

Chapter 10: Babies on His Brain

A baby can change a man's mind. Take Peter's mind as an example. After having two young girls, he finds himself perceptive of the cries and squirmings of little ones, whether in a grocery store, in an airplane, on a playground, or in a coffee shop. Babies surrounded him in all of these same places before he had kids. Yet somehow he did not perceive them. It wasn't until he had his own kids that babies entered his brain—and his social vision. He's probably not alone. In a study that measured changes in pupil area (an index of a person's social orientation) in response to looking at pictures of various things, babies elicited no changes in men's eyes, and mothers and babies together barely altered men's eyes, yet either type of image noticeably altered women's eyes. So what did modify men's attention? Men's pupils opened up at the sight of naked women (Eibl Eibesfeldt 1989: 255).

In this chapter, we focus on two issues concerning babies on the male brain. First, what are the psychological impacts of parenting on men? As men transition into fatherhood, they experience a variety of changes in their emotional life and quality of life, and we want to describe and understand these. Second, what are the physiological mechanisms underlying the psychological and behavioral transitions associated with fatherhood? In what is essentially a new science of human fatherhood, we can begin to tease apart the physiological substrates underlying these transitions to fatherhood. Grab a place in a functional imaging machine, listen to infant cries, and watch your brain respond to these infant stimuli. Or let researchers measure your hormone levels while you

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interact with a baby. These are some of the ways that we can begin revealing the proximate mechanisms underlying our responses to babies.

Emotional Impacts of Fatherhood

Impending fatherhood can elicit a variety of emotional responses. Often these are positive! Fatherhood serves as a social marker of full adult achievement in many societies: you are not a complete man unless you have fathered children. Among the Sambia of New Guinea, a “fully masculine” man has fathered children, and in many circum-Mediterranean societies an ultimate litmus test of manhood is impregnating one’s wife (Gilmore 1990). In these contexts, the recognition of a partner’s pregnancy and a man’s own fatherhood can be validating. If a child is desired, the recognition of impending fatherhood also tends to be positive. The arrival of a child is awaited eagerly and with excitement.

The expectation of a child’s arrival can also be an emotional mixed bag. Several qualitative studies of men’s prepartum lives illustrate the vagaries of prepartum life. Through interviews with U.K. men, sources of ambivalence during a partner’s pregnancy centered on how men would perform as fathers, on changes in lifestyles and on changes in marital relationships (Donovan 1995). In a different study entailing interviews with prospective U.K. fathers, additional sources of ambivalence emerged: “While the pregnancy generated positive feelings it also precipitated worries and concerns. These were mainly in response to the demands of the pregnancy, what it signified in terms of its potential effects on the health of the partner and unborn, its impact upon the conjugal

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relationship and other siblings, financial commitment, accommodation space, prospective parenthood, antenatal preparation and maternal care” (Brennan et al. 2007a: 27).

Several biomedical studies have tracked the emotional lives of men pre- and postpartum, and sometimes in contrast with control “non-father” men (reviewed in Bartlett 2004; Brennan et al. 2007b). What do these kinds of studies find concerning the emotional lives of would-be fathers? Clinton (1987) studied about 150 Wisconsin men, both expectant and non-expectant, across the course of a year. During the first trimester, expectant fathers reported greater irritability and more colds than non-expectant men. While no differences appeared in the second trimester, during the third trimester, expectant fathers reported more weight gain, restlessness, and insomnia. In a study of about 160 Australian men, participants contrasted their health symptoms during a partner’s pregnancy with those they experienced prior to their partner’s pregnancy. The main symptoms affected were sleep disturbances, lack of energy, diminished libido, appetite changes, and aches/pains (cited in Bartlett 2004). In a 1960s U.K. study investigating physical symptoms of over 500 men, a higher percentage (57%) of men whose partners were pregnant experienced pregnancy symptoms compared with men whose partners were not pregnant (46%) (Trethowan and Conlon 1965). The pregnancy symptoms men commonly reported included anxiety, loss of appetite, and nausea. Symptoms were most severe during a partner’s first and third trimester, a pattern that appears quite common, and appears to reflect responsiveness to a newly recognized pregnancy (in the first trimester) and concern over the partner’s well-being and the challenges of an expanding family (third trimester).

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The main engine of emotional change takes place during the first few months postpartum. In Clinton's (1987) study of pre- and postpartum Wisconsin fathers contrasted with control "non-fathers", she investigated a battery of emotional and health outcomes. Postpartum, fathers exhibited more fatigue, irritability, headaches, difficulties concentrating, insomnia, nervousness, and restlessness, but no differences in backaches, depression or colds compared with controls (Clinton 1987: 65). Other studies elicit men's emotional ups and downs during early postpartum life; interviews with Australian dads suggest that men struggled to cope with changes in a relationship with a mate, with demands of work, and with ambivalence over their interactions with an infant (Barclay and Lupton 1999).

In the face of family turmoil, men commonly exhibit postpartum depression. Since paternal postpartum depression is relatively little appreciated, we consider it in some detail. In a meta-analysis of 20 relevant studies, all from North America, Western Europe, or Australia, rates of postpartum male depression varied from 1-26% (Goodman 2004). Variation in the timing of assessment, how depression was assessed, in the study populations, and other factors help account for this wide-ranging variation, and almost all of the studies had sample sizes less than 100 men. Still, several key patterns stood out from this analysis. Perhaps the most important finding was that the largest risk-factor for men experiencing postpartum depression was if their partner also displayed it. Between 24-50% of men reported postpartum depression if their partner also had postpartum depression.

In perhaps the most rigorous investigation yet of male postpartum depression, a nationally representative study of approximately 5000 U.S. families revealed that 10% of

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fathers with 9 month old infants exhibited clinically significant rates of depressive symptomology (Paulson et al. 2006). That rate was less than postpartum female depression in the same study (14%), but was twice the expected rate of male depression among non-father controls (Paulson et al. 2006). Male depression in the study was also associated with less male involvement in parenting behaviors such as reading to his child.

