DATING AND MATING IN ADOLESCENCE: HOW HORMONES AND PUBERTY INFLUENCE ADOLESCENT MATING MOTIVATION

by

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A DISSERTATION

Presented to the Department of Psychology
and the Division of Graduate Studies of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

September 2022

DISSERTATION APPROVAL PAGE

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Title: Dating and Mating in Adolescence: How Hormones and Puberty Influence Adolescent Mating Motivation.

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Degree awarded September 2022

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DISSERTATION ABSTRACT

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Doctor of Philosophy

Department of Psychology

September 2022

Title: Dating and Mating in Adolescence: How Hormones and Puberty Influence Adolescent Mating Motivation.

Puberty marks the physical transition towards sexual maturity, culminating in the ability to reproduce. It follows that maturing cognitive, affective, and social skills develop concurrently to support reproductive competence, transitioning the mind towards identifying and exploring mating relationships. While there is much research on the link between earlier pubertal timing and earlier onset of sexual behaviors, the specific underlying psychological changes occurring prior to the enactment of these behaviors is understudied. This dissertation explores how different aspects of puberty influence the development of mating motivations in early to middle adolescent girls. The first section of this dissertation reviews the literature on the development of adolescent social cognition and points to key ways in which these processes may support mating-relevant psychology. The following two empirical studies explore the development of mating motivation and behaviors in early to middle adolescence, and investigate whether testosterone or other pubertal indices play a role in these emerging romantic ideations and experiences. Results suggest that age of menarche has a more nuanced relationship with mating indices than previously thought, as an older age of menarche is associated with increased enjoyment of mating behaviors and a greater number of romantic partnerships (Chapter III), while an earlier age of menarche is associated with poorer performance in a mate-learning task. However, neither

changes in T nor current levels of T were related to the development of mating motivation as assessed in this dissertation (Chapter III) and did not influence performance on a social learning task (Chapter IV). It is likely that more detailed explorations of romantic development will provide additional clarity on emerging romantic experiences in early to middle adolescents, and whether other hormonal mechanisms influence mating motivation in adolescent girls.

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Welling, LM, Mitchell, VE, Mogilski, JK, **Donaldson, SH**, Nicholas, SCA (2020). Sexual motivation and satisfaction among consensually non-monogamous and monogamous individuals. *Journal of Sexual Medicine.*

Mogilski, JK, Mitchell, VE, Donaldson, SH, Nicholas, SCA, Welling, LM. (2020) Sexual motivation and satisfaction among consensually non-monogamous, open relationship, and monogamous individuals. *Journal of Sexual Medicine.*

Mogilski, JK, Mitchell, VE, Reeve, SD, Donaldson, SH, Nicholas, SCA, Welling, LM (2020). Life history and multi-partner mating: A novel explanation for moral stigma against consensual nonmonogamy. *Frontiers in Psychology* 10:3033.

Mogilski JK, Reeve SD, Nicolas SCA, Donaldson SH, Mitchell VE, & Welling LLM (2019). Jealousy, consent, and compersion within monogamous and consensually non-monogamous romantic relationships. *Archives of Sexual Behavior* 48 (1811–1828).

Donaldson, S.H., Welling, L.L.M., Reeve, S.D. (2017). The influence of hormone replacement therapy on mating psychology among post-menopausal women. *Personality and Individual Differences* 115 (13-18).

ACKNOWLEDGMENTS

I want to express my sincerest gratitude for the guidance of my advisor, Jennifer Pfeifer, who took me in as a second-year graduate student when I had nowhere else to go. You encouraged me to explore my passions and supported my interests, even when they stretched beyond the bounds of the Developmental Social Neuroscience lab. Thank you for your patience and kindness throughout my time with you! I am also grateful for the input of my other dissertation committee members, Kate Mills, Nick Allen, and Leslie Leve. I would like to extend a special thank you to Kate Mills – thank you so much for your supportive, thoughtful feedback throughout the writing process of our chapter, and for cheering me on in meetings and while working in the lab! I so admire your brilliance and advocacy towards building a better graduate school experience. I would also like to acknowledge the contribution of Sam Chavez who provided endless hours of statistical training and guidance, vastly improving the scientific design and rigor of the empirical chapters in this dissertation. Thank you so much, Sam, for your valuable input and patience with me – I could not have made it through these analyses without you! To my other lab mates, thank you so much for your feedback and encouragement throughout my graduate school journey.

I am eternally grateful for my wonderful family. To my father and stepmother, thank you for teaching me the value of working hard for your dreams, and to keep pushing forward when things get difficult. To my mother, thank you for all the ways you supported me from letters in the mail, fielding my sobbing phone calls, and providing a safe haven whenever I needed one. A special thank you to my grandmother, Dorothy Donaldson, who instilled in me a love of education from a very young age and helped get me started on my graduate school journey. To all my aunts, uncles, and cousins, thank you for believing in me when I didn’t believe in myself.

I've felt all the love and support from each of you, which helped me overcome both physical and mental barriers in my way. I am so lucky to have you all in my corner!

Thank you to all my graduate school friends, especially Katie Denning, who helped me through the hardest of times – always with a smile, a hug, and/or a big glass of wine. Finally, to my dog Izzy who provided unconditional love and endless cuddles during our short years together. You were my sunshine during my darkest days, my family when I felt lonely, and my eternal best friend. You saved me in more ways than I can express. I miss you dearly and am so thankful for the time we spent together.

Dedicated to my grandmother, Dorothy Ann Donaldson.

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CHAPTER I

INTRODUCTION

Across species, the biological purpose of puberty is the transition into sexual maturity, culminating in the ability to reproduce (Schulz & Sisk, 2016). It follows that maturing cognitive, affective, and social skills develop concurrently to support reproductive competence, transitioning the mind towards identifying and exploring mating relationships. While the biological trajectory of physical changes towards sexual maturity throughout puberty and early adolescence is well documented, less research investigates how these biological changes organize and activate underlying social and cognitive abilities that aid in successful coupling and reproduction (Suleiman et al., 2017). While there is much research on the link between earlier pubertal timing and earlier onset of sexual behaviors (Baams et al., 2014), the specific underlying cognitive, affective, and social changes that likely occur prior to the enactment of these behaviors is understudied. The purpose of this dissertation is to explore how different aspects of puberty influence the development of mating motivations in adolescent girls. This work will inform our understanding of the normative processes of sexual development in adolescence, which highlights the need for (and could support the development of) more comprehensive sex education for young people – specifically, that which incorporates both the physical and mental aspects of romantic and sexual relationships. By framing adolescence as a sensitive period for learning about healthy romantic and sexual relationships, teachers, families, and other youth-serving individuals can provide additional scaffolding for positive sexual development throughout adolescence (Patton et al., 2016).

Defining Adolescence

Adolescence is typically characterized by profound biological and psychological changes in the prolonged window between childhood and adulthood. During this time, youths experience a vast expansion in the complexities of their social environment and undergo significant development in underlying cognitive processes. According to developmental scientists, adolescence begins as early as 7-10 years old with the biological initiation of puberty (Blakemore, 2008), while the end of adolescence is less well-defined. The World Health Organization (WHO) defines an 'adolescent' as anyone between 10 and 19 years old, while 'young person' refers to anyone between the ages of 10 and 24 (WHO, n.d.). However, some researchers refer to the same time period (ages 10-24) as 'adolescence' (Patton et al., 2016). Alternatively, the American Academy of Pediatrics (AAP) defines the adolescent age range as being between 10-21 years old, and this definition of adolescence will be used throughout this dissertation. AAP's breakdown of age periods will also be utilized in this dissertation, with early adolescence ranging from 10-13 years old (when pubertal changes typically begin), middle adolescence including anyone 14-17 years old (during which time many teens report interest in sexual and romantic relationships), and late adolescence spanning between 18 -21 years old (AAP, n.d.). Compared to pubertal changes which mark the onset of adolescence, the delineation between adolescence and young adulthood is more ambiguous and can vary across cultures. The WHO states that adolescence ends "when an adult identity and behavior are accepted" (WHO, n.d.). These can include taking on employment, leaving the rearing environment to live alone or with friends, or financial independence (Patton et al., 2016). However, one common hallmark of an adult identity involves the establishment of romantic life partnerships (e.g., marriage, domestic partnership) where one begins to live with one or more long-term partners (Ember et al., 2017). Thus, understanding psychological development related to finding mating partners is essential to understanding adolescent development, and can lead to translational opportunities that support this age group throughout this intense period of reproductive growth.

Measuring Puberty

Because puberty is a core feature of both adolescence and this dissertation, it is worth carefully defining in this introduction. Puberty is typically characterized using pubertal *stage* (i.e., one's current status of physical development), *timing* (i.e., when specific pubertal markers appear, or one's development compared to peers), and *tempo* (i.e., one's pace of changes across puberty).

Pubertal stage is typically assigned by doctors or nurse practitioners though physical examination. Tanner stages (Marshall & Tanner 1969) are used to classify physical development across puberty, which assign numbers ranging from 1 (*not at all developed*) to 5 (*completely developed*) based on secondary sexual characteristics (e.g., pubic hair, breast development, genital size). In psychological research studies, pubertal status is typically self-evaluated through Tanner stage line drawings (TLDs; Marshall & Tanner 1969; 1970) or the Pubertal Development Scale (PDS; Peterson et al., 1988). These measures allow individuals to select either statements (in the PDS) or line drawings (TLDs) that most accurately represent their current physical development. These self-assessments map directly onto Tanner stages, resulting in a number between one and five that represents pubertal stage.

There are several methods used to characterize pubertal timing. Pubertal status can become a "stage-normative" measure of pubertal timing by comparing how far advanced someone is in their pubertal development compared to peers of the same age and biological sex (Baams et al., 2014). Another "peer-normative" measurement is a more subjective account where participants are asked how far along they think they are in puberty relative to their peers. From this item, researchers can determine whether subjects consider themselves to be more advanced than their peers, right on time with their peers, or slower than their peers. Finally, individuals can report the age at which certain events first occurred, such as first ejaculation for boys, or first menstruation (i.e., menarche) for girls.

Finally, pubertal tempo is an assessment of how quickly or slowly changes occur through puberty. Pubertal tempo can be represented in two ways. One is simply measuring the length of time between pubertal events, such as time from breast development to menarche. Another tempo estimate can be made using statistical modeling to determine rate of changes across puberty (Beltz et al., 2014; Lee & Dennis, 2013; Mendle et al, 2014). Fast tempo appears to be linked to externalizing problems (Castellanos-Ryan et al., 2013; Mendle et al., 2014) and with age of first sexual experience (Mendle et al., 2014). However, the mechanisms via which timing and tempo influence sexual behaviors are relatively under-studied.

Pubertal Status, Timing, and Sexual Behavior

Formation of romantic relationships and new sexual experiences comprise a large part of the adolescent experience, and there is much evidence to suggest that different aspects of puberty influence the onset of sexual behaviors. A recent meta-analysis found that those with early pubertal timing - using either stage-normative or peer-normative measures - engaged in earlier and more advanced sexual behavior, and that these links were strongest among girls (Baams et al., 2014). Furthermore, researchers found a moderate to large positive association between pubertal status and combined sexual behavior (including non-penetrative sexual behaviors such as kissing, touching, oral sex, etc.; ES*r* = .42). Moderation analyses indicated that this link was also much stronger for girls and for younger samples. Finally, there was a small, positive association between age at menarche and sexual intercourse status such that adolescents with a younger age at menarche were more likely to have engaged in sexual intercourse (ESr = .15). Overall, results from this meta-analysis suggest that especially among young participants, sexual behavior was affected by a more advanced pubertal status, earlier pubertal timing compared to peers, and an earlier age of menarche (Baams et al., 2014).

While much research has focused on initiation of sexual behaviors, these behaviors are likely preceded by the development of underlying psychological processes such as sexual attraction/arousal, interpretation of other's intentions or emotions, sensitivity to social feedback, and various aspects of executive functioning (Donaldson & Mills, 2021). However, the pathway by which pubertal timing affects initiation of sexual behaviors is understudied. Given PDS scores correlate well with salivary hormone levels (Shirtcliff et al., 2009) one strong possibility is that reproductive hormones activated at puberty coordinate the development of physical, social, affective, and cognitive processes that lay the foundation for the initiation of sexual behaviors.

Pubertal Hormones and Romantic Experiences

There is some early research investigating relationships between reproductive hormone fluctuations during puberty and emerging sexual behaviors. Prior research has found that hormonal changes beginning with puberty influence adolescents' motivations to engage in romantic and sexual behaviors. In both males and females, increases in gonadal hormones—primarily in testosterone (T)—during puberty drive increased motivation and goal-oriented behavior, particularly when the outcomes result in social rewards (Cardoos et al., 2017). Pubertal increases in testosterone in both sexes have been associated with increased motivations to seek out rewarding experiences (Braams et al., 2015) and with increased motivation to engage in highly arousing, exciting experiences associated with peer relationships (Forbes & Dahl, 2010). In the context of romantic and sexual behaviors, increased motivation to seek out peer-related rewarding experiences may lead to increased behaviors such as experiences of romantic attraction, asking someone out, spending more time holding hands or kissing, or focusing attention on a new crush. During adolescence, increases in testosterone and estrogen contribute to increases in goal-oriented behavior related to sexual and romantic relationships and in social behavior that increases the likelihood of first sexual experience (Suleiman et al., 2015). Although these changes in behavior do not automatically translate into increased sexual activity, this suggests the peri-pubertal period is an important time for relevant social learning related to romantic and sexual behavior.

Focusing on T in this current study makes sense as it has previously been found that T increases sensitivity to social engagement cues by enhancing attention to social threat (Wirth & Schultheiss, 2007), motivation to act (Bos, Panksepp, Bluthé, & van Honk, 2012), sensitivity to social rewards (van Honk et al., 2004), and risk-taking (Braams et al., 2014) in adolescence - all of which play vital roles in status maintenance and intrasexual competition for mates. There is also much research supporting evolutionary models that proclaim testosterone's role in mediating status-seeking and mate-seeking motivations in adults (Eisenegger, Haushofer, & Fehr, 2011; Ellis et al., 2012; Mazur & Booth, 1998; Wingfield, Hegner, Dufty, & Ball, 1990). Due to these mating-relevant motivations associated with testosterone described above, participant T measures will be used throughout this dissertation.

Mating Motivation

While there is extensive research on the importance of romantic and sexual relationships during adolescence (Capaldi et al., 2002; Schalet, 2011; A. Suleiman & Deardorff, 2015), there is little research on sexual development as it relates to *motivation*. Recent work views mate-seeking as a normative developmental process important for development of an empowered and responsible sexual identity (Fine & McClelland, 2007; Suleiman et al., 2017). Yet, direct measurement of mating motivation is absent. Most research to date has focused on adolescent sexual behaviors from a risk-taking perspective (Braams et al., 2014, 2015; Capaldi et al., 2002) which neglects the importance of sexual motivation and desire in developmentally-appropriate stages (Suleiman et al., 2017). Although sexual desire is recognized rhetorically as an important component in emerging adolescent romantic and sexual behavior, direct investigation into the trajectory of these desires is lacking.

Asking adolescents directly about romantic relationships, sexual desires, crushes, and sexual behaviors (including behaviors outside of intercourse) is one way to understand their self-reported sexual interests. However, behavioral measures that can assess underlying, subconscious motivations will also be a valuable tool in elucidating mating motivations. One previously developed measure experimentally manipulates motivational domain-relevant cues during a reinforcement learning task (Flournoy, 2018). According to the basic reinforcement learning paradigm, the salience of presented stimuli should directly impact learning rates (Cunningham & Brosch, 2012), and this phenomenon has been well established in both humans and rodents in behavioral economics literature (Collins & Frank, 2012; Glimcher, Camerer, Fehr, & Poldrack, 2009; Jones et al., 2011). Using this type of task with mating-relevant stimuli should reveal the strength of underlying evolutionarily relevant motivations (Flournoy, 2018).

From an evolutionary perspective, selection pressures for the development and refinement of both mate-seeking and status-seeking motivations are likely high during the adolescent period (Ellis et al., 2012). Relative to other primate species, humans have a longer adolescent period, with a wider time between biological sexual maturity and the onset of sexual behaviors (Onyango et al., 2013; Silk et al., 2010). This essentially represents a ‘pause’ in development during which physiology, psychology, and behaviors become more adult-like at a relatively slower pace (Del Giudice et al., 2009). The adolescent period as a sensitive time for the development of mating relationships has been studied in primates (Onyango et al., 2013), yet similar work for human adolescence is limited. This dissertation seeks to elucidate the step-wise progression from puberty to the onset of sexual behaviors by identifying how reproductive hormones influence the development of mating motivations in early- to mid-adolescence, and whether these motivations are reflected in a social learning task related to identifying potential mates.

Present Research

The first section of this dissertation (Chapter II) reviews the literature on the development of adolescent social cognition and points to key ways in which these processes may support mating-relevant psychology. In this chapter (previously written), Donaldson and Mills (2021) review the development of social cognition in adolescence within a mating context and identify areas where cognitive processes may be specialized for reproductive competence. To achieve full reproductive competence adolescents must be able to identify potential mates, practice engaging in romantic relationship experiences (including sexual experiences) and develop coping mechanisms for relationship dissolutions. Hormonal and neurological changes at puberty form dynamic interactions with new and increasingly more complex social environments in the adolescent experience, allowing for more nuanced social-cognitive strategies across development. This is evidenced by findings that many social cognitive processes that mature during adolescence share underlying mechanisms with mating-focused behaviors and cognition. This chapter stresses the importance of investigating how adolescent social cognition supports romantic and sexual development during this period of development, and how mating-focused cognition and experiences in adolescence represent normative developmental milestones necessary for health and well-being into adulthood (Donaldson & Mills, 2021).

The next section (Chapter III) has two overarching aims. First, it explores whether it is possible to create a single factor of sexual motivation in adolescents, using existing measures of sexual motivation. Next, it tests whether current testosterone levels mediate the effect of pubertal tempo on mating motivation. While different measures of pubertal timing have been associated with sexual behaviors (e.g., Baams et al., 2014; Mendle et al., 2014), little is known about whether the tempo of puberty also influence sexual and romantic motivations in adolescents. It could be that those who advance through puberty faster than others may also be more likely to experience increased mating motivations compared to their same-aged peers. Given T's rise during puberty, its correlation with PDS scores (Shirtcliff et al., 2009), and its associations with mating psychology in adults, it is proposed that T represents the mechanistic pathway by which puberty influences mating motivation in adolescents. Specifically, it is hypothesized that the tempo of change in T over puberty influences current T levels at any given time point, and that this pathway then leads to differences in mating motivations during early to mid-adolescence.

The second study of this dissertation (Chapter IV) first explores emerging romantic ideations and experiences at a single timepoint during early to middle adolescence. It assesses whether daily T levels (as opposed to T exposure over the course of one month, as in Chapter III) influence measures of mating motivation. Given prior work finding more acute effects of testosterone on sexual behavior in adults (Gangestad et al., 2010; Gildersleeve et al., 2014), it could be that daily T levels have a more proximal effect on mating motivation than distal T fluctuations. Next, this study assesses whether testosterone levels, pubertal indices, and sexual motivation predict individual differences in learning about mating cues. Using a task previously designed to relate underlying motivations to salience of social learning cues (Flournoy, 2018), this study will explore whether this task is a valid representation of underlying sexual motivations in a sample of early to middle adolescents. It is hypothesized that reproductive hormones, pubertal stage, age of menarche, and sexual motivation (as measured using two mating-relevant indices) will influence the ability to learn about mating-relevant information, either as unique indicators, or when combined with other variables.

