Türk Psikiyatri Dergisi 2010;
Turkish Journal of Psychiatry

Neurobiology of Motherhood

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Abstract

Motherhood is a physiological status in which certain behavioural patterns are exhibited. Maintenance of the life of the species in mammals is dependent upon the presentation of motherhood services in a certain period that the child is dependent on the mother. Absence of the mother causes some deficiencies in social, behavioural and cognitive abilities, an abnormal development of the stress response system, learning and memory disorders, and later, inadequate motherhood skills of the mature offspring during their own maternity period. Because maternal care is extremely important for the survival of the child and thus, for the species to maintain, nature seems to have provided the development of a healthy mother-child relationship. Therefore, motherhood is programmed by the evolutionary process in the female brain before birth. It is certain that the brain of the mother is very different from the brains of the nulliparous women who are within the same age range, and is very sensitive to her own child's needs. For maternal behaviour to develop in human beings and animals, special neural networks, which are cooperatively developed by genetic, environmental and hormonal factors, are necessary. It also seems likely that non-genetic (epigenetic) transmission responsible for the internalization of maternal behaviours learned from the mother and hormonal exposure of the brain both during the foetal period, throughout the growth, and during the gestation of the woman as well as genetic factors, play an important role in the development of these maternal neural networks and systems. In this paper, which was prepared by obtaining the necessary publications by means of a search for the words related to motherhood in the PubMed search engine, the physical and mental changes that prepare females for motherhood and enable them to tolerate it will be reviewed.

Key Words: motherhood, evolutional psychology, neuroendocrinology

Motherhood is a physiological status in which certain behavioural patterns are exhibited. Maintenance of the life of the species in mammals is dependent upon the presentation of precise maternal care in that period when the child is dependent on the mother (Swain et al. 2007). A new mother displays behavioural changes immediately after parturition. These behaviours serve the immediate provision of care and defence for the offspring, and are called "the maternal behaviour" (Brunton and Russell 2008).

In human beings and animals, the development of maternal behaviour requires particular neural networks evolved under the influence of genetic (such as oxytocin, prolactin, and oestrogen alpha receptor genes), environmental (parental behaviour modelled during infanthood and childhood, facing the babies before and after the birth, stimulation by the baby), and hormonal [oestrogen and progesterone before the birth, and oxytocin, prolactin and corticotropin-releasing-hormone (CRH) during and after the birth] factors (Leckman and Herman 2002). The process of the development of these particular neural networks originates in neuronal plasticity. Starting after birth and accelerating during the productive years (cycles occurring at adolescence, pregnancy, the postpartum period, and finally, during the mother-child relationship), the development and stabilization of maternal behaviour in the female's brain is a product of progressive particular neural plasticity (Kinsley and Lambert 2008).

Received: 18.03.2009 - **Accepted:** 29.05.2009

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In animals, typical maternal behaviours are induced by parturition and generally not observed outside this period (de Bono 2003). The reward system of the mother's brain is activated to enable this motherhood service to take place (Curley and Keverne 2005). In this article, we aimed to review the neurobiological grounds for maternal behaviour, which is not well understood at present, in the light of the latest advances in neural sciences. When presenting the biological bases of maternal behaviour, we are going to frequently refer to animal studies in order to point to the evolutionary origins of this behaviour. Necessary publications were obtained for the preparation of this review article from the PubMed search engine using the words "motherhood, maternal behaviour, fatherhood, neurobiology, brain, evolution, neuro-imaging, and attachment" between the years 1980 and 2008.

Maternal behaviour in mammals

In many mammal species, care for the newborn is provided by females. Because of the mother's a good deal of preparations before the birth and ability to produce milk, the responsibility for the maternal care has been given by nature to females.

Since the current human brain has developed as a result of the evolutionary processes of millions of years, it is now essentially under the influence of the general experiences that the human species has acquired over a long period rather than individual decisions or styles, especially when vital functions are in question. For this reason, our emotions and instinctive behaviours are more influential than our intelligence on vital processes, although our individual ability to make decisions has become very advanced. , Maternal care is also one such ability (von Ditfurth 2007).