As research in male postpartum depression grows, so too do factors helping account for its variation. Apart from a partner's own depression, a variety of additional factors appear linked to variable rates of male postpartum depression. Step-fatherhood is associated with a higher rate of postpartum male depression than genetic fatherhood (Deater-Deckard 1998), but that effect disappears when adjusting for other factors associated with depression such as male education, age, social support and network, and a partner's lack of affection. A history of depression, poor relationship quality with a partner, young paternal age, and poor health status of an offspring may also be linked with increased postpartum depression (Johns and Belsky 2007). Poverty appears linked with male depression, with higher rates of paternal depression among more economically challenged men (Anderson et al. 2005). When the time between births is short, this too can amplify problems in family relationships.

Importantly, it is unclear whether men experience elevated postpartum depression in broader cross-cultural perspectives. Almost all studies are restricted to western samples. While cross-cultural data on women's postpartum depression have recently emerged, the same kinds of data are lacking for fathers (see Halbreich and Karkun 2006; Oates et al. 2004). Thus, at this time, we are unable to determine whether fathers experience postpartum depression in various cultural contexts and, if this is the case,

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whether predictors such as the quality of a marital relationship help account for variation. We are sorely lacking data from small-scale societies in South America, Africa, and elsewhere. We suspect that future research will someday find that male postpartum depression exists in these wider social contexts too.

Still, in light of the available depressing evidence, why have kids in the first place? The weight of depression may be counterbalanced by other factors. Baumeister (1991) finds that despite reductions in marital satisfaction postpartum, men and women commonly find their lives enriched. Life has more meaning, even with a crying baby in hand. Furthermore, that decline in marital satisfaction may not be eternal: Hakim (2003) found that after children left the home (admittedly a long time), marital satisfaction rebounded. And from an evolutionary perspective, the reason why men strive to father children is because we attend to nature's bottom line: reproductive success. A father may feel compelled to sacrifice for his children because it feels right, and in this course enable his genes to survive another generation. Our offspring are, quite literally, reproductive successes.

Several large Danish studies speak further to the favorable sides of fatherhood. In a twin study consisting of over 2000 men (Kohler et al. 2005), subjects responded to the question, "How satisfied are you with your life, all things considered?" The presence of children, especially first-born sons, led to slightly more positive responses. The effect of parenting in this study was small compared to partnership status (partnered men reported much larger, more positive responses compared with unpartnered men), yet still indicated an up side for kids. Moreover, a huge study of approximately 390,000 Danes investigated the effects of parenting on suicide risk; two thirds of the approximately 18,000 suicides

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taking place between 1981 and 1997 were males, consistent with the finding that most suicides around the globe involve males (Qin and Mortensen 2003). Across all men, fathering 5 or more children or having a child aged 2 or younger was associated with reduced risk of committing suicide. When splitting fathers into those involved in cohabitating relationships or not, among cohabitating fathers having more children was protective against suicide, whereas among single fathers (who typically lived apart from their children), having more children was associated with increased suicide risk.

Couvade in Cross-cultural Perspective

Against the backdrop of these recent forays into fatherhood and mental health, earlier scholarly research on prenatal and postnatal changes in men's psychology and behavior traces to a substantial literature on the so-called couvade (Elwood and Mason 1995). The etymology of couvade derives from a French word suggesting "hatching" or "brooding." Findings of this couvade literature relate to male psychological transitions occurring alongside fatherhood. The idea is that men experience symptoms prior to and shortly after a partner's pregnancy during the development of a paternal role. While study of the couvade traces to the anthropologist Edward Tylor's work during the 19th century, ongoing research has been conducted largely by two disparate intellectual communities: anthropologists and biomedical scientists. Academic study of the couvade has used inconsistent definitions, time frames (prepartum vs. postpartum, variable lengths postpartum), symptomology (emotions, physical effects), and so forth, making much of the scholarship unstandardized. The couvade literature has given rise to some sensible and testable accounts of paternal transitions, but also to some strange ones: Bohem (cited

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in Brennan et al. 2007b) suggested that men experience couvade symptoms because of a latent, unattainable desire to give birth.

All that said, there are some interesting features of the couvade literature that help shed light on the psychological transformations men experience with fatherhood. The couvade research also covers cross-cultural terrain, providing much-needed insight into the patterns and function of men's paternal transitions around the world. In a study of 172 Thai men whose wives were pregnant, these men described couvade symptoms quite similar to those identified in western societies (cited in Brennan et al. 2007b). Common symptoms included poor concentration, anxiety, fatigue, and sleep alterations. Couvade symptomology has also been addressed in a study of 300 Chinese married men. The majority (68%) of those husbands whose wives were pregnant (in the third trimester) reported more pregnancy symptoms than men whose wives were not pregnant (Tsai and Chen 1997). The anthropological scholarship suggests that the couvade appears in a variety of societies but primarily in two regions: aboriginal South America and Southeast Asia. More ink has been spilled on South America, a trend we continue here too.

Throughout much of aboriginal South America, fathers are subject to a variety of late pregnancy and postpartum taboos and psychological effects resembling those experienced by their partners. Men may be confined for days to months, shift from a meat-heavy diet to a vegetarian one late in a partner's pregnancy and postpartum, be restricted from engaging in subsistence practices, and claim to report physiological symptoms. Among the Witoto of northwestern Amazonia, for example, "[T]he husband rests for a week or more in his hammock, observes food taboos, and receives the congratulations of his friends while the new mother is almost ignored. During this

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couvade, which is practiced until the child's navel is healed, he cannot eat meat or touch his weapons" (Paige and Paige 1981: 189).