Finally, the last section of this dissertation (Chapter V) provides an overall discussion of how the results from both studies relate to one another and to the current scientific literature on adolescent sexual development. This section also addresses limitations of study findings and what future researchers can do to bolster understanding of emerging romantic motivations and behaviors in early to middle adolescence. Findings from this dissertation can inform family members, teachers, policy-makers, and other youth-focused personnel on developmentally appropriate interventions that support the normative development of sexuality in adolescence.

CHAPTER II

DEVELOPMENT OF SOCIAL COGNITION IN ADOLESCENCE AND THE IMPORTANCE OF MATING

Sarah Donaldson & Kathryn Mills

Abstract: Adolescents experience rapid growth in biology, cognition, and behaviours, which are essential for navigating social complexity within the human environment. One added complexity includes the development of romantic relationships. The onset of puberty prepares the body for biological processes of reproduction, allowing for the ability to conceive, carry, and rear offspring. It follows that maturing cognitive and affective systems develop concurrently to support reproductive competence, transitioning the mind towards identifying and maintaining mating relationships. This chapter reviews current literature in the development of adolescent social cognition, and proposes ways in which these mechanisms also support the emergence of a mating-focused mentality in adolescent youth. Hormonal and neurological influences on social cognition during adolescence are discussed, followed by more focused assessments of research investigating (1) face perception, (2) mentalizing, and (3) emotional regulation/executive control. How these processes support the advancement of mating cognition across adolescence will be highlighted.

Introduction

Adolescence is a time of intense changes in biology, cognition, behaviour, and social contexts (Burke et al., 2017). A primary function of adolescence is to master the social complexities of humans, a main tenet of which includes navigating romantic relationship dynamics. Despite the clear necessity for acquiring the skills to successfully mate during this time of reproductive development, current developmental cognitive literature lacks a framework for understanding how social cognitive development benefits mating psychology during adolescence.

Beginning with puberty, vast biological changes occur that are critical for the development of social, emotional, and cognitive maturation as it relates to romantic and sexual experiences. This chapter will highlight aspects of social cognitive development in adolescence, including underlying neurological changes, in which a mating-focused perspective could improve our understanding of the interrelated dynamics of this period of life. Indeed, the formation of romantic relationships and new sexual experiences comprise a large part of the adolescent experience, and underlying cognitive processes, such as sexual attraction/arousal, interpretation of others' intentions or emotions, sensitivity to social feedback, and various aspects of executive functioning, likely develop concurrently that both influence and are influenced by this new social context. These various cognitive processes involved in navigating mating interactions are referred to as 'mating intelligence' (Geher et al., 2008) and have been extensively investigated in adults, yet the developmental trajectory of these processes is lacking. To achieve full reproductive competence, adolescents must be able to identify potential mates, practice engaging in romantic relationship experiences (including sexual experiences) and develop coping mechanisms for relationship dissolutions. While there have been many investigations focused on the risks associated with sexual activity in adolescence (Ewing et al., 2015; Victor & Hariri, 2016), few have identified the normative, healthy behaviours and cognitive mechanisms related to dating and sex that are necessary for psychological adjustment and well-being into adulthood (Suleiman et al., 2017).

Defining Adolescence

Adolescence is often understood as the period of time between childhood and adulthood, when youths experience a vast expansion in the complexities of their social environment and undergo significant development in underlying cognitive processes. This period begins with the biological initiation of puberty, which in some can begin as early as 7–10 years old, yet the ending of adolescence varies by different organizational definitions. For example, the World Health Organization defines an 'adolescent' as anyone between the ages of 10 and 19 years old, while the term 'young person' is used for anyone between 10 and 24 years old (www.who.int) . Alternatively, the American Academy of Pediatrics (AAP) uses a more inclusive definition of the adolescent age range as being between 10 and 21 years old, and this is the definition of adolescence used throughout this chapter. We also use AAP's breakdown of age periods, with early adolescence ranging from 10 to 13 years old (when pubertal changes develop), middle adolescence including anyone 14–17 years old (during which many teens report interest in sexual and romantic relationships), and late adolescence as anyone between 18 and 21 years old (www.healthychildren.org). The end of adolescence is somewhat ambiguous and can be marked by substantially different processes across cultures (Schlegel & Barry III, 1991). However, a common hallmark involves the transition away from parental dependency to more adult-typical roles and responsibilities, including a socially recognized union of a romantic, intimate partnership (i.e., marriage) where one begins to live with one or more long-term partners (Ember et al., 2017). Thus, understanding social cognitive processes related to mating is essential to understanding adolescent development, and can lead to translational opportunities that support this age group throughout this intense period of reproductive growth. This chapter will cover social cognitive development across adolescence, with a special focus on how these cognitive processes facilitate maturation in the realm of intimate relationships.

Adolescent Social Cognition

Investigating social cognitive development in adolescence means exploring the mental processes required to navigate an increasingly complex social environment. With the advancement of neuroimaging methods, there has been much growth in the understanding of general adolescent social cognition. However, there is very little research identifying how the maturation of social cognitive processes relates to reproductive competence (i.e., mating intelligence). For example, while prior research has found evidence for neurological and cognitive development in perspective-taking processes during adolescence (Dumontheil et al., 2010; Garcia & Scherf, 2015; Sebastian et al., 2012), there is a gap in our understanding of how these advancements facilitate romantic interactions among youth. In the following sections, we will first discuss changes in the adolescent social environment. Then, we will describe how underlying hormonal and neurological changes during puberty influence the development of adolescent social cognition in order to support more nuanced social interactions, particularly in the realm of dating. Then, we will focus discussion on cognitive processes related to social a) perception, b) information processing, and c) regulation. Throughout, we will emphasize how incorporating a mating perspective to these processes may reveal a fuller picture of adolescent social cognitive development.

Social Changes

From an evolutionary perspective, it is important to consider the social environment in which our human ancestors evolved. Hunter-gatherer societies provide a relatively close approximation of early human culture (Ember et al., 2014) because it has been argued that, for the vast majority of primate evolution, humans and other great apes existed in small cooperative groups, subsisting on hunted animals and foraged wild plants (Fitzhugh, 2003). Although current human cultures differ substantially from evolutionary environments, the slower timescale of evolution by natural selection indicates that cognitive, emotional, and behavioural adaptations that address evolutionary survival pressures are still with us today (i.e., mismatch hypotheses; Li et al., 2018). Thus, modern societies can both reflect and influence evolved psychological adaptations relevant to survival and reproduction. Similar to past environments, in modern hunter-gatherer societies, young males focus their peer interactions on physical competitions, while young females are encouraged to focus on enhancing attractiveness in order to signal reproductive capacity (Ember et al., 2017; Schlegel & Barry III, 1991). Such intrasexual physical competition and displays of sexual receptivity are core aspects of sexual selection (the ability to attract and engage in reproduction opportunities across primate species; for review, see Puts, 2016), thus interactions with members of the same- and opposite-sex likely take on new meaning during this developmental window. Not only do these physical displays influence attraction between peers (Little, 2015), but they also serve as indicators of status and sexual maturation to the group as a whole, likely influencing societal and parental decisions regarding mating partnerships.

Globally, adolescents begin to take on more roles and responsibilities and enter more complex social environments compared with younger children. In developing countries, adolescents typically take on more adult-like responsibilities modeled by older, same-gender family members, but leisure time is spent primarily among peers, distinctly apart from adults. In industrialized societies, it is common for children to transition to new schools, grouped with same-age peers, and encounter new status hierarchies where many are initially relegated to lower standing (Eder, 1985; Eder & Kinney, 1995). Even those who may have gained popularity in primary school must navigate new social standings when entering a different school with older, more experienced youth (Ojanen & Nostrand, 2014). As mentalizing structures continue to mature from childhood through adolescence (4.2.3.2. Mentalizing C4.S10, C4S11), it is likely that secondary schoolers continue to develop increasingly nuanced conceptualizations of self, including an understanding of how peers view or accept them (e.g., Burrow & Rainone, 2017). This likely facilitates the exploration of more independent social identities available within this expanded social network. However, empirical evidence for this is lacking.

Indeed, adolescents are particularly sensitive to social feedback (Platt et al., 2013; Silvers et al., 2017, 2012). This sensitivity might facilitate a preoccupation with status (i.e., popularity), which is evident among adolescents (van den Berg et al., 2019; van den Broek et al., 2016). For example, the social reorientation hypothesis proposed by Nelson and colleagues (2005) states that adolescent social development is characterized by a marked increase in interest and time spent with peers as they establish individual identities. While the salience of peer evaluation likely represents a continuation of processes initiated during childhood, there is evidence of increased neural activation in brain regions supporting a social reorientation, with some changes related to pubertal development (medial prefrontal cortex; Pfeifer et al., 2013) and some related to age (temporoparietal junction; Blakemore and Robbins, 2012). Moreover, different types of social feedback differentially affect social cognitive networks, with social rejection increasing connectivity between the anterior cingulate cortex (ACC)and the insula (McIver et al, 2019), while social inclusion is related to decreased functional connectivity between the ventral ACC and the medial prefrontal cortex (mPFC) (Bolling et al., 2011). Social rejection and acceptance give adolescents valuable feedback in understanding their own social status within a particular context (e.g., high school, sports teams, youth clubs) and may provide motivation to achieve social approval, or to avoid social rejection. Thus, advancing and maintaining social status (i.e., popularity) among peers should represent a primary motive as adolescents enter the new social environments of secondary school (Mansfield & Wosnitza, 2010), particularly given its association with increased access to resources and mating opportunities among many primate species, including macaques (Rodriguez-Llanes et al., 2009) and humans (Bercovitch, 1991; Hopcroft, 2006).

One of the most notable differences in social dynamics between primary school-aged groups and secondary school-aged groups is the formation of romantic relationships that are more intimate and contain a sexualized component. For example, there is cross-cultural evidence that first sexual experiences and romantic relationships occur during the teenage years. In Western societies, the average age of first intercourse is around 17 years, however other sexual (non-intercourse) behaviours begin earlier (CDC, 2017). In non-Western cultures, the average age of first sexual intercourse is estimated to be between 18 and 19 years (Bearinger et al., 2007). Age of first sexual behaviours other than intercourse in developing countries has yet to be investigated, but is assumed to occur prior to intercourse (Bellizzi et al., 2019; Patton et al., 2012). It is not surprising that interest and engagement in dating and sexual activity blossom at the same time that youths experience biological changes that signal sexual receptivity (i.e., secondary sex characteristics). However, research linking pubertal development with the emergence of social cognitive processes that support sexual attraction and romantic relationship initiation is only just beginning (Cornwell et al., 2006; Harden et al., 2018; Suleiman et al., 2017). Exactly how adolescent social cognition supports mating interactions over adolescent development is essential to understanding how youths navigate this new social context.

Pubertal Hormones, Brain Development, and Social Cognition

Puberty and Hormones. While adolescents encounter new and increasingly complex social situations, underlying biological functions and supporting social-cognitive structures show concurrent development. Puberty can be considered as a coordinated suite of rapid, physical, and cognitive changes transitioning children into reproductively capable adolescents (Ellis et al., 2012), and is driven by secretions of adrenal androgens and gonadal steroids, beginning in late childhood/early adolescence, around ages 7–10 years old (Sisk & Foster, 2004; Sisk & Zehr, 2005). Adrenarche refers to the release of androgens (DHEA, DHEA-S) from the matured adrenal gland and gonadarche refers to hormonal secretions from the hypothalamus that stimulate production of reproductive hormones (e.g., oestradiol, testosterone, progesterone) as part of the hypothalamic-pituitary-gonadal (HPG) axis (Peper et al., 2010). Once adrenarche and gonadarche are initiated, puberty is marked by sharp increases in testosterone in both sexes, although the developmental shift is stronger in males compared with females (Booth et al., 2006; Braams et al., 2015). While males show a steady increase in testosterone across adolescence, peaking in early adulthood, female testosterone shows more cyclic patterns, coupled with hormonal changes across the menstrual cycle (Judd & Yen, 1973).

The rise in testosterone during puberty influences neural structures associated with general and social cognitive processes, such as sensation seeking (Campbell et al., 2010; Harden et al., 2018), reward sensitivity (Braams et al., 2015; Dreher et al., 2016; Lombardo et al., 2012;

Spielberg et al., 2014), social aggression (Dreher et al., 2016; Rowe et al., 2004), and social information processing (Cservenka et al., 2015; Nelson et al., 2016). Through neural organization, pubertal hormone secretions help activate a set of new drives and perceptual processes associated with sexual reproduction (Ellis et al., 2012; Schulz & Sisk, 2016). Testosterone levels influence social information processing systems in youth, such as interpreting facial emotions (Cservenka et al., 2015; Nelson et al., 2016) and perceiving gender cues (Johnston et al., 2003). Subcortical brain structures that are influenced in-utero by testosterone are later affected by the same hormone in early adolescence to be more responsive to positively, compared with negatively, valenced facial cues (Lombardo et al., 2012). Reproductive hormone mechanisms also modulate identification and attraction towards mating-relevant facial cues, such as jaw size, brow projection and height, eye size, and other facial proportions that correlate with estimates of facial masculinity or femininity (Roney et al., 2011). Therefore, linking social cognitive shifts and perception of specific mating cues in the face and body would be an important next step in revealing how pubertal hormones attune cognitive systems towards mating and reproduction (Suleiman et al., 2017).

Testosterone also increases sensitivity to social engagement cues by enhancing attention to social threat (Wirth & Schultheiss, 2007), motivation to act (Bos et al., 2012), and sensitivity to social rewards (van Honk et al., 2004), all of which play vital roles in status maintenance and intrasexual competition for mates, supporting evolutionary models that proclaim testosterone's role in mediating status-seeking and mate-seeking motivations in adults (Eisenegger et al., 2011; Ellis et al., 2012; Mazur & Booth, 1998; Wingfield et al., 1990). The biosocial model of status (Mazur & Booth, 1998) claims that testosterone reactivity in adults motivates competitive and risky decisions that serve to increase status and, ultimately, greater reproductive opportunities (for review, see Apicella & Dreber, 2015). Testosterone levels are also related to increases in reward sensitivity and risk taking observed during adolescence (Braams et al., 2015). In a longitudinal study of participants aged 8–27 years old, changes in testosterone levels were positively associated with reward sensitivity, as reflected in both self-report accounts and activity in the nucleus accumbens (NAcc) (Braams et al., 2015). Further, this study found that NAcc sensitivity followed a quadratic pattern (peaking in adolescence), as did risk taking, providing evidence for a link between pubertal hormones, reward sensitivity, and risk taking (Braams et al., 2015). Given the high concentration of testosterone (and other androgen) receptors in the NAcc (Lu et al., 1998), it is likely that changing hormone levels during puberty influence neurological changes in the NAcc, mediating the link between the NAcc and risk taking behaviours. Other neuroimaging studies have shown a link between oestrogen and risk taking in girls, particularly aggressive risk taking, in the middle window of their menstrual cycle (Vermeersch et al., 2008). Notably, risk-taking behaviour in laboratory tasks has been found to increase in adolescence particularly when peers are ostensibly watching, indicating a distinct social influence on these cognitive processes (Gardner & Steinberg, 2005; Peake et al., 2013). It could be that the presence of peers motivates status concerns leading to increased risky decisions (in order to gain or maintain popularity), yet this link has not been empirically investigated. Given hormonal influences on physical, neurological, and cognitive development related to reward sensitivity and risk taking, it is likely that natural selection has favoured motivations, behaviours, and cognitions that appear at the same time as reproductive capability (e.g., puberty and adolescence). For example, perhaps adolescents who were willing to take risks in order to increase their status among peers were likely to have early and more frequent copulatory encounters (and therefore higher reproductive success) compared with those who did not. An understanding of how risk taking and supporting neurological structures relate to status motivation in adolescents would give valuable insight into the normative mating experiences during adolescence.

While hormone fluctuations likely interact with social cognitive processes to guide status-maintenance and mating behaviours, specific hormone relationships with mating cognition is understudied. For example, the link between testosterone and reproductive behaviours is well established in non-human animal models (Romeo et al., 2003; Rupp & Wallen, 2007). However, evidence in adults and youth is mixed, with some studies finding a positive association (Braams et al., 2014; Buster et al., 2005; Halpern et al., 1997; 1998) and others finding a negative association (Burnham, 2007; Gray et al., 2004) or no relationship (Halpern et al., 1997, 1998; Roney & Simmons, 2013). Reproductive behaviour is presumably mediated by several processes, including attraction and sexual desire, which are also influenced by pubertal hormones. In terms of sexual motivations, researchers have found that, rather than testosterone, oestradiol and progesterone are linked with sexual desire and behaviour in females. However, the direction of the association differed by hormone. While oestradiol correlated with an increase in sexual desire, progesterone associated with declines in sexual motivation (Rupp & Wallen, 2007). Social neuro-endocrinology work would benefit from advancements in understanding the developmental trajectory of the link between reproductive hormones (i.e., oestrogen, progesterone, and testosterone) and social cognition that facilitates mating behaviours, such as arousal, sexual attraction, and desire.

The Social Brain. There is much research devoted to understanding how puberty and pubertal hormones relate to underlying neurological development in brain structures that support social cognition related to decision making, sensation seeking, risk taking, reward, and mood control (Vijayakumar et al., 2018). A particularly important aspect of social living is interpreting and understanding the thoughts, beliefs, perspectives, and intentions of others, a collection of social-cognitive processes known as 'mentalizing' (Blakemore & Mills, 2014). Modern neuroimaging research has revealed brain networks associated with mentalizing processes that show substantial structural and functional growth during adolescence. This network, often referred to as 'the social brain' (Blakemore, 2008; Blakemore & Mills, 2014) includes the (mPFC), the temporoparietal junction (TPJ), the posterior superior temporal sulcus (pSTS) and the anterior temporal cortex (ATC; Frith & Frith, 2010; Mills, et al., 2014). The mPFC is recruited more by adolescents, compared with adults, during social cognitive tasks, and is implicated in identifying the mental states and intentions of others (Blakemore, 2008). TPJ activation is evident when youths and adults attempt to infer mental states of others, rather than simply receiving information about another individual. In close anatomical proximity to the TPJ, the pSTS is activated when processing social information conveyed through gestures, eye gaze, and other body movements (Puce & Perrett, 2003). The ATC has been shown to underlie the interpretation of social narratives and processing of social scripts (Olson et al., 2013). While many of these structures and cognitions are evident in childhood, it is proposed that the specialization of these anatomically distinct regions influence the mastery of increasingly complex social interactions during adolescence (Blakemore & Mills, 2014). In the following sections, we will demonstrate how the development of the social brain can both influence, and be influenced by, the development of social cognition across adolescence, with particular focus on how these underlying mechanisms may support the development of mating cognition.