In mammals, the mother-child relationship is the essential source of social stimulation; therefore, maternal care is one of the main resources for socialization. Human beings might have so highly developed skills such as "mind-reading" (theory of mind or ToM), understanding emotions and empathy because of the mother's obligation to know the needs of her baby. .

Human babyhood lasts for a long period. The reason for this is that the human brain is the biggest among those of all primates and that the completion of the development of this brain lasts for years. In animals, individuals belonging to predatory species are less developed at birth and need a longer period of maternal care. The offspring of prey species however, are born more mature and can move quickly to evade predators. Thus, the maternal care lasts longer in predatory species (Debiec 2007).

In humans, the long period of childhood is associated with certain obligations and consequences:

– Long-term maternal care
– Long-term education near the mother and therefore, a longer time to transfer the culture
– The father has to provide the required food through hunting because the mother is unable to leave the home for several years. Thus, male-female collaboration developed and the human being first stood upright because of the necessity for the male to carry the food home in his hands after hunting, which additionally stimulated the evolution of the cerebral cortex (Roberts 2004).

Importance of the mother for the child

For normal physical and mental maturation, the child needs maternal care and to be touched. Especially in mammals, maternal care, including touching and licking, is important during a particular phase (e.g., the first week after birth in rodents). Absence of the mother causes some deficiencies in social, behavioural and cognitive functions, abnormal development of the stress response system, learning and memory disorders in children of both gender and finally, inadequate motherhood skills in the female offspring (De Bellis 2005, Leckman and Herman 2002, Kaffman and Meaney 2007).

Some impairment during the development of the brain in neglected children was reported because of the ratios of certain substances increasing due to stress. These are disorders such as delayed myelinization, inappropriate pruning, suppression of neurogenesis and decline in brain growth factors (De Bellis 2005). It has been reported that, in mammalian animals separated from the mother during babyhood, a permanent down-regulation develops in the glucocorticoid receptors in the hippocampus and prefrontal cortex, which mediate the inhibitory feedback on the hypothalamo-pituitary-adrenal (HPA) axis, and that these individuals show exaggerated HPA axis reactivity to stress (Kaffman and Meaney 2007). The converse is also true; researchers found that monkeys and rats whose mothers had displayed abundant caring behaviours such as touching, patting, licking and hugging in their childhood were also more compassionate to their children and less anxious mothers when they matured themselves (Caldji et al. 1998). It has been observed, again in animal studies, that even when the pups of careless mothers are separated from their biological mothers and placed with a surrogate mother who frequently licks her offspring, the pups become good mothers later themselves (Francis et al. 1999).

Changing gene expression in a manner of suppressing or activating the transcription by way of DNA methylation or histone modification depending on the stimulation arising from the environment, is called " epigenetic regulation" (Feng et al. 2007). Long-term neuroplastic changes in the synaptic connections, which develop especially in dependence on learning, are formed by this kind of epigenetic regulation on the gene expressions, but not by changes in the genes themselves. The permanence of these epigenetic regulations varies depending on the function itself, the importance for survival and on whether environmental stimulation continues in a stable way, and thus some of them endure throughout a lifetime. The changes in the gene expression also can alter depending on the learning processes and the changes in environmental stimulation. Experiences, particularly those occurring in childhood, cause long-term changes in expressions in the genes which operate brain functions. When these changes persist into adulthood, they are called "epigenetic transfer". Therefore, the transfer type of the maternal behaviour mentioned above, from mother to daughter over generations, is different from the heritability of genes and this heritability type is an example of epigenetic transfer (Kaffman and Meaney 2007, Champagne 2008). Confirming this heritability in humans, it has been found that 70% of parents abusing their children had experienced abusive parenting in their own childhood (Chapman and Scott 2001). Epigenetic transfer in humans is supported also by findings of increased frequencies of antisocial personality disorder, depression, anxiety disorder and substance dependence in individuals exposed to inadequate maternal care in childhood, and of increased self-esteem among persons who received a high quality of maternal care (Champagne 2008).

Is there any advantage of motherhood to the mother?

