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10 Girl Uninterrupted: The Neural Basis of Moral Development among Adolescent Females

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The nature of our moral selves has intrigued and eluded scholars in religion, philosophy, and psychology for centuries. Advances in modern science have given us many reasons to think that we are increasingly close to uncovering the substrates of what makes a person "moral." Morality can be described as an intricate system of beliefs, values, and ideas that ultimately influences how an individual distinguishes between right and wrong and acts upon these judgments (Kalsoom, Behlol, Kayani, & Kaini, 2012). In fact, our evolved morality is thought to be one of the things that, along with complex language, sets us apart from other species. It is interesting that both language and morality appear to be uniquely human as they share critically important attributes. Moral and linguistic development are not hard-wired abilities but, rather, intricate capacities that are shaped by the context of our experience (Caravita, Gini, & Pozzoli, 2012; Kalsoom et al., 2012; Nelson & Buchholz, 2003). The plasticity observed in both moral and linguistic development is at once the most fascinating and mysterious feature of both abilities. Like language, morality has a developmental course (see Baird, 2007 for a review) that is shaped by an idiosyncratic interaction of nature and nurture; this interaction has made it nearly impossible to construct a single model for how humans come to be moral creatures. Ironically, those whose moral standards we often question the most, namely adolescents, may have the most to teach us about how we acquire our moral reasoning as adults. Although children as young as three years old have been shown to exhibit an understanding of moral versus immoral behaviors (Caravita et al., 2012), morality develops throughout the life span, with the most profound period of moral development occurring during adolescence (Walker, 1989). Adolescence is a particularly crucial period of development given the significant changes that occur during this time. Moral development during

this period is aided by a complex combination of biopsychosocial factors, including neuronal maturation, changes in cognition, and a shift from a parent-centered to peer-centered social world.

People are never more certain about what is right or wrong as they are during adolescence (independent of the accuracy of these thoughts). Unprecedented gains in abstract thinking that follow the neural maturation of puberty enable adolescents to think about their own thoughts, as well as the thoughts of others, from a third-party (or non-egocentric) point of view for the first time in their lives. The ability to contemplate their own thinking, as well as the thoughts of those around them, fills most adolescents with a great sense of accomplishment, often misperceived as self-righteousness or egocentrism. What young adolescents have yet to realize, however, is that this ability is just the beginning of a learning process, driven by context, that will provide them with the skills needed to engage in adult levels of moral reasoning and, in most cases, moral behavior. The means by which an individual comes to integrate his/her own beliefs with those of the people and larger society around her/him is precisely what prepares an adolescent to enter the adult social world. This process is so critical to the survival of the human race that it may in fact be the best lens through which to understand how our brains contribute to moral reasoning.

The very nature of adolescence makes a compelling case for using it as a vantage point from which to study the brain bases of moral thought because it brings two critically important factors to the forefront of the discussion. The first of these resides in the functional purpose of adolescence—namely to differentiate the sexes from one another in order to eventually enable procreation. Although sex differences have been studied a bit in the extant literature, individual differences also need to be considered in terms of gender—the social construct that accompanies the presentation of biological sex. Second, although few would argue that morality is contextually bound, at no other point in one's life is the context more influential to brain development than during the transition into adult society. For most adolescents, context will consist largely of the community and culture in which they reside, mixed with a healthy dose of the contemporary culture within their peer group. The discussion that follows explores these ideas by first briefly reviewing the most recent literature on the brain bases of moral reasoning in adults and the sex differences that have been reported. Next we turn to the importance of sexual dimorphism during adolescence and

how this manifests in unique aspects of female peer relationships. Finally, we attempt to integrate these ideas and suggest possible directions for future research on the neural substrates of moral thought.

The Moral Brain circa 2015

Although recent years have produced a number of exciting findings from the study of the neurophysiological underpinnings of adult moral reasoning, most investigations have referenced, albeit to different extents, the same "characters" (i.e., neuroanatomical regions). It is worth a short review before we think about how we might revise our conceptions of moral development. As previously discussed, moral behavior among most adults is the result of the coordination of a number of neural regions and networks. Each component of morality, from emotional recognition and empathy to the evaluation of outcomes and decision making, involves a number of brain regions, all of which work together in various combinations to eventually allow an individual to engage in moral behavior. Although a complete review of these regions is beyond our scope here, the most fundamental are worth mentioning. It is possible to divide the neural regions associated with moral reasoning in the adult brain into three groups on the basis of their function: emotional experience, mentalizing, and behavioral regulation.