Specific Advancements in Adolescent Social Cognition

Face Perception. While obtaining information from faces is an ability that matures throughout infancy and childhood, adolescents begin to use the face to process more complex social cues, which likely include judgements of attraction (Saxton et al., 2009), social status, and inference of intention and emotion (Maner et al., 2007). Accordingly, the neural systems underlying facial processing have been found to change across adolescence (Monk et al., 2003; Pfeifer et al., 2011; Yurgelun-Todd & Killgore, 2006). Advancements in neuroimaging and electrophysiological measurements have allowed researchers to examine the neurological underpinnings of person-perception, particularly in the pSTS. Activation patterns in this area have been found to relate to interpreting complex social gestures (Pelphrey et al., 2004; Puce & Perrett, 2003). Cohen Kadosh and colleagues (2011; 2013) sought to identify functional connectivity of the face-processing network in the brain across development, comparing children, adolescents, and young adults as they detected various facial cues while in a functional magnetic resonance imaging (fMRI) scanner. Participants were instructed to detect eye-gaze direction, facial identity, and emotional expression in a series of facial images. Researchers found that, while a core face-processing network was activated for all three age groups, modulation of this network connectivity according to a face-processing task showed age-related growth. For adults, detecting facial identity was related to increased connectivity between the inferior occipital gyrus (IOG) and the fusiform gyrus, while detecting an emotional expression modulated connectivity between the IOG and superior temporal sulcus (STS). No such modulation was identified for children aged 7–11 years old (Cohen Kadosh et al., 2011), implying that specialization of this network must develop over adolescence. Follow-up work found that changes in this face-processing network connectivity were related to continued structural development of underlying brain structures, which may relate to more advanced cognitive strategies used in perceiving information from the face (Cohen Kadosh et al., 2013; Kilford et al., 2016).

Missing from adolescent person-perception literature is identifying ways in which neural facial processing networks become specialized for specific mating cues. Given the body's biological transformation towards reproduction, it is likely that concurrent neurological and cognitive processes also shift towards the detection of mating cues from facial features. In the field of evolutionary psychology, researchers have identified facial cues linked with reproductive fitness (Cornwell et al., 2006; for review, see Little, 2015) and have demonstrated that adults are more attracted to facial aspects that signal health and reproductive capacity (reviewed in Little, 2015). Therefore, it is proposed that natural selection has favoured cognitive strategies that direct attention towards reproductively fit individuals, capable of conceiving and caring for children. For example, naturally cycling females (those who have natural menstrual cycles with no hormonal birth control) report increased attraction to men with highly masculine faces, particularly during her window of ovulation (the 2–3 day period when women are most likely to conceive; Barrett & Marshall, 1969; Dixson et al., 2018; Little & Jones, 2012). Facial masculinity has a direct positive association with testosterone in men, and indicates high immunocompetence (Furman et al., 2014; Penton-Voak & Chen, 2004; Rhodes et al., 2003). Indeed, there is some evidence to suggest that ovulating women have a specialized ability to detect fitness cues in men's faces (Durante et al., 2012; Jones et al., 2019; Peters et al., 2009).

Taken together, this points to a putative shift in motivational systems during the ovulatory window when females are more interested in obtaining good genes for offspring, while favouring less masculine faces and more long-term mating strategies during other parts of the menstrual cycle (for review, see Jones et al., 2019). Additionally, adult heterosexual males (Roberts et al., 2004) and females (Lobmaier et al., 2016) are able to detect ovulation cues in the faces of females, finding that facial images of ovulating females are more attractive compared with the same female when she is not ovulating. It is likely that detecting ovulation cues from the face helps motivate and direct attention towards females who are especially likely to conceive. These proposed evolutionary adaptations have yet to be explored from a developmental perspective, which would provide essential information on how face-perception becomes attuned to mating cues as part of the body's biological shift towards reproduction (i.e., puberty). This evolutionary psychological theory around face perception requires further evidence from developmental investigations identifying how these neural structures and associated facial preferences begin to incorporate mating cues over adolescence.

Mentalizing. A fundamental aspect of social cognition involves the ability to detect, interpret, and understand the intentions, thoughts, and feelings of others, collectively known as 'mentalizing'. This ability requires the integration of a wide range of advanced perceptual, social cognitive, and affective skills, such as perspective-taking, emotion attribution, and interpreting the intentions of others, which develop from infancy and throughout childhood (Blakemore & Mills, 2014; Garcia & Scherf, 2015). The ability to reason about another individual's mental state is crucial to the development and maintenance of pair bonds, which facilitate biparental care, coordinating behaviours, and resource investments geared towards rearing young (Wlodarski & Dunbar, 2014). Ascertaining the beliefs and intentions of a potential or bonded romantic partner (referred to as 'cross-sex mind reading'; Geher & Kaufman, 2011) ensures directed reproductive behaviours (e.g., focusing efforts on someone who likely reciprocates your feelings, or who shares your desire for an exclusive romantic relationship) and better cooperation (e.g., perceiving another's needs or intentions) with a partner during child-rearing. This points to unique cognitive processes within a mating context, including cross-sex mind reading, flexible mating strategies (weighing risks and benefits of enacting short-term versus long-term mating strategies), being able to read cues that reliably indicate fitness or infidelity, and identifying and out-competing intrasexual rivals, that directly aid in romantic relationship formation and maintenance (Geher et al., 2008). However, it has yet to be examined whether the continued development of mentalizing during adolescence incorporates mating-focused social cues along with concurrent biological shifts towards reproductive competence.

As mentioned earlier (The Social Brain), key regions responsible for attributing mental states to others involve many parts of the social brain, including the TPJ, pSTS, ATC, and the dorsal medial prefrontal cortex (dmPFC). Notably, many researchers have found a decrease in dmPFC activation between adolescence and adulthood (reviewed in Blakemore, 2008). Tasks used to investigate mentalizing in adolescents include identifying preferences and attitudes of oneself versus a hypothetical 'other' (Burrows et al., 2016), and understanding others' intentions (Blakemore et al., 2007) and emotional states (Gunther Moor et al., 2012; Overgaauw et al., 2015), as well as understanding irony (Wang et al., 2006). A common paradigm for studying mentalizing is the Reading the Mind in the Eyes task (RMET; Baron-Cohen et al., 2001), where participants view cropped facial photos showing just the eyes and are asked to interpret the mental and emotional state of the person in the photo. Gunther Moor et al. (2012) compared neural activity in social brain networks during this task between early, mid, and late adolescents. These researchers found that all ages recruited the pSTS during the mentalizing task (compared with a control condition where participants estimated age and gender of photographed subjects). However, only the youngest group of participants showed additional engagement of the dmPFC (Gunther Moor et al., 2012). Follow-up work demonstrated the same pattern in a longitudinal analysis—namely, that the dmPFC follows a quadratic growth pattern such that it is heavily recruited in early and late adolescents during the RMET, but not so much during mid-adolescence (Overgaauw et al., 2015). The modulated activation of the dmPFC likely reflects an increase in cognitive control strategies engaged during social situations for adolescents compared with adults (Dumontheil et al., 2012; Kilford et al., 2016; Mills et al., 2014).

Reasoning about another's emotions and intentions in tasks such as the RMET is particularly useful in targeting potential romantic partners (e.g., identifying those who are attracted to you) and maintaining romantic relationships (e.g., understanding needs, wants, and desires of a romantic partner). Specifically, compared with children, adolescents encounter a completely new set of mentalizing demands when it comes to mating, such as (1) recognizing that others may view them in a sexualized way, and (2) determining whether romantic feelings are reciprocated. These new mentalizing requirements add an additional layer of processing when interpreting others' desires or feelings, and could therefore influence demands on the cognitive control system. Wlodarski and Dunbar (2014) investigated whether a romantic versus a neutral prime influenced performance on the RMET for adults in current romantic relationships. Results showed that participants were significantly better at interpreting the emotional states of others after a love prime compared with a neutral prime. A good next step would be to use facial images of neutral versus potential romantic partners in the RMET with adolescents to determine whether this mating context influences recruitment of pSTS and mPFC structures, which may reveal a particular mating-focused specialization within mentalizing processes.

A crucial aspect of mentalizing is the ability to take another person's perspective while inhibiting one's own, a process that requires effortful cognitive control. While perspective taking shows substantial development in childhood, there is evidence that the propensity to take another's perspective continues to develop throughout adolescence as well (Dumontheil et al., 2010). However, perspective-taking performance has been found to decrease under cognitive load, suggesting that general cognitive resources are required to successfully inhibit one's own perspective to take another's (Mills et al., 2015). Further, individual differences in inhibitory control can partly account for errors in perspective taking above age differences (Symeonidou et al., 2016).

Neuroimaging work examining perspective taking in adults and adolescents found that adults recruited more fronto-parietal cognitive control regions than adolescents when inhibiting one's own perspective (Dumontheil et al., 2012). Further, adolescents recruit the social brain when engaging in both cognitive mentalizing (understanding thoughts, perspectives, and intentions of others) and affective mentalizing (recognizing and interpreting other's affective states) (Sebastian et al., 2012). Increased perspective-taking has also been linked to the left TPJ and dorsolateral PFC during economic interactions involving trust and reciprocity (Fett et al., 2014; van den Bos et al., 2011), indicating an interaction of social cognition and cognitive control systems during adolescence.

Within a mating context, cross-sex mind reading involves not only assessing whether the desired 'other' is interested in you, but also estimating what they want and desire in a potential partnership. In a study conducted by De Backer et al. (2007) , 481 participants (65% female) stated their current desire for either a short-term or long-term sexual relationship and wrote a 'personal ad' to look for a potential mate. They then selected their preferred potential mating partner from a set of personal ads written by other participants. To engage in cross-sex mind reading, participants were then asked to estimate which personal ads the opposite sex might pick. A significant interaction was found between sex and mating strategy such that males were more accurate at assessing female long-term mating desires (selecting more long-term-focused ads when cross-sex mind reading for females), and females were more accurate in guessing the short-term mating desires of men (selecting more short-term focused ads when cross-sex mind reading for males). From an evolutionary context, accuracy in this realm is essential for reproductive fitness, given the sex-differentiated risks associated with errors. According to error management theory (Haselton & Buss, 2000) men tend to overestimate a woman's preferences for short-term encounters because of the high cost of passing up a conception opportunity (lowering their overall reproductive fitness) while women tend to underestimate a man's willingness to engage in a long-term relationship, because the costs of being wrong are extremely high. If a woman's assumption about a man's long-term mating intentions is incorrect (believing a partner is interested in a long-term, committed relationship when he is not), women must then spend extensive time and energy resources towards child-rearing with little help. Thus, perspective-taking within a mating context is an essential skill that must be developed post-puberty, because detecting the mating intentions of another individual has vast implications for intimate relationship formation. Given that these mating-focused perspective-taking abilities were explored primarily with heterosexual adults, future work should seek to identify how perspective-taking abilities become specialized for mating-relevant inferences during adolescence, particularly when adolescents begin to explore sexual orientation and identity.

Executive Functioning and Emotional Regulation. Executive functioning includes several skills such as sustained attention, motivation, planning and prioritization, goal-directed persistence, response inhibition, and emotional regulation (Dawson & Guare, 2018). Executive functioning and affective/motivational systems can interact in two key ways. First, bottom-up processes can cause the modification or disruption of executive control strategies with interference by intense emotional responses. Second, top-down processes refer to ways in which cognitive control systems exert influence over affective responses, such as re-structuring interpretations of emotional events (Dawson & Guare, 2018; Kilford et al., 2016).

Research investigating the relationship between affective processes and cognitive control often assess inhibitory control (i.e., the ability to focus attention on particular stimuli while ignoring competing emotional information). In these studies, participants must suppress goal-irrelevant stimuli while given emotional contexts or distractions. This ability to suppress affective responses to social stimuli appears to develop over the course of adolescence (for review, see Kilford et al., 2016). While processing feelings and emotions, there is evidence for increased functional connectivity between vmPFC and both the amygdala and ventral striatum in youth (Herting et al., 2015; Pfeifer et al., 2011; Somerville et al., 2013; Spielberg et al., 2014; van den Bos et al., 2012). The vmPFC, and its connectivity to the amygdala, is central in affect regulation systems, in habituation of affective stimuli, and in the formation/pursuit of socially relevant goals (Pessoa, 2009). Youths show decreased activation in the vmPFC in response to emotional stimuli (Barbalat et al., 2013; Hare et al., 2009; Kilford et al., 2016), suggesting that adolescents show decreased activity in frontal regulatory regions and increased connectivity with the emotionally sensitive amygdala. Researchers have described this imbalance in terms of Dual-Systems (or the Imbalance) Model, proposing that the under-developed cognitive control system, along with the highly developed affective and emotional system, leads to increased risk taking in adolescence (Steinberg, 2010; Casey et al., 2008). According to this perspective, youth are overly influenced by rewards, and unable to regulate reward-motivation towards more safe choices because of the relatively protracted development of frontal lobe areas. Indeed, motivational/reward pathways are more sensitive in affective contexts during adolescence, which may underlie the increase in risky choices in this age group compared with adults (Blakemore &

Robbins, 2012; Burnett et al., 2010). However, given the extreme variability in fMRI studies investigating cognitive control and affective/motivational processes, the evidence in support of the Dual-Systems Model is more nuanced (Kilford et al., 2016).

More recently, social cognitive work has investigated the Dual-Systems Model as it relates to social context. PFC recruitment is more flexible during adolescence, and is particularly sensitive to social and affective stimuli (Casey, 2015; Pfeifer & Allen, 2016; van den Bos & Eppinger, 2016). For example, the presence of peers is a social context that influences brain regions in the motivational/affective processing system, such that adolescents take more risks with peers present (Chein et al., 2011; Smith et al., 2014, 2015). Adults showed greater activity in lateral PFC during decisions, regardless of social context, while adolescents show increased use of ventral striatum and lateral orbitofrontal cortex when making decisions when peers are present versus when alone (Chein et al., 2011). Similar responses are seen in adolescence when playing another laboratory task assessing risk taking (McCormick & Telzer, 2016). Responses that vary according to social context might allow for more creative and adaptive responses that help navigate new, complex, and rapidly changing social contexts adolescents encounter (Kilford et al., 2016). Indeed, different behavioural responses can be adaptive or maladaptive depending on the particular social situation, wherein a seemingly ‘risky’ choice actually yields better overall adaptive value for the individual.

According to evolutionary literature, behaviours often associated with inhibitory control capacities are related to trade-offs one makes between ‘fast’ or ‘slow’ life history strategies (Wenner et al., 2013). Life history theory relates a suite of behaviours and biological milestones to the environmental context such that certain strategies are more useful in particular environments. In unstable, unpredictable, impoverished environments, a faster life history strategy would be beneficial, including traits such as early menarche, earlier age of first sexual encounter, earlier age at first birth, and having multiple births across the lifespan. This is because one's life expectancy is pretty low in these relatively dangerous environments so procreating early and often leads to higher overall reproductive success. Alternatively, later menarche, longer sexual abstinence, and investing heavily in only few children is most beneficial in stable, predictable, and resource-rich environments (Kaplan & Gangestad, 2015). These traits and behaviours are mediated by executive functions that motivate and organize behaviours within particular contexts. In more unpredictable environments, actions focused on short-term gains are increasingly adaptive, whereas actions biased towards long-term benefits are advantageous within stable, resource-rich environments (Wenner et al., 2013).

Therefore, viewing adolescent risk taking with this evolutionary lens could partially explain variance in the neural correlates of risky behaviour in regard to sexual activity and romantic relationship formation. Adolescents who experience early sexual development, or who make risky sexual choices such as not using protection or having multiple sex partners, or who enjoy more casual romantic relationships, could be making the most adaptive decisions for their genetic background and environment. A more holistic approach incorporating both proximate and ultimate influences on mating behaviours in adolescence will give a clearer picture on how youth navigate new and more complex social situations.

A likely motivator of potentially risky choices involves one's emotional state, or 'affect'. Social affect refers to the interaction between emotions and behaviour when communicating with others (Kilford et al., 2016), and social affective interpretations increase in salience during adolescent development (Rubia et al., 2006; Silvers et al., 2012; Somerville et al., 2013). This social affect becomes highly sensitive during adolescence, resulting in strong emotional responses to social feedback and social situations. In particular, negative feedback or social rejection from peers typically results in more distress and anxiety in youth compared with adults and children, and this effect is strongest in early adolescence (Burke et al., 2017; Kilford et al., 2016; Platt et al., 2013). Older adolescents and adults are better able to regulate emotional responses to social rejection and show heightened responses in the right ventrolateral PFC (vlPFC; Silvers et al., 2017, 2012). Studies using a simulated computer game (Cyberball) in which the participant experiences rejection from peers who do not throw the ball to them have furthered this finding. Specifically, compared with adults and children, adolescents show reduced activation of right vlPFC, indicating a positive association between right vlPFC activation and emotional regulation in response to rejection in Cyberball (Bolling et al., 2016; Cheng et al., 2019; Vijayakumar et al., 2017). Additionally, functional connectivity between right vlPFC and ventral ACC increases with age during adolescence, but only when participants feel excluded (Bolling et al., 2011, 2016; Vijayakumar et al., 2017). One such emotional regulation strategy includes emotional re-appraisal, or the ability to change one's thoughts and feelings about an emotional event (Jazaieri et al., 2014; Xie et al., 2016), a process which requires the integration of cognitive control processes and perspective-taking (McRae et al., 2012; Vijayakumar et al., 2017). While this research looks at rejection from a peer group during a simulated game, it has yet to be investigated whether neural responses to social rejection differ between peers and a potential romantic partner. More evidence is needed to determine at what age mating motivations begin to become salient, the developmental trajectory of mating motivations, and cognitive control strategies used to mitigate emotional reactions to success or failure in this realm. For example, how does rejection from a potential mate influence one's identity or self-esteem, and can emotional reappraisal help adolescents decrease negative feelings when such events occur?

In adults, ‘love’ as an affective state has been investigated from a neurological and cognitive perspective. However, the developmental trajectory of these neural underpinnings have yet to be explored. Passionate or romantic love is defined as a ‘state of intense longing for union with another’ (Acevedo et al., 2012). Recent fMRI research on individuals who claim to be ‘deeply in love’ have revealed unique patterns of brain activation when viewing images of the romantic partner versus images of acquaintances. Specifically, images of the romantic partner correlated with increased activation in the brain’s reward system, such as caudate nucleus and putamen, as well as regions related to reward processing, emotion regulation, and sensory integration, including the insula, ACC, and the subcortical ventral tegmental area (VTA). Follow-up work asked participants to rate the intensity of their romantic feelings towards their partner, and found a dose–response relationship between self-reported intensity and activations in these regions. Similarly, implicit romantic love primes activated regions associated with representations of others and the self—namely, the fusiform and angular gyri (Ortigue et al., 2010).

Neuroimaging work has also found differing neural activation patterns between initial romantic pairing and established romantic relationships. Symptoms associated with early-stage love include craving for union, focused attention, increased energy when with the partner, sexual attraction, and thinking about the partner when apart (Acevedo et al., 2012). Regions implicated in early-stage romantic love include the right VTA and the caudate nucleus, which are important in motivation, reinforcement learning, and decision making (Acevedo & Aron, 2014; Aron et al., 2005; Beauregard et al., 2009; Carter et al., 2009; Cooper et al., 2014). Importantly, the VTA also plays a role in neural networks underlying motivational and reward systems implicated in behaviours necessary for survival (Carter et al., 2009). For example, similar regions are activated in response to food (Hare et al., 2009) and monetary gains, as well as highly motivational stimuli (Carter et al., 2009; Knutson & Greer, 2008). This is consistent with romantic love as a 'desire for union with another', which must influence reproductive motivations. Furthermore, the dorsal striatum is activated during romantic relationship initiation, which is also associated with goal-directed behaviour necessary to attain rewarding stimuli (Knutson & Greer, 2008). Together, these activation patterns within romantic relationships suggest underlying motivational mechanisms for seeking and maintaining romantic pair-bonds (Acevedo & Aron, 2014). Thus, investigating neural activity in adolescents who are interested in romantic relationships would strengthen the argument for adolescence representing an inflection point in the development of mating-specific social cognition.