In a study from Poland, it was reported that each child born shortened the mother's lifespan by 95 weeks on average (Jasienska et al. 2006). In contrast, it was further found that children did not shorten the father's lifespan and that each daughter increased the father's longevity by 74 weeks on average although sons had no impact on the lifespan of fathers. The authors suggested that this difference originated from being open to diseases and maternal energy loss as a result of reproduction, pregnancy and hard work after the birth. On the other hand, the fathers are possibly better nourished and helped by their daughters at no cost.

The development of a good mother-child relationship

Nature seems to guarantee the development of a good mother-child relationship, since the maternal care is extremely important for the survival of the offspring and therefore for the perpetuation of the species. To achieve this mission, nature makes arrangements for the female to prepare for, and more easily tolerate motherhood, and provides necessary devices for her, such as the following:

1. Preparing the female for motherhood from childhood on
2. Preparing the female for motherhood during pregnancy
3. Secretion of hormones which trigger motherhood with birth
4. Rewarding effects of motherhood so that the mother can carry out maternal care "with love"
5. Enhancement of the mother's memory
6. Increased aggression of the mother toward strangers
7. The mother perceiving her baby as more adorable
8. Responding quickly to her offspring's cries
9. The child's attachment to the mother
10. The mother's ability to understand the child's emotions
11. The necessity of the mother's thoughts focusing on her child and of the mother's being meticulous about protecting and caring for her child

Preparing the female for motherhood from childhood on

Nature handles the process of preparing females for motherhood from infancy on meticulously, since maternal care is extremely important for the perpetuation of the species. In humans and other primates, females beginning in their infancy display more interest in the newborn and touch them more than males do (Herman et al. 2003). It is suggested that this sexual dimorphism becomes prominent in adolescence and may be related to the brain's exposure to the gonadal hormones during the perinatal period. Oestrogen is thought to play an important role at this stage. Indeed, it is noted that rhesus macaques, bilaterally ovariectomized at 1 year of age, displayed normal interest in their infants and that this interest did not change with oestradiol replacement and that this continuity might be related to the perinatal exposure to oestrogen (Maestripieri and Zehr 1998).

Women are more successful in establishing social relationships from childhood on. In humans, the ability to establish social relationships is inversely related to levels of foetal testosterone both in females and males (Knickmeyer et al. 2005). Hence, it is suggested that different reproductive strategies underlie the different social behaviours displayed by females and males. Women need to establish good social relationships with their children and the other females around them (particularly with their female relatives), because rearing children in a high quality environment is more essential than the quantity of the children for women (Keverne and Curley 2004). This evolutionary requirement may account for women being more social. Especially in primates, females other than the mother can display maternal behaviour and this enables the other females to rear the offspring (Curley and Keverne 2005). Since the hormones making this possible also facilitate social recognition and relations, primates are social animals.

Preparing the female for motherhood during pregnancy

The process of preparing the female for motherhood during pregnancy is generally carried out by those hormones which increase in level during pregnancy. Here, especially oestrogen and progesterone play important roles. If oxytocin secretion is induced by vaginocervical stimulation after priming with oestradiol and progesterone, maternal behaviour starts automatically in nulliparous sheep (Keverne et al. 1983). It was noted that there was a direct correlation between the levels of oestradiol during pregnancy and a mother's attachment to her child after birth in humans (Fleming et al. 1997).

It has been suggested that high levels of progesterone and oestrogen during pregnancy increase oxytocin and prolactin receptors in the brain regions involved in maternal behaviour and, in this way, initiate motherhood. Levels of oestrogen and progesterone decrease immediately after birth; however, this does not have a negative influence on motherhood once maternal behaviour is triggered (de Bono 2003).

Another change during pregnancy is the mother's diminished sensitivity to the bad smells of the baby. It has been suggested that the mother perceives these bad smells in a neutral and sometimes even rewarding way, because of the possible hormonal influences on the amygdala during pregnancy, since the amygdala regulates responses to bad smells (Numan and Sheehan 1997, Numan et al. 1993).

Initiation of maternal behaviour after birth

The brain structures primarily related to maternity are known as the medial prefrontal cortex; medial orbitofrontal cortex; anterior cingulate; thalamocingulate pathway; medial preoptic area (MPOA), ventral medial nucleus (VMN) and paraventricular nucleus (PVN) of the hypothalamus; ventral tegmental area (VTA) and its associations with dopaminergic reward systems; the bed nucleus of the stria terminalis (BNST); and locus ceruleus (LS) (Bartels and Zeki 2004, Brunton and Russell 2008).

