocin receptors is associated with variation in responsiveness to oxytocin, with some alleles associated with high responsiveness and increased touching of offspring by fathers (Feldman et al, 2012).

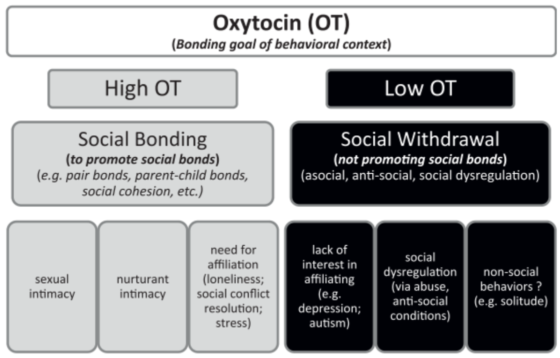

Figure 4. Behaviors resulting from high and low oxytocin (OT) levels. Oxytocin promotes social bonding. Low levels of this hormone result in social withdrawl. From: Van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The Steroid/Peptide Theory of Social Bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, *36*(9), 1265–1275. https://doi.org/10.1016/j.psyneuen.2011.06.001

Vasopressin

Vasopressin is another peptide hormone that is involved in pair-bonding and parenting (Grande et al., 2020). This hormone could be very interesting to look at in human fathers. However, research on this hormone in human fathers is scares. Only a few studies over the years incorporated measurements of vasopressin.

Table 1. The steroid-peptide matrix of social bonds. Arrows indicate high and low levels of steroid or peptide hormones in individuals or populations. Testosterone is indicated with 'T'. Antagonistic aggression is aggression that has to do with protecting territory or acquiring mates. Protective aggression is a form of aggression to protect social bonds. Levels of hormonal combinations give a prediction of the behavior. From: Van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The Steroid/Peptide Theory of Social Bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, *36*(9), 1265–1275. https://doi.org/10.1016/j.psyneuen.2011.06.001

		Oxytocin		Vasopressin	
		↑	↓	↑	↓
T	↑	Sexual intimacy	Antagonistic aggression; social dysfunction	Protective aggression	Antagonistic aggression; social dysfunction
	↓	Nurturant intimacy (need or presence)	Depression? Withdrawal?	Nurturant intimacy (need or presence)	Depression? Withdrawal?

Fathers that have younger children, show higher levels of vasopressin (Gray et al., 2007). Fathers that are playing with their children more actively also showed this increase in vasopressin (Abraham et al., 2018).

Research done on prairie voles discovered that polymorphisms in the promoter region of vasopressin receptors altered the distribution and density of these proteins in the brain (Hammock and Young, 2005). This contributed to differences in paternal care between monogamous and polygynous males (Hammock and Young, 2005).

A promising finding for future research on human paternal behavior, is that vasopressin alters brain region activation in fathers but not in mothers (Nishitani et al., 2017; also see ''Hormones, brain, and paternal behavior'').

Steroid-peptide theory of social bonds

An explanation for paternal behavior because of hormone changes, could be given by the steroid-peptide theory of social bonds. This theory depends on testosterone (steroid), oxytocin (peptide), and vasopressin (peptide) levels.

Vasopressin and oxytocin have both been linked to pair-bonding and at the same time aggression towards intruders that might harm their infants (Figure 4; Van Anders et al., 2011). Testosterone on the other hand does not facilitate pair-bonding and stimulates aggression (Figure 2; Van Anders et al., 2011).

Combining different levels of these hormones could make a prediction of the expressed behavior in an individual or a population (Table 1; Van Anders et al., 2011). For example, a man that has high testosterone levels is in a ''competing state'', meaning that he wants to keep and acquire resources (Figure 2). Often these high testosterone levels result in aggressive behavior.
A combination of high testosterone levels with low oxytocin and vasopressin levels, results in antagonistic aggression (Table 1). A man that experiences these hormone levels is socially dysfunctional. When testosterone and oxytocin are both present in high concentrations, sexual intimacy is observed. Whereas a combination of high testosterone and high vasopressin levels result in protective aggression (Table 1). Protective aggression is often seen in men protecting their mate or infants (Van Anders et al., 2011). This could explain high testosterone peaks in fathers when exposed to infant cries and not being able to help (Storey et al., 2000; Fleming et al., 2002). Fathers have increased vasopressin levels (Gray et al., 2007) and combining this with high testosterone levels, in response to infant cries, leads to protective aggression (Table 1).