Implications for Mental Health

Understanding the development of social cognitive development in the context of mating can inform potential translational opportunities for adolescents with depression, an illness characterized by low self-esteem, worthlessness, and negative rumination (Manani & Sharma, 2013). Depression symptoms typically increase during adolescence, and are related to high levels of interpersonal stress (Davey et al., 2008) and decreased quality in peer relationships (Mendle et al., 2012). Uniting both social-cognitive and evolutionary-based frameworks, specific interventions may be formed to help adolescents navigate mating interactions that might otherwise lead to poorer self-evaluations. Given that adolescents experience almost constant fluctuations in social dynamics (e.g., many short-term romantic relationships, changing friend groups) and are especially sensitive to social rejection from peers during this time (Burke et al., 2017; Kilford et al., 2016), it is likely that rejection from a potential romantic interest can have a severe impact on an adolescent's self-esteem and feelings of worthiness. Further, several underlying neural structures involved with self-referential processing (i.e., mPFC, ACC, precuneus) are still developing as the ‘social brain network’ matures across adolescence. Therefore, peer rejection (particularly from a potential love interest) or the dissolution of a romantic relationship may influence the development of these structures, or perhaps negative reflections about the self within these situations result from processing deficits in these areas. Moving forward, researchers should identify how the mating context may influence the development of psychopathology in adolescence, and design interventions targeted for healthy development, maintenance, and dissolution of romantic relationships as part of a normative developmental process.

Conclusion.

As Suleiman et al. (2017) succinctly stated, ‘while existing neurodevelopmental models have integrated our current understanding of adolescent brain development . . . there has been surprisingly little focus on the importance of adolescence as a sensitive period for romantic and sexual development (p. 209)’. Given the importance of reproduction and pair-bonding from an evolutionary perspective, the period of adolescence may serve to foster the development of social cognition within a mating context at the same time as biological changes ready the body for copulation and conception. Hormonal and neurological changes at puberty form dynamic interactions with new and increasingly more complex social environments in the adolescent experience, allowing for more nuanced social cognitive strategies across development. This is evidenced by findings that many social cognitive processes that mature during adolescence share underlying mechanisms with mating-focused behaviours and cognition; however, integrating these fields of research is only just beginning. It will be important for future investigators to identify how adolescent social cognition supports romantic and sexual development during this time, and how mating cognition and experiences in adolescence represent normative developmental milestones necessary for health and well-being into adulthood.

CHAPTER III

STUDY 1

Introduction

One of the primary developmental tasks embarked upon during adolescence is the transition to sexual maturity. During puberty, reproductive hormones such as estrogen, progesterone, and testosterone organize and activate the development of sexual characteristics and sexual behavior. Adolescent boys and girls undergo internal and external biological changes that prepare the body for successful reproduction. The activation of the hypothalamic–pituitary–gonadal axis at puberty results in elevated levels of sex steroid hormones, the maturation of gametes, the appearance of secondary sex characteristics, and fertility (Sisk, 2016). However, being fertile is not sufficient for reproductive fitness in most mammals. Sexual reproduction requires a series of complex social behaviors for bringing sperm and egg together. Thus, while these hormonally mediated biological processes change the physical body, it is likely that the same hormones also influence cognitive mechanisms that shape the mental strategies of reproduction, namely interest in mate-seeking and copulatory behaviors such as kissing, touching, and later, sexual intercourse. While the development of physical reproductive maturity (i.e., primary and secondary sex characteristics) and links with risky and non-risky sexual behaviors has been investigated in recent years, the development of mating cognition in adolescence is not yet well understood. This paper seeks to investigate the mechanistic pathway between physical reproductive development and the beginning of sexual behaviors; namely, the cognitive processes that aid in navigating this new social context.

According to evolutionary biology, “mating” is a term encompassing a wide range of patterns and processes leading to successful reproduction within a species. This includes finding a partner to mate with, engaging in behaviors to attract and keep that mate, desire and willingness to copulate. Each of these activities require a subset of physical and cognitive adaptations that aid species in successfully completing each step. Indeed, across primate species, puberty marks the onset of sexual maturity along with concurrent sex-specific physiology and behaviors designed to attract and engage with potential mates. For example, females in many primate species begin to show physical signs of sexual maturity (i.e., sexual swelling and bright colorations) during their estrus cycle post-puberty (Wallen, 1990). At the same time, both receptive and proceptive behaviors begin to be displayed wherein the female either receives copulatory advances, or she herself initiates sexual interaction with conspecifics, respectively (Rooker & Gavrilets, 2020). However, humans differ from other primates in that many pubertal processes are relatively hidden and occur over an extended period of time. Thus, while animal models of sexual development and mating behavior are helpful, they are also limited in their ability to explain normative developmental trajectories of human romantic relationships and experiences. Furthermore, animal models leave out the cognitive strategies involved in the transition to sexual maturity. Therefore, mapping out the cognitive pathway from childhood through to more sophisticated romantic relationship dynamics is needed. It is likely that the same mechanisms that work towards the physical transition to sexual maturity also influence mental adaptations related to romantic relationships and experiences.

Mating Motivation

Evolutionary psychologists investigate mental adaptations associated with mating processes such as attraction (i.e., mate selection), jealousy (i.e., mate retention), sexual desire and copulation, and even parental investment. Each of these areas have a wide foundation of scientific literature in adults, however the development of these adaptations during adolescence has not yet been investigated. Here, mating motivation refers to the desire to enact mating behaviors, including interest in obtaining a short-term or long-term mate, the desire to flirt with others, and to engage in sexual activities, including kissing, touching, oral sex or intercourse. The interest and desire to engage in romantic relationships presumably precedes enacting any actual mating behaviors, and this mating motivation represents one of the starkest contrasts between children and adolescents in terms of social relationships. Therefore, exploring the cognitive mechanisms underlying the transition from childhood friendship to adolescent romance is essential to understand the adolescent social experience.

Indeed, adolescence is the time when most individuals first report having a “crush” on someone, begin dating, and engage in sexual behaviors for the first time. A “crush” typically begins with initial interest and curiosity about someone (Seiffge-Krenke, 2003), and can move into an infatuation stage where the person becomes distracted and hyper-focused on a single individual (Connolly et al., 2004). This stage can be highly emotional, with intense joy or sadness depending on whether these feelings are reciprocated (or not; Seiffge-Krenke, 2003). Next, dyadic dating typically begins at approximately 13 years of age, and about 80% of adolescents report having had a date prior to graduating high school (Tolman & McClelland, 2011). According to a large, longitudinal study, Connolly et al., (2014) found support for a three-stage normative trajectory of romantic development across adolescence. In this study, most adolescents (52.3%) reported an “on-time” romantic development, gradually maturing from simple, group-based romantic affiliations around puberty, exploring dyadic romantic relationships during mid-adolescence, and consolidating dyadic romantic bonds during late adolescence, when more adult-like, exclusive, and stable romantic partnerships are formed. Additionally, researchers found that deviations in both sequencing and timing relative to peers had negative impacts on adolescent externalizing symptoms across adolescence (Connolly et al., 2014). Furthermore, some aspects of adolescent romantic relationships can influence psychological wellbeing into adulthood, including hostile conflict or support (Kansky & Allen, 2018), connectedness (Shulman & Schachar-Shapira, 2011), and family support (Connolly et al., 2004). Thus, it is likely that adolescence is a critical window for developing both physical and mental skills for successful mating relationships. However, research has yet to identify how pubertal markers influence cognitive mating strategies during adolescence.

One meta-analysis investigated the effects of pubertal timing and status on sexual behaviors across adolescence (Baams et al., 2014). Results showed that earlier pubertal timing and more advanced pubertal status were related to earlier and more sexual behaviors. Pubertal status was significantly associated with combined sexual behavior (i.e., touching, kissing, oral sex), and pubertal timing was positively associated with both combined sexual behaviors and sexual intercourse. Furthermore, these effects were stronger for girls compared to boys, and stronger for younger adolescents compared to older adolescents (Baams et al., 2014). This meta-analysis provides evidence for relationships between pubertal indices (i.e., timing and status) and sexual behaviors, particularly in early adolescent girls.

Prior research has attributed these links between pubertal timing and sexual debut to genetic and environmental influences, consistent with life history theory (Moore et al., 2014; Belsky et al., 1991). Life history theory developed from evolutionary science and predicts that early stressful environments (e.g., parental conflict, absence, or abuse, low socioeconomic status) triggers early puberty, particularly in adolescent girls. From a biological perspective, it presumes that early stressful or unstable environments encode a shift in reproductive strategy whereby organisms differentially invest energetic resources towards earlier and more frequent reproductive opportunities (Kaplan & Gangestad, 2015; Moore et al., 2014). In humans, some evidence has suggested that early ongoing stressful environments is associated with earlier menarche in girls. For example, children who experience insecure attachment to their parents, father absence, or food insecurity early in life are more likely to reach sexual maturity earlier and more quickly than those raised in less stressful environments. (Belsky et al., 2012; Webster et al., 2014). It is likely then, that earlier maturing girls and/or girls that experience faster pubertal tempo may also develop cognitive facets of mating earlier. However, research has yet to investigate how pubertal indices relate to the cognitive processes that occur *prior* to the onset of sexual behaviors, such as sexual attraction, interest in dating or flirting, and sexual desire. This study provides an investigation into how hormones - as one physical marker of puberty - relate to underlying cognitive processes (i.e., mating motivation) in adolescent girls.

Testosterone and Mating

Given romantic (aka mating) interest and dating behavior begins during puberty and early adolescence (Connolly et al., 2014), some view this time period as a coordinated suite of events that transform both the body and the mind towards mating efforts (Ellis et al., 2012). According to the Organizational-Activational Hypothesis, hormone exposure both in-utero and during puberty serve to organize and activate sex-specific behaviors in primates and other animals (Wallen, 2015). Much of the literature on the organizational-activational hypothesis comes from rodent studies (Heck & Handa, 2019). In the foundational study testing this hypothesis, it was found that male and female guinea pigs must have been exposed to appropriate levels of T, estrogen, and progesterone in-utero and at 4-8 weeks postnatally (during their adolescent phase) to display successful mating behaviors (i.e., mounting in males and lordosis in females; Phoenix et al., 1959). Since then, this hypothesis has been expanded to explain a wide variety of sex differences in mating morphology and behavior in mammals (for review, see Wallen, 2015). Schulz et al. (2015) found that male and female behaviors in Syrian hamsters also undergo steroid-dependent organization during gestation and activation during adolescence, modulated by social experience, such as the presence of a receptive female or an intruding male. However, little work to-date has been done to investigate how reproductive hormones at puberty activate sexual motivations and behaviors in human adolescents.

In human adults, T plays an important role in mating psychology. It is correlated with the initiation of sexual relationships and preferences for more casual sexual encounters (Ellison, 2000; Bakker & Walker, 2020; Jones et al., 2018). Further evidence suggests that single men and women have higher levels of T compared to those in committed, monogamous relationships (van Anders & Siciliano, 2010). Indeed, male T increases after divorce, and lowers again upon remarriage (Mazur & Mchalek, 1998). Women with multiple sex partners in polyamorous relationships had higher T compared to women in single, monogamous relationships (Alvergene et al., 2009; van Anders et al., 2007), suggesting a role for T in one’s desire for sexual partners. Similarly, Penke and Asendorpf (2008) showed that women’s sexual behaviors uniquely predicted laboratory flirting behavior, and that this relationship was moderated by T, such that high T women were more likely to engage in flirting with a confederate compared to low T women. In another study, Anders and colleagues (2007) found that T was positively associated with women's (but not men's) number of past and expected future sexual partners. Taken together, these studies provide evidence for a clear link between T and mating efforts in *adult* men and women. Yet, little is known about how T fluctuations across puberty influence mating cognition during early to middle adolescence.

Puberty and Adolescent Sexual Relationships

The rise of T during puberty in both boys and girls may be one mechanism by which the body and mind transition towards mating efforts. Changes in T have been associated with increased motivation and goal-oriented behaviors during adolescence, which may encourage adolescents to try new things (Bradshaw et al., 2012). Changes in T have further been associated with increased motivation to seek out exciting and rewarding experiences along with enhanced experience of rewards. This new propensity likely interacts with the new social context of dating where adolescents may experience heightened rewards within romantic relationships and may spend a larger proportion of time seeking these sexual or romantic rewards.

This general relationship between T and motivation likely influences romantic and sexual motivations in both sexes. Halpern and colleagues (1997; 1998) longitudinally tracked adolescent boys and girls over 3 years and found that sexual debut correlated in boys with increased levels of salivary testosterone (1998). Similarly, girls who experienced greater increases in testosterone during puberty were also more likely to initiate sexual intercourse, independent of pubertal stage (1997). Finkelstein and colleagues (1998) exposed pre-pubertal boys to testosterone and found an increase in boys touching others and experiencing nocturnal emissions. Thus, increases in T at puberty likely prime adolescent mating cognition, preparing individuals for experiencing romantic relationships (Bradshaw et al., 2012). However, no research to-date has investigated how T changes during puberty influence sexual attraction, desire or interest in romantic relationships during early to middle adolescence.

The Current Study

The first goal of this study (Aim 1) is to determine the best combination of instruments for assessing sexual motivation in adolescents. The second goal of this investigation (Aim 2) is to determine whether the rate change in T across three waves of data collection and current basal T levels predict individual differences in sexual motivation as calculated either by a single composite factor, or calculated with separate scales depending on the results from Aim 1. It is predicted that the tempo of change in T will positively predict mating motivation, such that faster increases in T over time will predict increased levels of mating motivation, and that this effect will be partially mediated by current T levels.

Methods

Participants

189 female adolescents aged 10.0 to 13.0 years were recruited from the local community in Lane County, Oregon (OR), USA. Participants were excluded if they had any developmental disabilities, psychotic or behavioral disorders, if they were currently using any psychotropic medications other than stimulants, or if they reported or suspected being pregnant. Of the total amount recruited, 7 failed to meet inclusion criteria, and another 8 withdrew before completing any study procedures, yielding a total of 174 participants at Wave 1 of the study. The primary recruitment method consisted of recruitment letters that were distributed by schools in the greater Eugene/Springfield area to families with children in grades 5 or 6 that were registered as female. Recruitment to a lesser extent came from secure databases of people who registered their interest in our lab's/department's research, recruitment flyers posted around the community or disseminated at community events, and through snow-balling efforts. Parents/guardians gave written informed consent and adolescents assented to participate. All study procedures and ethics were approved by the Institutional Review Board of the University of Oregon.

The race and ethnicity distribution of the final sample of 174 participants was as follows: 66.1% white, non-Hispanic/Latinx/Chicanx 8.6% white Hispanic/Latinx/Chicanx, 0.6% Asian and Hispanic/Latinx/Chicanx, 0.6% African American and Hispanic/Latinx/Chicanx, 2.9% not further specified Hispanic/Latinx/Chicanx, 0.6% American Indian/Alaskan Native, 0.6% Asian, 0.6% African American, and 19.5% multiracial. This distribution showed higher racial and ethnic diversity than in the overall population of Lane County, OR (U.S. Census Bureau, 2020). All 174 participants were assigned female at birth, however 1.7% of the sample identified as non-binary at Wave 1 of the study.

Timeline and Procedure

Timeline. This longitudinal study took place over the course of approximately five years, comprising three testing waves: W1, W2, and W3. The first wave (W1) took place from December 2015 through March 2018, when participants were 10.0 to 13.0 years old (*M*age 11.64, *SD* = 0.81); the second wave (W2) took place approximately 18 months after W1 (July 2017 – October 2019; *M*age = 13.11, *SD* = 0.83); and the third wave (W3) started approximately 18 months after W2 (February 2019). However, the COVID-19 pandemic interrupted data collection during W3, so there is a wider range of data collection for this time point (February 2019 – June 2021; *M*age = 14.88, *SD* = 0.85). The average time between W1 and W2 was 1.57 years (SD = 0.12 years) and 163 participants completed W2 (retention rate of 94%). The average time between W2 and W3 was significantly longer (1.97 years) given the interruption of the COVID-19 pandemic, and 151 participants completed W3 (retention rate of 93% from W2; 87% from W1). Only participants who completed either the K-SRQ or the FSMI at W3 were included in analyses, yielding a final sample size for this study of 148. Additional waves of the study (W4, W5, and W6) are planned and currently underway, however this study only used data from W1-W3.

At each wave, participants completed two laboratory sessions (each 2–3 hours in length) approximately one month apart, as well as a questionnaire and saliva sampling component at home between sessions (see *Measures* below). Sessions were on average 33 days apart at W1, 32 days apart at W2, and 34 days apart at W3. Both lab sessions took place at the Developmental Social Neuroscience laboratory at the University of Oregon. Data for this study was collected at all three waves, however some questionnaires were only provided at W3 (see *Measures* below).

Procedure. Participants were screened for eligibility over the phone prior to scheduling their first lab session (S1). Eligible participants came into the lab with their parents or guardians and first provided written informed consent and children assent to participate. Subjects then completed a structured diagnostic interview with trained study personnel and completed a subset of questionnaires. At the end of S1, participants and their parents/guardians received supplies and instructions for completing additional questionnaires and collecting saliva samples at home prior to the second session (S2). Adolescents were asked to respond to another subset of study questionnaires, and to collect four saliva samples, one per week, between the two lab sessions. About a month later, participants returned to the lab for S2, which included an MRI scan, a self-narrative video, hair sampling, anthropometric measures, and the remaining questionnaires. They also returned the saliva samples at this session. Procedures described in this paragraph were followed for all three waves, although some questionnaires were added in subsequent waves. While participants completed several study protocols at home and at both S1 and S2, data for this study came from the at-home portion (saliva and questionnaires), and from S2 questionnaires. Therefore, detailed information about data used specifically in this study will be presented. For additional information about the remainder of the study protocol, see Barendse et al., (2020).

Measures

Testosterone. Testosterone (T) was measured through multiple saliva samples provided at each timepoint, between S1 and S2. Participants were asked to collect four saliva samples through passive drool of 2 ml each at home, in the weeks between the two laboratory sessions. Given short-term fluctuations in T throughout the day and across the menstrual cycle, adolescents were instructed to provide the sample in the morning, directly after waking, one week apart, on a weekend day. Further, participants were instructed not to eat or brush their teeth before collecting the sample. They recorded the time of day at each collection, and stated any illnesses, medication use, caffeine, and birth control use in the 24 hours before sample collection. Samples were stored in the freezer at home and brought to S2 on ice in a cooler bag. Once brought to the lab, samples were stored in a -80°C freezer until they were shipped (overnight on dry ice) to the Stress Physiology Investigative Team at Iowa State University. There, they were assayed in duplicate for dehydroepiandrosterone (DHEA), T, and estradiol using Salimetrics Enzyme-Linked Immunosorbent Assay (ELISA) kits, however only T concentrations are used in this study. Samples were rerun if the optical density coefficient of variation (CV) was greater than 7% and enough sample was left over to do so. All hormones for each participant were assayed on the same day to minimize freeze-thaw cycles, and all saliva samples from each participant are assayed on the same plate to minimize variation in hormone concentrations that may be attributable to plate differences.