Oestrogen, prolactin and oxytocin stimulate maternal behaviour after birth via their receptors located in the MPOA. Lesions in the vicinity of the MPOA completely abolish all aspects of maternal behaviour in mammals (Swain et al. 2007). The MPOA is an area in which a broad range of ritualistic parenting behaviours such as breast-feeding and nest building are regulated. The oxytocin is necessary for the initiation of motherhood immediately after parturition, but it is not so important for the continuation of motherhood (Leckman et al. 2004). It has been suggested that oestrogen, prolactin and norepinephrine trigger maternal behaviour through increasing the "cyclic AMP (adenosine monophosphate) response element-binding protein" (CREB), which is an intracellular transcription factor in the MPOA and VTA (Jin et al. 2005).

Vaginocervical stimulation in the course of parturition induces oxytocin secretion and then the increased oxytocin simultaneously initiates several events related to parturition and motherhood. The oxytocin not only facilitates parturition but also contributes to milk production. Moreover, it initiates maternal behaviour by stimulating its receptors in the MPOA, BNST, amygdala and olfactory bulb; makes the mother recognize her baby's smell; and suppresses sexual desire via its receptors in the basal hypothalamus (de Bono 2003, Bales et al. 2004, Curley and Keverne 2005). It has been shown that the oxytocin secreted during breast-feeding also reduces anxiety and levels of stress in the mother (Legros et al. 1988). Furthermore, it is proposed that oxytocin positively contributes to the mother's ability to understand the signals from the baby and to recognize her baby (Swain et al. 2007). In crowded groups of animals, oxytocin plays a role in the mother recognizing her own newborn (Neumann 2008).

It has been noted that oxytocin is needed to initiate maternal behaviour after the first parturition, but maternal behaviour continues regardless of oxytocin stimulation throughout the following births. The inhibition of oxytocin does not prevent maternal behaviour if it is not the mother's first parturition (Debiec 2007). Briefly, the rule that "once you are a mother, it lasts a lifetime" seems to work for this subject.

In animals, nulliparous females generally do not get too close to newborns and do not display maternal behaviour. However, these females start to display maternal behaviour if they live together with newborns for a while (sensitivity). On the other hand, the new mothers can comfortably rear even newborns other than her own (Leckman and Herman 2002). Former mothers can quickly start to display maternal behaviour when they meet a newborn. In summary, it has been concluded that maternal behaviour becomes permanent after first parturition (Pawluski and Galea 2006).

Prolactin also plays an important role in the initiation of maternal behaviour with the birth of a child. In mammals, a prolactin increase is observed in both mothers and fathers after childbirth (Dixson and George 1982). Prolactin reinforces maternal behaviour by stimulating its receptors in the MPOA (Stack et al. 2002). When female animals meet newborns, prolactin secretion increases. Mice carrying null mutation of the prolactin receptor gene cannot show maternal behaviour to pups (Lucas et al. 1998). As the female's reproductive experience increases, the sensitivity of the prolactin receptors in the central nervous system increases, and hence when maternally experienced females meet babies, they can start to display maternal behaviour far sooner than nulliparous ones do (Anderson et al. 2006).

Attachments of mother and child to each other

In social animals and humans, the first example and basis of social bonding is the construction of the mother-child bond. In animals, the construction of the mother-child bond requires the occurrence of an "attachment" in both the mother and offspring to each other. In birds and mammals, this attachment develops easily, beginning at birth. In contrast to fish and reptiles, which do not care about their offspring's fate after spawning, mammals make a huge investment of time and effort in the quality rather than the quantity of their offspring. Mammals feed, defend and keep their offspring warm for a certain period. As the animal becomes wiser, this period gets longer and takes years in monkeys, and thus it is the longest in humans. The reward and stress response systems are involved in the mother's attachment and love for her baby. It is known that women, especially mothers, are more sensitive to baby faces than men are. When baby faces are shown to subjects in electrophysiological studies, the P1 component of evoked response potentials (ERP) is observed far sooner and wider in women than in men; that is to say, women seem to be more sensitive to baby faces (Proverbio et al. 2006).