When all 3 hormones are present in low concentrations, depressed behavioral patterns are observed (Table 1). Low testosterone and high oxytocin and vasopressin levels result in nurturant intimacy (Table 1). This behavior is

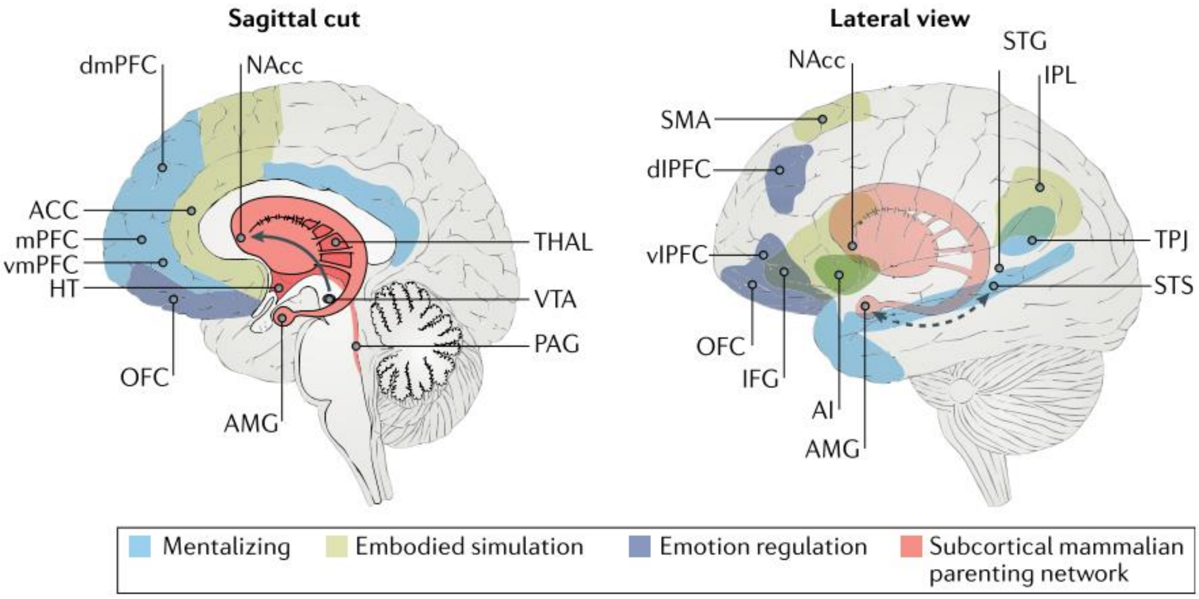

Figure 5. The global human paternal caregiving network. This figure includes both the cortical areas involved in mentalizing, embodied simulation and emotion regulation as well as the subcortical areas. Solid arrows indicated connectivity patterns based on animal research and dashed arrows indicated connectivity patterns seen in human research. ACC, anterior cingulate cortex; AI, anterior insula; AMG, amygdala; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; HT, hypothalamus; IFG, inferior frontal gyrus; IPL , inferior parietal lobe; mPFC, medial prefrontal cortex; NAcc, nucleus accumbens; OFC, orbitofrontal cortex; PAG, periaqueductal grey ; PFC, prefrontal cortex; SMA , supplementary motor area; STG, superior temporal gyrus; STS, superior temporal sulcus; THAL , thalamus; TPJ, temporoparietal junction; vlPFC, ventrolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex; VTA , ventral tegmental area. From: Feldman, R., Braun, K., & Champagne, F. A. (2019). The neural mechanisms and consequences of paternal caregiving. *Nature Reviews Neuroscience*, *20*(4), 205–224. https://doi.org/10.1038/s41583-019-0124-6

also observed in fathers that have these hormone levels.

