

# UC Berkeley

## UC Berkeley Previously Published Works

### Title

Becoming a sexual being: The 'elephant in the room' of adolescent brain development

### Permalink

<https://escholarship.org/uc/item/0xx2z3xv>

### Authors

Suleiman, Ahna Ballonoff

Galván, Adriana

Harden, K Paige

et al.

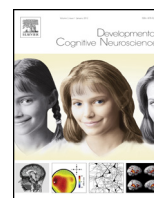
### Publication Date

2017-06-01

### DOI

10.1016/j.dcn.2016.09.004

Peer reviewed



## Becoming a sexual being: The ‘elephant in the room’ of adolescent brain development



Ahna Ballonoff Suleiman<sup>a,\*</sup>, Adriana Galván<sup>b</sup>, K. Paige Harden<sup>c</sup>, Ronald E. Dahl<sup>a</sup>

<sup>a</sup> University of California Berkeley—Institute for Human Development, 1121 Tolman Hall #1690, Berkeley, CA 94720-1690, USA

<sup>b</sup> University of California Los Angeles, Department of Psychology, 1285 Franz Hall, Box 951563 Los Angeles, CA 90095-1563, USA

<sup>c</sup> University of Austin, Texas, Population Research Center, 305 E. 23rd St., Stop G1800, Austin, TX 78712-1699, USA

### ARTICLE INFO

#### Article history:

Received 22 May 2016

Received in revised form 25 August 2016

Accepted 26 September 2016

Available online 29 September 2016

#### Keywords:

Romantic development

Sexual development

Adolescence

Developmental neuroscience

Puberty

### ABSTRACT

The onset of adolescence is a time of profound changes in motivation, cognition, behavior, and social relationships. Existing neurodevelopmental models have integrated our current understanding of adolescent brain development; however, there has been surprisingly little focus on the importance of adolescence as a sensitive period for romantic and sexual development. As young people enter adolescence, one of their primary tasks is to gain knowledge and experience that will allow them to take on the social roles of adults, including engaging in romantic and sexual relationships. By reviewing the relevant human and animal neurodevelopmental literature, this paper highlights how we should move beyond thinking of puberty as simply a set of somatic changes that are critical for physical reproductive maturation. Rather, puberty also involves a set of neurobiological changes that are critical for **the social, emotional, and cognitive maturation necessary for reproductive success**. The primary goal of this paper is to broaden the research base and dialogue about adolescent romantic and sexual development, in hopes of advancing understanding of sex and romance as important developmental dimensions of health and well-being in adolescence.

© 2016 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

### Contents

1. Introduction .....	210
2. Expecting to learn about love, bonding and romantic attachment .....	211
3. Pubertal hormones, neurodevelopment, and behavior .....	212
3.1. Testosterone .....	212
3.2. Estradiol .....	213
4. Social context .....	213
4.1. Parents .....	214
4.2. Peers .....	214
4.3. Media .....	214
5. Promising translational opportunities for developmental neuroscience .....	215
5.1. Example 1: extended adolescence .....	215
5.2. Example 2: contraception innovation .....	216
5.3. Example 3: childbearing and parenting .....	216
6. Conclusion .....	217
References .....	218

“In childhood people depend for their very life on the natal family; in adulthood, they are responsible for the well-being

of spouses and children and for pursuing the interests and position of the marital family. For the brief period of adolescence, they are neither so dependent as they were nor so responsible as they will be. It is then that peer relationship can take on an intensity of attachment that they will lack at other stages in the life cycle. . .” – (Schlegel and Barry, 1991 Schlegel & Barry III, 1991, p. 68)

\* Corresponding author.

E-mail address: [asuleiman@berkeley.edu](mailto:asuleiman@berkeley.edu) (A.B. Suleiman).

## 1. Introduction

Neurodevelopmental models have identified the onset of adolescence, marked by the biological transition into puberty, as a time of profound changes in motivation, cognition, behavior, and social relationships. These models have helped to identify the peripubertal time as a sensitive period of learning, particularly the social and emotional learning necessary to navigate new social contexts and process emerging self-relevant emotions (Telzer 2016; Crone and Dahl, 2012). However, despite the emergence of many excellent models highlighting the importance of puberty for neural development and new, adaptive learning (e.g. (Blakemore 2012; Braams et al., 2015; Crone and Dahl, 2012; Giedd et al., 2006; James et al., 2012; Peper and Dahl, 2013)), these models give limited consideration to the importance of adolescence as a sensitive period for romantic and sexual development. In the few cases when romance and sexuality are considered in these developmental models, they tend to emphasize sexual development as negative risk behavior (i.e., a risk-framework of sexual behavior) (Ewing et al., 2014; Goldenberg et al. 2013; James et al., 2012; Victor and Hariri, 2015). Although we acknowledge the importance of considering negative developmental trajectories related to risky or reckless sexual behavior, it is equally important to consider the normative, healthy aspects of sexual and romantic development, and the neurodevelopmental underpinnings of learning about romantic and sexual behavior.

Studies using a sexual risk framework have helped to identify some of the underlying neural correlates associated with health-harming sexual decision-making, but, unfortunately, these studies have done little to expand our understanding of normative sexual development trajectories. For example, among sexually active older adolescents (15–17 years old), self-reported sexual risk taking negatively correlated with activation of the prefrontal cortex (PFC) during a laboratory response inhibition task (Goldenberg et al., 2013). Similarly, in a study of 14–15 year-old young women, making a high-risk sexual decision on a laboratory task was associated with activation in the anterior cingulate (Hensel et al., 2015). These studies suggest that individuals with increased cognitive control during response inhibition and less activation in the anterior cingulate may make more responsible sexual decisions, but do little to enhance our understanding of normative developmental trajectories. Moving beyond a risk framework in neurodevelopmental research is essential for identifying neural processes associated with positive romantic and sexual development.

Beyond the handful of neurodevelopmental studies exploring sexual risk taking, there has been limited effort to explore the neural underpinnings of the normative developmental trajectory of increased interest and engagement in romantic and sexual behavior. As young people enter adolescence, one of their primary tasks is to gain knowledge and experience that will allow them to take on the social role of adults, including engaging in romantic and sexual relationships (Crone and Dahl, 2012). Young people's romantic relationships, ranging from primary school crushes where two people might interact very little, to relationships that involve a significant investment of emotion, time, and energy, are often dismissed as insignificant. In fact, these relationships serve important developmental purposes, and are the primary context for young people to explore their sexual identity and gain sexual experience (Furman and Shaffer, 2003; Furman et al., 2007). In hopes of gaining social status and winning the companionship of desirable partners, adolescents are highly motivated to learn how to navigate the complex social interactions involved with establishing and maintaining romantic relationships. A person's ability to engage in behaviors that facilitate intimate relationships and that create opportunities for sex and reproduction is the normative developmental outcome of puberty.

Puberty, a biological process starting in the brain, involves a cascade of hormonal changes and profound physical and physiological transformations that ultimately result in the ability to reproduce (Sisk 2016; Sisk and Foster, 2004). The development of some elements of adult sexuality, including changes in physical anatomy, sexual arousal, and orgasm, are well understood. Although puberty motivates mating and sexual behavior, there has been very limited research exploring the emergence of sexual behavior in adolescent humans. In contrast, pubertal research on other species includes in-depth exploration of the onset of sexual and mating behavior associated with puberty, acknowledging that the emergence of these novel behaviors requires immense coordination of developmental transitions in the brain, endocrine system, and nervous system. As such, animal researchers perceive early sexual experiences not only as behavioral outputs, but also as physiologic inputs that shape neural and hormonal function and development (e.g., Nutsch et al., 2014, 2016; Will et al., 2015). The dearth of knowledge about the learning and the reciprocal feedback loops involved in the onset of human mating and sexual experiences highlights important oversights in existing models of human adolescent development. At the same time, while animal models offer important insights into understanding sexual developmental trajectories, they do not expand our understanding of romantic relationships and experiences, nor do they identify developmental changes relevant to these important social milestones. Moreover, the mating framework of animal models offers solely a heterosexual framework for sexual development, and thus limits our understanding of the diversity and fluidity of attraction, behavior, and identity present in human sexuality.

The animal literature serves as a critical reminder of the biological purpose of puberty and the reciprocal feedback loops involved in romantic and sexual experiences, which have been largely ignored in models of human adolescent development. In addition, animal models and limited human research have done little to explore how puberty shapes the opportunities for learning about the *meaning* of romantic and sexual behaviors (Fortenberry, 2013). On one hand, a basic capacity for procreative behavior can be achieved with relatively little skill, knowledge or experience; on the other hand, from an evolutionary perspective, social competition in attracting a mate and success in coupling relies heavily on mastery of a complex set of social and emotional skills and behaviors. The learning relevant to acquiring the skills and knowledge necessary to navigate the intertwined social and sexual motivations emerging with puberty is core to the normative trajectory of social, affective, and cognitive development in humans. Therefore, pubertal maturation (and the natural increase in social motivations including interest in sexual and romantic behavior) is likely to represent a normative window of learning—not simply about the mechanical aspects of sexual behavior, but also about the complex emotional and social cognitive processes that are part of navigating the charged, high-intensity emotions involved in developing an identity as a sexual being.

In this paper, we explore how cognitive and social-affective development occurring at puberty creates a unique window of opportunity for adolescents to engage in developmentally appropriate learning opportunities relevant to navigating romantic and sexual experiences. We propose that changes in underlying neural circuitry associated with social and emotional processing may open a second developmental window (following the one in early childhood) for learning about love and attachment relationships. We further hypothesize that these learning processes begin with the pubertal physical and neurobiological transitions that influence motivation, yet are highly dependent on context and interpersonal relationships during this time. Next, drawing on both animal and human research, we will review how the hormonal, neural, and biological transitions at puberty prime young people to engage in

romantic and sexual behavior. Finally, we highlight some important, outstanding questions about the developmental trajectories of romantic and sexual behaviors and relationships, including how development is impacted by the social elongation of adolescence, which has increasingly uncoupled sexual maturity from cultural definitions of adulthood. Throughout the paper, we also identify opportunities for researchers to explore a number of unanswered questions. The ultimate goal of this paper is to broaden the research base and the dialogue about adolescent romantic and sexual development, in hopes of strengthening the potential for neuroscience research to be used to improve these critical trajectories.

## 2. Expecting to learn about love, bonding and romantic attachment

Many neurodevelopmental models highlight that the neuroplasticity occurring at puberty opens sensitive windows in the brain, which prime the individual for unique types of learning (Crone and Dahl, 2012). In its broadest usage, the term **neuroplasticity** includes a wide range of synaptic and non-synaptic processes that underpin the brain's capacity to instantiate learning, along with the concept of 'sensitive windows' for specialized learning. Greenough et al's (1987) early childhood 'experience-expectant framework' proposes that the infant brain expects specific types of learning, which naturally motivates them to engage in repeated practice and mastery of learning experiences (e.g. walking). These learning experiences, in turn, contribute to critical neural development (Greenough et al., 1987). Recent research into the molecular processes and mechanisms of neuroplasticity has progressed rapidly and highlighted that adolescent brain development, beginning with the onset of puberty, may represent a unique combination of stability and plasticity. This combination creates an important window of opportunity for learning and experience to shape developing neural networks in enduring ways (Hensch 2014; Takesian and Hensch, 2013; Werker and Hensch, 2015).