What are the functions of couvade behavior (Elwood and Mason 1995; Munroe et al. 1971)? Numerous functions have been advanced, but several stand out as most reasonable given current understanding of human behavioral biology. One broad function is that the couvade fosters male emotional commitment to a partner and child, thus favoring continued investment in them. By this logic, men experience "sympathy" with a partner's pregnancy and postpartum, leading men to experience similar feelings of nausea and fatigue. This function presumably has physiological substrates that encourage emotional commitment and thereby continued investment in the offspring. This is an account that links both proximate (physiological bases of couvade) and ultimate (function) causation. Unfortunately, because descriptive accounts of the emotional experiences—and not just symptom reports and behavioral transformations—of men are typically lacking in the relevant cross-cultural literature, we cannot determine how reliably the posited psychological changes unfold.

A second broad function is that the couvade serves as a social signal, potentially in several ways. By men marking their fatherhood experience with behavioral and psychological adjustments witnessed by others, paternity is conferred upon those men experiencing the couvade. Indeed, in native South American societies recognized for the possibility of "multiple paternity," any man, even a married man, who has had intercourse with a pregnant or postpartum woman is supposed to publicly engage in couvade behaviors (Paige and Paige 1981). Recognized as fathers, all such men have a responsibility to help care for the offspring thereafter.

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As an extension of this second function, the couvade experience may legitimize a partnership within the broader community, thus having signaling value outside the immediate family. Consistent with this view, couvade constraints that reduce the ability of a couple to feed themselves for days, weeks or even longer inherently demand that others provide sustenance during these times. As part of a legitimizing process, extended family or a broader portion of the local community may provide that support. As an illustration of this function, Rival (1998) contends that the couvade serves this latter social function—legitimizing a reproductive union within the longhouse community—among the Huaoroni of Ecuador. The longhouse community, by witnessing and supporting the constrained couple, effectively says “we sanction your union and the baby it has produced.”

Cross-cultural perspectives on the couvade suggest it cannot be divorced from a larger social context like those described here. Paige and Paige (1981) make a compelling point that the couvade is more prevalent among matrilineal societies than among patrilineal, patrilocal ones. To be sure, cultural inertia must play a large role in the geographic distribution of the couvade, given its prevalence in a few regions such as Amazonia. More than that, however, there exists a sensible rationale to account for its presence or not depending on the matrilineal vs. patrilineal basis of a society. The idea is that among patrilineal, patrilocal societies men commonly provide bridewealth or some other compensation for acquiring a wife, and in the course of doing so also acquire rights to sexual access and the resulting children. Among matrilineal societies, men enter women’s and her kin’s terrain, often without providing the same sort of compensation for reproductive rights inherent in the formation of a long-term bond. Men’s unions and

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offspring born from them may thus benefit from the social signaling occurring during the couvade.

Impacts of Children on Parents' Relationship Quality

While this couvade literature suggests behavioral transformations with fatherhood, what about other changes? Father's emotional barometers are not the only thing adjusting postpartum. So too are men's marital relationships. The arrival of baby tends to go hand-in-hand with declines in a couple's relationship quality. A meta-analysis of 90 studies, largely drawn from North American and Western European samples, found that parents experienced lower marital satisfaction than non-parents (Twenge et al. 2003). The effect was slightly larger for women, especially with infants, but the effect held for men too and was not related to the age of their children. Other variables "moderating" the relationships between marital satisfaction and parenting were socioeconomic status and when a study was conducted. Couples of higher socioeconomic status and who were studied more recently exhibited greater deficits on marital satisfaction associated with parenting. Married fathers in Beijing, China reported lower marital satisfaction than married non-fathers, providing some evidence that the postpartum marital declines described among western societies may apply more widely (Gray et al. 2006).

A variety of factors may contribute to postpartum declines in relationship satisfaction. In Chapter 9, we saw how conflicts over sexuality exist and are amplified after birth, and these may serve as a postpartum sore point. Findings from the meta-analysis above suggest that a waning in "pronatalist" outlooks in places like the U.S. help contribute to greater reductions in marital satisfaction with parenting among couples

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studied more recently. To the degree socioeconomic status is linked with greater freedom in one's (and a couple's) behavior, the intrusion of a demanding baby may be perceived more negatively. Challenges to a couple's communication abilities, including the lack of time for spending leisurely time together, appear to play a role too. Belsky and Kelly (1994) found that communication strategies were linked with changes in marital satisfaction in their longitudinal study of parents in Pennsylvania.

Physiological Effects of Fatherhood: The Neuroendocrine System

With all of these emotional and social changes, what is happening “under the skin?” This is a question concerning the physiological substrates underlying men's transition to fatherhood. This is a natural complement to the focus on the psychology of fatherhood discussed so far in this chapter. To begin addressing that question, we need to cover some basics of the neuroendocrine system. It is the workings of this system that illuminate the physiological effects of fatherhood.

The neuroendocrine system consists of the interlinked nervous and endocrine systems (Breedlove et al. 2007; Ellison and Gray 2009; Nelson 2005). The function of this system is to integrate information both within and outside an organism and then use that information to guide appropriate behavioral responses for its environment. The system can work across variable speeds and specificities too, with neurons enabling rapid and direct communication between parts of the body, and hormones permitting more diffuse signaling throughout the body and over slower paces. Putting some flesh on these concepts, suppose a father holds a child, acquiring sensory information through touch, smell, hearing, and visual pathways. His brain integrates that information with brain areas

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devoted to memory and emotion. Neural pathways favor responses suitable for the moment: facilitating release of hormones that travel throughout the body to foster integrated behavioral responses, for example, or making a conscious decision to continue holding the child. Effectively, the neuroendocrine system serves as the body's primary means of engaging sensory, cognitive, emotional, and motor mechanisms to enable the kinds of behavior such as childcare or mating that enhances an organism's survival and reproductive success.