Entering fatherhood is associated with a decline in testosterone, increase in oxytocin and an increase in vasopressin (Grey et al., 2007; Grodon et al., 2010; Gettler et al., 2011; Weisman et al., 2014; Abraham et al., 2018). According to the steroid-peptide theory, these hormone levels could explain the nurturant behavior that is observed in fathers (Table 1; Van Anders et al., 2011).

Neuronal changes in fathers

The global human caregiving network

A new term was introduced in 2019 by Feldman et al. A network of subcortical and cortical regions that underpin human parental behavior was called the global human caregiving network (Feldman et al., 2019). This network plays a major role in simulating internal feelings of others (empathy), understanding thoughts and beliefs of others (metalizing) and the motivation to approach and nurture children (Rilling et al., 2017; Diaz-Rojas et al., 2021).

It is known that up to four months postpartum, brain structures change in both mothers and fathers (Storey et al., 2020). Some regions in both mothers and fathers undergo volume increases, whereas other regions decrease in volume only in the brain of the father (Storey et al., 2020).

The global human caregiving network consists of different cortical and subcortical regions. One of these cortical regions is the insular-cingulate empathy network. This network includes the anterior insula (AI) and the anterior cingulate cortex (ACC) (Figure 5; Rilling et al., 2017). These brain regions show a reduction in volume in new fathers (Kim et al., 2014; Storey et al., 2020). The insular-cingulate network has been connected to processing uncertainty and ambiguous information (Kim et al., 2014). Therefore, the reduction of volume in these brain regions is believed to reduce stress because of experience and interaction between father and child (Kim et al., 2014).

Besides the empathy network, the mirror simulation cortical network also plays an important role in simulating actions and facial expressions of others (Rilling et al., 2017). This network consists of the inferior parietal lobe (IPL) and the inferior frontal gyrus (IFG) (Figure 5; Rilling et al., 2017). The ability to identify the meaning of facial expressions of an infant is very important for fathers to be able to give the appropriate care (Rilling et al., 2017).

Another cortical region that plays a role in parental caregiving, is the temporoparietal mentalizing network. Mentalizing is the ability to understand thoughts and beliefs of others (Rilling et al., 2017). Several brain regions are involved in this network; temporo-parietal junction (TPJ), medial prefrontal cortex (MPC) and the superior temporal sulcus (STS) (Figure 5; Feldman et al., 2019). These regions show an increase in grey matter when a man transitions to fatherhood (Storey et al., 2020). This is associated with understanding an infant's intention through non-verbal signaling (Allison et al., 2000; Feldman et al., 2019).

The empathy, mirror and mentalizing cortical networks seem to be very important in paternal care. All networks undergo significant changes in the paternal brain and are involved in identifying the feelings and needs of an infant, needed to provide the best care (Feldman et al., 2019).

Besides the cortical networks, the global human caregiving network also consists of subcortical regions (Figure 5; Feldman et al., 2019). These subcortical regions are connected to the 3 cortical networks (Figure 5; Storey et al., 2020). Subcortical regions involved in paternal care are the hypothalamus, amygdala, and the dopamine reward circuit (Figure 5; Feldman et al., 2019).

Changes in activation of the global human paternal caregiving network

Activation of brain regions in response to infant cues, was assessed in the brains of fathers compared to non-fathers. Interestingly it was found that all regions of the global human caregiving network showed increased activity in fathers (Feldman et al., 2019). When comparing the neuronal response of fathers to their own infant and another infant that was not theirs, fathers showed greater neural activation as a response to stimuli from their own infant (Feldman et al., 2019).

Another study compared the activation of the global caregiving network in mothers and fathers. They found in mothers that the activation of the amygdala increased after childbirth, whereas in father's cortical activity went up, specifically in the superior temporal sulcus (STS) (Abraham et al., 2014). From this finding, cortical areas seem to be more important in paternal behavior compared to maternal behavior. Fathers that took part in childcare, showed greater connection of the STS and amygdala (Abraham et al., 2014). Suggesting that childcare experiences strengthen a father's connection between the cortical and subcortical regions of the global human caregiving network.