The onset of puberty seems to re-orient greater attention and salience toward social and emotional information-processing streams, which are particularly relevant to interest in romantic relationships and sexual behavior (Dahl 2016; Nelson et al., 2016). More specifically, puberty leads to the development of novel social behaviors and responses to newly emerging social contexts (Brown et al., 2015). At the same time that young people begin to spend increasingly more time with their peers, they experience new, sexualized feelings of attraction that motivate relationship-facilitating behaviors. Given that the biological purpose of puberty is to achieve reproductive maturity, it makes sense that the balance between plasticity and stability in the unique peripubertal neural system would create a window of opportunity for learning and motivation relevant to romantic and sexual behavior. Consider the skills that an adolescent must learn in this domain, including coping with emotions related to finding someone attractive, building communication skills in order to ask someone out on a date, experiencing sexual arousal with a stranger, navigating the social consequences of dating someone more or less popular, coping with rejection or break up, and balancing the biological desire to have sexual experiences with the complex emotions associated with maintaining a romantic relationship. The wide range of early romantic and sexual experiences likely shapes developing neural networks in enduring ways to support lifelong romantic and sexual trajectories.

One of the most important transitions occurring during puberty is the motivation and desire to engage in romantic love. Whereas infants learn early in life the value of stable attachment and parental love, it is not until after the onset of the pubertal transition that young people become interested in romantic love. Romantic love

has been conceptualized as an important attachment process, and adults' romantic attachment styles frequently mirror the styles they experienced with their parents as infants (Hazan and Shaver, 1987). In addition, both romantic love and parental love facilitate bond formation, and make the formation and maintenance of these bonds positive and rewarding experiences (Bartels and Zeki, 2004). Despite significant overlap in the purpose, qualities, neurohormone binding sites, and neural correlates between parental and romantic love, there are also important distinctions (Bartels and Zeki, 2004). Both parental and romantic love facilitate nurturing, sensitive, responsive caretaking, but romantic love also includes distinct components, such as reciprocal power sharing and sexual desire. We propose that the hormonal changes associated with puberty contribute to neural transitions that prime the brain to learn about this new type of love, in order to facilitate mating, childbearing, and childcare.

Although it has been established that many of the neural systems involved in romantic love and sex undergo significant structural, connectivity, and functional transformation during puberty, little is known about how this intersects with a normative romantic and sexual developmental trajectory. Integrating what is known about the neural underpinnings of romantic love and sexual desire/arousal in adults with the literature on pubertal neurodevelopment points to some intriguing questions. While it is beyond the scope of this paper to summarize this body of literature, adolescent neurodevelopmental models have clearly demonstrated significant sex-specific restructuring of the brain during puberty (Dennison et al., 2013; Giedd and Denker, 2015). Despite sex differences in these trajectories, all adolescent brains are sensitized to reward learning (Galván, 2013). By activating dopamine-rich, reward processing and motivational systems, both romantic love and sex are goal-oriented motivations accompanied by strong emotional responses (Aron et al., 2005; Fisher et al., 2010). Beginning with puberty, the developmental transitions in brain networks involved in motivation, reward, and social-emotional processing likely create a unique inflection point for romantic love and sexual arousal to be experienced as positive rewards.

Both love and sexual desire are dopaminergically-mediated motivation states that can globally affect cognition (Diamond and Dickenson, 2012). Given the developmental transitions that occur during adolescence related to emotional processing and cognitive control, it has been proposed that adolescence is an opportune time to explore the cognitions and emotions associated with romantic relationships (Collins, 2003). These new motivational states significantly increase in salience at the same time that youth develop an increased capacity for self-regulation of other appetitive behaviors (Fortenberry, 2013). It therefore makes sense that physical maturation is accompanied by increased neural plasticity and a heightened motivation to seek out a range of highly arousing, slightly scary, highly rewarding, novel experiences, and that increases in sensation seeking make adolescents more likely to find these high-intensity experiences, such as having a first crush or engaging in a first kiss, enjoyable (Spielberg et al., 2014). The co-release of dopamine and oxytocin associated with repeated interactions with a specific partner contributes to additional reward-driven learning about romantic behaviors. Once a young person has a crush and begins to build a relationship with someone, they develop a conditioned partner response in which the dopaminergic reward is expected and experienced greatest with that specific bonded partner (Love 2013; Ortigue et al., 2010). As with all learning, partner preference takes time, as well as repeated experience, to develop. Once this partner-specific response has been established, engaging in arousing, novel activities creates enhanced experiences of relationship satisfaction among couples (Aron et al., 2000). Because of the neural development occurring with puberty, a partner-specific response in early romantic rela-

tionships, when both the emotional and physical intimacies are novel, makes them particularly exciting, rewarding, and satisfying. In order to engage in romantic and sexual relationships successfully, adolescents need to want, like, approach, and learn from the high-stakes activities of asking someone out on a first date, falling in love, experiencing a broken heart, and trying again.

Romantic love involves increased activation in dopamine-rich subcortical regions associated with processing emotion, rewards, and motivation; in the higher-order cortical brain regions associated with social cognition and self-representation; and decreased activation in the amygdala (Ortigue et al., 2010). Although sexual desire/arousal and love involve many overlapping areas of activation, particularly in the subcortical regions, there are also distinct areas of activation. For example, romantic love, both while someone is actively in love and after they have experienced rejection from a break-up, but not sexual arousal, involves ventral tegmental activation (generally associated with pleasure, focused attention, and motivation to pursue rewards), whereas sexual arousal, but not love, involves ventral striatal activation (associated with motivation and predictive reward value) (Fisher et al., 2010; Diamond and Dickenson, 2012). Due to limitations in developing tasks appropriate for the scanner, neuroimaging research has not successfully distinguished sexual desire—a cognitively-mediated motivation state to pursue sexual activity—from sexual arousal—a physiological state of sexual readiness (Diamond and Dickenson, 2012). Most laboratory paradigms use sexual stimuli of strangers rather than loved ones, and thus likely better represent arousal than desire, but this remains unclear. Research on the developmental trajectory of love in the human brain is incredibly limited. Puberty offers a unique developmental inflection point when romantic love emerges. Uncovering the neural developmental trajectories that contribute to the emergence of romantic love and sexual arousal could help to expand our understanding of these motivational states. In addition, research that helps to unpack how neurodevelopmental transitions occurring at puberty interact with early experiences of desire, romantic love, and sex would greatly increase our understanding of how the inflection point of puberty creates a unique developmental window for learning about these complex social activities.

As with any important learning experience, young people benefit from having supports and scaffolding to facilitate positive trajectories. We need a better understanding of the contexts and conditions that contribute to positive learning experiences relevant to sexual development, as well as those that minimize the risks of negative trajectories. Just as we understand the importance of providing a safe environment for toddlers who are learning to walk (and falling repeatedly), we can pose questions about the corollary environments that help youth to explore and experiment with their powerful desires and feelings, while developing the skills for dealing with these feelings and integrating them into their self-identity. Developmental science can give important insights about the types of scaffolding that can best support healthy versions of these high-intensity learning experiences for all young people, including those who are experiencing their first feelings of desire, attraction, or arousal, and those who are already dating and/or sexually active.

### 3. Pubertal hormones, neurodevelopment, and behavior

Hormonal increases are a cornerstone of the pubertal transition. The same hormones that contribute to the developmental of the secondary sex characteristics also play a critical role in reorganizing neural circuitry (Schulz and Sisk, 2016; Sisk 2016; Sisk and Zehr, 2005). As a result, adolescents experience greater motivation to seek out rewards, enhanced experience of rewards, and increased motivation to engage in social relationships—including romantic

and sexual behavior (Crone and Dahl, 2012). Additionally, pubertal hormones might contribute to the increase in sensation-seeking that makes the high-intensity novel feelings more appealing. Beyond gonadal hormones, a number of other hormones and neurotransmitters are activated or enhanced during puberty, and are involved in how people experience romantic love, including oxytocin, vasopressin, dopamine, serotonin, and cortisol (De Boer et al., 2012). For instance, as increases in pubertal hormones enhance socially-motivated behavior and feelings of desire, increases in dopamine and oxytocin augment feelings of love and connection (Love, 2013). Collectively, these changes in hormones and neurotransmitters create an ideal physiological climate for fostering young people's interest in learning about romantic love and sexual attraction. Below, we review, more specifically, results on how two key pubertal hormones – testosterone and estradiol – contribute to the sexual and romantic development in adolescence.

#### 3.1. Testosterone

Testosterone has been associated with changes in social information processing, reward sensitivity, and sensation seeking during puberty. Often thought of in relation to aggression, testosterone has also been described as a social hormone, motivating status-seeking and status-maintenance behaviors through a number of diverse mechanisms, including changes in fear processing, stress response, threat vigilance, and reward from increasing social status (Eisenegger and Naef, 2011). Pubertal increases in testosterone have been associated with changes in neural activation to threat cues in the amygdala (associated with threat avoidance) and the nucleus accumbens (associated with reward processing) (Spielberg et al., 2014). In addition, increased testosterone has been associated with increased risk-taking on laboratory tasks among both boys and girls (Op de Macks et al., 2011; Peper and Dahl, 2013). The nucleus accumbens and amygdala, which are social information-processing brain networks that are extensively reorganized during puberty, have large populations of testosterone receptors (Nelson et al., 2005). These testosterone-related processes all likely influence changes in romantic and sexual behavior during adolescence. Consistent with the idea that adolescence is a sensitive period for the behavioral effects of gonadal hormones, animal models suggest that the behavioral response to gonadal hormones differs between pre- and post-pubertal animals. Unlike the pre-pubertal brain, the post-pubertal brain is primed for steroid hormones to activate reproductive behavior (Sisk and Zehr, 2005).

There has been extensive research into the neurodevelopmental trajectories of sexual and mating behavior in male mammals. For instance, in male Syrian hamsters, it is well-established how pubertal hormones influence the structure and function of neural circuits that integrate steroidal and sensory information, and how these changing neural circuits alter the way males respond to social stimuli and engage in mating behaviors (Romeo et al., 2002). Furthermore, research in nonhuman primates has identified that, distinct from most mammalian species, gonadal hormones in primates primarily influence sexual *motivation*, rather than *ability* to copulate (Wallen, 2001). Because the effects of gonadal hormones are specific to stimulating sexual motivation, this line of research suggests that shifts in social experience and context are critical influencers of learning about sexual behavior (Wallen, 2001). Non-human primate research has also illustrated the importance of the learning component associated with puberty and sexual experience. Although undergoing endocrine puberty and the associated increase in testosterone results in increased sexual behavior, the experience of successful coupling—ejaculating during intercourse with a female—is the best predictor of future sexual behavior independent of elevated testosterone (Wallen, 2001). Even males who have not experienced endocrine puberty increase their sex-

ual behavior following successful sexual experiences. Collectively, the animal research highlights the importance of learning experiences that occur in tandem with the hormonal transition, and suggests new questions for research in humans regarding how hormonal, neurodevelopmental, learning, and contextual changes in adolescence shape the development of sexual behavior and sexual relationships during adolescence.