Evolution is a tinkerer, and natural selection has “discovered” that by tinkering with the neuroendocrine system it is possible to alter a species' and indeed an individual's behavioral tendencies, including family proclivities. Beginning with highly conserved neuroendocrine mechanisms, evolution can play with the knobs of brain tissue development, the affinity of a receptor to bind a specific neurotransmitter, or the structure of a peptide hormone, among other possibilities. Since life evolved once on this planet, the neuroendocrine machinery of all life forms has the deepest of shared ancestry, helping account for why the progesterone in a woman is like that of a yam (which helped when first creating birth control pills) or why the pharmacological drugs that work on us (e.g., selective serotonin reuptake inhibitors) also commonly work on our distantly related pets like cats and dogs. Yet from those basics, nature can throw some switches to alter the specifics of these processes in ways suitable for more specific selective pressures, including family ones.

When it comes to the neuroendocrine mechanisms of paternal care, we will see shortly how many of these processes have been illustrated through intricate and invasive research on small rodents known as voles as well as less invasive work on humans.

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Before we fully jump into this story, however, a few other concepts deserve attention.

One is that the mechanisms of paternal care are effectively parasitic tweakings on preexisting neuroendocrine substrates. Sometimes it appears that mechanisms of paternal care take systems operating in females and co-opt them among males too (e.g., effects of the hormone prolactin); in other cases, it seems that the system alters male-specialized circuitry (e.g., effects of the hormone vasopressin); in still other examples, the relevant mechanisms appear more generalized before being coaxed into aiding in paternal care (e.g., functions of the vagus nerve or prefrontal cortex). Lastly, the evolutionary story likely entails developmental plasticity (potential for change across a lifespan) leading the way rather than, as we have pretended, a conscious process of natural selection (West-Eberhard 2003). Put another way, the relevant mechanisms provide for species-specific and even individual tendencies. But the specifics of an organism's interaction with its environment during development will shape how these tendencies play out, enabling a range of outcomes (such as a rhesus monkey male, who in the wild would never provide paternal care, doing so in a captive setting: Smith 2005). Effectively, a push toward paternal care during development can create a new environment favoring the evolution of heritable neuroendocrine mechanisms that in turn increase the tendencies toward paternal care.

Sensing a Baby

Babies can reach their fathers through several sensory modalities. This is the first step toward making impacts on fathers' neuroendocrine systems and in turn shaping paternal behavior. Among most mammals, including various rodent species on which the majority

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of paternal physiological research has been conducted, smell factors heavily into how an offspring impacts its father. This insight is as apparent as noticing a mouse or rat's relatively large, wet nose (by which dad smells various things, including its pups). A human reliance on smell is diminished greatly compared with our non-human relatives. This diminished reliance on smell manifests in various ways, including our relatively smaller olfactory bulbs and recent comparative genomics research revealing a reduction in the reliance on smell among our ancestors—even compared with chimpanzees.

All that said, Peter can still remember the intoxicating smell of his first baby's forehead. For the first several weeks of her life, his daughter exuded a profound, glorious smell that he could breathe in at close distance. Given the cross-cultural variation in paternal proximity to infants, much less hygiene and other factors, this experience may not be widely generalizable; it may be something of an evolutionary holdover, and more functional in maternal-offspring dyads, but it does raise several issues concerning smell and fatherhood.

Can human fathers recognize their offspring by smell? Sometimes. Studies of dads sniffing around revealed that blindfolded fathers (unlike mothers) could not recognize their offspring by smell when allowed to smell their babies' heads. If given a shirt worn by the baby, however, then dads could identify their baby. When fathers of older children (aged 6-15) were asked to identify by smell who had worn shirts placed inside a container, they correctly recognized 31/42 children (Weisfeld et al. 2003). However, the dads in this latter study preferred the scents of unrelated females over those of their daughters, a finding the authors suggested fits with incest avoidance.

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In a more recent study of 39 Dutch fathers, who had children around 9 years of age, two thirds of the dads were able to identify their children's smells (Dubas et al. 2009). Paternal recognition of children's smells was positively associated with paternal investment, affection and attachment. Fathers who recognized their children's smells ignored these children less. Results from this study do not enable determining whether smell recognition favors or is instead a reflection of paternal care. Yet the data do suggest that smell may continue to infuse paternal physiology, at least to some degree.

Visual cues provide important infant lifelines to fathers. This is hardly surprising given the importance humans place on vision for navigating our social worlds. We possess a dedicated face recognition neural circuitry, enhanced facial musculature allowing a breadth of expressiveness, and newborns keen on seeking eye contact with a caregiver (Cozolino 2006). We even possess a different sort of eye (which, unlike other primates, exhibits a vivid contrast between the white background and pupil) that arguably may have arisen to enhance our capacities for visual communication. Given our sensory worlds, how does vision shape paternal physiology? As noted in Chapter 5, fathers may seek and be given visual confirmation of a child's resemblance to him. This visual alignment suggests that a man's investment is being channeled into his genetic offspring rather than those of another man.

Further illustrating the importance of vision to paternal physiology, Platak et al. (2004) constructed a virtual paternal world by computer morphing facial photographs of non-fathers and non-mothers with those of 3 unrelated babies. The researchers then asked these men and women a host of questions concerning their likely paternal investment in the morphed and unmorphed children's images. Across the positive investment items—

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e.g., Which one of these children would you spend the most time with?—the men preferentially selected the morphed children’s images more often than did the women. When men and women were subject to fMRI in a similar photo morphing scheme, men also displayed different neural activity than women when faced with self-morphed vs. unmorphed stimuli. More specifically, men exposed to self-morphs exhibited increased left frontal cortical activation, thought to be involved in an inhibitory process. The implication is that facial resemblance matters more to men than women in anticipating parental investment, and this sex difference has observable neural substrates.

Touch can have powerful physiological effects. We know it when someone scratches our backs or rubs our feet. Touch can have physiological effects on the “toucher” as well as the “touched.” The levels of cortisol (a stress hormone) in depressed moms declined after touching their infants (Onozawa et al. 2001). Dog lovers playing with and scratching dogs for about 15 minutes experienced elevations in beta endorphins as well as hormones including oxytocin and prolactin (Odendaal and Meitje 2003). If playfully rolling around with a dog can have these effects on people, it is little surprise that touching and holding an infant can have physiological effects too.

