

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/287272797>

The Neurobiological Basis of Morality

Article · January 2012

DOI: 10.1093/oxfordhb/9780199570706.013.0023

CITATIONS

8

READS

201

2 authors, including:



Pat Churchland

University of California, San Diego

127 PUBLICATIONS 6,188 CITATIONS

SEE PROFILE



The neurobiological platform for moral values

Patricia S. Churchland*

Department of Philosophy, University of California, San Diego, La Jolla, CA 92093, USA

* Author's e-mail address: pschurchland@ucsd.edu

Accepted 8 October 2013; published online 27 November 2013

Abstract

What we humans call ethics or morality depends on four interlocking brain processes: (1) caring (supported by the neuroendocrine system, and emerging in the young as a function of parental care); (2) learning local social practices and the ways of others — by positive and negative reinforcement, by imitation, by trial and error, by various kinds of conditioning, and by analogy; (3) recognition of others' psychological states (goals, feelings etc.); (4) problem-solving in a social context. These four broad capacities are not unique to humans, but are probably uniquely developed in human brains by virtue of the expansion of the prefrontal cortex (this formulation is based on Chapter 1 of my book, *Braintrust: What neuroscience tells us about morality*).

Keywords

morality, oxytocin, vasopressin, hypothalamus, epigenetics.

1. Where do values come from?¹

Values are not in the world in the way that seasons or the tides are in the world. This has sometimes provoked the idea that moral values come from the supernatural world. A more appealing hypothesis is that moral values are not other-worldly; rather they are social-worldly. They reflect facts about how we feel and think about certain kinds of social behavior. Those processes are drivers of behavior.

The values of self-survival and self-maintenance are not in the world either. But we are not surprised that they shape the behavior of every animal. No one suggests self-survival values are other-worldly. Instead, it is easy

¹ The text that follows is adapted from Chapter 4 in Churchland (2013).

to see how the biological world came to be organized around such values. Unless the genes build a brain that is organized to avoid danger, and seek food and water, the animal will not long survive nor likely reproduce. By contrast, an animal that is wired to care about its own self-maintenance has a better shot at having offspring. So certain self-oriented values are favored by natural selection.

The hallmark of moral values is that they involve self-cost in the care of others. Self-care seems to be in conflict with other-care. How can the neuronal organization to support such values be selected for?

2. The hungry brains of homeotherms

The evolution of the mammalian brain marks the emergence of social values of the kind we associate with morality (this story is probably true of birds too, but for simplicity I shall leave birds aside for now, regrettably). Sociality appears to have evolved many times, but the flexibility associated with mammalian sociality is strikingly different from the sociality of insects. The evolution of the mammalian brain saw the emergence of a brand new strategy for having babies: the young grow inside the warm, nourishing womb of the female. When mammalian offspring are born, they depend for survival on the mother. So the mammalian brain has to be organized to do something completely new: take care of others in much the way she takes care of herself. So just as I keep myself warm, fed and safe, I keep my babies warm, fed and safe.

Bit by evolutionary bit, over some 70 million years, the self-care system was modified so that care was extended to babies. Now, genes built brains that felt pain when the babies fell out of the nest. Also new, when the babies felt pain owing to cold or separation or hunger, they vocalized. This too caused the mother pain and made her respond to diminish the pain. These new mammalian brains felt pleasure when they were together with their babies, and the babies felt pleasure when they were cuddled up with their mother. They liked being together; they disliked being separated. The pleasure and pain systems were extended to respond to social stimuli.

What was so advantageous about the way early mammal-like reptiles made a living that set the stage for this whole new way of having babies and extending care? The answer is energy sources.

The first reptiles that happened to be *homeotherms* had a terrific advantage — they could hunt at night when the cold-blooded competition was

sluggish. Pre-mammals probably feasted on sluggish reptiles lying around waiting for the sun to come up, or at least they could forage without fear of reptilian predators. Homeotherms also managed well in colder climates, thus opening new feeding and breeding ranges.

Homeothermy requires a lot of energy, so warm-blooded animals have to eat about ten times as much as comparably sized poikilotherms (Lane, 2009). If you have to take in a lot of calories to survive, it may help to have a brain that can adapt to new conditions by being smart and flexible. Biologically speaking, it is vastly faster to build brains that can learn prodigiously than to rig a genome that builds brains with reflexes for every contingency that might crop up. To accommodate learning, the genome has to have genes that get expressed to make new protein to add wiring to embody new information. That is much less complex than altering a genome so that it builds a brain that can know at birth how to react in many different circumstances (Quartz & Sejnowski, 1999, 2003). Notice that using a learning strategy to tune up the brain for strategic survival also means that at birth the offspring have only basic reflexes. Mammalian babies are dependent.