The *emotional experience* group consists of the amygdala, the anterior insula, and the dorsal anterior cingulate cortex—all of which contribute to the experience and memory of emotion. The *amygdala* is particularly important in the process of evaluating potential rewards or punishments of a given situation. It is typically associated with the "fight or flight" response and is most reactive to visual and potentially threatening stimuli (Adolphs, 1999; Blair, 2007). The amygdala is a structure that is active, in some form, in nearly every study of human emotion. The experience of emotion relies most heavily on interoception. *Interoception* refers to the dynamic processing of afferent homeostatic sensory information and the ability for that information to reach conscious awareness. This also includes the creation of abstracted feeling states (cold, hunger, pain) from the diverse set of discrete sensations that arrive from multiple internal sensory systems.

The *anterior insula*, which is home to the primary cortical representation of the body's internal state, is consistently referred to as the critical hub (along with the anterior cingulate) for interoceptive (emotional) experience.

It seems that a major function of the anterior insula is to assemble diverse sensory information into coherent feeling states and to assess the salience of those states in service of executive control (Craig, 1996, 2004; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). Another critical aspect of interoception is the experience of physical pain. A number of studies have validated both the anterior insula (Ostrowsky et al., 2002) and the posterior portion of the anterior cingulate cortex (see Price, 2000, for a review) as being critical to the experience of physical pain.

What is most relevant about the function of these two regions is that human beings have overlaid prosocial emotions onto the primary sensory function of these regions, co-opting their function for the underpinnings of moral behavior. In the same way that the posterior portion of the anterior cingulate aids in the experience of physical pain, a series of elegant studies led by Eisenberger have demonstrated that this same tissue also processes social pain and exclusion (see Eisenberger, 2012, for a review). In addition to physical pain, guilt may be the most powerful emotion in terms of moral motivation. Studies have reliably shown that the anterior insula is highly active during the experience of interpersonal guilt, as a derivative of the more primitive interoceptive state of disgust (Phillips et al., 1997; Shin et al., 2000). Disgust is a universal human emotion tied to a set of nonverbal behaviors that clearly and rapidly convey a visceral, repulsive sensation. Together, the evidence described above suggests that the relatively complex emotion of guilt has, over the course of evolution, co-opted the neural hardware that enables enduring avoidance of noxious stimuli, following just a single experience. This primary response has been expanded in the social realm, where the very same social signals that reduce the probability of an individual ingesting toxic substances are also able to significantly reduce the chances of an individual violating important moral standards. The insula and anterior cingulate cortex produce aversive visceral responses associated with witnessing or engaging in immoral behaviors (Bechara, 2001; Krach et al., 2011; Vogt, Finch, & Olson, 1992), such as experiencing nausea accompanied by feelings of guilt or anxiety, which are likely to reduce future immoral behavior. Finally, insula-driven guilt has been associated with a desire to compensate others and engage in self-punishment (Berthoz, Grèzes, & Armony, 2006; Yu, Hu, Hu, & Zhou, 2013).

The *mentalizing group* is comprised of the posterior cingulate, precuneus, retrosplenial cortex, as well as the dorsolateral portion of the parietal cortex

(which includes the supramarginal and angular gyri). Collectively, these regions support processes that require understanding the perspective of others and integrating it with one's own experience. These regions have also been shown to participate in the creation of the individual's socioemotional "narrative" (Greene & Haidt, 2002) through the integration of emotion, mental imagery, and contextually specific memory (Fletcher et al., 1995; Moll, Eslinger, & de Oliveira-Souza, 2001). More specifically, the posterior cingulate cortex (PCC) is consistently described as the central node in the default mode network (see Buckner et al., 2008, for a review as well as Fair et al., 2009, for a review of its developmental course). The PCC has been shown to play a prominent role in the processing of both pain and contextually relevant episodic memory (Maddock, Garrett, & Buonocore, 2001; Nielsen, Balslev, & Hansen, 2005). Additionally, previous results have suggested that the PCC inhibits the parietal cortices to avoid distractions and simultaneously activates the medial prefrontal cortex to redirect attention so the individual can internally generate mental strategies (Small et al., 2003). In sum, the PCC subserves a constellation of functions that relate, most fundamentally, to intrinsic experience and the flexible nature of thoughtful and self-preserving behavior (Pearson, Heilbronner, Barack, Hayden, & Platt, 2011).