Just a few days postpartum, fathers were able to identify their infants by touch alone (not looking) (Kaitz et al. 1994). In a sense, the feel of our baby makes its mark on our minds. Research with titi monkeys suggests further links between touch and the brain, particularly the somatosensory cortex. The somatosensory cortex forms a strip along the front portion of the parietal lobe in the brain. It contains a miniaturized map of our body’s experience with the world, with enlarged areas for our faces, our fingers, our genitals, and toes. Among titi monkeys, in which males devote an inordinate amount of

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time tending their young, portions of the somatosensory cortex are enlarged in association with enhanced hand and forelimb touch (Padberg et al. 2005).

Paternal proximity may activate several sensory pathways in the course of linking a father's physiology with his child. A man sees and hears his infant. He holds his child's hand. The child's mother is often present too, fostering a family atmosphere. Imagining an intimate sensory world like this one, however, we step back to consider the variable paternal roles men fulfill around the globe. Among some societies, such as the Thonga of Africa, men may avoid all forms of touch with their young children. In the vast majority of societies, fathers spend relatively little time directly interacting with their infants and toddlers during day hours, but perhaps more time with older children, including sons. At the other extreme, among the Aka, dads are within reach of infants the bulk of the day as well as the night.

While there is variation in paternal proximity (and hence fathers' sensory experiences with children) during daylight, what about during sleeping times? Even if men spend relatively little time with their young children during day hours, sleeping arrangements commonly place father and child closer together, and may contribute to the formation of an attachment between them. A father may awaken to his child's movements and cries. Perhaps that same father loses sleep but gains an enhanced bond. Research has barely scratched the surface of this interesting interface, however. In a preliminary study of 32 U.K. children, those children who had co-slept with parents had lower cortisol levels than those children who had not (Waynforth 2007). This study suggests an impact of sleeping arrangements on children. However, there is no research investigating the effects of sleeping arrangements on paternal physiology.

Babies and Brain Imaging

Through various sensory pathways, babies can crawl into our brains. New brain imaging studies reveal some of the specific neural pathways taken by these baby stimuli (reviewed in Swain et al. 2007). In these types of studies, subjects are put inside a scanner (e.g., fMRI machine) and given standardized stimuli such as photos of children and adults to determine which areas of the brain respond with heightened activity. Brain areas associated with elevated activation also shed insight on the cognitive and emotional processes that make up paternal psychology and behavior. If emotional centers of a father's brain light up in response to an infant's face, we infer that part of the way a baby elicits paternal care is by pulling on these emotional strings. Furthermore, these imaging studies also reveal ways in which information about a baby can be integrated with other information in the brain to generate integrated neuroendocrine responses. If the hypothalamus is activated by baby stimuli, we might imagine how this could lead to release of hormones from it that would in turn initiate hormone release from the pituitary gland which in turn would travel throughout the body to help coordinate an individual's behavior.

The first of these types of imaging studies compared patterns of neural activation among parents and non-parents, men and women, to infant cries (Seifritz et al. 2003). The parents exhibited more pronounced neural responses to infant crying than laughter in the right amygdala. The amygdala is a small brain structure active in emotional processing, especially fear. So the interpretation of this infant cry activation could be that parents experience the cry as more emotionally salient, including perhaps a vigilance response.

Swain and colleagues (Swain et al. 2007) have conducted fMRI studies of fathers exposed to both visual and auditory stimuli. Men responded differently to cries of their own vs. other infants. Among those men listening to cries from their own infant, these fathers experienced increased activation in several brain areas including the hypothalamus, hippocampus, midbrain, and anterior cingulate. The activation of the hypothalamus is striking because, as noted above, of its role transducing neural information into release of hormones that can in turn have effects on further hormone release throughout the body (e.g., the hypothalamus releasing a hormone, GnRH, that in turn stimulates the pituitary gland to release LH, which in turn increases testosterone release from the testes). The hippocampus plays an important role in long-term memory formation, suggesting that it may play a role in the neural distinction between own vs. other baby. The midbrain consists of the superior and inferior colliculi as well as the substantia nigra; to find the midbrain more activated is interesting because the substantia nigra contains dopaminergic neurons associated with psychological reward.

Activation of the anterior cingulate cortex in the fMRI studies is also notable. The anterior cingulate rests at the intersection between the emotional (limbic) and higher cognitive (neocortex) functions (Cozolino 2006). It appears to play a broad role in social orientation. The cingulate cortex appears to have evolved among animals involved in parental care (which includes a very distant ancestor of ours). By linking emotional activation with higher association areas, an organism is better able to evaluate the emotional significance of its social world, including an offspring in its charge. So the increased activation of dads' anterior cingulate cortices to their own babies' cries suggests an enhanced social attention and evaluation in progress.

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Fathers displayed increased neural activity in specific brain areas when exposed to photos of babies compared with houses (Swain et al. 2007). This observation suggests that babies impact the brain differently than do inanimate objects. While that may hardly surprise anyone, the details of neural activation are more compelling. Some of the areas more activated by babies include the thalamus, anterior and middle cingulate, and midbrain. Some of these areas such as the anterior cingulate thus overlap with ones activated by infant cries. The patterns of activation also make some sense. The thalamus serves as a relay station for neural information, and babies appear to generate more information transit than houses. The anterior cingulate appears equally capable of facilitating social evaluation for infant visual or auditory stimuli.

Interestingly, fathers' brains also responded differently to images of their own babies compared with unrelated ones. The brain areas more highly activated by own baby photos were almost exactly the same ones activated when viewing babies compared with houses. The inference is that babies activate the brain differently than houses, and fathers' own babies are more salient stimuli compared with unrelated babies.