Learning requires circuitry that can respond to experience in an adaptive manner yet also work hand in hand with the old motivational, pain and drive systems long in place. Laminar cortex is a remarkable computational solution to the Big Learning problem. It can provide the kind of power and flexibility needed for learning, and also for advantageous planning, and efficient impulse control. Gene duplication allows for the smooth addition of cortical subfields, since the basic recipe for a patch of six-laminar organization of cortex appears to be easily repeatable. Hence size of cortex is expandable in response to ecological pressures.

Exactly how the six-layer cortex emerged from the loosely organized one-to-two layer of reptilian dorsal cortex is largely lost in our ancient past. Nevertheless, comparisons of the brains of different existing species as well as studies of brain development from birth to maturity can tell us a lot (Krubitzer & Kaas, 2005; Krubitzer, 2007). It is known that cortical fields supporting sensory functions vary in size, complexity, and in the connectivity portfolio as a function of a particular mammal's lifestyle and ecological niche. For example, flying squirrels have a very large visual cortical field, whereas the platypus cortex has a tiny visual field but large somatosensory fields. The ghost bat, a nocturnal mammal that relies on precise echo-location

to hunt, has a relatively huge auditory field, a small visual field, and a somatosensory field much smaller than that of the platypus (Krubitzer et al., 2011). Among rodents there are very different styles of moving — flying squirrels, swimming beavers, tree-climbing squirrels, for example. This means that there will also be organizational differences in the parts of the brain that are associated with skilled movement, including motor cortex. In all mammals, frontal cortex is concerned with motor function. In front of the motor regions is prefrontal cortex — areas concerned with control, sociality, and decision-making. All of these cortical fields have rich pathways to and from the whole range of subcortical regions.

Brains are energy hogs, and the calorie intake of homeotherms is high not just to keep body temperature constant, but also to keep their big brains in business. Moreover, because young mammalian are so immature at birth, their calorie intake is especially high. Because mammals eat so much more than reptiles, a given range supports fewer of them. Dozens of lizards can feed quite well on a small patch but a patch that size will support fewer squirrels and even fewer bobcats. The implication for litter size is that the more successful strategy may to produce fewer rather than many offspring, and to invest heavily in their welfare to independence and reproductive maturation.

3. Social bonding

Why do mammalian mothers typically go to great lengths to feed and care for their babies? After all, such care can be demanding, it interferes with feeding, and it can be dangerous. Two central characters in the neurobiological explanation of mammalian other-care are the simple nonapeptides, *oxytocin* and *vasopressin*. The hypothalamus regulates many basic life-functions, including feeding, drinking, and sexual behavior. In mammals, the hypothalamus secretes oxytocin, which triggers a cascade of events with the end result that the mother is powerfully attached to her offspring; she wants to have the offspring close and warm and fed. The hypothalamus also secretes vasopressin, which triggers a different cascade of events so that the mother protects offspring, defending them against predators, for example (Keverne, 2007; Porges & Carter, 2007; Cheng et al., 2010).

The lineage of oxytocin and vasopressin goes back about 500 million-years, long before mammals began to appear. In reptiles these nonapeptides play various roles in fluid regulation and in reproductive processes such as

egg-laying, sperm ejection, and spawning stimulation. In mammalian males, oxytocin is still secreted in the testes, and still aids sperm ejaculation. In females it is secreted in the ovaries and plays a role in the release of eggs. In mammals, the roles of oxytocin and vasopressin in both the body and the brain were expanded and modified, along with circuitry changes in the hypothalamus to implement post-natal maternal behavior, including suckling and care (Carter et al., 2008; Young & Alexander, 2012).

During pregnancy, genes in the fetus and in the placenta make hormones that are released into the mother's blood (e.g., progesterone, prolactin, and estrogen). This leads to a sequestering of oxytocin in neurons in the mother's hypothalamus. Just prior to parturition, progesterone levels drop sharply, the density of oxytocin receptors in the hypothalamus increases, and a flood of oxytocin is released from the hypothalamus.