In humans, whether or not increases in testosterone during puberty directly affect individual differences in sexual motivations and behavior is less clear. Higher testosterone modestly correlates with increased sexual fantasies in pubertal boys, but the effect disappears in models that include onset of spontaneous nocturnal ejaculations and age (Campbell et al., 2005). Increasing testosterone in pre-pubertal boys seems to be associated with increased sexual behavior, including touching others and nocturnal emissions (Finkelstein et al., 1998). In cross-sectional studies, independent of pubertal stage and age, girls and boys with higher levels of testosterone are more likely to engage in sexual intercourse (Halpern et al., 1997, 1998). In contrast, in longitudinal studies, individual changes in testosterone are associated with sexual debut (first sexual intercourse) for girls, but not for boys (Halpern et al., 1997). For boys, pubertal stage is more strongly associated with sexual debut than testosterone (Halpern et al., 1993). These findings highlight the difficulty of disentangling the biologically-mediated effects of gonadal hormones from the socially-mediated effects of bodily changes. For boys, the physical capacity to produce gametes and reproduce occurs relatively early in the pubertal transition, although few boys engage in sexual behavior during that time. Over the course of puberty, testosterone levels increase, boys become taller and more muscular, their voices deepen and their facial hair thickens. These secondary sex characteristics, which are readily apparent and may be seen as attractive or desirable by potential sex partners, may contribute more substantially to a boy's chances of experiencing sexual intercourse than reproductive capacity or the neurodevelopmental changes in motivation associated with testosterone *per se* (Halpern et al., 1993). Thus, despite the fact that increases in testosterone are associated with increases in socially-motivated, goal-oriented behavior, they do not automatically translate into increased sexual behavior or activity.

Results from studies that have attempted to unpack the relationship between testosterone and sexual behavior in adults further complicate the picture. For example, studies with young adult men have found that being in a committed romantic relationship is associated with more frequent sexual intercourse and simultaneous declines in testosterone (Burnham et al., 2003; Gray and Campbell, 2009). Among adult women, *endogenous* testosterone does *not* show significant correlations with sexual behavior (Roney and Simmons, 2013), but *exogenous* testosterone treatment in women has been found to increase sexual desire, sexual activity, and sexual self-image (Buster et al., 2005; Davis et al., 2006; Shifren et al., 2006). Both these data suggest that the association between testosterone and sexual behavior may depend heavily on developmental stage, as well as on relationship context.

What we know about testosterone and sexual behavior collectively suggests that there may be some threshold effect for testosterone that leads to the possibility of engaging in sexual intercourse, but no linear relationship between testosterone and subsequent sexual experience. Given the developmental transitions in neural regions with high volumes of testosterone receptors and the increases in testosterone during puberty, we still have much to learn about the relationship between testosterone and romantic and sexual behavior in humans. More nuanced exploration of the relationship between testosterone, sensation seeking, pubertal development and factors associated with learning about sexual behavior, would help clarify the contributions of the biological versus social components that contribute to sexual debut

and subsequent sexual activity. In particular, longitudinal studies that can delineate changes in secondary sex characteristics from changes in gonadal hormones can be helpful in identifying specific hormonal mechanisms (Harden, Kretsch, Moore, & Mendle, 2014).

### 3.2. Estradiol

In addition to testosterone, increases in estradiol and progesterone contribute to remodeling and activation of neural circuitry for both males and females during puberty. Both estradiol and progesterone have been found to play important roles in sexual, social, and risk-taking behavior (Romeo 2003; Tackett et al., 2015; Vermeersch et al., 2009). Compared to other hormones, among girls, estradiol has the strongest correlation to breast development, a very early sign of puberty (Drife, 1986). In contrast to boys (and all other primates) who begin producing gametes before looking sexual mature, human girls develop secondary sex characteristics well before achieving full reproductive capacity. This results in pubertal girls being socially perceived as sexually attractive and desirable before they are reproductively mature or experiencing the neurodevelopmental changes in motivation associated with testosterone. The evolutionary purpose of this divergence is not well understood, but point to the importance of understanding the role of estradiol and progesterone in female sexual behavior.

Limited research has explored the relationship between female hormones in pubertal brain development, sexual behavior, and risk-taking. Among pubertal girls, increased estradiol levels have been associated with increased white matter growth and decreased pubertal grey matter pruning (Herting et al., 2014). Limited functional neuroimaging research has associated estrogen with risk taking in adolescent girls (Vermeersch et al., 2008). The majority of neurodevelopmental studies in humans have identified testosterone, rather than estradiol, as the hormone most correlated with striatal activity related to risk-taking and social motivation in females (Op de Macks et al., 2011; Peper and Dahl, 2013; Peters et al., 2015). Primate studies, on the other hand, suggest that estrogen and progesterone, rather than testosterone, are associated with changes in female sexual behavior, and that the relationship between hormones and behavior is dependent on social context (Wallen, 2001). Tests of this model in humans, also suggest that estradiol is associated with increases in sexual desire and progesterone is associated with declines (Wallen, 2001). In addition, exposing pre-pubertal girls to increased estrogen results in increased kissing and necking behavior (Finkelstein et al., 1998). Although the overwhelming majority of girls choose not to engage in sexual behavior during puberty, understanding the brain, hormone, behavior transitions occurring during this sensitive window may increase our understanding of factors that lead to different behavioral outcomes.

## 4. Social context

The influence of pubertal hormones does not occur in a vacuum. Many of the individual differences in when youth engage in romantic relationships are aligned with pubertal timing, yet social and cultural factors also play a critical role in framing the sexuality of youth (Collins, 2003). For example, in one study, the association between testosterone and experiencing first sexual intercourse was statistically mediated by less frequent attendance at religious services. This study points to the potential power of environment-behavior-development feedback loops and the importance of social institutions as adolescents are experiencing neurohormonal changes (Halpern et al., 1997). At the same time, attendance at religious services is known to be inversely associated with sensation seeking personality traits (Gaither and

Sellbom, 2010), which have been linked in other work with differences in testosterone and estrogen levels (Campbell, 2010; Roberti, 2004) (although this link is not consistent across all studies e.g. Rosenblitt et al., 2001). Therefore, the extent to which the effects of testosterone are truly driven by changes in social experience, versus driven by changes in motivation, is ambiguous. This further underscores our earlier point: Disentangling the different strands of hormonal, motivational, and social change during puberty is highly challenging methodologically. Nevertheless, additional research focused on identifying which environmental factors can most effectively mediate and moderate the behavioral sequelae of neurohormonal development is needed. Given the transitions occurring in a number of neural systems associated with social processing and motivation during puberty, and the fact that romantic and sexual relationships are social phenomena, it is important to understand how social and contextual factors influence brain structure, brain function, and how these neural changes mediate social effects on learning and behavior.

#### 4.1. Parents

Parents play a key role in providing support and information about romantic and sexual behavior. The quality of parent-child relationships affects both sexual behavior and neural development and activation, specifically in the amygdala, which has been associated with reward processing (Ernst et al., 2005), emotional processing (Whalen et al., 2013), and fear response (LeDoux, 2003). The quality of maternal relationships in early adolescence has also been associated with changes in the trajectory of brain maturation. Specifically, more positive relationships between mothers and early adolescents have been associated with decreased volumetric growth of the amygdala (Whittle et al., 2014). These results suggest that maternal relationships may influence brain development trajectories associated with behavior regulation.

The functional role that parental presence has on brain activation also shifts in adolescence. Both children and adolescents have high amygdala reactivity to their mothers' faces, but amygdala reactivity to the faces of strangers declines from childhood to adolescence. These results suggest that, while positive maternal response remains constant, fear of, and anxiety towards strangers declines across development, facilitating more social exploration (Tottenham et al., 2012). Research has also highlighted that maternal presence can buffer cortisol stress response in children, but it does not have the same buffering effect for adolescents (Hostinar et al., 2014). This suggests that mothers serve to buffer stress for younger children, and as children follow the normal trajectory of development into adolescence, accompanied by declining fear and anxiety about novel people and situations and increased exploration, the physiological effect of parental presence shifts.

Complementing neuroscience research on parent-child relationships, behavioral research has found that positive parent-adolescent relationships are associated with decreased intention to have sex and later age at first sexual intercourse (Van de Bongardt et al., 2014), and adolescents who perceive their parents to be caring have delayed first sex (Longmore et al., 2009). Youth who report having positive relationships and open communication with their parents also have less sexual experience, increased condom use (Parkes et al., 2011), later sexual debut (Price and Hyde, 2008), fewer unintended teen pregnancies (Miller et al., 2001) and fewer sexual partners (Kan et al., 2010; Kerpelman et al., 2016).

Despite the fact that the transition into adolescence is usually accompanied by more autonomy and less parental monitoring, this neuroscience and behavioral research highlights the need for parents not to pull back from parenting during adolescence, but instead shift from providing basic emotional support to providing more constructive support and scaffolding to facilitate the next stage of

development. Unfortunately, few resources exist to support parents into caring for adolescents and even fewer resources prepare them for the transition into young adulthood.

#### 4.2. Peers

Peers have also been demonstrated to influence adolescents' decisions about sexual behavior (Choukas-Bradley et al., 2014; Hampton et al., 2005; Suleiman and Deardorff, 2015). Some research has demonstrated that the presence of peers, or even the suggested presence of peers, increases activation of adolescents' neural reward circuitry, specifically the ventral striatum (VS), and risk-taking behavior in a way that does not occur for children or adults (Chein et al., 2011; Telzer et al., 2014). One interpretation of this could suggest that adolescents are uniquely vulnerable to take risks in the presence of peers, however, understanding the relationship between increased VS activation and risk taking behavior is far from straight forward. Some studies have found increased VS activation to be associated with increased risk taking on laboratory tasks in the presence of peers (Chein et al., 2011), while other studies have not replicated this result (Peake et al., 2013). Instead these studies have found activation in the temporal parietal junction, an area of the brain involved in self-other metalizing, to mediate the relationship between adolescents' increased risk taking and their ability to resist peer influence, specifically after experiencing social exclusion (Peake et al., 2013). To further complicate things, other studies have found that increased VS activation during the processing of emotional faces, specifically happy and sad expressions, have been associated with increased self-reported resistance to peer influence (Pfeifer et al., 2011). Collectively, this research suggests that the affective and social context of peer presence may lead to differences in neural activation and to differences in behavior. The transitions occurring in social and affective neural processing systems are priming young people to be open to and enjoy the novel social experiences associated with romantic and sexual relationships. Both platonic and romantic peers influence adolescent sexual behavior and adolescents' decisions to engage in romantic and sexual relationships (Ali and Dwyer, 2011; Baumgartner et al., 2011; Crockett et al., 2006; Kennett et al., 2012; Potard et al., 2008). In addition, sexual activity is strongly peer-mediated; having sexually active platonic peers is associated with earlier first sexual intercourse, more frequent sexual activity, and more sexual partners (Ali and Dwyer, 2011; Furman et al., 2007; Santor et al., 2000).

#### 4.3. Media

In addition to social relationships "in real life," traditional media and social media may also shape sexual behavior. Messages about sexuality and romantic relationships are persistent throughout the media. Over 70% of television programming contains some type of sexual content or dialogue (Kunkel et al., 2005). Depending on the context and population, between 23 and 95% of 10–19-year-olds report having ever viewed online pornography, and between 28 and 84% reported that the exposure was unwanted or unintentional (Peter and Valkenburg, 2016; Wolak et al., 2007). Mass media has been identified as a "sexual super peer" having significant social influence, particularly for girls who experience puberty earlier than their peers (Brown et al., 2005).