Hormones and Paternal Care: Lessons of the Voles

Several of the paternal imaging studies above reveal activation of brain structures involved in hormone release (e.g., hypothalamus). Moreover, some of those areas responding to paternal stimuli also contain specific hormone receptors—molecules that bind hormones such as vasopressin or prolactin. These observations suggest that hormones are involved in the regulation of paternal behavior.

Leave it to voles (small, furry rodents) to illustrate some of the specific ways in which hormones facilitate paternal behavior. Because the lessons of the voles are immensely useful in our understanding of hormones and paternal care generally, including how we conceptualize this area in humans, we discuss these rodents in some detail. Elegant experimental research has been conducted on several sister species of voles differing in mating system and paternal care. By comparing the neuroendocrine substrates of closely related species characterized by long-term pair bonding and considerable paternal care on one hand (e.g., prairie voles) with ones involved in polygynous mating relationships and little paternal involvement on the other (e.g., montane voles), proximate mechanisms underlying these behavioral proclivities have been revealed. Much of the story centers on the vasopressin system.

Males tend to have higher vasopressin levels than females. While we commonly recognize sex differences in steroid hormone levels (e.g., estradiol, progesterone, testosterone), this sex difference in vasopressin is less recognized, even though vasopressin levels (and densities of the hormone receptors to which it binds) are modulated by androgens such as testosterone (Carter 2007). Effects of vasopressin are also more pronounced in males, suggesting this hormone warrants more attention for its roles in sexually dimorphic behavior.

What are the physiological effects of vasopressin (Caldwell et al. 2008)? Vasopressin is classically recognized for two functions: increasing blood pressure, and acting as an anti-diuretic. It also serves to psychologically and behaviorally activate an organism, especially a male, in response to the appropriate stimuli. A male competitor, a courtship opportunity, a helpless rodent pup—these may elicit a vasopressin response,

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including potentially adaptive psychological effects of heightened anxiety and enhanced social memory, both of which may prime a male's readiness and physiologically mark the importance of the interaction. To exert its effects, vasopressin is bound to one of three receptor types: AVP1a, AVP1b, and AVP2, each of which has a different distribution in the body. For our purposes, it is notable that AVP1a receptors are found in several key brain structures including the ventral pallidum, itself involved in "reward" pathways. The links between vasopressin and reward pathways, which themselves rely on the neurotransmitter dopamine, enables linking a vasopressin response to a social stimulus like a mate or pup with a positive emotional association.

Experiments with prairie and montane voles reveal differences in the distribution of AVP1a receptors between their brains (Carter 1998; Young and Wang 2004). These differences have been traced to differences in the promoter region of the AVP1a receptor gene. Most remarkable have been the results of transgenic experiments—those which involve moving a gene from one species into another—demonstrating that expression of the AVP1a receptor in the normally polygynous montane vole's forebrain can lead to enhanced interest in spending time with a single female partner, thereby facilitating partner preferences and likely pair bonding (Lim and Young 2006). Similar results have been found in normally polygynous mouse and other vole species (Lim & Young 2006). Stop and think about these results for a moment. The introduction and expression of a single gene—one involved in the vasopressin system—has proven capable of behaviorally altering a male's family life. Such exciting research has spurred interest in the roles of hormones, neurotransmitters, and neural pathways in human male social behavior too. Ethical and logistical constraints mean that we often cannot perform the

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kinds of experiments on humans that can be done on lab rodents like these voles. We do not know if human transgenic experiments involving the AVP1a receptor would alter family proclivities. Yet non-human animal research like this can serve as a rich source of testable hypotheses for less invasive human research.

Testosterone and Human Male Family Life

In the world of hormones and paternal care, the so-called “Challenge Hypothesis” represents a wonderful example of nonhuman animal work influencing human research. The hypothesis posits that male testosterone levels increase in reproductively relevant contexts; consequently, male-male competition and courtship may elicit adaptive increases in testosterone levels, while involvement in long-term bonds and paternal care may be linked with lower testosterone levels (Wingfield et al. 1990). The hypothesis originally integrated a body of research on North American migratory birds, including dark-eyed juncos and song sparrows, in which males commonly exhibit peak testosterone levels during spring male-male competition and courtship, but decreased testosterone levels after forming long-term bonds and raising offspring. In some cases, injecting birds in the wild with synthetic testosterone could also affect family life, including reductions in feeding rates but increases in courtship of extra-pair mates (Ketterson and Nolan 1999).

An obvious question spurred by the “Challenge Hypothesis” is: do human males involved in long-term affiliative pair bonds and/or paternal care have lower testosterone levels? The data on human male testosterone and family life have been piling up recently, including from a variety of international samples, enabling us to address that question.

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The short answer is that in samples of men living in the U.S. and Canada men involved in long-term relationships like marriage and/or fatherhood almost uniformly have lower testosterone levels than their single and childless counterparts. However, outside North America, the answer is muddier, probably in good measure due to the cross-cultural variation in human family relationships. Let's walk through some of the key findings in this research on men's testosterone and family relationships.

Among North American testosterone and pair bonding studies, 10 of 11 have found lower testosterone levels among men involved in committed relationships such as marriage (Gray and Campbell 2009; van Anders and Gray 2007). In the earliest of these studies, Booth and Dabbs (1993) showed that among approximately 4000 U.S. Army veterans, men's testosterone levels were higher if they had never married, ever divorced, separated, or had extramarital sex. In a longitudinal study of approximately 4000 U.S. Air Force veterans, Mazur and Michalek (1998) observed that married men had lower testosterone levels, but also found that men's testosterone increased around the time of divorce. Research among Harvard undergraduates and Harvard Business School students revealed that men involved in a long-term committed relationship, whether married or not, had lower testosterone levels than unpaired men. A study on Canadian men revealed that men involved in either same-city or long-distance relationships had lower testosterone levels than single men.