The brain is not the only target of oxytocin, however. It is released also in the body during birth, facilitating the contractions. During lactation, oxytocin is needed for milk ejection, but is also released in the brain of both mother and infant with a calming influence. Assuming the typical background neural circuitry and assuming the typical suite of other resident neurochemicals, oxytocin facilitates attachment of mother to baby. And of baby to mother (Keverne & Curley, 2004; Broad et al., 2006).

Physical pain is a 'protect myself' signal, and these signals lead to corrective behavior organized by self-preservation circuitry. In mammals, the pain system is expanded and modified; protect myself and protect my babies. In addition to a pathway that identifies the kind of pain and locates the site of a painful stimulus, there are pathways responsible for emotional pain, prominently associated with the cingulate cortex, but also subcortical structures such as the amygdala. So when the infant cries in distress, the mother's emotional pain system responds and she takes corrective action. Another cortical area, the insula, monitors the physiological state of the entire body. When you are gently and lovingly stroked, this area sends out 'emotionally-safe' signals (*doing-very-well-now*). The same emotionally-safe signal emerges when the baby is safe and content. And of course the infant responds likewise to gentle and loving touches: *ahhhhh, all is well, I am safe, I am fed*. Safety signals down-regulate vigilance signals such as cortisol. When anxiety and fear are down-regulated, contentment and peacefulness can take their place.

The expression of maternal behavior also depends on the endogenous opioids. This means that during suckling and other kinds of infant care, the opioids down-regulate anxiety, allowing for peaceful responses. If opioid receptors are experimentally blocked, maternal behavior is blocked. This has been observed, for example, in rats, sheep, and rhesus monkeys (Martel et al., 1993; Keverne, 2004; Broad et al., 2006). A reasonable speculation is that the endogenous cannabinoids also play an important role, but much about the extensive cannabinoid system remains unknown.

Although some mammals, such as marmosets and titi monkeys are biparental, in many species, the father takes no interest in parenting and shows none of the mother's attachment to the infant. There are many variations on the basic circuitry regulating parental behavior, depending on a species' ecological niche and how it makes its living. For example, sheep refuse to suckle any lamb that is not their own, whereas pigs and dogs will often suckle nonkin, and even infants of other species.

Studies on rodents of the effect of separation of a pup from the mother (3 h a day for the first two weeks of life) reveal experience-dependent changes in oxytocin and vasopressin synthesis, as well as changes in brain-specific regions of receptors for oxytocin and vasopressin. Behaviorally, the pups that were separated from their mothers showed heightened aggression and anxiety. In some way that is not yet entirely understood, the rats' brains and behavior were altered in a deprived social environment (Veenema, 2012). In a set of important findings on the relationship between stress regulation, gene expression and social behavior, Michael Meaney and colleagues have shown in rodents that during infancy, licking and loving stimulates gene expression that affects the density of receptors for oxytocin in the hypothalamus. More generally, parental tending, or lack thereof, regulates neuroendocrine responses to stress (Meaney, 2001). They also showed that variations in maternal care of female infants is associated with subsequent variations in maternal care displayed by those same females to the next generation of infants. This is a remarkable epigenetic effect. It suggests that neglect or abuse adversely affects the capacity for normal caring, and hence for normal socialization. Further research will explore this matter further.

Here is where we are in the values story: that anything has value *at all* and is motivating *at all* ultimately depends on the very ancient neural organization serving survival and well-being. With the evolution of mammals, the rudimentary 'self-caring organization' is modified to extend the basic values

of being alive and well to selected others — to *Me and Mine*. Depending on the evolutionary pressures to which a species is subject, caring may extend to mates, kin, and to friends. Social mammals do tend to show attachment and caring behavior to others besides their own offspring. Exactly which others come within the ambit of caring depends, as always, on the species, how it makes its living, and whether it is thriving. The pain of another's distress and the motivation to care seems to fall off with social distance. By and large, motivation to care seems to be stronger for offspring than for affiliates, for friends than for strangers, for mates than for friends, and so on.

If the maternalization of the brain means that care extends to offspring via mechanisms in the hypothalamus, are those same mechanisms modified to extend care to mates and others? The answer is not entirely clear at this point. Nevertheless, prairie voles (*Microtus ochrogaster*), who tend to bond for life, have provided an important avenue of research on this question. In this context, bonding means that mates prefer the company of each other to that of any other vole. Bonded mates like to be together, the male guards the nest, and they show stress when separated. Male prairie voles also participate in rearing the pups. In prairie voles, permanent bonding typically occurs after the first mating. Bonding does not imply sexual exclusivity, but regardless of other mating interactions, the pair remains as mates that spend a lot of time together and share parenting.