Both romantic love and a mother's love for her baby activate the same structures of the reward system in the brain (the brain's reward structures, such as the VTA, caudate nucleus and nucleus accumbens) (Bartels and Zeki 2000, Aron et al. 2005). As such, attachment to the child has a rewarding effect and therefore, contributes to the perpetuation of the species (Bartels and Zeki 2004).

In addition, there are deactivations in some brain structures (such as the medial prefrontal, inferior parietal and posterior cingulate cortices, and amygdala) related to negative emotions, social judgement and criticizing thoughts during the period of a mother's love. In other words, the mother's love reduces the likelihood of criticizing assessments towards the child (Bartels and Zeki 2004). It was found that 73% and 66% of mothers and fathers, respectively, thought that their baby was "excellent" during the first 3 months following the birth (Leckman et al. 2004). This favourable view is necessary for the development of a positive relationship between mother and child.

In a functional magnetic resonance imaging (fMRI) study conducted on humans, it was reported that when the mothers were shown a smiling photograph of their offspring, which they had not seen before, they reported more loving emotions in comparison with a photograph of a baby other than her own. Moreover, they showed a more evident activity increase bilaterally in both orbitofrontal cortex (positively related to affirmative emotions) and bilateral visual cortex (Nitschke et al. 2004). In another study, when the mothers were shown videos of their babies recorded while playing, it was observed that there was an activity increase in the orbitofrontal cortex, periaqueductal gray substance, anterior insula and putamen in comparison with seeing videos of other children (Noriuchi et al. 2008). In summary, seeing their children happy generates a rewarding influence in mothers and seems to stimulate the reward structures of the brain. Moreover, it can also be concluded from these studies that the orbitofrontal cortex is the core region in the case of affirmative emotions related to the mother's attachment to her child.

It has also been reported that oxytocin and vasopressin are important hormones for a mother's attachment to and rearing of her child. Oxytocin and vasopressin are hormones that play an important role in maternal behaviour and a mother's attachment to her child (Leckman and Herman 2002). An increased rate of oxytocin receptor binding in the MPOA (Francis et al. 2002) and the expression of oestrogen alpha receptors on these oxytocinergic neurons (Champagne et al. 2003) were found in animals frequently licking their pups and in their female pups. Therefore, the MPOA oxytocin neurons appear to play a role in the mother's attachment to her child as well as in the transfer of motherhood styles from generation to generation (from mother to daughter).

Finally, the stress system also has a role in the mother's attachment to and rearing of her child. The HPA axis is the core element of the stress system, and its function and response severity to stress are decreased during pregnancy. This decline is explained by the fact that oestrogen produces desensitization in the pituitary CRH receptors and thus causes the decreased secretion of adrenocorticotropic hormone (ACTH) (Brunton and Russell 2008). The mother's stress system further undergoes an adaptive functional increase with the approximation of birth. In humans, it was found that mothers with high levels of cortisol immediately after giving birth, were more sensitive to their children's smell and exhibited more affection for their children (Fleming et al. 1997). Nevertheless, the administration of corticosteroids and exposure to stress reduces maternal behaviour in virgin female animals (Rees et al. 2006).

If the mother's environmental conditions are unfavourable, especially during gestation (for some reasons such as poverty, having many children, or having a bad spouse), her care and affection for the child decline, and this leads the child's future behaviour to change in a permanent manner (Champagne and Meaney 2006). In mice, mothers under stress during pregnancy display decreased licking and grooming of their pups. Consequently the oxytocin receptors in the child's MPOA decline, and thereby the child is prevented from being a good spouse or mother. Here, the mediator of transferring maternal stress to the child's behaviour is also the biological structure of "maternal behaviour" (especially the oxytocin system) (Champagne and Meaney 2006). It has also been proposed that this epigenetic transfer may have an evolutionary adaptive value. That is to say, offspring receiving less maternal care in their childhood will be more fearful, nervous and anxious in their adulthood. Hence, the mother's unfavourable environmental conditions make the child, as an individual, less gregarious and more inclined to avoid risks, and these features may contribute towards the child living longer in these dangerous settings (Champagne and Meaney 2006).