In the first study considering sexual orientation, testosterone, and men's relationships, testosterone levels of Canadian gay men involved in relationships were not different from gay men not involved in relationships, although paired heterosexual men had lower testosterone levels than unpaired heterosexual men (van Anders et al. 2006). In

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this same study, testosterone levels of heterosexual women did not differ depending on relationship status, whereas paired lesbians had lower testosterone levels than unpaired lesbians. The inference from this study is that being paired to a woman (but not a man) appears to be associated with lower testosterone levels, for both men and women.

Several North American studies also point to lower testosterone levels among fathers. In a study of Canadian men undergoing the transition to fatherhood, men's testosterone levels shortly after birth were 33% lower than shortly before birth (Storey et al. 2000). In a different Canadian sample of 67 men, fathers had lower testosterone levels than control non-fathers (Fleming et al. 2002). Men's testosterone levels, whether they were fathers or not, were also negatively related to their sympathy and desire to respond to tape-recorded infant cries. In other words, men with lower testosterone levels were more paternally responsive. Put these testosterone and fatherhood data together with the other North American studies and there exists a consistent link between lower testosterone and men's involvement in affiliative pair bonds and paternal care.

Step off the North American continent and the links between testosterone and men's family relationships become less clear. In only 3 of 7 studies outside North America do we find that monogamously married men have lower testosterone levels compared with their unmarried counterparts (reviewed in Gray and Campbell 2009). For example, among urban Bangladeshi men, testosterone levels did not differ depending on whether men were married. Results regarding testosterone and polygyny have also differed. Among Swahili on the Kenyan coast, men married to two wives had higher testosterone levels than other men. This result was not replicated among Ariaal

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pastoralists, however: in fact, older, polygynously married Ariaal men had lower, rather than higher, testosterone levels compared with older, monogamously married men.

Several international studies have also tested whether fathers outside of North America have lower testosterone levels. In 4 of 6 such studies, fathers had lower testosterone levels than controls. Married fathers in Beijing, China had lower testosterone levels than married non-fathers or unmarried men (Gray et al. 2006). Fathers in urban Jamaica had lower testosterone levels than single controls, although this effect was largely and surprisingly due to the lowest levels of “visiting fathers” (fathers who live separately from their partner and child) rather than “coresidential fathers” (Gray et al. 2007). Fathers in urban Bangladesh, by contrast, did not have lower testosterone levels compared with married non-fathers or single men.

What accounts for some of these globally discrepant results? Perhaps a major factor underlying the variable patterns is the cross-cultural variation in men’s family relationships. These studies outside of North America encompass a range of family contexts, including ones in which polygyny is common and acceptable, ones in which fathers may spend little time with their infants and toddlers, and ones in which extramarital affairs may be less stigmatized.

To illustrate the importance of social context, and its likely helping account for these cross-culturally variable data, contrast findings from two human societies living in the same northern Tanzania bush. Here, the Hadza live as hunter-gatherers, and men engage in relatively frequent interaction with their children. The neighboring Datoga are pastoralists with a high degree of polygyny and less paternal involvement with young children. Based on differences in family life, researchers predicted that Hadza fathers

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would have lower testosterone levels than single men, but no differences in testosterone levels would be found between Datoga fathers and non-fathers (Muller et al. 2009). Once the researchers asked men about their family relationships and collected saliva samples from which testosterone levels were measured, the results supported the predictions. Indeed, Hadza fathers, but not Datoga fathers, had lower testosterone levels compared with controls. So given the social context of fatherhood, we might generally expect where men engage in a reasonable degree of direct interaction with young children during day hours and perhaps also associated with co-sleeping, they may be more likely to have lower testosterone levels.

Hormones and Human Paternal Care: Vasopressin, Prolactin, and More

While the birds helped inspire research on human testosterone and family life, let's go back to the rodents to ask what further insights they might offer concerning the possible hormonal correlates of human paternal care. The vole work described above suggests we ought to be testing for links between vasopressin and paternal care. Experimental research on male voles shows that simultaneously blocking the effects of vasopressin and oxytocin can compromise paternal care (Bales et al. 2004). Rodent work has also suggested a conceptual bridge between androgenic hormones such as testosterone with other hormones like vasopressin. In an integrative model of social affiliation derived primarily from experimental rodent research, Depue and Morrone-Strupinsky (2005) suggest interactions between the social context of an organism and facilitatory roles for gonadal steroids such as testosterone that in turn can have facilitatory roles on peptide hormones like vasopressin. Hormones such as vasopressin play important integrative

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functions in part through their effects on dopaminergic reward pathways in brain structures such as the ventral pallidum. Depue and Morrone-Strupinsky (2005) also postulate important roles for endogenous opioids in the continuation of a relationship. Let's draw on these concepts to ask about vasopressin and human male family life.

The only study investigating vasopressin and human paternal care is the Jamaican one previously described (Gray et al. 2007). In this study of Jamaican fathers and control non-fathers, vasopressin levels did not differ according to whether men had children. Among the 27 fathers in the study, however, the age of their youngest child was negatively correlated with their urinary vasopressin levels. In other words, the younger the child a father had, the higher his vasopressin levels. That finding resonates with the recent report in common marmosets that age of youngest offspring and fathers' AVP1a receptor density in the prefrontal cortex were negatively correlated (Kozorovitskiy et al. 2006). In this Jamaican sample, vasopressin levels were positively correlated with blood pressure. Based on that link with blood pressure, along with non-human research on psychological and behavioral effects of vasopressin, we can offer interpretations of this preliminary study. Fathers interacting with younger children may have higher vasopressin levels for several reasons: responding to unpredictable and potent infant stimuli like cries, carrying and holding their young, and experiencing greater anxiety and promoting social memory.

Prolactin has been linked with paternal care in numerous vertebrates (Nelson 2005). If males play important roles caring for offspring, one of the most consistent hormonal correlates of this care is elevated prolactin. In species as diverse as emperor penguins, wolves, meerkats, ring doves, and common marmosets, involved males exhibit

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increases in prolactin associated with offspring care. Even that paragon of paternal investment—the pipefish, containing a pouch in which he incubates eggs before “giving birth”—develops that brood pouch under the stimulation of prolactin (Stolting and Wilson 2007).