The precuneus is known to contribute to processes of reflective self-awareness and autobiographical recall (Kjaer, Nowak, & Lou, 2002; Lundstrom, Ingvar, & Petersson, 2005). In close collaboration with the precuneus, the retrosplenial cortex also contributes to self-relevant aspects of memory. Specifically, it has been shown to support processes related to planning and hypothetical reasoning (Vann, Aggleton, & Maguire, 2009). Both regions contribute to moral reasoning by recognizing socially significant visual cues, aiding in the theory of mind process, and reflecting on complex conceptions of "humanness" (Allison, Puce, & McCarthy, 2000; Brothers & Ring, 1992; Frith, 2001). Together, the supramarginal and angular gyri are often referred to as the *inferior parietal cortex*, the *parietal operculum*, or the *temporoparietal junction*. This area has been shown to correspond with tasks that require an individual to make inferences about the mental states of others, especially when compared to physical qualities about people. It is among the most commonly observed areas of activity during tasks that require theory of mind strategies (Saxe & Kanwisher, 2003) and/or the ability to distinguish between one's own thoughts and the thoughts of others (Decety & Sommerville, 2003).

Finally, the medial prefrontal cortex makes up the *behavioral regulation group* of regions. The group includes the ventral anterior cingulate cortex, the dorsomedial and ventromedial prefrontal regions, and the hippocampus. Collectively, these regions contribute to the attentional, organizational, and regulatory aspects of emotional information as it pertains to the individual. Generally, the *medial prefrontal cortex* enables individuals to integrate their emotions with decision-making processes. Additionally, this region is critical to the development of conscious moral planning (Damasio, 1994; Reiman, 1997). The ventral portion of the ACC is most reliably engaged during conditions in which, under high arousal, it is important to direct attention to the processing of emotional information. In these instances, the ventral ACC seems to work closely with the ventromedial prefrontal cortex in terms of attention to potentially rewarding information (see Phillips, Drevets, Rauch, & Lane, 2003, for a review). The ventromedial prefrontal cortex is primarily responsible for evaluating rewards and punishments and for providing individuals with the ability to control and inhibit potentially disadvantageous behaviors (Blair, 2001; Damasio, 1994; Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994; O'Doherty, Kringelbach, Rolls, Hornack, & Andrews, 2001). The dorsomedial prefrontal cortex has been shown to be critical for making highly adaptive, very rapid real-world social decisions (Cooper, Dunne, Furey, & O'Doherty, 2012). It has been consistently linked with cognitions about the "self," making distinctions between "self" and "other" (Mitchell, Banaji, & Macrae, 2005; Pfeifer, Lieberman, & Dapretto, 2007), and contributing to the manipulation of information related to the "self" (Ochsner et al., 2004).

Finally, our ability to experience emotion, organize and perform cognitive functions on acquired emotional information, and regulate our behavior using previous experience all critically rely on the functionality of the hippocampus. Among the innumerable functions the hippocampus subserves, it is critical for the consolidation of cohesive experiences in which all of the functions described above (and more) are meaningfully integrated and stored in long-term memory (see Murray & Kensinger, 2013, for a review).

Theories of Moral Development

There has always been a great deal of variance in how morality is defined, both theoretically and operationally. The variations in the most basic ideas

of moral theory are critical to understanding why modeling moral development is such a herculean (or possibly Sisyphean) task. In the psychological literature, the work of Lawrence Kohlberg forms the backbone of how we understand moral development. Kohlberg's (1974) theories of moral development describe the progression from an obedience and punishment orientation, to the native hedonistic and instrumental orientation, to the good boy/girl orientation, and, finally, to the law and authority orientation. Although Kohlberg's theories set a framework for psychologists to gauge developmental milestones in relation to morality, other theorists (Baumrind, 1986; Gilligan, 1982) have suggested that his orientations contain a bias that favors traditionally "male" reasoning and, in doing so, fail to address decision-making processes and morality formation as typically experienced by females.