All previous studies focused on the neuronal changes in activation of the male brain after childbirth. A new study, by Diaz-Rojas in 2021, focused on brain region activation in response to infant stimuli during early pregnancy in expectant fathers. The neuronal activation in expectant fathers and non-fathers was measured in response to infant interaction videos. Both groups showed similar activation of the global human caregiving network (Diaz-Rojas et al., 2021). This would suggest that the paternal brain would develop during late pregnancy or after childbirth.
However, the degree in which certain brain regions were activated, different between the expectant and non-fathers (Diaz-Rojas et al., 2021). Expectant fathers showed a higher

activation of the left anterior insula. This brain region is involved in the cortical empathy network and could mediate parental behavior (Figure 5; Rilling et al., 2017).
In the left inferior frontal gyrus, increased neuronal activation was also observed (Diaz-Rojas et al., 2021). These findings show that the paternal brain is developing during early pregnancy. It is not known how these developments continue over the entire pregnancy.

Hormones, brain, and paternal behavior

The degree of activation in the global human paternal caregiving network is associated with paternal behavior and hormone levels (Feldman et al., 2019). Hormones that are known to be involved in the brain-hormone-behavior connection are oxytocin, vasopressin, and testosterone (Feldman et al., 2019).

Oxytocin administration led to a higher STS activation in fathers (Abraham et al., 2014). STS is known to play a role in the mentalizing network (Figure 5; Feldman et al., 2019). High oxytocin levels were previously associated with increased paternal care (Gordan et al., 2010). Paternal behavior could in this way be the result of increased STS activation through increased oxytocin levels (Abraham et al., 2014)

Another study showed that fathers that expressed more vasopressin receptors in the prefrontal cortex, showed greater bonding with their child (Nishitani et al., 2017). Interestingly, this was only found in fathers and not in mother. Mothers showed more oxytocin receptors in the prefrontal cortex (Nishitani et al., 2017).

Infant stimuli increase testosterone for a short period of time as well as neuronal activation of the caregiving network, resulting in paternal behavior (Storey et al., 2000; Kuo et al., 2012; Feldman et al., 2019). Fathers with higher testosterone levels showed stronger neuronal responses to infant cry (Khoddam et al., 2020). How this brain-testosterone-behavior connection works is still unknown.

The relation of other hormones, discussed in this essay, to the brain, is still unknown.

Discussion

Hormones

Early research on testosterone in man after birth, showed a significant decline in testosterone levels after birth (Berg et al., 2001). However, this research was done on American males only. Making it less reliable. Later, a longitudinal study was conducted in the Philippines (Gettler et al., 2011). This study observed the same testosterone decline in males after birth. Making the conclusion, that testosterone levels drop in fathers after birth, plausible.

Drops in testosterone levels are associated with increased paternal care for a long time (Figure 1). This theory seems to hold in human fathers. The mechanism of this testosterone lowering is not yet understood.

A theory could be that after birth, sexual intimacy between parents is probably lower. Sexual intimacy is related to high testosterone levels in men (Table 1). Since fathers do not experience this sexual intimacy after childbirth, testosterone levels could decline.

Another explanation could be that cortisol suppresses testosterone (Kuo et al., 2018). In the period leading up to childbirth, cortisol levels increase (Storey et al., 2000; Berg et al., 2001; Kuo et al., 2018). This increase could result in the suppression of testosterone and thus explain the testosterone drop after birth. Only, after the testosterone drop, testosterone levels remain lower than before entering fatherhood (Figure 3). These lower testosterone levels cannot be explained by cortisol levels yet. Further research is needed to determine how these hormones affect each other.