Hormone Processing and Basal Estimates. Raw T concentrations for all three timepoints were log-transformed and winsorized prior to calculating "basal" hormone estimates. Next, multilevel linear regressions were used to investigate potential confounds, examining the effects of 1) waking time, and time between waking and collecting the sample, 2) medication use, 3) illness, and 4) additional variance explained by collecting samples during a weekend day. At W1, time between waking and sample collection was a significant confound, and therefore included in the basal estimate equation. At W2, collecting a sample on a weekday (versus a weekend day), use of glucocorticoid sprays/inhalers, contraceptives, and antibiotics/antifungals were confounds and therefore included in basal estimates for this time point. Initially, no significant confounds were observed at W3. However at the time of writing, only half of the hormone assays for W3 were completed due to a combination of delays related to the COVID-19 pandemic and the relocation of the lab providing assays. Therefore, in order to create a more conservative basal estimate, confounds from W1 (time between waking and sample collection) and W2 (collecting a sample on a weekday, and use of glucocorticoids, contraceptives or antibiotics/antifungals) were included in the equation for W3 basal estimates. Missing data was multiply imputed using the Amelia package in *R* (Honaker et al., 2021), which uses a bootstrapping-based algorithm for time series data. Basal T levels were then calculated across the four saliva samples using the lmer linear mixed models package in *R* (Bates et al., 2015; Vijayakumar et al., 2019). Specifically, the following model was run for each wave: $Y_{ij} = \beta_0 + \beta_1$(time between waking and collection) + β_2(weekday) + β_3(glucocorticoids) + β_4(contraceptives) + β_5(antibiotics/antifungals) + $u_j + e_{ij}$. All models accounted for i^{th} time point for each j^{th} subject, with a random intercept (u_j) and residual error term (e_{ij}). The random effects from these models reflect "basal" hormone concentrations across the repeated measurements that accounts for within-individual variance. These random effects were extracted and used in subsequent analyses (Vijayakumar et al., 2019).

Change in Testosterone Across Waves. To obtain the tempo of changes in T across waves, the following mixed model was used: $Y_{ij} = \beta_{0j} + \beta_{1j}$(wave) + e_{ij}. All models accounted for i^{th} wave (W1, W2, W3) for each j^{th} subject and residual error term (e_{ij}). Each β in this model represents the combination of fixed and random intercepts per person j (β_{0j}), and fixed and random linear slopes per person j (β_{1j}). Thus, β_{1j} was extracted from the model and used to represent pubertal tempo (i.e., each person's linear change in T across the three waves). T estimates for two waves of data were used to obtain the slope of T for participants who did not provide all three samples, or if their W3 sample was not yet assayed (n = 72). Participants who provided a hormone sample at only one wave were excluded (n = 21).

Sexual Motivation. Items from two questionnaires presented in W3 were used to assess interest in dating and/or sexual behaviors: The Fundamental Social Motives Inventory (FSMI; Neel et al., 2015) the child version of the Social Rewards Questionnaire (K-SRQ; Foulkes et al., 2017).

Fundamental Social Motives Inventory. The FSMI was developed from an evolutionary psychology framework to capture individual differences in social motives that directly relate to elements of survival and reproductive fitness (Neel et al., 2015). The inventory contains seven subscales, however, only the 6-item mate seeking subscale is relevant to this investigation. Sample items from this subscale include "I am interested in finding a new romantic/sexual partner," and "would like to find a new romantic/sexual partner soon." However, wording of the questionnaire was adjusted to be more appropriate for adolescent participants, and to encompass a wider range of dating behaviors. See Table 4 for a list of items used from this scale. Participants report their agreement with each statement on a seven point Likert scale ranging from 1 (*strongly disagree*) to 7 (*strongly agree*). Thus, higher scores on this subscale indicate greater motivation for mate-seeking. This subscale is associated with other motive-relevant self-report instruments and behaviors (Neel et al., 2015). For example, Neel et al., 2015 found that scores on the mate-seeking subscale were significantly correlated with short-term and long-term mating orientations (depending on relationship status) and with asking someone out on a date and reported sexual behaviors. Questions were added to the FSMI to assess sexual and gender identity, and whether or not the participant had ever had any romantic relationships (and if so, how many). This inventory was only administered at W3 and 133 participants responded.

Kid' Social Reward Questionnaire. The K-SRQ was adapted from an adult instrument intended to measure individual differences in the kinds of social interactions people find rewarding (Foulkes et al., 2017). In the creation of the original inventory, results for the 3-item sexual relationships subscale correlated strongly with sociosexual orientation measures (Foulkes et al., 2014). The K-SRQ was modified to be more appropriate for adolescents by replacing questions explicitly about sex (e.g., "I enjoy having an active sex life"), with questions that are closely related to sexual and romantic experience. The three items used in this investigation include "I like kissing," "I like having a crush on someone," and "I like flirting" (Foulkes et al., 2017). See Table 4 for the list of items used in this analysis. Participants report their agreement with each statement on a seven point Likert scale from 1 (*strongly disagree*) to 7 (*strongly agree*). Thus, higher scores on this subscale indicate greater enjoyment of the activity. Rewarding and valuable experiences as assessed in the K-SRQ should be directly related to what people find motivating, with greater reward derived from a particular experience indicating greater motivation to seek out that experience. This questionnaire was only administered at W3 and 148 participants responded.

Pubertal Timing. Pubertal timing was assessed using age of menarche, and pubertal status was assessed using scores on the Pubertal Development Scale and line drawings, which map onto Tanner stages.

Age of Menarche. First, adolescents were asked whether they had ever had their period and if yes, to report the date of menarche. If participants did not remember the exact date, we imputed the middle of the range they reported (e.g., June 2018 became June 15, 2018).

Pubertal Development Scale. Measures of pubertal timing were assessed at all three waves. Participants responded to the Pubertal Development Scale (PDS; Petersen et al., 1988), a self-report measure of physical development for youth under the age of 16. The PDS has been shown to correlate with measures of pubertal development derived from physical examination (Shirtcliff et al., 2009). The female version of the PDS asks participants to report whether growth has not begun, barely begun, is definitely underway, or has finished in regard to body hair, skin change, breast development, and a growth spurt. Adolescents in our sample also viewed Tanner stage line drawings (TLDs) which depict increasing levels of secondary sex characteristics, including breast development and presence of pubic hair. Answers on the PDS were recoded to correspond with the TLDs and a composite pubertal development score was created using validated conversion methods (Barendse et al., 2022; Shirtcliff et al., 2009). This composite score ranged from 1 (*not at all developed*) to 5 (*completely developed*).

Analysis Plan

To investigate construct validity, demographics will be obtained and relationships among mating motivation, puberty, and number of romantic relationships will be explored in this sample. Next, an exploratory factor analysis was run to determine whether the two measures of mating motivation - the FSMI and the K-SRQ - could be combined to represent a single, composite factor (Aim 1). Finally, mediation analyses investigated whether current levels of T (aggregated from the month prior to the W3 session) mediated the relationships between the rate of T changes across W1-W3 and measures of mating motivation completed at W3 (Aim 2).

Results

Relationships Between Mating Motivation, Puberty, and Romantic Partners

133 participants responded to the question regarding relationship status on the FSMI. At W3, 16% of participants reported currently being in a romantic relationship, and 27% participants reported no interest in seeking a romantic relationship. The remainder stated they had previously been in a romantic relationship (34%) or had never been in one but would like to be (18%). Of those currently in a relationship, the majority (88%) stated they had been in the relationship for less than 6 months. Notably, at W3 this sample displayed some variability in terms of sexual and gender identity, and in attraction preferences (see Table 1).

Table 1

Frequency Table for Adolescent Sexuality, Gender Identity, and Attraction at W3

Variable	*Counts*	*Percent of Total Sample (148)*
Relationship Status (n = 133)		
Had Past Relationships	52	34%
Not Interested	40	27%
Current Relationship	23	16%
Want Relationship	18	12%
(Missing)	(15)	(10%)
Gender Expression (n = 132)		
Female	119	80%
Questioning	10	7%
Male	3	2%
(Missing)	(16)	(11%)
Sexuality (n = 117)		
Straight	76	51%
Bisexual	16	11%
Other	11	7%
Questioning	9	6%
Gay or Lesbian	5	3%

Table 1 continued

Variable	*Counts*	*Percent of Total Sample (148)*
(Missing)	(31)	(21%)
Attraction (n = 117)		
Only Males	64	43%
Mostly Males	20	14%
Equally Both	11	7%
Not Sure	9	6%
Mostly Females	8	5%
Only Females	5	3%
(Missing)	(31)	(21%)

Note: These questions were added to the FSMI to obtain demographic information. Only 133 subjects completed the FSMI. One participant did not respond to the gender identity question. Due to a coding error some participants (n = 16) did not see the gender identity or attraction questions. The remaining 16 participants only completed the K-SRQ. The number and percentage of participants missing responses to a given item are listed in parentheses.

First, it is important to identify whether our mating motivation indices relate to pubertal timing, stage, and behavior (number of romantic relationships). Table 2 displays the descriptive statistics for each measure. Given previous findings of differences in FSMI scores depending on relationship status (Neel et al., 2015), one-way analysis of variances (ANOVAs) was run to test this in our sample for both FSMI scores ad K-SRQ scores. K-SRQ scores were not normally distributed, so Welch's *f* test was used to assess this measure. Significant differences were found in both FSMI ($F(3, 124) = 12.94$, $p < .001$) and K-SRQ scores (Welch's $F(3, 50.40) = 10.39$, $p < .001$) depending on relationship status (see Figure 1 for plots). For FSMI mate-seeking scores, Tukey post-hoc tests found significant differences between those currently in a relationship or not interested in one and those who were previously in one or wanted to be. Those currently in a relationship scored lower than both participants who were previously in a relationship ($t(124) = -3.13$, $p = .011$) and those who wanted to be in a relationship ($t(124) = -4.47$, $p < .001$). Similarly, scores in the not interested group were significantly lower than those who were previously in a relationship ($t(124) = 4.21$, $p < .001$), and from those who have never been in a relationship but want to be ($t(124) = -5.29$, $p < .001$). Those who were currently in a relationship scored similarly to those who were not interested in one ($t(124) = 0.44$, $p = .972$), and those who were previously in a relationship scored similarly to those who wanted to be in one ($t(124) = -1.17$, $p = .109$).

Tukey post-hoc tests for K-SRQ found that that those who were not interested in a romantic relationship scored significantly lower compared to all other groups, including those who are currently in a relationship ($t(127) = 4.21$, $p < .001$), those who were previously in one ($t(127) = 4.68$, $p < .001$), and those who do not want to be in one ($t(127) = -3.83$, $p < .001$). Therefore, it appears that the FSMI and K-SRQ perform well in capturing interest in romantic relations compared to those who are not interested.

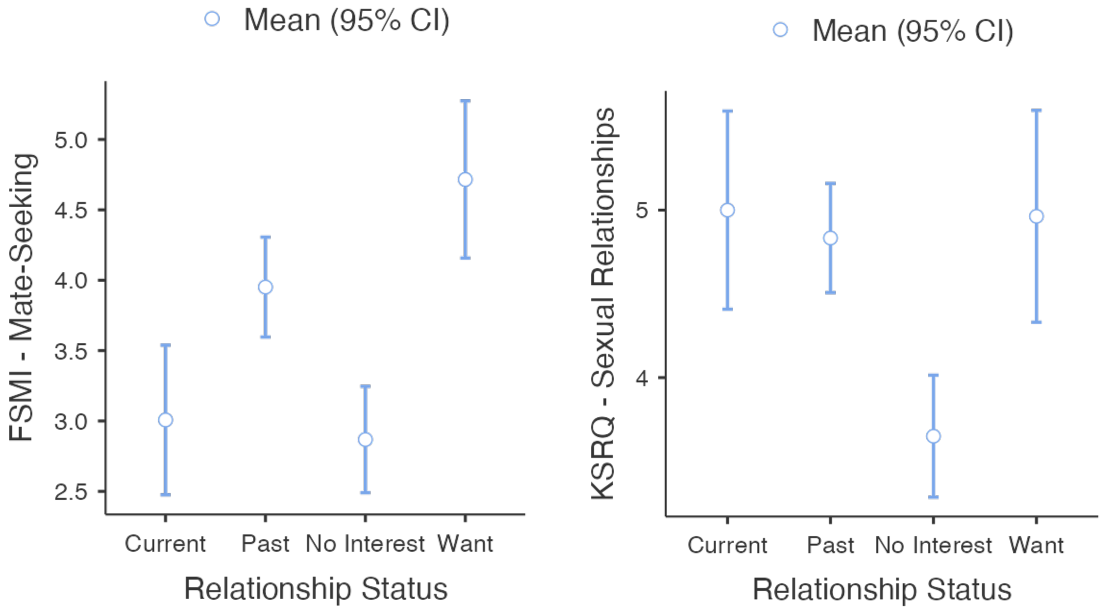
Table 2

Descriptive Statistics for FSMI and K-SRQ subscales at Timepoint 3

	N	*M*	*SD*
FSMI Mate-Seeking	**127**	**3.56**	**1.36**
Current Relationship	22	2.96	1.24
Past Relationship	50	3.95	1.25
Want Relationship	17	4.72	1.09
Not Interested	38	2.87	1.15
K-SRQ Sexual Relationships	**132**	**4.52**	**1.32**
Current Relationship	22	5.00	1.33
Past Relationship	52	4.83	1.77
Want Relationship	18	4.96	1.27
Not Interested	40	3.65	1.14

Note: Overall group means are listed in bold

Correlation analyses were also run to explore relationships between FSMI, K-SRQ, pubertal indices at W3, and number of reported romantic relationships. Spearman's rho was used to deal with non-normal distributions (see Table 3). It was predicted that both FSMI and K-SRQ



(a) Plot of means for FSMI mate-seeking subscale, grouped by relationship status.

(b) Plot of means for K-SRQ sexual relationships subscale, grouped by relationship status.

Figure 1. Mean plots for FSMI (a) and K-SRQ (b) scores grouped by relationship status

should be positively correlated with W3 pubertal indices and with the number of romantic relationships. FSMI and K-SRQ scores correlated with one another ($r(126) = .49, p < .001$) as did pubertal stage at W3 and age at W3 ($r(130) = .27, p = .002$). Additionally, age of menarche significantly correlated with age at W3 ($r(124) = .23, p = .011$). No other significant correlations were found (all *p*'s > .068). However, age at menarche was marginally related to FSMI ($r\ (120) = .17, p = .068$) and age at W3 was marginally related to K-SRQ ($r\ (131) = .16, p = .068$).

Aim 1: Exploratory Factor Analyses for Sexual Motivation

An exploratory factor analysis (EFA) was used to determine the factor structure underlying items from the mate-seeking motive sub-scale on the FSMI, and the sexual relationships subscale of the K-SRQ. See Table 4 for the items used from each scale. This factor

Table 3

Correlation Matrix for FSMI, KSRQ Scores, Pubertal Indices, and Romantic Relationships

		FSMI	*K-SRQ*	*Number of Relationships*	*Pubertal Stage*	*Age at Menarche*	*Age at Wave 3*
FSMI	Spearman's rho	—					
	p-value	—					
	N	—					
K-SRQ	Spearman's rho	0.49 ***	—				
	p-value	< .001	—				
	N	128	—				
Number of Relationships	Spearman's rho	-0.09	-0.10	—			
	p-value	0.524	0.482	—			
	N	55	55	—			
Pubertal Stage	Spearman's rho	-0.06	0.11	0.05	—		
	p-value	0.468	0.212	0.727	—		
	N	128	132	55	—		
Age at Menarche	Spearman's rho	0.17	0.08	0.00	-0.15	—	
	p-value	0.068	0.347	0.991	0.094	—	
	N	122	126	55	126	—	
Age at Wave 3	Spearman's rho	0.11	0.16	-0.05	0.27 **	0.23 *	—
	p-value	0.199	0.068	0.726	0.002	0.011	—
	N	128	133	55	132	126	—

Note. * p < .05, ** p < .01, *** p < .001

structure would then determine whether items from each subscale could be combined to represent a unified factor of sexual motivation, or if each scale should remain separate in future analyses.

First, a correlation plot was created to investigate correlations among the individual items from both the FSMI and the K-SRQ (See Figure 2). FSMI items showed medium to large

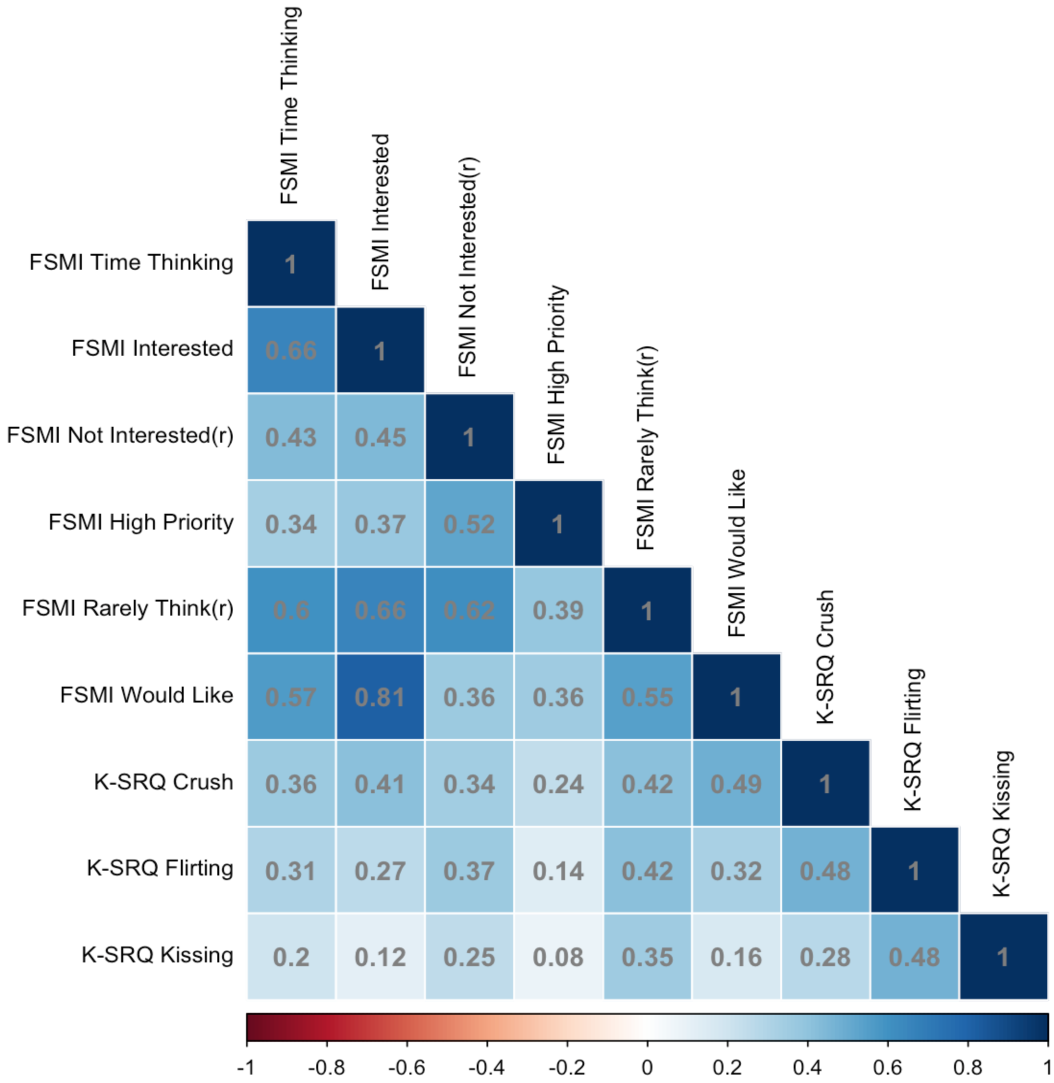
Table 4

Items Used to Measure Sexual Motivation in the FSMI and K-SRQ

FSMI - Mate Seeking Subscale (Neel et al., 2015)	**K-SRQ - Sexual Relationships Subscale (Foulkes et al., 2017)**
I spend a lot of time thinking about meeting people who could become my boyfriend or girlfriend.	*I like having a crush on someone*
I am interested in finding a new boyfriend or girlfriend.	*I like flirting*
I am not interested in meeting people to flirt with or date (reverse-scored).	*I like kissing*
Getting a new boyfriend or girlfriend is not a high priority for me (reverse-scored).	
I rarely think about finding a boyfriend or girlfriend (reverse-scored).	
I would like to find a new boyfriend or girlfriend soon.	

correlations with each other (r = .34 - r = .81) while the K-SRQ items showed more moderate correlations (r = .28 - r = .48). The K-SRQ item "I like kissing" showed the lowest correlations with each of the FSMI items (r = .08 - r = .35), yet it correlated most strongly with the reverse coded FSMI item "I rarely think about finding a boyfriend or girlfriend" (r = .35).