Carol Gilligan (1982) has offered a more feminist perspective of moral development. Kohlberg theorized that females rarely progress past the third (good girl/boy) stage of moral development, whereas males consistently exhibit morality development through the fourth (law and authority) stage (Muuss, 1988). Gilligan argues that females are just as morally developed as males but that they simply approach morality from a different perspective. According to her theoretical framework, females employ an interpersonal outlook that fosters interdependent relationships, emphasizes responsibility toward others, and focuses on sensitivity toward humanity. Males, on the other hand, employ a justice-oriented approach that focuses on upholding rules, engaging in logical thinking, and preserving autonomy (Kalsoom et al., 2012; Muuss, 1988; Silfver & Helkama, 2007; Walker, 1989). Gilligan is careful to explain that the two approaches are neither hierarchical nor mutually exclusive. That is, both approaches are equally valid, and individuals of both sexes tend to engage in a combination of interpersonal- and justice-oriented moral development. Thus, although women and men engage in morality formations that bring them to the same conclusions of "right" and "wrong," they often prefer different routes of processing, which urge them to rely more heavily on one orientation than the other.

Although Gilligan's morality theories have been widely referenced throughout the field of psychology, most researchers have been unsuccessful in their attempts to find empirical validation for her ideas. One possible explanation for this lack of evidence results from the fact that tests of moral reasoning have traditionally compared participants on the basis of

biological sex, as opposed to gender. Although it is beyond the scope of the present discussion to explore this idea entirely, it is worth consideration.

"Sex" and "gender" are different despite the fact that there is most often a great deal of overlap between the two. Whereas sex refers to the chromosomes and biology that make one male or female, gender is more difficult to define. Gender is often influenced by both context and the individual's beliefs about her or his own identity. When a baby is born (with a small number of exceptions), the child is immediately identified as male or female based on its visible genitalia, but it will be a few years before the child's gender develops (see Bussey & Bandura, 1999, for a thorough review). If we are to responsibly seek out models of moral development, the effects of both neurobiological factors associated with sex and the sociocultural influences of gender must be prominently considered.

Young children do not possess secondary sex characteristics, such as facial hair or full breasts, physical signs meant to signal their biological sex to others. These traits do not emerge until adolescence simply because they are physical manifestations of the increases in sex hormones that accompany puberty. Evolutionarily, these differences have evolved because they enable people of reproductive age to recognize each other with greater ease and speed. It was once believed that the way in which these traits appeared determined how masculine or feminine a person was, but it is now understood that feelings and perceptions of gender are much more complex and nuanced ideas. Simply, as societies evolve, so do their gender norms. At present, males still show more "traditionally male," and females "traditionally female" behavior, but there are increasing numbers of individuals who show a mix of the two (Gilligan, 1982; Muuss, 1988). In terms of understanding individual differences in moral reasoning, adding gender (in addition to biological sex) might enable us to forge a more parsimonious model of moral development by integrating the work of both Kohlberg and Gilligan.

Although there are few consistently reported sex differences in moral reasoning, research has indicated a number of small, albeit important, distinctions on the basis of gender. For example, girls have been shown to exhibit an increased tendency toward guilt, and they often employ a more implicit and empathic processing route in order to reach these conclusions. Boys, on the other hand, exhibit guilt less frequently, and they usually rely more on cognition and reasoning to form these feelings (Silfver & Helkama, 2007). Additionally, girls tend to prefer evaluations of social desirability

(i.e., being considered kind or well-liked), as opposed to boys who more readily strive for social status (i.e., being considered popular or socially influential) (Caravita et al., 2012).