Oxytocin increases in fathers seem to benefit pair-bonding (Figure 4). When oxytocin was artificially administered, fathers had better quality interactions with their child (Weisman et al., 2014). Besides its role in pair-bonding, oxytocin also alters hormone levels of vasopressin and cortisol (Weisman et al., 2014). Vasopressin is also known for its role in pair-bonding (Grande et al, 2020), therefore the effect on paternal behavior of only oxytocin, is hard to investigate.

Prolactin also has its role in paternal behavior. High levels of prolactin in both mothers and fathers were associated with better responsiveness to infant cry (Fleming et al., 2002). Its exact influence on paternal behavior is possibly overlapping with oxytocin and vasopressin (Van Anders et al., 2011).

It is important to understand the effect that hormones have on each other, before concluding that one hormone causes paternal behavior. The steroid-peptide theory explains observed behavior using multiple hormone levels (Van Anders et al., 2011). Nurturant behavior is seen as paternal behavior towards infants. Fathers show this behavior when their testosterone is low, oxytocin is high, and vasopressin is also high (Table 1). These hormone levels overlap with the findings in this essay on hormone levels in fathers. Other hormones mentioned in this essay could possibly have similar effects on behavior as oxytocin and vasopressin.

Vasopressin seems to play an important role in paternal behavior compared to maternal behavior. Testosterone levels shortly increase in fathers that hear their infant cry (Fleming et al., 2002). These increase in testosterone combined with high vasopressin levels, is associated with protective aggression (Table 1). This combination of hormones in response to infant cry is not seen in mothers and may be exclusive for paternal behavior.

Neuronal changes

Structural changes in the brain occur up to 4 moths postpartum in both mothers and fathers (Storey et al., 2020). Some brain regions in the global human paternal caregiving network (Figure 5) increase in volume, where others undergo a decrease (Storey et al., 2020). In response to infant stimuli, all regions of the global human caregiving network are activated (Feldman et al., 2019). Cortical activation in fathers went up significantly compared to that of mothers (Abraham et al., 2014). Specifically, in the superior temporal sulcus (STS). Father-child interactions strengthened the connection of the STS and the amygdala in the male brain (Abraham et al., 2014). Indicating that structural brain changes occur because of father-child interactions.
However, new research showed that structural changes in the male brain, are also happening before birth and do not depend on father- child interactions (Diaz-Rojas et al., 2021). Triggers for these early changes are unknown, but it is possible that close contact with the mother could already change some brain regions.

Future directions

20 years ago, research on paternal behavior in humans started. A basis has been made in the understanding of human paternal behavior. However, the research that has been conducted always has compared caregiving fathers to non-fathers. Some fathers know they have children, but do not participate in childcare. It could be interesting to see if neuronal and hormonal changes occur in these fathers. Or that they are limited to caregiving fathers that experience father-child interactions. To further investigate the effect of father-child interactions on physiological changes and paternal behavior, parents of adopted children could also be and interesting group to investigate.

Human research comes with lots of limitations like ethical considerations, making it hard to study paternal behavior in humans. Therefore, animal studies could be very useful. Preferably animals that display similar social behavior as humans.

Research in titi monkeys showed that a lesion in the prefrontal cortex of the father's brain made the father spend more time with its mate and offspring (Fernandez-Duque et al., 2009). They were also more tolerant of others group members. The offspring, of the fathers with lesions, were more likely to engage in a friendly way with their siblings and later in life with their own offspring. Indicating that paternal behavior towards infants is very important for the development of behavior in infants later in life. This is an example of how animal research can contribute to the understanding of human paternal behavior.

Future research should also try to determine causation of paternal behavior. Do physiological changes result in paternal behavior or does paternal behavior lead to physiological changes? This causation is not clear and animal models could help in the understanding of the relation between physiological change and behavior.

Conclusion

After childbirth, paternal behavior is observed in human fathers. This change in behavior is accompanied by changed hormone levels and structural changes in the brain. Hormones that are believed to be involved in paternal behaviors are: testosterone, cortisol, prolactin, oxytocin, and vasopressin. Structural changes in the brain are seen in the global human caregiving network. Future research is needed to understand human paternal behavior.

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