Although the name prolactin refers to its classical function of lactation support (literally, promoting lactation), this hormone, secreted from the anterior pituitary, serves a variety of functions, including ones related to offspring care. Prolactin promotes adaptive weight gain, and anxiety, and inhibits reproductive function, all good things if one is focused on extensive care of dependent offspring rather than looking for mates (Sobrinho 2003). Under the right sex steroid hormone milieu, along with nipple stimulation, a man can also produce small amounts of milk under the influence of prolactin (Bribiescas 2006). Relatively few men have pursued this breastfeeding potential, despite the potential to revolutionize paternal involvement. However, several human studies have also investigated links between prolactin and paternal care.

The first of these human studies, published in 2000, initiated a new era in human hormones and fatherhood research (Storey et al. 2000). Although researchers had linked elevated prolactin levels with fatherhood in common marmosets almost 20 years earlier, no human study on this subject had been published until the new millennium dawned. In this study of 34 highly invested Canadian men recruited from prenatal classes, men’s prolactin levels were highest shortly before the birth of their offspring. Across samples collected before and after birth, men who reported concern when listening to tape-recorded infant cries had higher prolactin levels than less-concerned men. Those men reporting two or more pregnancy symptoms such as nausea and fatigue also had higher

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prolactin levels. Results of this study thus suggested, like among many other paternal vertebrates, links between prolactin and human paternal care. Additionally, the findings were relatively unique in bridging the psychology and physiology of fatherhood. It was not just the case that men's prolactin levels were associated with infant cries, but also that some of the couvade symptoms discussed earlier in this chapter could also be linked with paternal physiology.

In a different study of Canadian men, fathers listened to either “control” background noise or the tape-recorded pain and hunger cries of unrelated infants (Fleming et al. 2002). The experienced fathers listening to the infant cries experienced acute increases in prolactin levels compared to experienced fathers listening to control noise or inexperienced fathers listening to noise or the same cries. Fathers with higher prolactin levels tended to respond with more alertness and positive feelings to infant cries. Among fathers listening to the infant cries, their prolactin levels were positively associated with experience changing diapers and holding babies.

In a third study investigating prolactin and human paternal interactions, the same Jamaican men described above participated (Gray et al. 2007). The prolactin levels of men were measured before and after a 20 minute session during which fathers interacted with their partners and youngest children and single non-fathers sat quietly. The prolactin levels of single men dipped during this period, whereas prolactin levels of fathers remained relatively flat across the test session. The result was different prolactin profiles according to paternal status. The contrast between single non-fathers and fathers was largely due to “visiting fathers,” a result mirroring the testosterone results in the same

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sample. This study, like the two Canadian ones, suggests that paternal interactions, including exposure to infant cries, can affect men's prolactin levels.

Non-human research has inconsistently pointed to roles of oxytocin or cortisol in paternal care. Oxytocin is typically viewed in other animals as fostering social affiliation and inhibiting the stress axis, including cortisol release (Carter 1998). What about in humans? In the same Jamaican study, no links between paternal status or age of youngest child and urinary oxytocin levels were found. Interestingly, however, one study did observe a link between oxytocin and human male pair bonding: Grewen et al. (2005) found that in a study of 38 couples who had been in a committed relationship for at least one year, both men and women with higher relationship quality had higher oxytocin levels. No differences in cortisol levels occurred with respect to paternal status or offspring age in the Jamaican study either. In the same Canadian hormone and fatherhood studies discussed above, one (Berg and Wynne-Edwards 2001), but not the other (Fleming et al. 2002), observed lower cortisol levels among fathers compared with non-father controls. Fleming et al. (2002) also found that fathers holding their infants experienced transient increases in cortisol levels. From these sparse and inconsistent preliminary data, perhaps we would anticipate the potential for fathers to experience transient increases in oxytocin during warm interactions with children (comparable to the human-dog study mentioned above, though not observed in this preliminary Jamaican one), and variable acute cortisol responses depending on the infant stimuli (e.g., increases in response to cries, but lowered levels during calm times). Indeed, Frodi et al. (1978) discovered that fathers experienced greater cardiovascular responses to premature infant

cries and faces, just one illustration of the ways that variable child stimuli are likely to elicit variation in paternal physiological responses.

By now, all of our brains, whether we are fathers or not, are steeped in babies. We have covered a lot of ground in attempting to address the two primary questions of this chapter concerning the psychological and physiological impacts associated with human fatherhood. We have found that men undergo a variety of psychological changes, ranging from excitement to anxiety, a heightened sense of life's worth to depression. We have seen that babies foster these variable psychological impacts by reaching through various sensory modes to affect men's neural and hormonal underpinnings. The specific ways in which all of these processes unfold depend on the sociocultural context.

As much terrain as we have covered this chapter, we can point to numerous roads researchers have yet to travel. We have said nothing about the ways development impacts the physiology of human paternal responses, an omission due to the lack of available data. We have said nothing about genetic bases of paternal behavior. In this case, there has been a modest amount of work suggesting that genetic differences contribute to some variation in paternal care (Pérusse et al. 1994); one might imagine that newly discovered polymorphisms in the human vasopressin or oxytocin receptor contribute small, but additive, amounts to variation in paternal behavior (see Walum et al. 2008). We have said nothing about variation in couvade symptoms, much less paternal physiology, depending on whether men are step- or biological fathers simply because there are no relevant data, whether among western societies or in broader cross-cultural samples. We have also yet to formally link some of the core psychological transitions with fatherhood—such as risk of postpartum depression and reduced marital quality—with the physiological bases of

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paternal responses discussed in the latter half of this chapter. We can clearly underscore large gaps in our knowledge of the psychology and physiology of human fatherhood.

Still, the progress made in recent years has been fast (note that the majority of studies cited in this chapter were published since 2000), and that pace will likely just get faster as babies continue to encroach upon our brains.