Because guaranteeing maternal care to the child is so important, the child's recognition of and bonding to the mother is also necessary. Evolutionary development appears to have solved this issue, too. In birds and mammals, the strong attachment of the offspring to the mother is a typical behaviour. The indicator of attachment is the distress which is revealed when the mother leaves.

The olfactor bulb, LS and amygdala participate in the attachment of the newborn to the mother, and the learning systems of newborns work substantially differently than those of adults (Moriceau and Sullivan 2005). In mammals, because the newborn has a hyperactive LS, learning to recognise the mother and her smell is commenced quickly. However, since the newborn's amygdala is hypoactive, the offspring does not feel fear or try to escape in spite of the mother's poor or rough treatment on occasion (the conditioned fear response has not yet come into existence), in any case the newborn attaches to the mother (Moriceau and Sullivan 2005). It has been proved that human babies become strongly attached to their caregivers, even if the caregiver is abusive. In conclusion, the newborn brain develops to provide an attachment to the nearest caregiver, in social animals, whether the caregiver behaves in a good or bad manner.

This automatic attachment occurs generally within a certain period, in mammals, the first days after birth. After this period, the animal learns to avoid individuals that treat it badly. The attachment constructed within this period is so important that an increased sexual performance was shown in adulthood when the individual had been exposed to the smells of the first days of babyhood (Moriceau and Sullivan 2005).

Enhancement of the mother's memory

The motherhood service also requires a strong memory. A strong memory is fundamental to the mother's functions such as recognizing the infant, especially in animals living in crowded groups, keeping the information related to the infant in memory, finding the place of the nest and keeping the places of resources in memory to provide food for the infant. It has been shown that 80% and 45% of mothers and fathers, respectively, could distinguish the sounds made by their own children on the 30th day after birth (Green and Gustafson 1983).

It has been reported that the spatial learning and memory of females get stronger during pregnancy and motherhood. These abilities are better in multiparous females than those of nulliparous ones (Kinsley and Lambert 2008). Moreover, it was reported that the mothers had higher levels of brain derived neurotrophic factor (BDNF) in the brain's hippocampal CA1 regions and septum in comparison to nulliparous animals (Macbeth et al. 2008). The long-term potentiation (LTP), regarded as the cellular equivalent of memory, has been found to have increased in the Schaffer collaterals, located in the mothers' hippocampus. Furthermore, there is an increase in the number of synapses of hippocampal CA1 pyramidal neurons in multiparous females compared to those of the nulliparous. It has been proposed that all these changes resemble the changes seen with "the enriched environment" in the brain during animal experiments (Kinsley and Lambert 2008).

These memory changes are, in general, connected to the effects of oxytocin (Pawluski and Galea 2006) or to proliferation of the hippocampal dendritic spines due to the effects of increased oestrogen and progesterone during pregnancy (Woolley and McEwen 1993). Moreover, meeting the newborn after giving birth also produces an enhancing effect on memory (Kinsley and Lambert 2008).

Motherhood aggression

In mammals, mothers become markedly aggressive, particularly while their offspring are in jeopardy, but this is not marked in humans. In animals, aggression is seen in behaviour such as attacking an animal coming too close to the nest. This behaviour also seems to be a gift from the evolutionary process to mothers for keeping their children safe. This aggressive tendency starts as pregnancy nears completion in expecting mothers and continues in a stable manner as long as the mother-child relationship goes on after birth. Motherhood aggression is associated with decreased anxiety and to fearlessness.

The brain areas involved in motherhood aggression have been identified as the olfactor areas, MPOA, BNST, the lateral septum, PVN, amygdala and lateral hypothalamus (Brunton and Russell 2008). Motherhood aggression is positively related to oxytocin levels, and is dependent on the effects of oxytocin on the central nucleus of the amygdala and on the PVN of the hypothalamus. Therefore, the oxytocin secretion triggered by parturition seems both to decrease anxiety due to its anxiolytic effects, and to raise aggression toward strangers in mothers (Brunton and Russell 2008).

Moreover, the finding that the female animals administered diethylstilbestrol during their babyhood display raised aggression in their motherhood period indicates the importance of oestrogen in this matter (Engell et al. 2006).