Montane voles, by contrast, do not exhibit comparable social behavior, nor does the male have any role in guarding the nest or rearing the pups. They are not social, and do not like to huddle or hang out with each other.

Because these two species are so very similar, save for their social behavior, the intriguing question is this: what are the relevant differences between the brains of prairie voles and montane voles? It turned out that the differences were not macrostructural. Rather, one major difference is microstructural, pertaining mainly to oxytocin, vasopressin, and differences in the density of receptors that can bind those hormones.

In one region of the reward system (the *nucleus accumbens*), the prairie voles contrast with the montane voles in having a higher density of receptors for oxytocin. In another region of the reward system (*ventral pallidum*) prairie voles have a higher density of receptors for vasopressin. It should also be noted that both males and females have oxytocin and vasopressin, along with their cognate receptors.

The differences in receptor density are one circuit-level difference that help explain long-term attachment of mates after the first mating, but there are other factors involved as well. For example, after mating, the mates need to be able to recognize one another as individuals. Recognition requires learning, which is mediated by the neurotransmitter, dopamine. So if you block the receptors for dopamine, the vole cannot remember whom it was she mated with, and so bonding with a particular mate does not occur. It should also be noted that the receptor density portfolio seen in prairie voles may not extend to all pair-bonders. For example, in mice, the density of vasopressin receptors in the ventral pallidum does not distinguish monogamous from promiscuous species of mice (Goodson, 2013). For technical and ethical reasons, essentially nothing is known about human nonapeptide receptor densities.

Though very common among birds, strong mate preference is somewhat uncommon in mammals. Only about three percent of mammals, including prairie voles, pine voles, California deer mice, beavers, titi monkeys and marmosets show mate attachment.

How exactly do oxytocin and vasopressin regulate other-care? A proper answer would involve the details of all the relevant circuitry and how the neurons in the circuits behave. Unfortunately, these details are not yet known (Goodson, 2013). What is known is that in rodents oxytocin down-regulates the activity of neurons in the amygdala, a structure mediating fear responses and avoidance learning, among other things (Panksepp, 2003; Panksepp & Biven, 2012). When animals are in high alert against danger, when they are preparing to fight or flee, stress hormones are high and oxytocin levels are low. When the threat has passed and the animals is among friends, hugging and chatting, stress hormones back off and oxytocin levels surge. So not only are the amygdala-dependent fear responses down-regulated, but the brain-stem switches from fight-and-flight preparation to rest-and-digest mode.

Is oxytocin the love molecule or the cuddle molecule, as has sometimes been suggested? No. The serious research on oxytocin reveals how very complicated is its action, and how complicated is the circuitry underlying social attachment (Churchland & Winkielman, 2012). Some remarkable claims about correlations between strength of love and blood levels of oxytocin are so astonishing as to raise a flag regarding experimental procedures (McCulloch et al., 2013). Caution is in order.

Lest it be thought that if something is good, more of it will be better, here is a cautionary note. If extra oxytocin is injected into the brain of a happily mated female prairie vole, her degree of mate attachment actually wanes, not rises, and she may become promiscuous.

4. Morality in humans

The foregoing constitutes a very brief overview of what is known about how oxytocin and vasopressin operate in the brain to create a platform for sociality, and hence for morality. But how do we get from a general disposition to care about others, to specific moral actions, such as telling the truth, respecting the goods of others, and keeping promises? How do we get from familial caring to broader community-wide values such as honesty, loyalty and courage? The answer has two intertwined parts: learning by the young, and problem-solving by everyone.

In group-living species such as humans, lemurs and baboons, learning the local conventions and the personality traits of individuals, knowing who is related to whom, and avoiding blackening one's own reputation become increasingly important. Learning, especially by imitation, is the mammalian trick that gets us both flexibility and well-grooved skills. Problem-solving, in the context of learning by trial and error, is the complementary trick that leads to stable social practices for avoiding such problems as conflict.