Despite this significant exposure to sexual content and messages throughout adolescence, little is known about the effect of sexual content on brain development. More generally, media content has been found to impact neural functioning. For example, limited exposure to violent media among adolescents has been found to affect the developmental trajectories of frontal inhibitory systems and subcortical limbic structures, as well as the connectivity between them, and may have some effect on violent behavior

(Hummer 2015; Kalnin et al., 2011). Although we are not aware of any imaging research that has been conducted specifically on sexual media, it is highly probable that sexual and romantic images, abundant in everything from general media to pornography, also likely affect neural development and behavior. At the same time, individual differences in neurodevelopment may shape exposure to sexual media. For example, more advanced pubertal young men with high sensation seeking tendencies are most likely to seek out online pornography intentionally, and there is a strong association between increased pornography exposure and less restrictive sexual attitudes (Peter and Valkenburg, 2016).

Developmental science offers strategies to expand our understanding of the impact of the media on neural development and sexual behavior. Developmental adaptations of innovative communications neuroscience research (e.g. Falk et al., 2015, 2012) coupled with behavioral research could help us better understand the neural activation associated with adolescents viewing different types of romantic and sexual media and better understand the types of affective learning experiences resulting from these media contexts. Applying a developmental framework to communications neuroscience could help inform the development of positive romantic and sexual media messages and increase our understanding of the potential negative trajectories associated with viewing more harmful messages. In the age of increased access to a wide range of romantic and sexual media content and the rapid emergence of virtual reality pornography, the need for these insights is urgent. Given that adolescence is a critical period of romantic and sexual identity development, we need a better understanding of the relationship between neurodevelopment, exposure to the romantic and sexual media, and subsequent behavioral trajectories.

## 5. Promising translational opportunities for developmental neuroscience

As highlighted above, there are many opportunities for neuroscientists to expand our understanding of the normative trajectory of adolescent romantic and sexual development. Beyond expanding our understanding of the normative developmental trajectories, there are specific ways in which understanding the underlying neural trajectories could inform policies and practices aiming to improve adolescent sexual and reproductive health outcomes. The period defined as adolescence continues to elongate across the globe, and understanding the effect of this elongation on neural development could contribute significantly to our understanding of the costs and benefits associated with this phenomenon. Similarly, expanding our understanding of the intersection between puberty, adolescent brain development, and sexual behavior could inform innovation, policies and practices aiming to support and improve these trajectories. Three examples of these opportunities are reviewed below.

### 5.1. Example 1: extended adolescence

Among humans, adolescence is a socially constructed period beginning with the hormonal, psychological, and physical changes occurring with puberty. The end of adolescence is much less clearly defined. Many of the features of adolescence are socially constructed, but, across species, it is observed as a “time of preparation for adult reproductive life,” spanning the period between achieving physical readiness to engage in sexual activity and having social permission to reproduce (Schlegel 1995, p. 16). Across primate species, young adolescents engage in mating and sexual behavior but rarely produce offspring (Schlegel, 1995). In humans, the length and experiences associated with adolescence can vary widely; nevertheless, the period, characterized by increasing autonomy, but

free of the full array of adult responsibilities, is culturally universal (Schlegel, 1995).

Today's youth face an especially protracted period between when they are physiologically capable of reproduction and when reproduction is socially and personally desirable. In countries across the globe, the age of puberty has continued to decline (Parent et al., 2003; Sørensen et al., 2012). For girls, this has been measured primarily by decline in menarcheal age. As menarche occurs rather late in the pubertal cascade, this metric may underestimate the extent of historical declines in the average age at pubertal onset. The average age of the most common early physical sign of puberty among girls, breast budding, has declined more rapidly than age at menarche, and as a result, girls are spending longer amounts of time in the pubertal transition (Mendle, 2014). Interestingly, the decrease in age of onset of breast development has not been clearly associated with early increases in the sex hormones associated with puberty, including gonadotropins and estrogen (Sørensen et al., 2012). In contrast, declines in the early physical sign of puberty for boys—primarily testicular growth—have been paralleled by secular shifts in hormones associated with puberty (Sørensen et al., 2012). The difference in the developmental trends between boys and girls is not well understood, but it highlights the importance of understanding the impact of these different trends on pubertal neural development, both within and between sexes. For both sexes, there is a clear declining trend in the age when humans are biologically capable of reproduction. Given that some brain development trajectories are closely tied to changes in pubertal hormones, it is likely (although an outstanding empirical question) that neural developmental changes associated with puberty have also begun to trend earlier.

At the same time that the age of reproductive capacity has declined, the age at which it is socially desirable for young people to bear children has continued to increase. The age at which young women in higher resourced countries first bear children has significantly increased over the past 40 years, and this trend is now beginning in many lower and mid-resourced countries as well (Bearinger et al., 2007; Bongaarts and Blanc, 2015; Mathews and Hamilton, 2009; Sedgh et al., 2015; Westoff 2003). Today, across the globe, the mean age of women at their first birth ranges from 20.9 years old in sub-Saharan Africa, to 25 years old in the US (Bongaarts and Blanc, 2015; Mathews and Hamilton, 2009).

Until recently, social acceptance of reproduction has been highly correlated with marriage, and the first child was often born within the first few years of marriage. This trend has also experienced disruption in recent years. First, even more sharply than the age of first birth, the age of marriage—highly correlated with socioeconomic and demographic variables—has increased for both men and women across the globe (Westoff, 2003). Second, particularly in higher resourced countries, there has been a trend towards uncoupling marriage and childbearing, with more births occurring outside of legal marriages, fewer marriages as a result of premarital conception, and married couples waiting longer after marriage for childbearing (England et al., 2013; Hayford et al., 2014). There is also an increasing number of people who go through the biological transition of puberty but never engage in marriage or parenting, and yet still have fulfilling romantic and sexual lives. Together these trends highlight the importance of gaining a better understanding about the intersection of social, cultural, and biological factors that influence normative trajectories of romantic and sexual development. This points to a wide range of yet unexplored empirical questions about how physical and neural development interact with contextual factors to shape and influence romantic and sexual behavior.

The secular trends of early puberty and later childbearing provide great opportunities for young people to have a longer period for increased maturation, educational attainment, and stabilization prior to assuming the full scope of adult roles and responsibilities.



At the same time, many individuals now spend a decade or more of their lives feeling biologically, physiologically, and motivationally primed to engage in romantic and sexual relationships outside of the context of reproduction. As such, we need to better understand the behavioral outcomes and neural developmental underpinnings of the motivations associated with early romantic love and sexual experiences, in order to provide young people supports and scaffolding that facilitate positive trajectories.

### 5.2. Example 2: contraception innovation

Over the course of the teen years, the majority of young people become sexually active. Globally, the average age of sexual debut ranges from 16.5 to 24.5 years old for males and from 15.5 to 21.5 years old for females (Wellings et al., 2006). In light of the fact that many young people engage in sexual intercourse before they want to parent, many young people choose contraception. Although condoms, cervical caps, diaphragms, and some intrauterine devices (IUDs) offer non-hormonal contraception, the primary methods of contraception used by adolescents include hormones. The recent global policy push to increase the use of long-acting reversible contraceptives (LARCs) among adolescents has promoted the use of some very effective non-hormonal methods, like hormone free IUDs, and has promoted increased use of IUDs, implants, and injectables containing progestin (Ott et al., 2014). Given the evidence that pubertal hormones influence neurodevelopment, it is important to identify if and when there could be negative implications of disrupting the normal hormonal trajectories, and specifically the potential influence on neural development, during critical developmental windows. To date, we are not aware of any published data exploring these effects.

Despite an array of other options and the promotion of LARCs, combined oral contraceptives (COCs), containing both estrogen and progestin, remain one of the most utilized contraceptive methods among young women (Ott et al., 2014). COCs, which are highly effective for preventing pregnancy when used correctly, have been found to significantly suppress both free and total testosterone levels by up to 50% in adult women (Zimmerman et al., 2013). This suppression of testosterone has been thought to be the underlying source of complaints associated with COCs, including diminished well-being and quality of life, reduced libido, cognitive disruptions, and decreased bone mass (Zimmerman et al., 2013). Although women on COCs have overall lower testosterone levels, additional research has suggested that the *change* in testosterone when women are engaged in a competitive tasks remains constant despite COC use (Edwards and O'Neal, 2009). Once again, this suggests interesting empirical questions about how COC use could affect testosterone levels in young women who are in the midst of the developmental testosterone increase associated with puberty (Braams et al., 2015).

In addition to the adverse effects reported by adult women, there are additional potential adverse effects of testosterone reduction during adolescence. Given that testosterone has been shown to motivate increased interest in arousing experiences, inhibiting testosterone levels during the peripubertal or adolescent period may diminish motivation to engage in a range of prosocial risk-taking behaviors that support positive developmental trajectories. It is also equally possible that inhibiting testosterone will not limit positive or negative risk taking, for although overall testosterone levels may be suppressed in young women taking COCs, their testosterone *responses* to stimuli may remain constant. Understanding the impact of testosterone suppression in adolescence on neural development would be essential to help better understand the mechanisms that may contribute to either of these potential trajectories. Furthermore, insights into the implications of chronic suppression of testosterone, in concert with the hor-

monal orchestration of puberty, may also help to bolster innovation as pharmaceutical companies develop new contraceptive methods. This is a place where animal neurodevelopmental models may offer important insights that can be later tested in humans. We do want to state explicitly that our goal is not to introduce new barriers to young women seeking reliable contraception, but instead propose that having more information about the interaction between hormonal contraceptives and neurodevelopmental trajectories would help increase the safety, efficacy and impact of contraceptives for young women.

### 5.3. Example 3: childbearing and parenting

The global trend towards later childbearing has been a positive trajectory, as there is clear consensus that very early childbearing, before age 15, has detrimental effects on the health, socioeconomic, educational and social outcomes of both mothers and infants (Brooks-Gunn & Furstenberg, 1986; Gibb et al., 2014; Hofferth and Reid, 2001; Brooks-Gunn and Furstenberg, 1986). Despite this knowledge on outcomes, we have very little insight into the neural developmental impacts of early childbearing. For over 100 years, we have understood that pregnancy, childbearing, lactation, and parenting involve a precise sequence of hormonal transitions. Pregnancy involves dramatic increases in human chorionic gonadotropin (HCG), estrogen, and progesterone. Labor follows a continued increase in placental production of estrogen and progesterone coupled with increases in oxytocin, endorphins, and prolactin. In contrast, lactation involves a rapid and severe drop-off in gonadal hormones and increase in prolactin (Russell et al., 2001). Rodent models illustrate that the voluntary, proactive, appetitive aspects of maternal behavior, including seeking out and retrieving pups, are highly linked to the effect of pregnancy hormones stimulating the development and activation of the mesolimbic dopamine system (Numan and Stolzenberg, 2009). This highlights how although primarily associated with rewards, the dopamine response systems are also important for learning about parenting. In an attempt to bridge from animal to human models, Moses-Kolko and colleagues tested, but were unable to find, that motherhood affected ventral striatal response in expectation of a financial reward (Moses-Kolko et al., 2016). The lack of replicability points to the importance of developing ecologically valid paradigms to test hypothesis about the impact of pregnancy on brain development trajectories, as financial reward is distinctly different from the social and emotional reward associated with nurturing an infant. Women of all ages describe a range of physical and cognitive changes associated with the hormonal transitions associated with childbearing, but little is known about how experiencing these hormonal events during the pubertal transition, or closely following it, affects neurodevelopmental trajectories.