It was predicted that items from both scales would load onto a single factor representing mating motivation. However, given the exploratory nature of this investigation, there was no *a priori* hypothesis regarding the number of items that would load onto the composite measure. The Kaiser, Meyer, Olkin (KMO) measure of sampling adequacy suggested that data seemed



	FSMI Time Thinking	FSMI Interested	FSMI Not Interested(r)	FSMI High Priority	FSMI Rarely Think(r)	FSMI Would Like	K-SRQ Crush	K-SRQ Flirting	K-SRQ Kissing
FSMI Time Thinking	1								
FSMI Interested	0.66	1							
FSMI Not Interested(r)	0.43	0.45	1						
FSMI High Priority	0.34	0.37	0.52	1					
FSMI Rarely Think(r)	0.6	0.66	0.62	0.39	1				
FSMI Would Like	0.57	0.81	0.36	0.36	0.55	1			
K-SRQ Crush	0.36	0.41	0.34	0.24	0.42	0.49	1		
K-SRQ Flirting	0.31	0.27	0.37	0.14	0.42	0.32	0.48	1	
K-SRQ Kissing	0.2	0.12	0.25	0.08	0.35	0.16	0.28	0.48	1

Figure 2. Correlation plot for all items used in EFA

appropriate for factor analysis (KMO = 0.83). Standardized cutoffs for factor loadings by sample size suggested a loading of at least .50 for a sample size of 120 to be considered significant (Kyriazos, 2018). First, the number of factors was explored using “nfactors” in *R* and identifying the number of recommended factors based on the root mean residual, yielding two factors as the most supported. However, given my first aim to determine whether a single, composite score could be used to assess mating motivation, the EFA was initially limited to one factor, and factor loadings were rotated using oblimin rotation. The results of this analysis shown in Table 5 reveal little support for combining items from both measures to represent a single composite measure. Thus, an additional EFA was analyzed and restricted to two factors in order to confirm whether items load onto their respective inventories. Table 6 shows the factor loadings for two factors, indicating that items used in this investigation are best represented by each individual questionnaire. Therefore, each measure was calculated by averaging items (after reverse coding where necessary).

Table 5

Factor Loadings for One-Factor Exploratory Factor Analysis

Items	*Factor Loadings*	*Uniqueness*
I rarely think about finding a boyfriend or girlfriend (reverse-scored).	.82	.33
I am interested in finding a new boyfriend or girlfriend	.80	.35
I would like to find a new boyfriend or girlfriend soon.	.76	.43
I spend a lot of time thinking about meeting people who could become my boyfriend or girlfriend.	.72	.49
I am not interested in meeting people to flirt with or date (reverse-scored).	.65	.58
I like having a crush on someone	.58	.67
I like flirting	.50	.75
Getting a new boyfriend or girlfriend is not a high priority for me (reverse-scored).	.48	.76
I like kissing	.34	.88

Table 6

Factor Loadings for Two-Factor Exploratory Factor Analysis

Items	*FSMI Factor Loadings*	*K-SRQ Factor Loadings*	*Uniqueness*
I am interested in finding a new boyfriend or girlfriend.	.97		.14
I would like to find a new boyfriend or girlfriend soon.	.80		.36
I spend a lot of time thinking about meeting people who could become my boyfriend or girlfriend.	.68		.48
I rarely think about finding a boyfriend or girlfriend (reverse-scored).	.61		.35
Getting a new boyfriend or girlfriend is not a high priority for me (reverse-scored).	.47		.76
I am not interested in meeting people to flirt with or date (reverse-scored).	.45		.58
I like flirting.		.76	.40
I like kissing.		.64	.62
I like having a crush on someone.		.39	.63

Aim 2: Mediation Analysis

First, basal estimates were created for each wave as described in the Methods section and in prior literature (Vijayakumar et al., 2019). See Table 7 for descriptives of basal T concentrations at each wave.

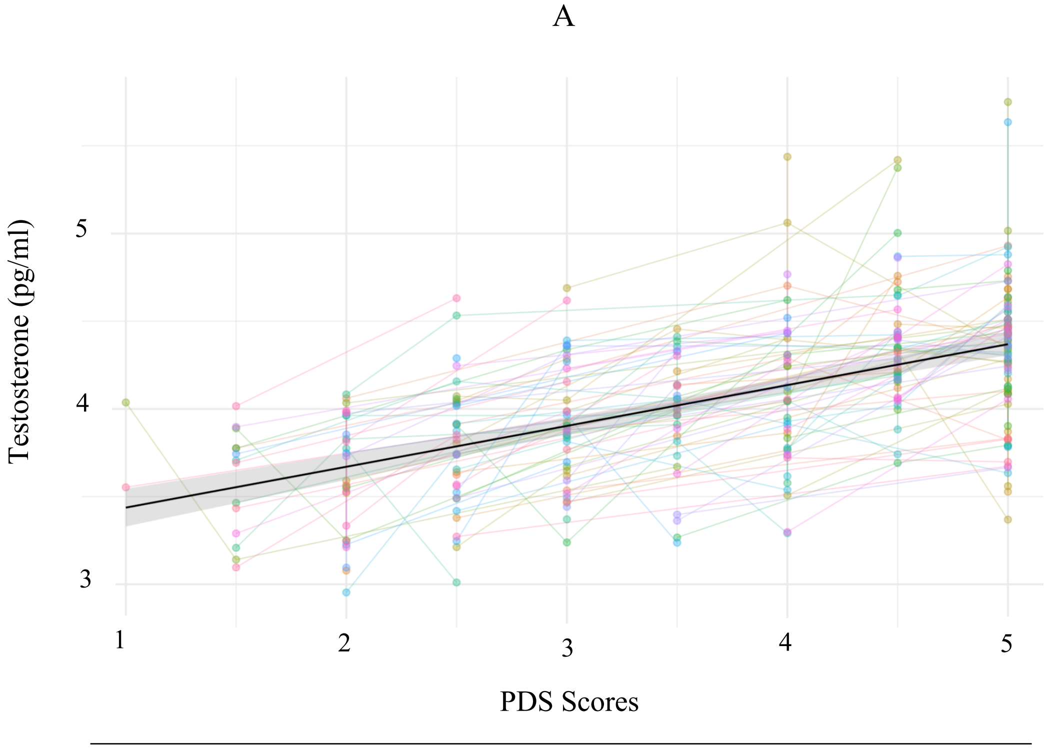
Next, it was important to assess whether T showed a linear relationship with pubertal development. Figure 3 displays the linear relationship between T and PDS scores and T across waves, indicating that T likely increases linearly across the age range used in this sample. To check this, a scatterplot was generated for levels of T across age, and residuals were graphed (Figure 4). Given even dispersion of the residuals, the assumption of linearity was appropriate.

Table 7

Descriptive Statistics for Basal T at each Timepoint in pg/ml.

	W1 Testosterone	*W2 Testosterone*	*W3 Testosterone*
Number of Samples	134	128	69
Adjusted Means	3.72	4.21	4.42
Raw Means	3.70	4.20	4.40
Standard Deviation	0.37	0.30	0.47
Minimum	2.90	3.21	3.37
Maximum	4.87	5.06	5.75

Testing the Mediation. A mediation analysis was conducted using the lavaan package in *R* (Yves, 2012). Participants were included in this analysis if they completed either the FSMI or K-SRQ, and provided saliva samples for at least two waves of data (N = 133). It was predicted that change in T would have an effect on mating motivation, and that this relationship would be mediated by current T levels. Following the results from Aim 1, the mediation analysis was run twice, once with the mate-seeking score from the FSMI as the dependent variable, and once with the sexual relationships score from the K-SRQ as the dependent variable. Missing data was handled using case-wise (or 'full information') maximum likelihood estimation within the lavaan package in *R* (Yves, 2012). See Figure 5 for results using both the FSMI and the K-SRQ as the dependent variable. There was no indirect effect of current T levels on the relationship between change in T and mating motivation in either the FSMI model ($\beta = 1.26$, $Z = 1.65$, $p = .098$) or the K-SRQ model ($\beta = 1.25$, $Z = 1.69$, $p = .090$). Further, there was no direct effect of change in T on either FSMI scores ($\beta = -0.87$, $Z = -.36$, $p = .719$) or K-SRQ scores ($\beta = -1.71$, $Z = -0.87$, $p = .383$). Finally, there was no effect of rate of change in T on mating motivation for either the



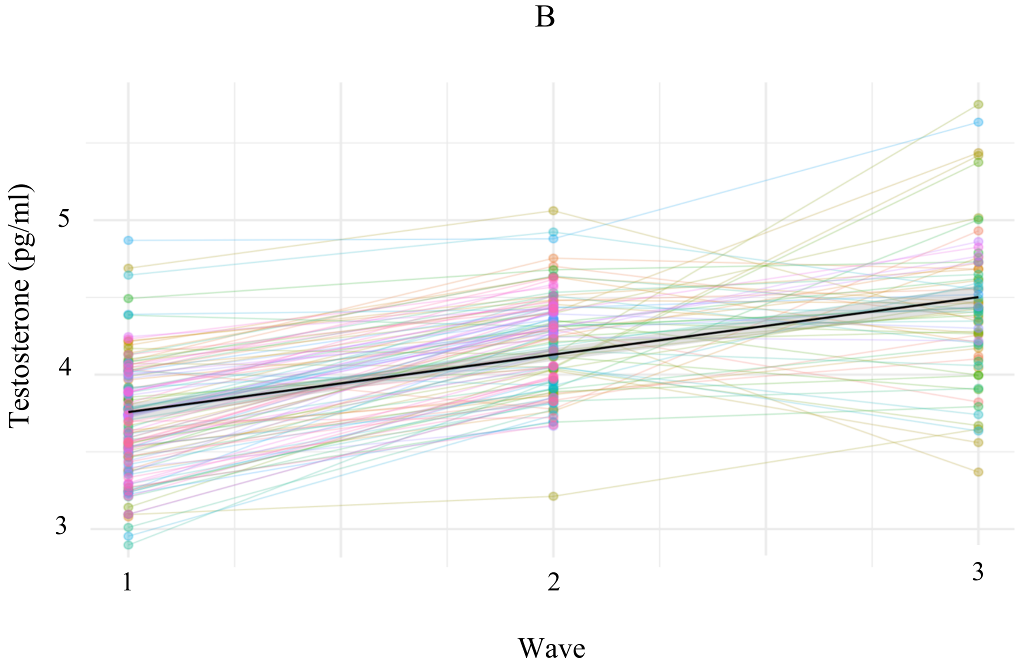


Figure 3. Linear relationship between testosterone and PDS scores (A) and change in testosterone across waves (B).

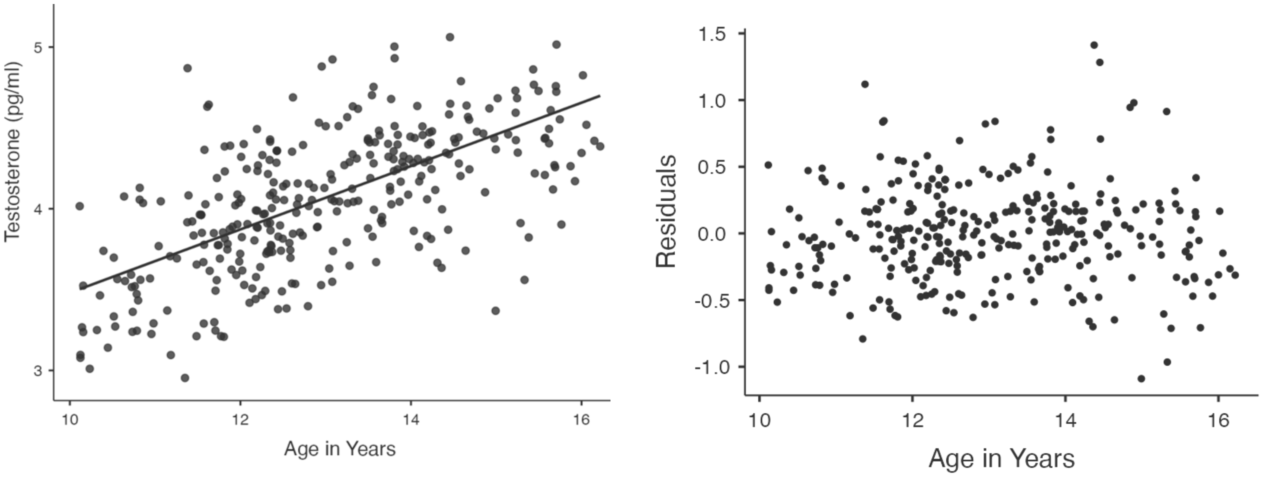


Figure 4. Testosterone's linear relationship with age in years.

FSMI mate-seeking scores (β = -0.71, Z = -0.51, p = .612) or the K-SRQ sexual relationship scores (β = 0.76, Z = 0.72, p = .475). The only significant pathway found in both models was the slope of T predicting current T (both $p < .001$). Given the overlap of the independent variable (slope of T) with the mediator (T and W3) another set of mediation models used change in T between W1 and W2 as the independent variable, so that W3 T was only included as the mediator. The same pattern of results were found (Figure 6), with only the change in T from W1 to W2 predicting T at W3 being significant in both the FSMI model (β = -0.70, Z = -2.29, p = .016). and K-SRQ model (β = -0.69, Z = -2.34, p = .019).

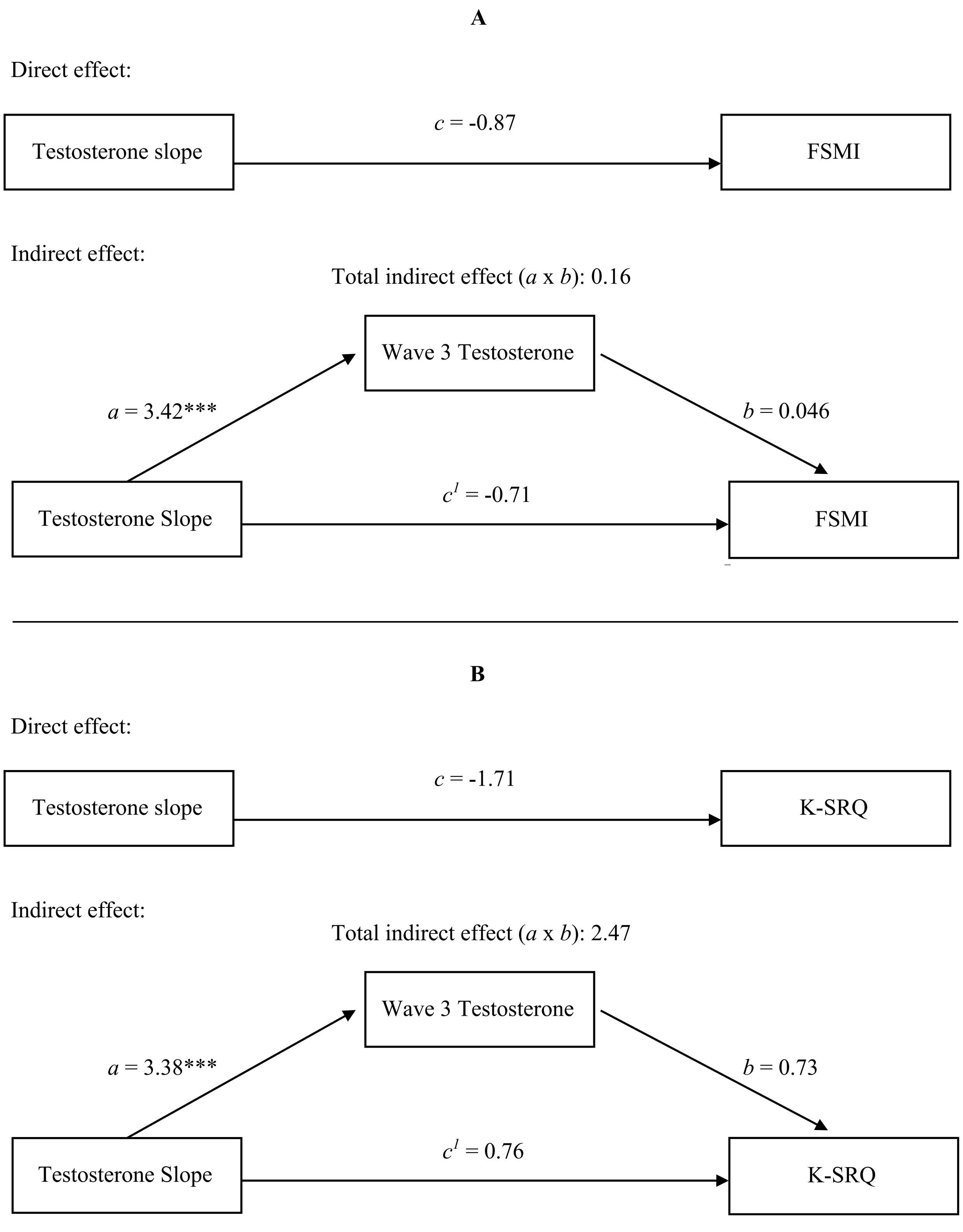


Figure 5. Estimates of the mediational model using the slope of testosterone as the independent variable and FSMI as the dependent variable (A), and K-SRQ as the dependent variable (B).