Children observe, sometimes quite automatically and implicitly, sometimes explicitly and with reflection, the advantages of cooperation. Two children rowing a boat gets them across the lake much faster; two turning the long skipping rope allows doubles skipping, turn-taking means everyone gets a chance so the games do not break down. Men working together can raise a barn in one day. Women working together feed all the men and the children. Singing in a group with parts makes beautiful music. Pitching a tent is easier with two people, and hiking together provides safety. A child quickly comes to recognize the value of cooperation (on the formation of group identity in children, see Killen & Rutland, 2013).

This does not mean that there is a gene 'for cooperation'. If you are sociable, and you want to achieve some goal, then a cooperative tactic can seem a fairly obvious solution to a practical problem. As philosopher David Hume observed, a crucial part of your socialization as a child is that you come to recognize the value of social practices such as cooperation and

keeping promises. This means you are then willing to sacrifice something when it is necessary to keep those practices stable in the long run. You may not actually articulate the value of such social practices. Your knowledge of their value may even be largely unconscious, but the value shapes your behavior nonetheless. Brosnan (2011) suggests this is true also of nonhuman primates.

In this context it is important to remember that although all mammals are born immature and learn a great deal during development, the period of human immaturity is especially long and the amount of learning is prodigious. For example, about 50% of a human brain's connections emerge after birth, and the human adult brain weighs about five times that of the infant brain. (Bourgeois, 1997; Huttenlocher & Dabholkar, 1997).

Moreover, in the period leading up to puberty the human brain undergoes substantial pruning and therewith a decrease in connectivity, whereas rodent brains and monkey brains do not show the same degree of pre-pubertal pruning. Jean-Pierre Changeux has argued that these particular epigenetic features of human brain development — extended immaturity and pre-pubertal pruning — enable learning of complex social and cultural organization. (Changeux, 1985). More succinctly, Changeux proposes that the unique developmental profile is what has made human culture, including its moral institutions, possible. Interestingly, this unusually long period of immaturity may depend only on a few regulatory genes that extend the period of epigenetic responsivity to the social and physical environments (Keverne & Curley, 2008).

What I call problem-solving is part of a general capacity to do smart things, and to respond flexibly and productively to new circumstances. Social problem-solving is directed toward finding suitable ways to cope with challenges such as instability, conflict, cheating, catastrophe and resource scarcity. It is probably an extension to the social domain of a broader capacity for problem solving in the physical world. Depending on what you pay most attention to, you may be more skilled in the social domain or in the nonsocial domain, or vice versa. From this perspective, moral problem-solving is, in its turn, a special instance of social problem-solving more broadly (Peterson, 2011).

Although evaluating how to proceed with a particular case is frequently the most pressing concern, the more fundamental problem concerns general principles and institutional structures that undergird well-being and stability.

The development of certain practices as normative — as the right way to handle *this* problem — is critical in a group's cultural evolution (Kitcher, 2012). These norms are established principles enjoining group members against such behavior as embezzlement and other specific forms of cheating. Motivated to belong, and recognizing the benefits of belonging, humans and other highly social animals find ways to get along, despite tension, irritation, and annoyance. Social practices may differ from one group to another, especially when ecological conditions are different. The Inuit of the Arctic will have solved some social problems differently from the Piranhã of the Amazonian basin in Brazil, if only because social problems are not isolated from the physical constraints such as climate and food resources (Hoebel, 1954; Everett, 2009).

Similarities in social practices are not uncommon, as different cultures hit upon similar solutions to particular problems. Subtle and not so subtle differences may also obtain. This is akin to common themes in other practices, such as boat-building or animal husbandry. Particular cultures developed skills for building particular styles of boats — dugout canoes, birch bark canoes, skin-backed kayaks, rafts with sails, junks for fishing on the rivers, and so forth. After many generations, the boats made by separate groups are exquisitely suited to the particular nature of the waters to be traveled on and the materials available. Notice too that many different cultures learned to use the stars for navigation. Some picked up the trick from travelers, others figured it out independently, just as conventions for private property occurred in different groups as their size expanded as agricultural practices became widespread. I am reasonably confident that there is no gene for navigating by the stars.

Though expressions of moral values can vary across cultures, they are not arbitrary, in the way that the conventions for funerals or weddings tend to be. Matters of etiquette, though important for smoothing social interactions, are not serious and momentous as moral values are. Truth-telling and promise-keeping are socially desirable in all cultures, and hence exhibit less dramatic variability than customs at weddings. Is there a gene for these behaviors? Though that hypothesis cannot be ruled out, there is so far no evidence for a truth-telling or a promise-keeping gene. More likely, practices for truth-telling and promise-keeping developed in much the same way as practices for boat building. They reflected the local ecology and are a fairly obvious solution to a common social problem (Hoebel, 1954).