Understanding the impact of delayed childbearing is equally as important as understanding the impact of early childbearing. Neural flexibility, defined as the extent to which cognitive control and social and affective motivation systems are engaged and activated under different circumstances, has been found to persist into the third decade of life (Crone and Dahl, 2012). Up until very recently in human history, it is during this time that the majority of individuals engaged in mating, bonding, and parenting activities. The recent trend to delay parenting, often well into the fourth decade of life, presents some intriguing questions about the interactions between biology and experience in influencing neural development. In addition, the increasing separation between the onset of reproductive maturity and first childbearing creates opportunities for both boys and girls to have an extended period when they have expanded autonomy and independence to pursue education and other life goals. It also minimizes the need for early pair-bonding and instead fosters an opportunity for young

people to explore romantic and sexual relationships with a number of different people. In higher resourced countries such as the US and Europe, the overwhelming majority of young people have romantic and sexual relationships before they commit to a single partner (Guttmacher Institute, 2014). Moreover, in countries where the span between puberty and childbearing has just begun to elongate, such as sub-Saharan Africa and South America, approximately 25–30% of adolescent girls engage in sex before coupling (Guttmacher Institute and International Planned Parenthood Federation, 2010). Developmental neuroscience may help identify the different neurodevelopmental trajectories associated with young people having multiple dynamic, high intensity romantic relationships with a broad range of people, and young people who have longer, more intense relationships with just a few. It may also identify different neural trajectories among people who engage in parenting during the first three decades of life and those who delay.

In addition to women, men also experience hormonal transitions associated with mating and parenting. In the US, single adult men who are seeking romantic partners and paired men who are seeking relationships outside of their primary partners have higher testosterone levels compared to men in committed relationship and furthermore, men who are fathers, regardless of relationship status, have the lowest testosterone levels (Gray and Campbell, 2009). Interestingly, this relationship trend holds in some countries, but not in others, begging important questions the causal direction and the reciprocal relationship between hormones and context (Gray and Campbell, 2009). Putting a developmental frame on this research about childbearing and parenting suggests that the pace of neural maturation from adolescence to adulthood is not entirely determined by a strict ontogenetic timetable but is rather shaped by the demands of an individual's social context. As an entire generation forestalls marriage and parenthood, in some cases entirely, it would behoove us to better understand what effect this has on "typical" trajectories of neural development into the third decade of life.

## 6. Conclusion

Research, policy, and practice focused on adolescent sexual and romantic relationships are often driven more by social values and rhetoric than by science. Given that the second decade of life spans the period during which almost all young people experience puberty, and many become interested in and engage in sexual and romantic relationships, often use hormonal contraception, and possibly experience pregnancy or childbearing, research into the reciprocal relationships between these experiences, social context, and neural development would significantly expand our understanding of adolescent development, and would inform efforts to improve these trajectories. Integrated developmental science, including developmental neuroscience, offers a pathway to expand our understanding of early romantic and sexual relationships and enhance our understanding of the types of mastery experiences that support positive trajectories.

For example, developmental neuroscience offers an opportunity to identify the conditions that increase the likelihood that early romantic and sexual relationships are prosocial, health promoting behaviors, rather than risk-taking behaviors. The developmental neuroscience research on peer relationships would be strengthened by having more nuanced measures to classify peer relationships that inform our understanding of the different types of neural activation that occur in the presence of romantic versus platonic peers. Adult neuroimaging research has illuminated important distinctions in neural activation associated with different types of love, and it would be helpful to understand how that aligns with the developmental trajectory of puberty.

We have limited research suggesting that the emotional experience of passionate love changes from adolescence into adulthood, and knowing more about the underlying neural mechanisms and developmental trajectories of this transition would help inform the timing and types of support and scaffolding needed. The pubertal transition also offers an exciting opportunity to explore how romantic and sexual arousal transforms peer relationships. Young people undergo a transition from relationships completely free of sexual and romantic attraction to a context where it is one of the highest priorities. As we continue to develop neurodevelopmental models that explore peer influence, developmental neuroscience is poised to provide unique insight into this social transition.

We recognize that proposing to conduct research on early adolescents' romantic and sexual relationships is not without its complexities. Parents and human subject review boards will likely have concerns about asking young people about their feelings of love, attraction and sexual arousal. It is essential to create developmentally-sensitive, validated measures to gather accurate information about the characteristics, meaning, and qualities of romantic and sexual relationships. To do this well will require careful attention, as adolescents are less likely than adults to conform to firm categories of sexual orientation or gender identity (Savin-Williams et al., 2012; van Anders, 2015). Even establishing whether a relationship is "romantic" can be challenging, particularly if adolescent partners disagree about how to categorize their relationship. As such, the high-intensity love an adolescent feels for a friend may vacillate between being platonic, romantic, and sexual, and we need measures that can accurately capture the dynamic nature of their peer relationships. We also recognize that given the complex relationship between biological sex, hormones, and neural development, there is likely a wide range of neural variability both between and within sexes relevant to romantic and sexual behavior. To address this, it will be necessary to design research robust enough to explore these differences. Despite these challenges, we believe that the benefits of these lines of inquiry make it worthwhile.

Adolescents have the cognitive capacity to navigate early romantic and sexual experiences safely, and yet they need appropriate support to do so successfully (Harden et al., 2014a,b). A primary goal for adolescents is to learn how to engage in and navigate romantic and sexual relationships. In addition, these early romantic relationships have important implications for identity development, learning about sexual behavior, and future relationship trajectories (Furman and Shaffer, 2003). Parents, clinicians, and educators can provide relevant learning opportunities in this area, but at the same time, the majority of relevant learning comes from personal experience (Fortenberry, 2014). Better understanding the neurodevelopmental underpinnings of the developmental trajectories of romantic and sexual behaviors holds great promise for informing intervention strategies and efforts to support more positive trajectories.

Developmental neuroscience, and more comprehensively integrated developmental science, is well positioned to move adolescent sexuality from the shadowy margins of adolescent identity into the forefront of normative development. Neuroimaging has the potential to better inform our understanding if early romantic relationships are more aligned with reward or self-identity processing. Similarly, given that puberty marks the onset of romantic love, neuroimaging research during this time could help us better untangle the distinct neural underpinnings of different types of love and expand our neurodevelopmental models. In addition, developmental neuroscience has the amazing opportunity to explore whether romantic love and sexual experience is something the adolescent brain *expects* to learn about and/or how the *experience* of romantic and sexual behaviors results in differing developmental trajectories. Lastly, it can also provide us with

important insights to inform advances in contraceptive technology and increase our understanding of the timing of childbearing. As we better understand the motivations and trajectories of these autonomous, high-intensity relationships in adolescence, we can transform the dialogue about the types of programs and policies we need to best scaffold them. This offers a way to enhance positive trajectories in early adolescence. Our failure to better understand adolescents' high intensity romantic and sexual relationships does not prevent them from happening. Adolescents are primed to learn about love and sex, and it would serve all of us to understand this learning process better.