The following sections focus on a female perspective. This point of view is presented not because moral dilemmas faced by boys are less important or complex; rather, we explore feminine experiences with morality because it is important to approach the topic from a rarely considered perspective. It will be equally important for future work to explore moral development from a male (sex), or masculine (gender), vantage point. For the purpose of this chapter, we refer only to the differences between self-identifying males and females, although future researchers may consider incorporating gender identifications that do not fit the typical binary model. Additionally, it should be noted that although "relational" people tend to be female, gender and relational personality are not direct correlates of one another and thus may produce variation in measured outcomes. Thus, "females" and "relational people" usually, although not universally, fall into Gilligan's model of interdependence/caring.

Female Puberty and Peer Relationships

The learning and organization of social behavior that takes place during adolescence occurs within a sensitive period, when the biology is uniquely attuned to socially relevant information that is able to be acquired at a particularly astounding rate (Nelson & Guyer, 2011). The remarkable developmental plasticity of the human brain enables adolescents to learn seemingly endless information about their unique and highly variable social contexts. As a result, it makes practical sense to think of the adolescent brain as a primarily social organ with the capacity to acquire knowledge and behavior that is essential for thriving in a highly complex social environment (Burnett, Thompson, Bird, & Blakemore, 2011; Sebastian, Viding, Williams, & Blakemore, 2010).

The myriad changes that occur in adolescence require substantial revision to the systems responsible for understanding one's experience. At puberty, females acquire the capacity to give birth and care for an infant; therefore, it is only logical that they would be predisposed to emotional, empathic, and sociocognitive processes that are unique. Taylor's (2006) "tend and befriend" model posits that women may be more likely to resort to forming

interdependent relationships in a time of physical or moral crisis. Rooted in an evolutionary perspective, her theory explains females' tendencies to engage in relationship formation during stressful situations as indicative of what was, historically, a necessary survival mechanism for families faced with a threat. In other words, a woman's act of engaging in relationship formation serves as a remnant of a mother's responsibility to protect her offspring in the face of danger. It follows logically, then, that this strategy would emerge following brain changes that occur during puberty. Humans universally agree that hurting children is a deplorable act, but few respond with the ferocity and tenacity of the mother of a child who has been injured. This development begins early in adolescence wherein adolescents become more prosocial than younger children (Fabes & Kupanoff, 1999) and friendships become increasingly important (Berndt, 1982; Brown, 2004; Larson & Richards, 1991; Richards, Crowe, Larson, & Swarr, 1998).

A large body of behavioral evidence has underscored the importance of same-sex peer relationships, especially among girls, during this time (Ma & Huebner, 2008; Prinstein, Cheah, Borelli, Simon, & Aikins, 2005; Rudolph, 2002). In general, girls have a greater propensity than boys to form close, intimate, self-disclosing friendships (Claes, 1992; Ma & Huebner, 2008). From an evolutionary perspective, greater affiliation among women is advantageous because it ensures group survival. Similarly, from a middle school perspective, a "tend and befriend" pattern (Taylor et al., 2000) among adolescent girls would seem to be advantageous because tightly knit friend groups tend to outline and adhere to common norms of behavior (which is often the bedrock of moral reasoning). These strategies serve to reduce individuals' uncertainty about how to "survive" within the larger school environment (Zwolinski, 2008). The socialization style observed among girls likely reflects the nature of both the biological changes initiated by adolescence and the sociocognitive transformations that accompany this maturation. For females, exploring and learning about interpersonal difficulties and moral dilemmas involving friends (i.e., engaging the interdependent orientation) may be an important step in shaping subsequent ideals of morality and determining future actions. Although there are certainly difficult, even painful, lessons to be learned during adolescence, this may be somewhat adaptive. It is important to remember that social pain (like physical pain) can facilitate memory of unpleasant or immoral actions and, in doing so, decrease the likelihood of their reoccurrence.

Within the context of their intense interpersonal relationships, gender roles and societal values often create a paradox for developing girls. For example, they are expected, as women, to be caring and relational, and yet, at the same time, patriarchal, individualistic Western culture rewards individuals who are less inclined to place central importance on relational thinking and behavior (Kalsoom et al., 2012). Again, it is likely that these opposing forces contribute to the lack of coherence in models of how moral reasoning develops.