Being reminded of the variability in what counts as morally acceptable helps us acknowledge that standards of morality are not universal. More generally, it reminds us that moral truths and laws do not reside in Plato's heaven to be accessed by pure reason. It reminds us that perorations about morality are often mixed with a whole range of emotions, including fear, resentment, empathy and compassion (Decety, 2011).

5. Tensions, conventions and balance

The mammalian brain is organized both for self-care and to develop care for others, but on many occasions, the two conflict. Social life brings benefits, but it also brings tensions. We compete with siblings and friends for resources and status; we also need to cooperate with them. Some individuals are temperamentally more problematic than others. Sometimes you have to tolerate others who are irritating or noisy or smelly.

Social life can often be very subtle, calling for judgment, not strict adherence to rules. As Aristotle and the Chinese philosopher, Mencius, well realized, you cannot prepare for every contingency or for every situation that may crop up in life. Judgment is essential. Sometimes telling a lie *is* the right thing to do — if it saves the group from a madman threatening to blow up a bomb, for example. Sometimes breaking a promise is the right thing to do — if it prevents a truly terrible catastrophe, such as the meltdown of a nuclear reactor. There are no rules for determining when something is a legitimate exception to prohibitions, such as do not lie, do not break a promise, and do not steal. Children quickly learn about prototypical exceptions, and apply fuzzy-bounded categories rather than hide-bound rules (Killen & Smetana, 2008; Park & Killen, 2010). Balance, as all wise moral philosophers have emphasized, may not be precisely definable, but it is needed to lead a good social and moral life. Not every beggar can be brought home and fed, not all your kidneys can be donated, not every disappointment can be remedied (Schwartz & Sharpe, 2010).

6. Concluding remarks

The capacity for moral behavior is rooted in the neurobiology of sociality, and in mammals depends on nonapeptides oxytocin and vasopressin, as well as on elaborated cortical structures that interface with the more ancient structures mediating motivation, reward, and emotion. The neural mechanisms

supporting social behavior are tuned up epigenetically by social interactions and by learning the social practices of the group, and by figuring out how to best deal with new social problems. Emerging after the advent of agriculture and the growth of large groups, organized religions would have built upon existing social practices, perhaps augmenting them in ways relevant to new social demands. Although it is known that oxytocin and vasopressin are critical in social behavior, much about their roles as well as the circuitry with which they interact remains unknown.

References

- Bourgeois, J.P. (1997). Synaptogenesis, heterochrony and epigenesis in mammalian neocortex. — *Acta Paediatr. Suppl.* 422: 27-33.
- Broad, K.D., Curley, J.P. & Keverne, E.B. (2006). Mother–infant bonding and the evolution of mammalian social relationships. — *Phil. Trans. Roy. Soc.* 361: 2199-2214.
- Brosnan, S.F. (2011). A hypothesis of the co-evolution between cooperation and response inequity. — *Front. Decis. Neurosci.* 5: 43.
- Carter, C.S., Grippo, A.J., Pournajafi-Nazarloo, H., Ruscio, M. & Porges, S.W. (2008). Oxytocin, vasopressin, and sociality. — *Progr. Brain Res.* 170: 331-336.
- Changeux, J.-P. (1985). *Neuronal man*. — Pantheon Books, New York, NY.
- Cheng, Y., Chen, C., Lin, C.-P., Chou, K.-H. & Decety, J. (2010). Love hurts: an fMRI study. — *NeuroImage* 51: 923-929.
- Churchland, P.S. (2011). *Braintrust: what neuroscience tells us about morality*. — Princeton University Press, Princeton, NJ.
- Churchland, P.S. (2013). *Touching a nerve*. — Norton, New York, NY.
- Churchland, P.S. & Winkielman, P. (2012). Modulating social behavior with oxytocin: How does it work? What does it do? — *Horm. Behav.* 61: 392-399.
- Decety, J. (2011). The neuroevolution of empathy. — *Ann. NY Acad. Sci.* 1231: 35-45.
- Everett, D. (2009). *Don't sleep, there are snakes: life and language in the Amazonian jungle*. — Pantheon Books, New York, NY.
- Goodson, J.L. (2013). Deconstructing sociality, social evolution and relevant nonapeptide functions. — *Psychoneuroendocrinology* 38: 465-478.
- Hoebel, E.A. (1954). *The law of primitive man*. — Harvard University Press, Cambridge, MA, Chapter 5.
- Huttenlocher, P.R. & Dabholkar, A.S. (1997). Regional differences in synaptogenesis in human cerebral cortex. — *J. Comp. Neurol.* 387: 167-178.
- Keverne, E.B. (2004). Understanding well-being in the evolutionary context of brain development. — *Phil. Trans. Roy. Soc. Lond. B* 359: 1349-1358.
- Keverne, E.B. (2007). Genomic imprinting and the evolution of sex differences in mammalian reproductive strategies. — *Adv. Genet.* 59: 217-243.
- Keverne, E.B. & Curley, J.P. (2004). Vasopressin, oxytocin and social behaviour. — *Curr. Opin. Neurobiol.* 14: 777-783.