## References

- Ali, M.M., Dwyer, D.S., 2011. Estimating peer effects in sexual behavior among adolescents. *J. Adolesc.* 34 (1), 183–190. <http://dx.doi.org/10.1016/j.adolescence.2009.12.008>.
- Aron, A., Norman, C.C., Aron, E.N., McKenna, C., Heyman, R.E., 2000. Couples' shared participation in novel and arousing activities and experienced relationship quality. *J. Pers. Soc. Psychol.* 78 (2), 273–284. <http://dx.doi.org/10.1037//0022-3514.78.2.273>.
- Aron, A., Fisher, H., Mashek, D.J., Strong, G., Li, H., Brown, L.L., 2005. Reward, motivation, and emotion systems associated with early-stage intense romantic love. *J. Neurophysiol.* 94 (1), 327.
- Bartels, A., Zeki, S., 2004. The neural correlates of maternal and romantic love. *Neuroimage* 21 (3), 1155–1166. <http://dx.doi.org/10.1016/j.neuroimage.2003.11.003>.
- Baumgartner, S.E., Valkenburg, P.M., Peter, J., 2011. The influence of descriptive and injunctive peer norms on adolescents' risky sexual online behavior. *Cyberpsychol. Behav. Soc. Networking* 14 (12), 753–758. <http://dx.doi.org/10.1089/cyber.2010.0510>.
- Bearinger, L.H., Sieving, R.E., Ferguson, J., Sharma, V., 2007. Global perspectives on the sexual and reproductive health of adolescents: patterns, prevention and potential. *Lancet* 369, 1220–1231. [http://dx.doi.org/10.1016/S0140-6736\(07\)60367-5](http://dx.doi.org/10.1016/S0140-6736(07)60367-5).
- Blakemore, S.J., 2012. Imaging brain development: the adolescent brain. *Neuroimage* 61 (2), 397–406. <http://dx.doi.org/10.1016/j.neuroimage.2011.11.080>.
- Bongaarts, J., Blanc, A.K., 2015. Estimating the current mean age of mothers at the birth of their first child from household surveys. *Popul. Health Metrics* 13 (1), 1. <http://dx.doi.org/10.1186/s12963-015-0058-9>.
- Braams, B., van Duijvenvoorde, A., Peper, J.S., Crone, E.A., 2015. Longitudinal change in adolescent risk-taking: a comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *J. Neurosci.* 35 (18), 7226–7238. <http://dx.doi.org/10.1523/JNEUROSCI.4764-14.2015>.
- Brooks-Gunn, J., Furstenberg, F.F., 1986. The children of adolescent mothers: physical, academic, and psychological outcomes. *Dev. Rev.* 6 (3), 224–251. [http://dx.doi.org/10.1016/0273-2297\(86\)90013-4](http://dx.doi.org/10.1016/0273-2297(86)90013-4).
- Brown, J.D., Halpern, C.T., L'Engle, K.L., 2005. Mass media as a sexual super peer for early maturing girls. *J. Adolesc. Health* 36 (5), 420–427. <http://dx.doi.org/10.1016/j.jadohealth.2004.06.003>.
- Brown, G.R., Kulbarsh, K.D., Spencer, K.A., Duval, C., 2015. Peripubertal exposure to testicular hormones organizes response to novel environments and social behavior in adult male rats. *Horm. Behav.* 73, 135–141. <http://dx.doi.org/10.1016/j.yhbeh.2015.07.003>.
- Burnham, T.C., Chapman, J.F., Gray, P.B., McIntyre, M.H., Lipson, S.F., Ellison, P.T., 2003. Men in committed, romantic relationships have lower testosterone. *Horm. Behav.* 44 (2), 119–122. [http://dx.doi.org/10.1016/S0018-506X\(03\)00125-9](http://dx.doi.org/10.1016/S0018-506X(03)00125-9).
- Buster, J.E., Kingsberg, S.A., Aguirre, O., Brown, C., Breaux, J.G., Buch, A., Casson, 2005. Testosterone patch for low sexual desire in surgically menopausal women: a randomized trial. *Obstet. Gynecol.* 105 (5 Pt 1), 944–952. <http://dx.doi.org/10.1097/01.aog.0000158103.27672.0d>.
- Campbell, B.C., Prossinger, H., Mbizvo, M., 2005. Timing of pubertal maturation and the onset of sexual behavior among zimbabwe school boys. *Arch. Sex. Behav.* 34 (5), 505–516. <http://dx.doi.org/10.1007/s10508-005-6276-7>.
- Campbell, A.1, 2010. Oxytocin and human social behavior. *Person. Soc. Psychol. Rev.* 14 (3), 281–295. <http://dx.doi.org/10.1177/1088868310363594>.
- Chein, J., Albert, D., O'Brien, L., Uckert, K., Steinberg, L., 2011. Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Dev. Sci.* 14 (2), F1–F10. <http://dx.doi.org/10.1111/j.1467-7687.2010.01035.x>.
- Choukas-Bradley, S., Giletta, M., Widman, L., Cohen, G.L., Prinstein, M.J., 2014. Experimentally measured susceptibility to peer influence and adolescent sexual behavior trajectories: a preliminary study. *Dev. Psychol.* <http://dx.doi.org/10.1037/a0037300>.
- Collins, W.A., 2003. More than myth: the developmental significance of romantic relationships during adolescence. *J. Res. Adolesc.* 13 (1), 1–24. <http://dx.doi.org/10.1111/1532-7795.1301001>.
- Crockett, L.J., Raffaelli, M., Shen, Y.-L., 2006. Linking self-regulation and risk proneness to risky sexual behavior: pathways through peer pressure and early substance use. *J. Res. Adolesc.* 16 (4), 503–525. <http://dx.doi.org/10.1111/j.1532-7795.2006.00505.x>.
- Crone, E.A., Dahl, R.E., 2012. Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat. Rev. Neurosci.* 13 (9), 636–650. <http://dx.doi.org/10.1038/nrn3313>.
- Dahl, R.E., 2016. The developmental neuroscience of adolescence: revisiting, refining, and extending seminal models. *Dev. Cogn. Neurosci.* 17, 101–102. <http://dx.doi.org/10.1016/j.dcn.2015.12.016>.
- Davis, S.R., van der Mooren, M.J., van Lunsen, R.H., Lopes, P., Ribot, C., Ribot, J., Purdie, D.W., 2006. Efficacy and safety of a testosterone patch for the treatment of hypoactive sexual desire disorder in surgically menopausal women: a randomized, placebo-controlled trial. *Menopause (New York N.Y.)* 13 (3), 387–396. <http://dx.doi.org/10.1097/01.gme.0000179049.08371.c7>.
- De Boer, A., Van Buel, E.M., Ter Horst, G.J., 2012. Love is more than just a kiss: a neurobiological perspective on love and affection. *Neuroscience* 201, 114–124. <http://dx.doi.org/10.1016/j.neuroscience.2011.11.017>.
- Dennison, M., Whittle, S., Yücel, M., Vijayakumar, N., Kline, A., Simmons, J., Allen, N.B., 2013. Mapping subcortical brain maturation during adolescence: evidence of hemisphere- and sex-specific longitudinal changes. *Dev. Sci.* 16 (5), 772–791. <http://dx.doi.org/10.1111/desc.12057>.
- Diamond, L.M., Dickenson, J.A., 2012. The neuroimaging of love and desire: review and future directions. *Clin. Neuropsychiatry* 9, 39–46.
- Drife, J.O., 1986. Breast development in puberty. *Ann. N. Y. Acad. Sci.* 464 (1 Endocrinology), 58–65. <http://dx.doi.org/10.1111/j.1749-6632.1986.tb15993.x>.
- Edwards, D.A., O'Neal, J.L., 2009. Oral contraceptives decrease saliva testosterone but do not affect the rise in testosterone associated with athletic competition. *Horm. Behav.* 56 (2), 195–198. <http://dx.doi.org/10.1016/j.yhbeh.2009.01.008>.
- Eisenegger, C., Naef, M., 2011. Combining behavioral endocrinology and experimental economics: testosterone and social decision making. *J. Vis. Exp.* 49. <http://dx.doi.org/10.3791/2065>.
- England, P., Wu, L.L., Shafer, E.F.1, 2013. Cohort trends in premarital first births: what role for the retreat from marriage? *Demography* 50 (6), 2075–2104. <http://dx.doi.org/10.1007/s13524-013-0241-1>.
- Ernst, M., Nelson, E.E., Jazbec, S., McClure, E.B., Monk, C.S., Leibenluft, E., Pine, D.S., 2005. Amygdala and nucleus accumbens in responses to receipt and omission of gains in adults and adolescents. *Neuroimage* 25 (4), 1279–1291. <http://dx.doi.org/10.1016/j.neuroimage.2004.12.038>.
- Ewing, S.W.F., Houck, J.M., Bryan, A.D., 2014. Neural activation during response inhibition is associated with adolescents' frequency of risky sex and substance use. *Addict. Behav.* <http://dx.doi.org/10.1016/j.addbeh.2014.12.007>.
- Falk, E.B., Berkman, E.T., Lieberman, M.D., 2012. From neural responses to population behavior neural focus group predicts population-level media effects. *Psychol. Sci.* 23 (5), 439–445. <http://dx.doi.org/10.1177/0956797611434964>.
- Falk, E.B., O'Donnell, M.B., Cascio, C.N., Tinney, F., Kang, Y., Lieberman, M.D., Strecher, V.J., 2015. Self-affirmation alters the brains response to health messages and subsequent behavior change. *Proc. Natl. Acad. Sci.* 201500247 (10.1073/pnas.1500247112/-DCSupplemental).
- Finkelstein, J.W., Susman, E.J., Chinchilli, V.M., D'Arcangelo, M.R., Kunselman, S.J., Schwab, J., Kulin, H.E., 1998. Effects of estrogen or testosterone on self-reported sexual responses and behaviors in hypogonadal adolescents 1. *J. Clin. Endocrinol. Metab.* 83 (7), 2281–2285. <http://dx.doi.org/10.1210/jcem.83.7.4961>.
- Fisher, H.E., Brown, L.L., Aron, A., Strong, G., Mashek, D., 2010. Reward, addiction, and emotion regulation systems associated with rejection in love. *J. Neurophysiol.* 104 (1), 51–60. <http://dx.doi.org/10.1152/jn.00784.2009>.
- Fortenberry, J.D., 2013. Puberty and adolescent sexuality. *Horm. Behav.* 64 (2), 280–287. <http://dx.doi.org/10.1016/j.yhbeh.2013.03.007>.
- Fortenberry, J.D., 2014. Sexual learning, sexual experience, and healthy adolescent sex. *New Dir. Child Adolesc. Dev.* 2014 (144), 71–86. <http://dx.doi.org/10.1002/cad.20061>.
- Furman, W., Shaffer, L., 2003. The role of romantic relationships in adolescent development. In: Florsheim, P. (Ed.), *Adolescent Romantic Relations and Sexual Behavior: Theory, Research, and Practical Implications*. Lawrence Erlbaum Associates Publishers, New Jersey, pp. 3–22.
- Furman, W., Ho, M., Low, S., 2007. The rocky road of adolescent romantic experience: dating and adjustment. In: Engels, R., Kerr, M., Stattin, H. (Eds.), *Hot Topics in Developmental Research: Friends, Lovers, and Groups*. John Wiley & Sons, Ltd, West Sussex, England, pp. 61–80.
- Gaither, G.A., Sellbom, M.1, 2010. The sexual sensation seeking scale: reliability and validity within a heterosexual college student sample. *J. Person. Assess.* 81 (2), 157–167. <http://dx.doi.org/10.1207/S15327752JPA8102.07>.
- Galván, A., 2013. The teenage brain sensitivity to rewards. *Curr. Direct. Psychol. Sci.* 22 (2), 88–93. <http://dx.doi.org/10.1177/0963721413480859>.
- Gibb, S.J., Fergusson, D.M., Horwood, L.J., Boden, J.M., 2014. Early motherhood and long-term economic outcomes: findings from a 30-year longitudinal study. *J. Res. Adolesc.* 25 (1), 163–172. <http://dx.doi.org/10.1111/jora.12122>.
- Giedd, J.N., Denker, A.H., 2015. The adolescent brain: insights from neuroimaging. In: Bourguignon, J.P. (Ed.), *Brain Crosstalk in Puberty and Adolescence*. Springer, pp. 85–96. <http://dx.doi.org/10.1007/978-3-319-09168-6.7>.
- Giedd, J.N., Clasen, L.S., Lenroot, R., Greenstein, D., Wallace, G.L., Ordaz, S., Chrousos, G.P., 2006. Puberty-related influences on brain development. *Mol. Cell. Endocrinol.* 254–255, 154–162. <http://dx.doi.org/10.1016/j.mce.2006.04.016>.