Female Brain Development and Moral Reasoning

Returning to the descriptions of the neural substrates related to moral reasoning in adults, it makes sense to examine the development of these networks during adolescence and to highlight the ways in which females may differ from males. It is important to recognize that, as differences in brain structure and/or function are reviewed, it is often impossible to know the precise relationship between the two. It is equally likely that observed sex differences in neural networks are the result of idiosyncrasies in behavioral strategies or that sex differences in neural networks are responsible for the variations in reported experience and/or behavioral strategies. The increasing presence of techniques that allow scientists to model developing networks of functional connectivity shows great promise with regard to understanding how the brain functionally develops. Although still in its methodological infancy, exciting work from Power and colleagues (see Power, Fair, Schlaggar, & Petersen, 2010) has reliably demonstrated that although some neural networks in the developing brain show increased distribution across regions, with the "beefing up" of long-range connections (e.g., the frontoparietal networks known to mature in late adolescence), there are other networks that become more locally coordinated (e.g., the improved coordination among functionally distinct prefrontal regions). Ultimately, the integration of behavioral data with structural, functional, and network data from human imaging holds great promise for improving our understanding of moral development.

Emotional Experience
Earlier in this review the brain regions described as being most closely related to the emotional experience component of moral development

included the amygdala, anterior insula, and the dorsal anterior cingulate cortex. All three of these regions have demonstrated relevant structural and functional differences as a product of sex across development. The amygdala is of particular interest as it is known to be a structure critical for social and emotional learning. In terms of human development it has also been implicated in the understanding of emotional "reactivity" or basic temperament (see Kagan, Snidman, Kahn, & Towsley, 2007, for a review). This could easily predispose an individual to a certain propensity toward a "fight or flight" response that is shaped by the dense connections among the amygdala, insula, and anterior cingulate cortex that are known to emerge during adolescence. The fluid coordination of these regions is what enables adolescents to use interoceptive information to inform moral reasoning.

Evidence from previous developmental research suggests these changes would likely be seen in areas that integrate internal sensory information with higher cognitive processes. Early sensory areas are typically mature before the end of childhood, reaching adult levels of cortical thickness by roughly the age of eight (Gogtay et al., 2004; Shaw et al., 2008). In contrast, many higher-order cortical regions, such as the dorsolateral prefrontal cortex and anterior cingulate, are not fully mature until the mid-twenties (Bennett & Baird, 2006; Gogtay et al., 2004).

One interoceptive structure that possesses a similar protracted maturation is the anterior insula (Shaw et al., 2008). This subregion of the insula is considered by many to bridge the interoceptive sensory system with higher-order cognitive processes (Craig, 2002; Critchley et al., 2004). If the anterior insula is involved in interoceptive imagery, it is likely to show developmental differences in activity between adults and adolescents. This would represent a kind of functional disconnection between the construction of abstract interoceptive feeling states and higher-order executive control.

Among the many functions related to moral reasoning, the emotional perception of empathy relies heavily on the functions subsumed by the anterior insula. It has been shown that females show greater activity in the anterior insula (relative to males) while witnessing others being treated unfairly. It has also been shown that changes to this experimental paradigm, such as the recipient of inequity treating others unfairly or an unfair individual being subjected to physical pain, resulted in diminished activity in the anterior insula in male participants; however, insula activity remained heightened among females (Bernhardt & Singer, 2012). Given that the

insula does not fully mature until relatively late in human development, it is reasonable to assume that the observed sex differences likely emerge as a result of complex social learning during adolescence. This idea is supported by the work of Decety and Michalska, who reported a positive correlation between age and activity in the anterior insula and a negative correlation between age and activity in the amygdala during a task in which participants observed other individuals in pain that has been inflicted by another (compared with pain inflicted on oneself). It is also noteworthy that pain inflicted by others was perceived as more painful by younger subjects than by adults; and further, individuals' ratings of pain correlated positively with amygdala activity. Given the rich connections between the amygdala and anterior insula, the authors posit a developmental transition from the more primitive, survival-based response of the amygdala to a more nuanced and integrated moral response (Decety & Michalska, 2010). Decety and colleagues have also demonstrated a developmental progression whereby greater emphasis is placed on intentionality with regard to interpersonal harm, which is the cornerstone of moral reasoning. The developmental transition from an immature amygdala-based affective response to a more mature approach to moral reasoning that relies on judgments of intent was reflected in a positive correlation between age and greater functional connectivity between the amygdala and ventromedial prefrontal cortex (Decety, Michalska, & Zinzler, 2011).