- Keverne, E.B. & Curley, J.P. (2008). Epigenetics, brain evolution and behavior. — *Front. Neuroendocrinol.* 29: 398-412.
- Killen, M. & Rutland, A. (2013). Children and social exclusion: morality, prejudice and group identity. — Wiley-Blackwell, Oxford.
- Killen, M. & Smetana, J.G. (eds) (2006). Handbook of moral development. — Lawrence Erlbaum Associates, Mahwah, NJ.
- Kitcher, P.S. (2012). The ethical project. — Harvard University Press, Cambridge, MA.
- Krubitzer, L. (2007). The magnificent compromise: cortical field evolution in mammals. — *Neuron* 2: 201-208.
- Krubitzer, L., Campi, K.L. & Cooke, D.F. (2011). All rodents are not the same: a modern synthesis of cortical organization. — *Brain Behav. Evol.* 78: 51-93.
- Krubitzer, L. & Kaas, J. (2005). The evolution of the neocortex in mammals: how is phenotypic diversity generated? — *Curr. Opin. Neurobiol.* 15: 444-453.
- Lane, N. (2009). Hot blood, Chapter 8. — In: *Life ascending: the ten great inventions of evolution*. W.W. Norton, New York, NY.
- Martel, F.L., Nevison, C.M., Rayment, F.D., Simpson, M.J. & Keverne, E.B. (1993). Opioid receptor blockade reduces maternal affect and social grooming in rhesus monkeys. — *Psychoneuroendocrinology* 18: 307-321.
- McCullough, M.E., Churchland, P.S. & Mendez, A.J. (2013). Problems with measuring peripheral oxytocin: Can data on oxytocin and human behavior be trusted? — *Neurosci. Behav. Rev.* 37: 1485-1492.
- Meaney, M.J. (2001). Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. — *Annu. Rev. Neurosci.* 24: 1161-1192.
- Panksepp, J. (2003). Feeling the pain of social loss. — *Science* 302: 237-239.
- Panksepp, J. & Biven, L. (2012). The archaeology of mind: neuroevolutionary origins of human emotions. — Norton, New York, NY.
- Park, Y. & Killen, M. (2010). When is peer rejection justifiable? Children's understanding across two cultures. — *Cogn. Dev.* 25: 290-301.
- Peterson, D. (2011). The moral lives of animals. — Bloomsbury Press, New York, NY.
- Porges, S.W. & Carter, C.S. (2007). Neurobiology and evolution: mechanisms, mediators, and adaptive consequences of caregiving. — In: *Self interest and beyond: toward a new understanding of human caregiving* (Brown, S.L., Brown, R.M. & Penner, L.A., eds). Oxford University Press, Oxford, p. 53-71.
- Quartz, S.R. & Sejnowski, T.J. (1999). The constructivist brain. — *Trends Cogn. Sci.* 3: 48-57.
- Quartz, S.R. & Sejnowski, T.J. (2003). Liars, lovers and heroes. — William Morrow, New York, NY.
- Schwartz, B. & Sharpe, K. (2010). Practical wisdom: the right way to do the right thing. — Riverhead Books, New York, NY.
- Veenema, A. (2012). Toward understanding how early-life social experiences alter oxytocin- and vasopressin-regulated social behaviors. — *Horm. Behav.* 61: 304-312.
- Young, L. & Alexander, B. (2012). The chemistry between us: love, sex and the science of attraction. — Penguin, New York, NY.