- Goldenberg, D., Telzer, E.H., Lieberman, M.D., Fuligni, A., Galván, A., 2013. Neural mechanisms of impulse control in sexually risky adolescents. *Dev. Cogn. Neurosci.* 6, 23–29. <http://dx.doi.org/10.1016/j.dcn.2013.06.002>.
- Gray, P.B., Campbell, B.C., 2009. Human male testosterone, pair bonding and fatherhood. In: Ellison, P.T., Gray, P.B. (Eds.), *Endocrinology of Social Relationships*. Harvard University Press Cambridge, MA, Boston, MA, pp. 270–293.
- Greenough, W.T., Black, J.E., Wallace, C.S., 1987. Experience and brain development. *Child Dev.* 58, 539–559 (0009-3920/87/5803-0017).
- Guttmacher Institute, & International Planned Parenthood Federation, 2010. In Brief: Facts on the Sexual and Reproductive Health of Adolescent Women in the Developing World. Guttmacher Institute, Washington DC (Retrieved from <http://www.guttmacher.org/pubs/FB-Adolescents-SRH.pdf>).
- Guttmacher Institute, 2014. Fact Sheet: American Teens' Sexual and Reproductive Health. Guttmacher Institute, Washington DC (Retrieved from <https://www.guttmacher.org/sites/default/files/pdfs/pubs/FB-ATSRH.pdf>).
- Halpern, C.T., Udry, J.R., Campbell, B., Suchindran, C.I., 1993. Testosterone and pubertal development as predictors of sexual activity: a panel analysis of adolescent males. *Psychosom. Med.* 55 (5), 436–447.
- Halpern, C.T., Udry, J.R., Suchindran, C., 1997. Testosterone predicts initiation of coitus in adolescent females. *Psychosom. Med.* 59 (2), 161–171.
- Halpern, C.T., Udry, J.R., Suchindran, C., 1998. Monthly measures of salivary testosterone predict sexual activity in adolescent males. *Arch. Sex. Behav.* 27 (5), 445–465. <http://dx.doi.org/10.1023/A:1018700529128>.
- Hampton, M.R., Jeffery, B., McWatters, B., Smith, P., 2005. Influence of teens' perceptions of parental disapproval and peer behavior on their initiation of sexual intercourse. *Can. J. Hum. Sex.* 14 (3–4), 105–121.
- Harden, K.P., 2014a. A sex-positive framework for research on adolescent sexuality. *Perspect. Psychol. Sci.* 9 (5), 455–469. <http://dx.doi.org/10.1037/0022-3514.85.2.197>.
- Harden, K.P., Kretsch, N., Moore, S.R., Mendle, J., 2014b. Descriptive review: hormonal influences on risk for eating disorder symptoms during puberty and adolescence. *Int. J. Eat. Disord.* 47 (7), 718–726. <http://dx.doi.org/10.1002/eat.22317>.
- Hayford, S.R., Guzzo, K.B., Smock, P.J., 2014. The decoupling of marriage and parenthood? Trends in the timing of marital first births, 1945–2002. *Family Relation.* 76 (3), 520–538. <http://dx.doi.org/10.1111/jomf.12114>.
- Hazan, C., Shaver, P., 1987. Romantic love conceptualized as an attachment process. *J. Pers. Soc. Psychol.* 52 (3), 511. <http://dx.doi.org/10.1037/0022-3514.52.3.511>.
- Hensch, T.K., 2014. Bistable parvalbumin circuits pivotal for brain plasticity. *Cell* 156 (1), 17–19. <http://dx.doi.org/10.1016/j.cell.2013.12.034>.
- Hensel, D.J., Hummer, T.A., Acurio, L.R., James, T.W., Fortenberry, J.D., 2015. Feasibility of functional neuroimaging to understand adolescent women's sexual decision making. *J. Adolesc. Health* 56, 389–395. <http://dx.doi.org/10.1016/j.jadohealth.2014.11.00>.
- Herting, M.M., Gautam, P., Spielberg, J.M., Kan, E., Dahl, R.E., Sowell, E.R., 2014. The role of testosterone and estradiol in brain volume changes across adolescence: a longitudinal structural MRI study. *Hum. Brain Mapp.* 35 (11), 5622–5645. <http://dx.doi.org/10.1002/hbm.22575>.
- Hofferth, S.L., Reid, L., 2001. The effects of early childbearing on schooling over time. *Fam. Plann. Perspect.* 33 (6), 259–267.
- Hostinar, C.E., Johnson, A.E., Gunnar, M.R., 2014. Parent support is less effective in buffering cortisol stress reactivity for adolescents compared to children. *Dev. Sci.* 18 (2), 218–297. <http://dx.doi.org/10.1111/desc.1219>.
- Hummer, T.A., 2015. Media violence effects on brain development: what neuroimaging has revealed and what lies ahead. *Am. Behav. Sci.* 59 (14), 1790–1806. <http://dx.doi.org/10.1177/0002764215596553>.
- James, J., Ellis, B.J., Schlomer, G.L., Garber, J., 2012. Sex-specific pathways to early puberty, sexual debut, and sexual risk taking: tests of an integrated evolutionary-developmental model. *Dev. Psychol.* 48 (3), 687–702. <http://dx.doi.org/10.1037/a0026427>.
- Kalnin, A.J., Edwards, C.R., Wang, Y., Kronenberger, W.G., Hummer, T.A., Mosier, K.M., Mathews, 2011. The interacting role of media violence exposure and aggressive-disruptive behavior in adolescent brain activation during an emotional Stroop task. *Psychiatry Res.: Neuroimaging* 192 (1), 12–19. <http://dx.doi.org/10.1016/j.psychres.2010.11.005>.
- Kan, M.L., Cheng, Y.A., Landale, N.S., McHale, S.M., 2010. Longitudinal predictors of change in number of sexual partners across adolescence and early adulthood. *J. Adolesc. Health* 46 (1), 25–31. <http://dx.doi.org/10.1016/j.jadohealth.2009.05.002>.
- Kennett, D.J., Humphreys, T.P., Schultz, K.E.1, 2012. Sexual resourcefulness and the impact of family, sex education, media and peers. *Sex Educ.* 12 (3), 351–368. <http://dx.doi.org/10.1080/14681811.2011.615624>.
- Kerpelman, J.L., McElwain, A.D., Pittman, J.F., Adler-Baeder, F.M., 2016. Engagement in risky sexual behavior: adolescents' perceptions of self and the parent-child relationship matter. *Youth Soc.* 48 (1), 101–125. <http://dx.doi.org/10.1177/0044118x1347961>.
- Kunkel, D., Eyal, K., Finnerty, K., Biely, E., Donnerstein, E., 2005. *Sex on TV 4 2005: A Kaiser Family Foundation Report*. In: Henry, J. (Ed.). Kaiser Family Foundation, Menlo Park, CA: California.
- LeDoux, J., 2003. The emotional brain, fear, and the amygdala. *Cell. Mol. Neurobiol.* 23 (4), 727–738. <http://dx.doi.org/10.1023/A:1025048802629>.
- Longmore, M.A., Eng, A.L., Giordano, P.C., Manning, W.D., 2009. Parenting and adolescents' sexual initiation. *J. Marriage Family* 71 (4), 969–982. <http://dx.doi.org/10.1111/j.1741-3737.2009.00647.x>.
- Love, T.M., 2013. Oxytocin, motivation and the role of dopamine. *Pharmacol. Biochem. Behav.* 119, 49–60. <http://dx.doi.org/10.1016/j.pbb.2013.06.011>.
- Mathews, T.J., Hamilton, B.E., 2009. Delayed Childbearing: More Women Are Having Their First Child Later in Life. US Department of Health and Human Services. Centers for Disease Control and Prevention, National Center for Health Statistics USA (Retrieved from <http://www.cdc.gov/nchs/data/databriefs/db21.pdf>).
- Mendle, J., 2014. Beyond pubertal timing new directions for studying individual differences in development. *Curr. Direct. Psychol. Sci.* 23 (3), 215–219. <http://dx.doi.org/10.1177/0963721414530144>.
- Miller, B.C., Benson, B., Galbraith, K.A., 2001. Family relationships and adolescent pregnancy risk: a research synthesis. *Dev. Rev.* 21 (1), 1–38. <http://dx.doi.org/10.1006/drev.2000.0513>.
- Moses-Kolko, E.L., Forbes, E.E., Stepp, S., Fraser, D., Keenan, K.E., Guyer, A.E., Hipwell, A.E., 2016. The influence of motherhood on neural systems for reward processing in low income, minority, young women. *Psychoneuroendocrinology* 66, 130–137. <http://dx.doi.org/10.1016/j.psyneuen.2016.01.009>.
- Nelson, E.E., Leibenluft, E., McClure, E., Pine, D.S., 2005. The social re-orientation of adolescence: a neuroscience perspective on the process and its relation to psychopathology. *Psychol. Med.* 35 (02), 163–174. <http://dx.doi.org/10.1017/S0033291704003915>.
- Nelson, E.E., Jarcho, J.M., Guyer, A.E., 2016. Social re-orientation and brain development: an expanded and updated view. *Dev. Cognit. Neurosci.* 17, 118–127. <http://dx.doi.org/10.1016/j.dcn.2015.12.008>.
- Numan, M., Stolzenberg, D.S.1, 2009. Medial preoptic area interactions with dopamine neural systems in the control of the onset and maintenance of maternal behavior in rats. *Front. Neuroendocrinol.* 30 (1), 46–64. <http://dx.doi.org/10.1016/j.yfrne.2008.10.002>.
- Nutsch, V.L., Will, R.G., Hattori, T., Tobiansky, D.J., Dominguez, J.M., 2014. Sexual experience influences mating-induced activity in nitric oxide synthase-containing neurons in the medial preoptic area. *Neurosci. Lett.* 579, 92–96. <http://dx.doi.org/10.1016/j.neulet.2014.07.021>.
- Nutsch, V.L., Will, R.G., Robison, C.L., Martz, J.R., Tobiansky, D.J., Dominguez, J.M., 2016. Colocalization of mating-induced Fos and D2-like dopamine receptors in the medial preoptic area: influence of sexual experience. *Front. Behav. Neurosci.* 10. <http://dx.doi.org/10.3389/fnbeh.2016.00075>.
- Op de Macks, Z.A., Moor, B.G., Overgaauw, S., Güroglu, B., Dahl, R.E., Crone, E.A., 2011. Testosterone levels correspond with increased ventral striatum activation in response to monetary rewards in adolescents. *Dev. Cognit. Neurosci.* 1 (4), 506–516. <http://dx.doi.org/10.1016/j.dcn.2011.06.003>.
- Ortigue, S., Bianchi-Demicheli, F., Patel, N., Frum, C., Lewis, J.W., 2010. Neuroimaging of love: fMRI meta-analysis evidence toward new perspectives in sexual medicine. *J. Sex. Med.* 7 (11), 3541–3552. <http://dx.doi.org/10.1111/j.1743-6109.2010.01999.x>.
- Ott, M.A., Sucato, G.S., Committee on Adolescence, 2014. Contraception for adolescents. *Pediatrics* 134 (4), e1257–e1281. <http://dx.doi.org/10.1542/peds.2014-2300>.
- Parent, A.S., Teilmann, G., Juul, A., Skakkebaek, N.E., Toppari, J., Bourguignon, J.P.1, 2003. The timing of normal puberty and the age limits of sexual precocity: variations around the world, secular trends, and changes after migration. *Endocr. Rev.* 24 (5), 668–693. <http://dx.doi.org/10.1210/er.2002-0019>.
- Parke, A., Henderson, M., Wight, D., Nixon, C., 2011. Is parenting associated with teenagers' early sexual risk-taking, autonomy and relationship with sexual partners? *Perspect. Sex Reprod. Health* 43 (1), 30–40. <http://dx.doi.org/10.1363/4303011>.
- Peake, S.J., Dishion, T.J., Stormshak, E.A., Moore, W.E., Pfeifer, J.H., 2013. Risk-taking and social exclusion in adolescence: neural mechanisms underlying peer influences on decision-making. *Neuroimage* 82, 23–34. <http://dx.doi.org/10.1016/j.neuroimage.2013.05.061>.
- Peper, J.S., Dahl, R.E., 2013. The teenage brain: surging hormones – brain-behavior interactions during puberty. *Curr. Direct. Psychol. Sci.* 22 (2), 134–139. <http://dx.doi.org/10.1177/0963721412473755>.
- Peter, J., Valkenburg, P.M., 2016. Adolescents and pornography: a review of 20 years of research. *J. Sex Res.* <http://dx.doi.org/10.1080/00224499.2016.1143441>.
- Peters, S., Jolles, D.J., Van Duijvenvoorde, A.C., Crone, E.A., Peper, J.S., 2015. The link between testosterone and amygdala-orbitofrontal cortex connectivity in adolescent alcohol use. *Psychoneuroendocrinology* 53, 117–126. <http://dx.doi.org/10.1016/j.psyneuen.2015.01.004>.
- Pfeifer, J.H., Masten III, C.L., Moore, W.E., Oswald, T.M., Mazziotta, J.C., Iacoboni, M., Dapretto, M., 2011. Entering adolescence: resistance to peer influence, risky behavior, and neural changes in emotion reactivity. *Neuron* 69 (5), 1029–1036. <http://dx.doi.org/10.1016/j.neuron.2011.02.019>.
- Potard, C., Courtois, R., Rusch, E., 2008. The influence of peers on risky sexual behavior during adolescence. *Eur. J. Contraception Reprod. Healthcare* 13 (3), 264–270. <http://dx.doi.org/10.1080/13625180802273530>.
- Price, M.N., Hyde, J.S., 2008. When two isn't better than one: predictors of early sexual activity in adolescence using a cumulative risk model. *J. Youth Adolesc.* 38 (8), 1059–1071. <http://dx.doi.org/10.1007/s10964-008-9351-2>.
- Roberti, J.W., 2004. A review of behavioral and biological correlates of sensation seeking. *J. Res. Person.* 38 (3), 256–279. [http://dx.doi.org/10.1016/s0092-6566\(03\)00067-9](http://dx.doi.org/10.1016/s0092-6566(03)00067-9).
- Romeo, R.D., Richardson, H.N., Sisk, C.L., 2002. Puberty and the maturation of the male brain and sexual behavior: recasting a behavioral potential. *Neurosci. Biobehav. Rev.* 26 (3), 381–391. [http://dx.doi.org/10.1016/s0149-7634\(02\)00009-x](http://dx.doi.org/10.1016/s0149-7634(02)00009-x).