The mother's perception of her baby as adorable

The faces of the babies are charming in all animals. Furthermore, babyish faces on adults are perceived as beautiful (Eşel 2007). The human baby has another feature that can attract a mother's attention: smiling. Social smiling appears in the human baby from the 2nd month after birth on. Biology makes the mothers love their own children. However, several evolutionary biologists suggest that mothers do not love their children because of their cuteness, but rather, the evolutionary process has designed the human brain in such a way that it perceives baby faces as adorable, since the mother's love is very important for the child's survival (Dennett 2006).

The mother's sensitivity to her baby's cry

Newborns cry while their mothers are away in rodents, monkeys and humans, and the mothers respond to the cry fast, searching for and getting close to the newborn (Maestripieri 1995). Typical mammalian social behaviour such as the separation scream of newborns are related to the pathways such as the amygdala-septal-hippocampal complex and connections of this complex with the hypothalamus, and cingulate cortex and connections of this with the thalamus (Insel and Winslow 1998). It has been reported that the serotonergic pathways are also important for pup screams in rats while the mother is away. It was shown that the 5HT1a agonists and 5HT2 antagonists reduced the separation scream, while 5HT1b agonists increased it (Insel and Winslow 1998).

An important part of motherhood is to recognize a mother's own child's voice, and if possible, to determine the meaning of this voice. In human studies, it was reported that a neural activation in the limbic forebrain structures was observed in the mothers of small children while they listened to a baby cry (Lorberbaum et al. 1999). In an fMRI study, decreased activity in the anterior cingulate cortex was observed in women while listening to baby cry or laugh, but there was no change in men (Seifritz et al. 2003). Mothers show higher emotional and brain activity responses to baby cries than neutral sounds, and these responses to baby cries are higher in contrast to nulliparous females. It was shown that mothers maltreating their children also displayed more negative and less empathetic responses to their own children's cries than those of others (Milner et al. 1995).

It has been proposed that the thalamocingulate pathway is important for the mother's response to the offspring's scream (Lorberbaum et al. 2002). Indeed, when there are lesions in these structures, the mother's response to a baby cry is impaired (Murphy et al. 1981).

Adult males and females who are not parents show an increased activity in brain structures such as the amygdala, insula and VTA while only listening to a baby laugh, but parents show a higher activity response in these structures while listening to a baby cry. That is to say, parents have a selective attention to the sound of children crying. This is probably a result of the associative learning in the parents' amygdala (Seifritz et al. 2003).

Furthermore, when mothers watch videos in which their babies are crying, they show more increased brain activity compared to when the babies are playing. This may be related to the fact that mothers are more sensitive when they have to carry out some kind of prompt action for their children (Noriuchi et al. 2008).

Mothers' understanding of their offspring's emotions

Understanding the meaning of facial expressions is critical in social animals such as human beings. The expression of emotions is shown with subtle changes on the face. This ability is well developed in humans (Kontsevich and Tyler 2004).

Women are known to be more successful in understanding emotions than men (Baron-Cohen 2003, Schirmer et al. 2004, Eşel 2005). Empathy is a necessity for social relations and keeps a man from harming others. Women are particularly known to process children's faces at a much higher speed (Proverbio et al. 2006). Women show far quicker and wider ERP responses, especially to distressed baby faces, than men do (Proverbio et al. 2006). When the photographs of their own and other children were shown to mothers, activity increases in the brain areas related to emotional responses such as the amygdala and insula, and in the brain areas playing an important role in the theory of mind, such as the anterior paracingulate gyrus and superior temporal sulcus, were observed only when looking at the photographs of their own children, but not at those of others (Leibenluft et al. 2004). In fact, a higher activity is observed in these areas when people see familiar faces compared to unfamiliar ones. Thus, it may be proposed that mothers feel more intense emotions for children and read their minds better as the degree of kinship and familiarity grows.