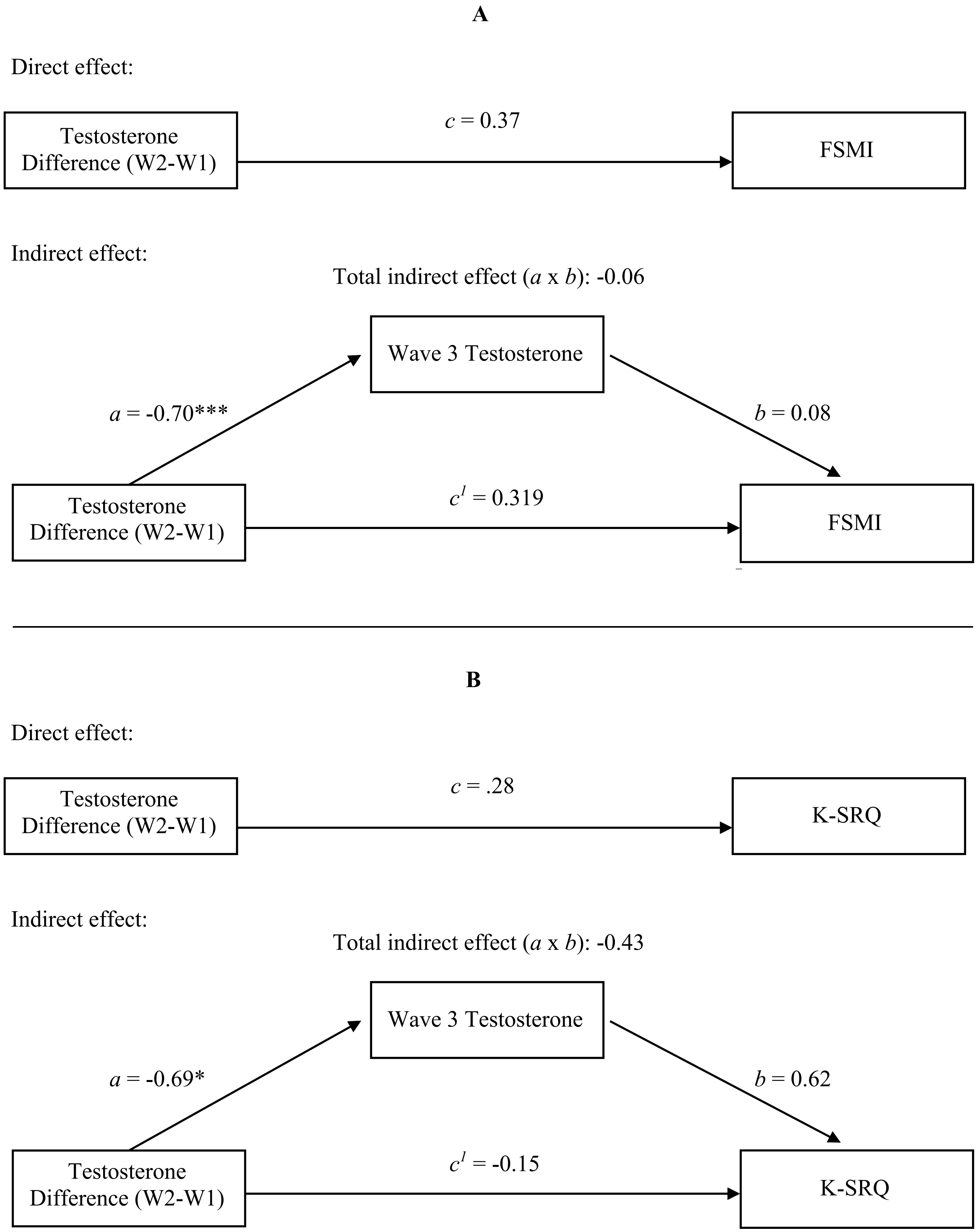


Figure 6. Estimates of the mediational model using the difference in testosterone between W1 and W2 as the independent variable and FSMI as the dependent variable (A), and K-SRQ as the dependent variable (B).

Discussion

This study investigated the mechanistic pathway by which pubertal hormones impact mating motivations in adolescent girls. To better understand this sample, relationships between each of the mating motivation scales, pubertal indices, and romantic partnerships were explored. While the mate-seeking subscale of the FSMI and the sexual relationships scale seemed to accurately capture *interest* in romantic relationships and activities, no relationships were found with pubertal timing, pubertal stage, or number of romantic relationships experienced. Additional exploratory analyses investigated whether the individual items on separate questionnaires could be combined to represent a single factor of mating motivation (Aim 1), finding that these scales were best kept as separate constructs. Finally, a mediation model tested whether T represented the mechanism linking pubertal indices (i.e., tempo and stage) with mating efforts (Aim 2). No links were found between the rate of change in T and mating motivation, nor between current levels of T and mating motivation. The two aims of this study are discussed below.

Aim 1: How do we measure sexual motivation?

The first aim of this chapter was to explore how best to measure sexual motivation in this dataset. Measures of mating motivation seemed to work well with their designed construct. For example, FSMI mate-seeking scores were higher for those who were previously in romantic relationships (and perhaps were interested in finding another one), and those who explicitly expressed a desire to be in one (although had never been in one previously). Further, those who were currently in, previously in, or wanted romantic relationships expressed greater interest in flirting, kissing, and having a crush on someone. Therefore, it is likely that seeking a boyfriend or girlfriend and enjoying romantic activities represents some motivation to engage in these activities.

It was proposed that items from both the mate-seeking subscale of the FSMI and the sexual relationships subscale of the K-SRQ should load onto a single factor representing mating motivation. However, factor loadings indicated that this data was best represented by two factors correlating to each individual questionnaire. Thus, the mate-seeking subscale of the FSMI and the sexual relationships subscale of the K-SRQ are likely measuring different aspects of sexual motivation.

The reason these scales could not be combined likely have to do with the different overall intent of each scale. The FSMI is specific to seeking a romantic partner (rather than interest in sexual behaviors) while the K-SRQ asks about enjoyment of specific behaviors (rather than seeking relationships). Although mating motivation likely encompasses a desire to engage with the opposite sex (e.g., Baker & Waller, 2020; Edelstein et. al., 2011; Suleiman et al., 2016), it could be that an exclusive romantic relationship (i.e., boyfriend or girlfriend) is not desired by adolescents in this study. The K-SRQ, on the other hand, expresses enjoyment of particular interactions (e.g., kissing, flirting), regardless of being in a romantic relationship or seeking a relationship. Recent evidence suggests adolescents are waiting longer to enter into romantic relationships (Rizzo et al., 2019) and are engaging in sexual behaviors later compared to earlier generations (Lindberg et al., 2021). This might be attributed to increased parental closeness and communication surrounding reproductive health (Prastika & Hasanah, 2022). Importantly, this data was collected during the COVID-19 pandemic, which likely impacted adolescent's desire and/or opportunities to have intimate interactions with peers (Stavridou et al., 2021). Taken together, current data indicates that the FSMI and K-SRQ likely measure different aspects of adolescent mating psychology.

There are other measures of mating motivation that could be used in future studies. The Sociosexual Orientation Inventory-Revised (SOI-R; Penke & Asendorpf, 2008) is a scale commonly used in adult evolutionary psychology literature to assess sexual attitudes, desires, and behaviors. When adjusted for developmentally appropriate questions (i.e., asking about "hooking-up" or other sexual behaviors rather than exclusively focusing on sexual intercourse), this scale could be a useful tool in assessing adolescent attitudes towards sex and sexual desires. While this questionnaire was used in a separate portion of this research project (see Chapter IV) it was not given to participants during any standard wave of TAG data collection. Previous research has also used a Dating Questionnaire assessing interest in obtaining a boyfriend or girlfriend, enjoyment of romantic activities, and the amount of time they spend with romantic partners (Connolly et al., 2013). Future work should also incorporate qualitative data to explore the adolescent experience of romantic attitudes, desires, and behaviors from their own perspective (Suleiman & Harden, 2004; Sueliman & Deardoff, 2015). Taken together, future work should build a more comprehensive mating interest inventory incorporating many aspects of the questionnaires described here and new items assessing motivation more explicitly.

Aim 2: Do current levels of T mediate the relationship between rate of change in T and mating motivation?

A mediation analysis was run to examine the relationship between T changes across puberty and mating motivation. It was predicted that current levels of T (as measured across four saliva samples prior to the lab visit) would mediate the relationship between the tempo of T increases across puberty and mating motivation. No relationship was found between the rate of change in T across waves and mating motivation, and there was no mediation effect of current T levels. The choice of repeated measures in these analyses could be problematic, given the mediation variable (T at W3) was also included in the calculation of the predictor variable (T slope). Thus, the link between T slope and W3 T would always be highly correlated. To examine this issue, a complementary set of mediation models used the difference in T between W1 and W2 as the predictor variable, so that W3 T was only used as a unique mediator. However, a similar pattern of results was found, given the logical connection between changes in T from W1 to W2 and T in W3. However, results were interpreted with this limitation in mind, understanding that the significance of the pathway between change in T and current T would logically have some degree of overlap. The paths important for this study were not significant, and therefore it was concluded that no mediation occurred. Indeed, there was no relationship between changes in T or current T on mating motivation measures.

Several factors could explain the lack of findings. First, it could be that pubertal tempo does not share the same relationship with sexual behaviors as pubertal timing does. It was assumed that if earlier pubertal timing was associated with earlier sexual debut (e.g., Baams et al., 2014) that a faster tempo should also lead to an earlier increase in mating motivation. However, statistical modeling has shown that links between pubertal timing and tempo is best explained by a logistic model (rather than linearly), such that those who enter puberty early show a slower pace of development while those with later timing show a relatively faster rate of development (Mendle et al., 2014). Thus, the original hypothesis for this study may have been based on the faulty assumption that those who started puberty early paced through pubertal development more rapidly, leading to higher T concentrations and increased mating motivations compared to peers. Similarly, while T does increase in boys and girls over pubertal development, prior research has suggested that the change over time may not be linear (e.g., Fung et al., 2020; Wierenga et al., 2018) particularly in girls. However, Figure 4 implies that testosterone increased linearly across the ages of this particular sample (10-16 years old). Further, due to the disruption in hormone assays due to the COVID-19 pandemic and change of lab location, only half of the salivary T was able to be used in these analyses. It could be that the additional data in the rest of the assays might reveal things like a different impact of control variables at W3, or a more parabolic relationship with PDS, which would then indicate that pubertal tempo cannot be measured linearly.

One reason current T exposure did not relate to mating motivation could be due to normative hormonal fluctuations across the menstrual cycle. As pubertal girls start experiencing hormone fluctuations correlating with the menstrual cycle (culminating in menarche), it could be that T was relatively low in some girls at the time they completed the questionnaires due to normal, monthly fluctuations. In adults, there is some evidence to suggest that sexual desire and motivation fluctuates along with the menstrual cycle (Jones et al. 2016; Haselton et al. 2014; Jones & Rooney 2018) so if many participants in this study were in a low T phase of their cycle, this could have impacted results in these analyses creating artificially lower scores on mating motivation. Relatedly, null findings could be due to temporal variation in when T influences mating behavior and motivation - not just surrounding the menstrual cycle but also in a more immediate manner. While the organizational - activational hypothesis suggests T exposure during particular developmental windows affect later behaviors, other research has found more acute effects of T by examining limited episodes of high T concentrations. For example, in some studies that administered T doses to their subjects, the rise in T was associated with increased motivation to act and sensitivity to social rewards (Bos et al., 2012; van Honk et al., 2004).

Therefore, current levels of T (i.e., T concentration on the day/time the questionnaires were answered) could have had some influence on responses. Future work should test T concentrations on the same day or time surveys are administered.

Next, it could be that T has a more nuanced relationship with puberty than expected. For example, some research has found no association between T and puberty in adolescent girls (Granger et al., 2003; Maskarinec et al., 2005) and still others found associations with different aspects of the PDS scale (Shirtcliff et al., 2009), indicating that the correlation between T and pubertal stages may depend on which aspects of puberty one is interested in. Further, there is some evidence to suggest that using ELISA kits may not be an adequate method to detect small levels of T, such as the low concentrations found in pubertal girls (Meta & Anderson, 2016). Perhaps a more accurate measure of T could be found with liquid chromatography tandem mass spectrometry (LCMS); a procedure that is more sensitive to detecting smaller testosterone levels (Moal et al., 2007; Welker et al., 2016).

It could also be that T simply doesn’t relate to mating motivation. Instead, other hormones, including estrogen and progesterone or their interactions could predict mating motivation in adolescent girls (Jones et al., 2019). According to the Dual Mating Strategy Hypothesis, women’s mate preferences and sexual attitudes are hormonally mediated, showing fluctuations across the menstrual cycle (Gildersleeve et al., 2014; Penton-Voak et al., 1999; Little et al., 2011). There is some evidence to support women showing a stronger sex drive and a preference for uncommitted sexual relationships during the high-fertility ovulatory phase of the menstrual cycle, when both T and estradiol are at their peak (Gildersleeve et al., 2014; Pillsworth & Haselton, 2006; Roney, 2018; Thornhill & Gangestad, 2006). A more recent theory proposes an Estrous Model, where the ovulatory phase of the menstrual cycle is characterized by an increase in overall sexual motivation rather than simple shifts in attraction or a preference for uncommitted sexual encounters (Jones et al., 2019). Thus, it could be that these preference shifts are due to estradiol and progesterone rather than T. For example, estradiol positively predicted sexual behavior in captive female macaques (Wallen et al., 1984; Zehr et al., 1998), while progesterone showed a negative relationship (Wallen et al., 1984; Zumpe et al., 1983). Further, administering estradiol to female macaques led to an increase in both sexual receptivity and proceptivity (Michael et al., 1987; Wallen et al., 1984). In humans, some studies report an increase in women's general sexual desire (Arslan et al., 2018; Shimoda et al, 2017; Roney & Simmons, 2013); interest in sex with attractive men, including those they do not know well (Gangestad et al., 2010); and assertiveness (Blake et al., 2017) during the ovulatory phase of the menstrual cycle. Given that estrogen peaks during ovulation, and progesterone is low, it seems likely that estrogen and/or progesterone (or their interaction) impact women's mating psychology. Thus, measuring associations between estrogen and progesterone and sexual motivation in young adolescent girls would be a logical next step in identifying the developmental trajectory of women's mating psychology.

Overall, this study found no associations between tempo of change in T or current levels of T with measures of mating motivation in adolescent girls. Further investigation into the developmental pathway of sexuality in early adolescence is needed to help explain the normative steps towards healthy, adult-typical romantic relationships. With better understanding of the motivations and trajectories of romantic relationships in adolescence, we can inform the types of programs and policies needed to support their navigation of this new social context.

CHAPTER IV

STUDY 2

Introduction

Adolescence begins with the onset of puberty, which marks the biological transition towards sexual maturity, and ends with taking on the rights, roles, and responsibilities of adulthood (Sawyer et al., 2018). During this time, adolescents must learn to navigate an increasingly complex social world with the added context of romantic relationships, which distinguishes the adolescent social world from childhood (Donaldson & Mills, 2021; Tolman & McClelland, 2011). Accordingly, the neurobiological changes associated with puberty include increased sensitivities to social evaluation, positive social rewards, and learning about high-intensity social relationships (Dahl et al., 2018). Indeed, adolescent romantic relationships differ from friendships in that they involve increased intensity, affection, and sexual behaviors (Collins, 2009; Gómez-López et al., 2019). Most adolescents report being in at least one romantic relationship by mid-adolescence (Connolly et al., 2014) and devote more time to romantic partners as they approach adulthood (Schulman et al., 2011). Yet, little is known about the normative trajectory of romantic development across early to mid-adolescence. It is likely that habits and skills learned during this time impact successful coupling into adulthood (Fincham & Cui, 2011; Simon & Barret, 2010). Therefore, adolescence could represent a sensitive window where information about romantic interactions is particularly salient and investigating factors that impact this learning should be explored.

Involvement in romantic relationships has been described as being a vitally important, normative developmental task during adolescence and into emerging adulthood (Brown et al., 1999; Collins et al., 2003; Furman & Collibee, 2014; Harden, 2014; Suleiman et al., 2018).

Indeed, adolescence is the time when most individuals report their first dating and sexual experiences (Connolly et al., 2014; Seiffge-Krenke, 2003) with some basic forms of romantic relationships starting as early as 10 years of age (i.e., having a “crush”, establishing romantic pairings, simple displays of affection; Connolly et al., 2013; Seiffge-Krenke, 2003) and about 80% of adolescents report having had a date or kissing someone prior to graduating high school (Tolman & McClelland, 2011). Some research has suggested that the social skills and behaviors learned in adolescent romantic relationships and experiences impact mental health and wellness into adulthood (Dahl et al., 2018; Gómez-López, 2019), pointing to the importance of these experiences during this developmental stage. Thus, understanding the trajectory of these developing relationships and sexual behaviors beginning with puberty is essential. While adolescent romantic experiences have been explored in middle to late adolescence and emerging adulthood (e.g., Connolly et al., 2013; Tolman & McClelland), there is relatively little research investigating early adolescent romantic thoughts experiences at the time they are first presented. We still know relatively little about engagement in these behaviors, let alone underlying motivations. The first aim of this chapter is to characterize the level of engagement in mating-relevant behaviors - romantic relationships and sexual experiences - in the first half of adolescence.

Evolutionary theory also points to adolescence as an inflection point for learning adaptive behaviors involved in mating and reproduction. Animal models point to how evolutionary forces have shaped the timing of different forms of social learning, with sensitive periods occurring when important information is most useful (Fawcett & Frankenhuis, 2015, as cited in Dahl et al., 2018). For example, some songbirds learn their songs through social interactions during a particular phase in development. Some learn their songs in the first few days of life from parents, while others learn their songs later in life, when the bird finds new territory and learns from peers (Doupe & Kuhl, 1999). Further, these learning periods are likely regulated by reproductive hormones (e.g., testosterone and estradiol) which likely influence the salience of social cues during particular stages of development (Marler et al., 1987; Templeton et al., 2012). It could be that similar processes shape human adolescent psychology, making mating cues particularly salient during this phase of life.

According to evolutionary psychologists, human "mating" involves much more than copulation for producing offspring. Rather, the term is used to encompass both physical and cognitive aspects of romantic experiences, including attraction preferences, jealousy, sexual desire, and perception of mating cues (e.g., De Baker et al., 2007; Geher & Kaufman, 2011; Little et al., 2015). However, the development of mating cognition in early to middle adolescence is not yet well understood. Given that puberty marks the transition towards biological reproductive maturity, it is likely that cognitive aspects of mating begin to develop around the same time (e.g., Donaldson & Mills, 2021). Specific to this chapter, the desire or motivation to engage in romantic experiences should precede the emergence of mating behaviors. Therefore, early to middle adolescence is a key time to explore the development of mating motivation along with the initiation of dating and sexual behaviors.

To test the salience of particular social cues and examine how they relate to underlying motivations, Flournoy (2018) developed a probabilistic reinforcement social learning task. Specifically, this task investigates how different social contexts impact learning rates in adolescents and young adults. This task was inspired by the fundamental social motives framework (originally proposed by Kenrick et al., 2010) which parses motives into subsets of adaptively-relevant categories believed to evolve from solving adaptive problems over human evolutionary history. According to this framework, the transition from childhood to adolescence comes with a change in fundamental social motives to include mating as a highly salient social goal. The initial study using this social probabilistic learning task found that adolescents and adults performed better in social learning contexts (including both mating-relevant cues and status-relevant cues) compared to a minimally social context, indicating the salience of social versus non-social learning (Flournoy, 2018). Although this initial study did not find associations between performance in the mate-learning condition and mating-relevant self-report questionnaires, these questionnaires were not given to adolescents in his sample, only young adults; and the stimuli presented were computerized depictions of young adult faces, which may not have been realistic-looking or relevant to the adolescents in the sample. It could be that adolescent youth are motivated to learn about social cues from their peers in a more realistic way rather than learning about hypothetical computer-drawn faces. Therefore, an updated version of this task may still be a useful tool for investigating whether underlying mating motives influence learning about mate-relevant cues.