- Romeo, R.D., 2003. Puberty: a period of both organizational and activational effects of steroid hormones on neurobehavioural development. *J. Neuroendocrinol.* 15 (12), 1185–1192, <http://dx.doi.org/10.1111/j.1365-2826.2003.01106.x>.
- Roney, J.R., Simmons, Z.L., 2013. Hormonal predictors of sexual motivation in natural menstrual cycles. *Horm. Behav.* 63 (4), 636–645, <http://dx.doi.org/10.1016/j.yhbeh.2013.02.013>.
- Rosenblitt, J.C., Soler, H., Johnson, S.E., Quadagno, D.M., 2001. Sensation seeking and hormones in men and women: exploring the link. *Horm. Behav.* 40 (3), 396–402, <http://dx.doi.org/10.1006/hbeh.2001.1704>.
- Russell, J.A., Douglas, A.J., Ingram, C.D., 2001. Brain preparations for maternity adaptive changes in behavioral and neuroendocrine systems during pregnancy and lactation. An overview. *Progress in Brain Research* 133, 1–38, [http://dx.doi.org/10.1016/S0079-6123\(01\)33002-9](http://dx.doi.org/10.1016/S0079-6123(01)33002-9).
- Sørensen, K., Mouritsen, A., Aksglaede, L., Hagen, C.P., Mogensen, S.S., Juul, A., 2012. Recent secular trends in pubertal timing: implications for evaluation and diagnosis of precocious puberty. *Horm. Res. Paediatr.* 77 (3), 137–145, <http://dx.doi.org/10.1159/000323361>.
- Santor, D.A., Messervey, D., Kusumakar, V.1., 2000. Measuring peer pressure, popularity, and conformity in adolescent boys and girls: predicting school performance, sexual attitudes, and substance abuse. *J. Youth Adolesc.* 29 (2), 163–182, <http://dx.doi.org/10.1023/A:1005152515264>.
- Savin-Williams, R.C., Joyner, K., Rieger, G., 2012. Prevalence and stability of self-reported sexual orientation identity during young adulthood. *Arch. Sex. Behav.* 41 (1), 103–110, <http://dx.doi.org/10.1007/s10508-012-9913-y>.
- Schlegel, A., Barry III, H., 1991. *Adolescence: An Anthropological Inquiry*. Free Press, New York.
- Schlegel, A., 1995. The cultural management of adolescent sexuality. In: Abramson, P.R. (Ed.), *Sexual Nature, Sexual Culture*. University of Chicago Press Chicago, Chicago, IL, pp. 177–194.
- Schulz, K.M., Sisk, C.L., 2016. The organizing actions of adolescent gonadal steroid hormones on brain and behavioral development. *Neurosci. Biobehav. Rev.*, <http://dx.doi.org/10.1016/j.neubiorev.2016.07.03>.
- Sedgh, G., Finer, L.B., Bankole, A., Eilers, M.A., Singh, S., 2015. Adolescent pregnancy, birth, and abortion rates across countries: levels and recent trends. *J. Adolesc. Health* 56 (2), 223–230, <http://dx.doi.org/10.1016/j.jadohealth.2014.09.007>.
- Shifren, J.L., Davis, S.R., Moreau, M., Waldbaum, A., Bouchard, C., DeRogatis, L., O'Neill, S., 2006. Testosterone patch for the treatment of hypoactive sexual desire disorder in naturally menopausal women: results from the INTIMATE NM1 study. *Menopause* 13 (5), 770–779, <http://dx.doi.org/10.1097/01.gme.0000227400.60816.52>.
- Sisk, C.L., Foster, D.L., 2004. The neural basis of puberty and adolescence. *Nat. Neurosci.* 7 (10), 1040–1047, <http://dx.doi.org/10.1038/nn1326>.
- Sisk, C.L., Zehr, J.L., 2005. Pubertal hormones organize the adolescent brain and behavior. *Front. Neuroendocrinol.* 26 (3), 163–174, <http://dx.doi.org/10.1016/j.yfrne.2005.10.003>.
- Sisk, C.L., 2016. Hormone-dependent adolescent organization of socio-sexual behaviors in mammals. *Curr. Opin. Neurobiol.* 38, 63–68, <http://dx.doi.org/10.1016/j.conb.2016.02.00>.
- Spielberg, J.M., Olino, T.M., Forbes, E.E., Dahl, R.E., 2014. Exciting fear in adolescence: does pubertal development alter threat processing? *Dev. Cogn. Neurosci.* 8, 86–95, <http://dx.doi.org/10.1016/j.dcn.2014.01.004>.
- Suleiman, A.B., Deardorff, J., 2015. Multiple dimensions of peer influence in adolescent romantic and sexual relationships: a descriptive, qualitative perspective. *Arch. Sex. Behav.* 44 (3), 765–775, <http://dx.doi.org/10.1007/s10508-014-0394-z>.
- Tackett, J.L., Reardon, K.W., Herzhoff, K., Page-Gould, E., Harden, K.P., Josephs, R.A., 2015. Estradiol and cortisol interactions in youth externalizing psychopathology. *Psychoneuroendocrinology* 55, 146–153, <http://dx.doi.org/10.1016/j.psyneuen.2015.02.014>.
- Takesian, A.E., Hensch, T.K., 2013. Balancing plasticity/stability across brain development. *Prog. Brain Res.* 207, 3–34, <http://dx.doi.org/10.1016/B978-0-444-63327-9.00001-1>.
- Telzer, E.H., Fuligni, A.J., Lieberman, M.D., Miernicki, M., Galván, A., 2014. The quality of adolescents' peer relationships modulates neural sensitivity to risk taking. *Social Cognit. Affective Neurosci.* nsu064, <http://dx.doi.org/10.1093/scan/nsu064>.
- Telzer, E.H., 2016. Dopaminergic reward sensitivity can promote adolescent health: a new perspective on the mechanism of ventral striatum activation. *Dev. Cognit. Neurosci.* 17, 57–67, <http://dx.doi.org/10.1016/j.dcn.2015.10.01>.
- Tottenham, N., Shapiro, M., Telzer, E.H., Humphreys, K.L., 2012. Amygdala response to mother. *Dev. Sci.* 15 (3), 307–319, <http://dx.doi.org/10.1111/j.1467-7687.2011.01128.x>.
- Van de Bongardt, D., de Graaf, H., Reitz, E., Deković, M., 2014. Parents as moderators of longitudinal associations between sexual peer norms and Dutch adolescents' sexual initiation and intention. *J. Adolesc. Health* 55 (3), 388–393, <http://dx.doi.org/10.1016/j.jadohealth.2014.02.017>.
- Vermeersch, H., T'sjoen, G., Kaufman, J.-M., Vincke, J., 2008. Estradiol, testosterone, differential association and aggressive and non-aggressive risk-taking in adolescent girls. *Psychoneuroendocrinology* 33 (7), 897–908, <http://dx.doi.org/10.1016/j.psyneuen.2008.03.016>.
- Vermeersch, H., T'sjoen, G., Kaufman, J., Vincke, J., 2009. The relationship between sex steroid hormones and behavioral inhibition (BIS) and behavioral activation (BAS) in adolescent boys and girls. *Person. Individual Differ.* 47 (1), 3–7, <http://dx.doi.org/10.1016/j.paid.2009.01.034>.
- Victor, E.C., Hariri, A.R., 2015. A neuroscience perspective on sexual risk behavior in adolescence and emerging adulthood. *Dev. Psychopathol.*, 1–17, <http://dx.doi.org/10.1017/s0954579415001042>.
- Wallen, K., 2001. Sex and context: hormones and primate sexual motivation. *Horm. Behav.* 40 (2), 339–357, <http://dx.doi.org/10.1006/hbeh.2001.1696>.
- Wellings, K., Collumbian, M., Staymaker, E., Singh, S., Hodges, Z., Patel, O., 2006. *Sexual behavior in context: a global perspective*. *Lancet Sex. Reprod. Health Ser.*
- Werker, J.F., Hensch, T.K., 2015. Critical periods in speech perception: new directions. *Ann. Rev. Psychol.* 66 (1), 173, <http://dx.doi.org/10.1146/annurev-psych-010814-015104>.
- Westoff, 2003. *Trends in marriage and early childbearing in developing countries*. In: *DHS Comparative Reports*. ORC Macro, Calverton, MD.
- Whalen, P.J., Raila, H., Bennett, R., Mattek, A., Brown, A., Taylor, J., Palmer, 2013. Neuroscience and facial expressions of emotion: the role of amygdala–prefrontal interactions. *Emotion Rev.* 5 (1), 78–83, <http://dx.doi.org/10.1177/1754073912457231>.
- Whittle, S., Simmons, J.G., Dennison, M., Vijayakumar, N., Schwartz, O., Yap, M.B., Allen, N.B., 2014. Positive parenting predicts the development of adolescent brain structure: a longitudinal study. *Dev. Cognit. Neurosci.* 8, 7–17, <http://dx.doi.org/10.1016/j.dcn.2013.10.006>.
- Will, R.G., Nutsch, V.L., Turner, J.M., Hattori, T., Tobiansky, D.J., Dominguez, J.M., 2015. Astrocytes in the medial preoptic area modulate ejaculation latency in an experience-dependent fashion. *Behav. Neurosci.* 129 (1), 68, <http://dx.doi.org/10.1037/bne0000026>.
- Wolak, J., Mitchell, K., Finkelhor, D., 2007. Unwanted and wanted exposure to online pornography in a national sample of youth internet users. *Pediatrics* 119 (2), 247–257, <http://dx.doi.org/10.1542/peds.2006-1891>.
- van Anders, S.M., 2015. Beyond sexual orientation: integrating gender/sex and diverse sexualities via sexual configurations theory. *Arch. Sex. Behav.* 44 (5), 1177–1213, <http://dx.doi.org/10.1007/s10508-015-0490-8>.
- Zimmerman, Y., Eijkemans, M.J.C., Coelingh Bennink, H.J.T., Blankenstein, M.A., Fauser, B.C.J.M., 2013. The effect of combined oral contraception on testosterone levels in healthy women: A systematic review and meta-analysis. *Human Reprod. Update*, 76–105, <http://dx.doi.org/10.1093/humupd/dmt038>.