Mentalizing

In terms of moral development, *mentalizing* is understood as the ability to understand the social and emotional perspective of another, to hold that person's emotional perspective in mind while keeping it separate from your own. Generally speaking, previous work has shown that children who perform better on mentalizing tasks are more sophisticated in their moral judgments as adults. This is likely because mentalizing lays the foundation for incorporating more diverse perspectives in adulthood, resulting in more complex and nuanced moral reasoning (Lane, Wellman, Olson, LaBounty, & Kerr, 2010). A simpler version of this process, theory of mind, emerges in early childhood. Saxe and Kanwisher (2003) provide elegant evidence for how the temporoparietal region becomes increasingly specialized for social information. Prior to about nine years of age, this region is shown to be highly responsive to general social information about others. However, as

individuals move closer to puberty, it becomes increasingly specialized in its responsiveness, becoming preferentially more active in response to the social and emotional states of others (Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009). This transition is critical for moral reasoning based on the experience and beliefs of socially relevant others. It is reasonable to speculate that these maturational improvements are the result of improvements in connectivity between the temporoparietal region and frontal regions, as it is well established that areas engaged in higher-order information processing take the longest amount of time to fully mature (Giedd et al., 1999; Gogtay et al., 2004).

In terms of gender differences, Harenski and colleagues (2008) have reported that adult females who responded to pictures of unpleasant moral violations showed a strong modulatory interaction between activity in the posterior cingulate cortex and anterior insula. Additionally, it was revealed that this activity was proportional to the intensity of their ratings of the degree of moral violation. Unlike females, male participants showed a greater response in the temporoparietal region that tracked with their ratings of moral transgression. Importantly, the ratings between males and females did not differ significantly, which indicates that while engaging in moral reasoning, female participants may rely more heavily on neural structures that support both emotional experience and mentalizing, whereas males may rely solely on mentalizing brain regions. This distinction is consistent with models of moral reasoning that suggest females may approach moral dilemmas from a more care-based or empathic strategy relative to males.

Behavioral Regulation

In adults, it is thought that the ventral anterior cingulate cortex, the dorsomedial and ventromedial prefrontal regions, as well as the hippocampus all contribute to the organizational and regulatory aspects of emotion as it pertains to socially appropriate (morally thoughtful) behavior. This grouping of regions has demonstrated some interesting sex differences among adolescents. For example, because the orbitofrontal cortex (OFC) and ventrolateral prefrontal cortex (vPFC) structurally mature earlier in females, females seem to be able to learn new social rules and engage in social inhibition at an earlier age than males (Nelson & Guyer, 2011). Nelson and Guyer further speculate that the interaction of pubertal hormones and gendered behavior also supports the notion that young adolescent females are likely to

be (relative to age-matched males) more adept at learning new social rules (e.g., rules related to peer relationships) and to possess better inhibitory control, especially in the presence of socially salient circumstances (e.g., moral transgressions).

Estrogen is the primary organizer when it comes to female adolescence. The deluge of estrogen circulating in the body during female puberty also affects the brain. Increased amounts of estrogen in the brain have major effects on both cognition and emotion. There are two brain structures in particular that are significantly shaped by female adolescence: the hippocampus and the prefrontal cortex. Studies have shown that both of these structures contain large numbers of estrogen receptors, and they vary in size and function as a result of estrogen's influence (Campbell, 2008; Giedd et al., 1996; Taylor, 2006). The increased maturation of these regions means that they are making new and more efficient connections with both local and distant areas of the brain (Power et al., 2010). The hippocampus is often referred to as the "seat of memory" in human beings, as it is known to be a key player in many aspects of human memory. Hu and colleagues (Hu, Prussner, Coupe, & Collins, 2013) found that controlling for pubertal change produced relative increases in hippocampal volume in females as a function of increased "puberty score" (while producing relative decreases in volume in males). Given the increasing complexity of adolescent girls' social lives, as well as the potential for child rearing, it makes sense to see a great deal of development in the hippocampus, a brain structure known for integrating and consolidating different aspects of memory to form cohesive personal narratives (Casebeer & Churchland, 2003).