The necessity for the mother being rigorous about her child

In the human motherhood period, mostly for several months after childbirth, the mother is in an intense state of mental preoccupation related to the child (anxiety related to the child's health, unnecessarily frequent observation of the child, thoughts as to whether she is a good mother, and obsessions and compulsions about the hygiene of food and drink, etc.). All these behaviours of the motherhood period partly resemble obsessive compulsive disorder (OCD) (Leckman and Herman 2002). As a matter of fact, the risk for the development of OCD increases during the pregnancy and postpartum period in mothers (Feygin et al. 2006). It has been found that there are intrusive thoughts, similar to those seen in OCD, in 95% and 80% of the mothers and fathers, respectively, during preceding weeks of the birth (Leckman et al. 1999). In the weeks after childbirth, it has been reported that mothers and fathers mentally focus on their child for 14 and 7 hours a day, respectively (Leckman et al. 1999). In essence, all these anxious and ritualistic behaviours are adaptive behaviour patterns developed over the evolutionary process in order to defend the offspring against jeopardy, and it is present in all mammals (Feygin et al. 2006).

Fatherhood

Paternal behaviour is observed in some groups of the mammals, especially in monogamous animals, and the male's benefit here is the increased reproduction and child survival rate. Fathers, in rats, attack the pups within hours after their birth. However, they start to display maternal-type behaviour (licking, retreating the pups home) after living together with the pups for a few days (Wynne-Edwards and Reburn 2000).

It is assumed that paternal behaviour is also controlled by the same brain pathways as maternal behaviour. Indeed, it is thought that these behaviours are originally present as software packages in the animal's brain and that these are, however, activated only after close contact with the child.

The neuroendocrine pathways of motherhood are also present and effective in fathers. Paternal behaviour seems to be related to prolactin rather than oxytocin and vasopressin (Wynne-Edwards and Reburn 2000). The levels of prolactin increase after childbirth and its increased levels trigger paternal behaviour in the father. Levels of prolactin remain elevated throughout the lifespan in experienced fathers and these fathers are ready to instantly display paternal behaviour (Wynne-Edwards and Reburn 2000). It was shown that fathers were more compassionate and protective of their child if they experienced a higher prolactin increase and testosterone decrease during the pregnancy of their spouses. Moreover, it has been proposed that fathers may display signs of pregnancy if they experienced a prolactin increase higher than expected (Wynne-Edwards and Reburn 2000).

In fathers, it has also been reported that there is an increase in the levels of oestrogen beginning from the first month of pregnancy and getting higher as the pregnancy progresses (Berg and Wynne-Edwards 2001). It is thought that the effects of oestrogen increase paternal behaviour. In contrast to the effects of oestrogen, the stimulation of progesterone receptors increases the father's aggression toward the child and decreases paternal behaviour (Schneider et al. 2003).

In addition, testosterone seems to be important in paternal behaviour. Testosterone generally inhibits paternal behaviour. In monkeys, the lower the levels of urinary testosterone, the higher the paternal care for newborns observed in new fathers is (Nunes et al. 2001). It has also been reported in humans that males having low levels of testosterone showed more reactivity to a child's cry (Fleming et al. 2002). The levels of testosterone generally decline with parturition in males (Wynne-Edwards 2001). This decline is possibly necessary to lessen the father's aggression toward the newborn, not to prompt the mother toward unnecessary sexual activity, and to develop paternal behaviour and social bonding with the newborn.

Fatherhood seems to be beneficial to the father in terms of cognitive functions. In marmoset monkeys, it has been reported that there is an increase in the intensity of dendritic spines of prefrontal cortex pyramidal neurons and consistently in the intensity of vasopressin V1a receptors in the brains of fathers, compared to those of other males (Kozorovitskiy et al. 2006).

CONCLUSION

Motherhood, consisting of very typical behavioural patterns, is a wholly natural process managed and executed by specialized brain neural systems. The maternal behaviour of human beings and the neural systems mediating this behaviour are products of the evolutionary development of millions of years. It is clear that the mother's brain is substantially different from the brains of nulliparous females of the same age and extremely sensitive, especially to her own newborn. Although maternal behaviour is mainly triggered and executed by genetic and hormonal factors, its expression may be changed by the mother's education dating from her childhood and by events experienced positively or negatively. In humans as well as in all mammals, survival of the newborn and thus, the perpetuation of the species, are guaranteed through the neurobiological systems which naturally and automatically initiate maternal behaviour.

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