Together, these findings underscore that although the outcomes of many tasks and behaviors may appear similar, there may be significant differences in the manner (or strategy) and concomitant neural regions that accompany similar performance. Differences in behavioral strategy should not be minimized, especially when reliably observed, as they likely are reflective of developmental commonalities among those being studied. Therefore, as quantifiable as some of these sex differences are, it is critical to appreciate that many of them are influenced by gender, a relationship that neuroscience is just beginning to explore. It is also the case that both sex and gender are only two of many "systems" along with culture, peers, temperament, and others that influence how adolescents develop (Mills, Lalonde, Clasen, Giedd, & Blakemore, 2012).

Final Thoughts

Cognitively, adolescents undergo a transformation in which they begin to engage in more logical, abstract, and idealistic thinking. Additionally, they develop the ability to reflect on past events and integrate them into the present. These changes in cognition allow individuals to approach moral dilemmas logically, apply moral codes of conduct in an abstract manner, consider ideal outcomes, and recall past outcomes in order to influence decision making in the present (see Blakemore, 2008 for a review). Changes in social environment during adolescence such as the shift from a parent-dominated to peer-dominated world must also be considered in the study of moral development, as individuals become more likely to learn through peer observations, punishments, and reinforcements than through experiences associated with parental figures (Caravita, Gini, & Pozzoli, 2012). The internalization of social norms—particularly gender norms—during adolescence can also lead to a deviation from dispositional traits and parental lessons and to a prioritization of external, as opposed to internal, values (Gilligan, 1982; Nelson & Buchholz, 2003). The work of the developing individual is to integrate her or his own inter- and intrapersonal characteristics with the vast number of cultural contexts in which they exist. Learning to balance and blend familial expectations, gender norms, peer demands, and broader cultural expectations is probably one of the many reasons that few adults would voice a desire to return to adolescence, and this is undoubtedly more true among the female population.

In terms of acquiring moral reasoning, adolescence and early adulthood represent an extended "practice time," during which adolescents begin to regulate their own frontal networks. Later, emerging adults become increasingly adept at self-regulation (by gradually wresting control away from external sources of behavioral regulation, namely parents and peers) and begin to more fluidly integrate their own cognitive and emotional processes and learn from the consequences of their actions.

As adolescents continue to mature, their frontal systems become increasingly coordinated and able to effectively regulate or communicate with more posterior regions in the brain. As young adults emerge from adolescence, their decision-making processes begin to approximate those observed among mature individuals. This highly functional and personally tailored process results from a great deal of experience in an infinite variety of contexts.

The neural maturation described above sets the stage for the integration of emotion and cognition, which is fundamental not only to adult decision making but also to the formation of adult-like social attachments. The adolescent has the capacity to discern future feelings and to make subtle distinctions regarding expressed emotion. Moreover, affective states become integrated with formal thought operations. The maturation that takes place during adolescence, namely the initial integration of visceral emotion (largely from the networks that support emotional and interoceptive experience) and social cognition, is essential for fully developed moral reasoning that functions intuitively and automatically (i.e., requiring minimal cognitive effort). This integration is the principal goal of adolescent development and comes about largely as a function of learning about both the self and the self in context. The integration of visceral emotion and social cognition is an elemental aspect of moral development (Hinson, Jameson, & Whitney, 2002). During adolescence, emotional experience as well as mentalizing and behavioral regulation are all translocated from the self to self-in-relationship, a domain in which the complex unfolding of visceral, mental, and behavioral states in both the self and other can be mutually recognized, integrated, and learned from. All of these critical processes are undoubtedly influenced by measurable individual differences in sensitivity to sex hormones and gender norms; and until we as scientists are able to start teasing apart these various factors, we are likely to continue to feel befuddled by the emergence of moral reasoning in adulthood.

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