There are several factors that may impact the development of mating motivation in adolescence. Given mating motivation should rise at and across puberty, it is likely that pubertal indices relate to the development of both cognitive and behavioral romantic experiences. Baams et al. (2014) conducted a meta-analysis to explore the effects of puberty on initiation and type of sexual behavior in adolescents. They identified 112 effect sizes across 50 independent studies and found a few consistent patterns. First, earlier pubertal timing was related to earlier initiation of sexual activities (including kissing, touching, oral sex), earlier sexual intercourse, and overall more sexual experiences compared to peers. Relatedly, more advanced pubertal status was also linked to earlier initiation of sexual behaviors. Furthermore, these effects were strongest among young, female adolescents compared to males and older adolescents (Baams et al., 2014). If both pubertal timing and status correlate with timing and number of sexual behaviors, it could be that these indices also impact motivation to engage in these behaviors. This chapter will explore whether pubertal timing and/or status relate to sexual behaviors of young, female adolescents in our study, and will extend this work to examine any influences on mating motivation and mating-relevant learning.

Testosterone (T) is one reproductive hormone that is linked with learning mating behaviors in many animal species. To return to the songbird example, one purpose of singing in zebra finches is to attract mates. Puberty-induced increases in T influence the development, type, and occurrence of these songs during their adolescent window (Templeton et al., 2012). Additionally, male rodents require T exposure during their adolescent period to successfully enact mating behaviors, and to learn from their sexual experiences. If these rodents are not exposed to T in adolescence but are instead given T during adulthood, similar mating postures and sexual learning are greatly diminished (Dahl et al., 2018; Schulz & Sisk, 2016). In humans, increases in T during puberty have been associated with increased motivation and goal-oriented behavior to achieve social rewards (Cardoos et al., 2017) and increased motivation to engage in highly arousing and exciting experiences with peers (Forbes & Dahl, 2010). These hormonally driven changes in a mating context likely lead to increased motivation to seek out and experience rewarding and meaningful romantic connections, including having a crush on someone, asking someone out on a date, kissing, or holding hands (Ballonoff Suleiman et al., 2015). Taken together, adolescence can be viewed as a special developmental window where reproductive hormones such as T influence the emergence of mating intentions and behaviors.

The temporal nature of T influences on mating psychology and behaviors has mixed findings, with some studies identifying acute influences of T on mating cognition, and others finding more distant effects. According to the organizational–activational hypothesis, T exposure in-utero organizes physiological structures that are later activated by T exposure in adolescence, and there is substantial support for this hypothesis in the animal literature (Heck & Handa, 2019; Phoenix et al., 1959; Schulz & Sisk, 2016; Templeton et al., 2012; Wallen, 2015). In this framework, T exposure earlier in development - in-utero and/or during puberty - prime physiological structures for behaviors that are seen days, months, or sometimes years later, as evidenced by the singing of zebra finches (Templeton et al., 2012) and sexual posture in rodents (Schulz & Sisk, 2016).

However, it is also important to take into account more dynamic indices of hormone levels, such as on a daily basis. There is some evidence to suggest that acute increases in T could impact female mating psychology, such as fluctuating sexual desires across the menstrual cycle. The dual mating strategy hypothesis (Gangestad & Thornhill, 1998) proposes that during the high-fertility phase of the menstrual cycle - when T is at its highest - women prefer more masculinized physical features and act more favorably towards uncommitted sexual relationships. A more recent "estrus model" proposes that around ovulation, women experience increased sexual motivation, similar to that reported in other non-human primates during the fertile phase of their reproductive cycles (Jones et al., 2018). In support of this hypothesis, it has previously been found that the peak in T during mid-cycle is associated with increased sexual desire (Thornhill & Gangestad, 2006), increased interest in sex (Roney & Simmons, 2013), and increased mate-retention behaviors (Gildersleeve et al., 2014). While previous work has focused on adult women, very little is known about how current levels of T impact mating psychology in adolescent girls on a daily basis. Therefore, capturing T concentrations on the same day mating motivation is assessed is a useful step in understanding hormonal influences on the development of mating motivation.

Current Study

One of the major transitions from childhood to adolescence is the emergence of romantic feelings, attitudes, desires, and motivations. Given animal models demonstrating links between pubertal hormones and mating behaviors (e.g., Schulz & Sisk, 2016; Templeton et al., 2012) it is probable that hormone increases during puberty create a critical window for learning about sexual behavior and mating. These changes in motivations during puberty lead adolescents to engage in entirely new social experiences related to dating and sexual behaviors, which in turn can ultimately affect their learning. The first aim of this chapter is to explore the romantic and attitudes and behaviors of this sample of early to middle adolescents, as the dating experiences during this phase of life is under-studied. Next, to determine whether learning is affected by this new social context, the second aim of study is to examine performance on a social probabilistic learning task that aims to capture shifts in underlying social motivations, and explores factors that may influence individual differences in the task. Given previously established links between pubertal timing and pubertal stage with sexual behaviors (Baams et al., 2014), it is hypothesized that these indices will also impact learning about mating cues, with earlier timing and later stages performing better in the mate-learning context. In-line with the estrus model of female mating psychology (Jones et al., 2018), it is proposed that current T levels (sampled on the same day as the learning task) will also influence mate-learning such that adolescents with increased T will perform better in this learning context compared to those with lower T concentrations.

Methods

Participants

77 Adolescents, aged 12 -16 years old (*Mage* = 13.90, *SD* = 1.08), were recruited as part of an existing longitudinal study of adolescent girls (the Transitions in Adolescent Girls (TAG) study; Barendse et al., 2020) and from the local community in Lane County, Oregon, USA. Detailed recruitment procedures and enrollment criteria are described in the previous chapter of this dissertation and in Barendse et al., (2020). Briefly, participants were recruited primarily through recruitment letters distributed by schools in the greater Eugene/Springfield area. Participants were excluded from the study if they were diagnosed with a developmental disability, psychotic disorder and/or behavioral disorder, including autism. Additional exclusions included adolescents who were taking psychotropic medications other than stimulations, and if they were currently or potentially pregnant, or had any other contraindications to undergoing magnetic resonance imaging. Given some variability in gender expression (two participants identified as male, two were "questioning" and three stated "other") it was confirmed with parents/guardians that all were assigned female at birth. Parents/guardians gave informed consent (and adolescents assent) to participate in the study and were financially compensated for participating. Ethics approval was received from the Institutional Review Board of the University of Oregon. Of the total dataset, 64 participants were part of the overall TAG study, and came into the lab for an additional session between Wave 2 and Wave 3. The remaining 13 participants were recruited specifically for this session and did not participate in the TAG study. Of these participants, at the time of writing, precise age was not calculated for nine, hence the missing data on this variable.

Measures

Current Relationships and Behaviors. To get a better understanding of the dating and sexual behaviors of our sample, modified versions of the Fundamental Social Motives Inventory (FSMI; Neel et al., 2015), and the revised sociosexual orientation inventory (K-SOIR; Penke & Asendorpf, 2008) were used. Questions added to the FSMI asked about current and previous romantic relationships, as well as sexual identity (e.g., heterosexual, bisexual, homosexual, etc.), gender expression, and attraction preferences (e.g., attracted exclusively to males or females or both). The K-SOIR is typically used to assess sexual behavior, number of partners, and attitudes towards uncommitted sex in adults. This inventory was revised to be more appropriate for adolescents by using the terminology “hooking-up” instead of having sex. The instructions for this revised inventory seen by all participants defined “hooking-up” as “any sexual behavior, including kissing, touching, oral sex and/or vaginal sex”. In this way, we obtained information about how many times adolescents engaged in any sexual behaviors, and with how many different partners, both in their lifetime and within the last six months.

Testosterone. Baseline T was measured through saliva samples, collected via passive drool at the start of the lab session. Participants were asked to collect 2mL of saliva while sitting alone in the lab. Participants also filled out a questionnaire to assess the time they woke up that day, the time they brushed their teeth, and whether or not they had taken any medications, caffeine, or birth control in the last 24 hours. Additionally, participants were asked if they felt ill and when their last menstrual period was. Samples were then stored in a -80°C freezer until they were shipped (overnight on dry ice) to the Stress Physiology Investigative Team at Iowa State University. Identical procedures were followed from previous work to estimate T concentrations: samples were assayed in duplicate using Salimetrics Enzyme-Linked Immunosorbent Assay

(ELISA) kits, and samples were rerun if the optical density coefficient of variation (CV) was greater than 7% and if there was enough sample left over to do so.

Raw concentrations were transformed using natural log transformations due to non-normality (+/-2 skewness and/or kurtosis), which resulted in a normal distribution, and time of day was controlled for. A small number of lower limit outliers remained after transformation (n = 4), which were then winsorized following recommendations (Shirtcliff et al., 2009).

Pubertal Indices.

Pubertal Timing (Age of Menarche). First, adolescents were asked whether they had ever had their period and if yes, to report the date of menarche. If participants did not remember the exact date, we imputed the middle of the range they reported (e.g., June 2018 became June 15, 2018). 21% of participants in our study were premenarcheal and the remaining 79% were postmenarcheal. Of those who had started menstruating, age at menarche was available for 78% of participants. The remaining 22% were postmenarcheal but did not remember or report any date. For participants who did not report starting their period by the time of this study, data was used from future waves (when available from the TAG study) to determine age of menarche.

Current Stage of Pubertal Development. Identical to the previous chapter, the current pubertal stage was assessed using the Pubertal Development Scale (PDS; Petersen et al., 1988) and Tanner stage Line Drawings (TLD; Morris & Udry, 1980). The PDS is a five-question, self-report measure of pubertal development, asking about the adolescent's secondary sexual characteristics. Subjects also viewed TLDs, which displayed various stages of breast and pubic hair development. Adolescents then indicated which image they most closely resembled. Answers on the PDS were recoded to correspond with the TLDs and a composite pubertal development score was created using validated conversion methods (Barendse et al., 2022;

Shirtcliff et al., 2009). This composite score ranged from 1 (*not at all developed*) to 5 (*completely developed*).

Mating Motivation.

Fundamental Social Motive Inventory. The FSMI (Neel et al., 2015) contains seven subscales, representing evolutionarily relevant motives. In the current study, only the 6-item mate-seeking subscale was used. Sample items from this subscale include "I am interested in finding a new romantic/sexual partner," and "I would like to find a new romantic/sexual partner soon." The wording for several items was adjusted to be more appropriate for adolescent participants, changing "romantic/sexual partner" to "boyfriend/girlfriend". Participants report their agreement with each statement on a seven point Likert scale ranging from 1 (*strongly disagree*) to 7 (*strongly agree*). Thus, higher scores on this subscale indicate greater motivation for mate-seeking. In adults, this subscale has been linked with short-term and long-term mating orientations (depending on relationship status), asking someone out on a date, and engagement in sexual behaviors (Neel et al., 2005).

Social Rewards Questionnaire. The Kid's version of the Social Rewards Questionnaire (K-SRQ; Foulkes et al., 2017) was adapted from an adult instrument intended to measure individual differences in the kinds of social interactions people find rewarding. In the creation of the original inventory, results for the 3-item sexual relationships subscale correlated strongly with sociosexual orientation measures (Foulkes et al., 2014). The K-SRQ was modified to be more appropriate for adolescents by replacing questions explicitly about sex (e.g., "I enjoy having an active sex life"), with questions that are closely related to sexual and romantic experience. The three items used in this investigation include "I like kissing," "I like having a crush on someone," and "I like flirting" (Foulkes et al., 2017). Participants report their agreement with each statement on a seven point Likert scale from 1 (*strongly disagree*) to 7 (*strongly agree*). Thus, higher scores on this subscale indicate greater enjoyment of the activity. Rewarding and valuable experiences as assessed in the K-SRQ should be directly related to what people find motivating, with greater reward derived from a particular experience indicating greater motivation to seek out that experience.

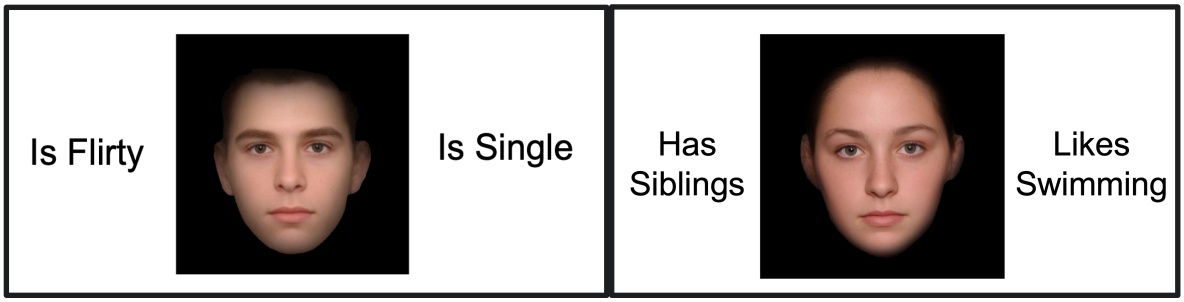
Social Probabilistic Learning Task. The Social Probabilistic Learning Task (SPLT) is a standard reinforcement learning paradigm developed by Dr. John Flournoy (2018) using several stimulus-word pairings that are grouped by motive relevance. Previous work used computer-generated drawings of faces as stimuli for this task, and these stimuli were improved upon in this study. Instead, photos of real adolescents were averaged to create six different stimuli - three female averages and three male averages. These stimuli are thus more realistic compared to prior tasks.

The SPLT motive context is manipulated by pairing realistic, averaged, adolescent faces (see Figure 7) with state or trait words related to mate-seeking and status motives. The purpose of this manipulation is to examine how motive framing alters learning, as well as how individual differences in mate-relevant learning are related to pubertal indices (including age of menarche, pubertal stage, and T) and measures of mating motivation.

On each trial, the participant sees one of six faces, along with two labels, and is asked to classify the face using one of the two labels. The labels are: *has siblings* versus *likes swimming* (neutral context), *is flirty* versus *is single* (mating-relevant context), and *is popular* versus *is wealthy* (status-relevant context; see Figure 8). The first iteration of the task used in this study contained different word pairings, including *flirty* versus *not flirty* (mating-relevant context), *popular* versus *not popular* (status context), and *has siblings* versus *does not have siblings*

Figure 7. An array of all computer-generated peer faces presented in the SPLT task. Faces were created using established methods (Tiddeman et al., 2001). Neutral adolescent faces of real participants were obtained from an online database and combined to create three distinct male and female average faces.

(neutral context). Nine participants completed this version of the task, while the remaining 61 saw the updated labels. Using one kin-related adjective and one activity is considered neutral for this project because this information should be less relevant (and therefore less salient) to adolescents who are potentially orienting to key features of their expanded social environment during this time (i.e., peer status and potential mates; Ellis et al., 2012; Nelson et al., 2005; 2016). Further, interest in whether someone has siblings or likes swimming is not expected to change across puberty, while it is expected that interest in mating-relevant and status-relevant information will increase with pubertal development. After participants choose the label, they are given feedback that they were correct and earned either 1/1 point or 5/5 points, or that they were incorrect and earned 0/1 point or 0/5 points. Each face is probabilistically associated with one label at P(Correct | Choice = Label) = .80. That is, there is a probabilistically optimal choice response, which precludes a memorization strategy and results in more automatic reinforcement learning (Knowlton et al., 1996). The participant is instructed that “the same word goes with the same picture most of the time, but not always,” and to “try to guess correctly as often as you can to get the most points.” For each participant, one male and one female face was randomly assigned to each label within condition (neutral, mating-relevant, status-relevant). On each trial, the participant had 3.5 seconds to respond, and was shown response feedback for 1 second. The task comprised a total of 384 trials across 8 blocks. Performance on this task was calculated by the number of times the adolescent correctly paired the face with the assigned label within each context.



(a) Example of a trial on the SPLT with a male stimulus in the mating-relevant context.

(b) Example of a trial on the SPLT with a female stimulus in the neutral context.

Figure 8. Example trials on the SPLT in the mating-relevant condition

Procedure

Adolescents and their caregivers came into the lab and first completed the informed consent process (and adolescents provided assent). Then, participants provided a baseline saliva hormone sample, and created an introduction video as part of the overall study. Participants then completed an MRI task unrelated to this project. After the MRI, participants completed the questionnaires used in this study and the SPLT.

Analysis Plan

First, sample characteristics were explored to identify romantic relationship and hook-up experiences in our participants (Aim 1). To ascertain how well our measures of mating motivation mapped onto romantic behaviors, correlations were examined between mating motivation measures (FSMI, K-SRQ) and romantic experiences (romantic relationships and hooking-up). Next, connections between our data and previous findings (in Baams et al., 2014) were examined by using binomial logistic regressions and correlations to test relationships between pubertal indices (pubertal stage, age of menarche, and T) and mating-related behaviors (ever being in a romantic relationship (yes/no), ever hooking-up with someone (yes/no), and number of romantic partners).

Next, predictive relationships were explored between FSMI scores in the mating context and age at menarche, pubertal stage, K-SRQ, FSMI, testosterone, or current age (Aim 2). First, a correlation plot was created to assess relationships among variables used in the model. Next, several simple regression models were run containing only one predictor variable at a time while accounting for performance in the neutral condition. A lenient cutoff ($p = .20$) was set to determine which predictor variables should be included in testing a larger model containing multiple predictors. Finally, model comparisons revealed the best fitting model that explained SPLT performance in the mating context.

Results

The first step was to explore dating status and hook-up behaviors in our sample. At the time of the study, eight (10%) adolescents stated they were currently in a romantic relationship, lasting from one week to approximately two months. Of the remaining 63 participants, 22 (29%) reported having at least one romantic relationship in their lifetime, 15 (19%) stated they were not currently in one, but they wanted to be, and 32 (42%) subjects were not in one and were not interested in one. Two (3%) participants did not answer this question. In our sample, 51 (66%) adolescents had never hooked-up before, while 22 (29%) participants reported hooking-up with someone at least once in their lifetime. Four (5%) participants declined to answer this question. Of those who endorsed hooking-up, 18 reported hook-up behaviors other than vaginal or anal intercourse (e.g., kissing, making out, touching), while the remaining four participants reported having sex at least once. In terms of hook-up partners, nine adolescents reported having only one partner in their lifetime, seven reported having two or three partners ever, and one subject reported having between four and seven partners in their lifetime. To explore more recent behaviors, participants were also asked about their dating and sexual behaviors in the last 6 months. Thirty-three subjects reported not hooking-up with anyone in the last six months, 11 reported one hook-up, and four adolescents reported two or three hook-ups. Information about our subjects' sexual identity, gender expression, and attraction preferences can be found in Table 8. Although two subjects taken from the overall TAG study self-identified as male, it was confirmed with caregivers that these subjects were assigned female at birth.

Table 8

Frequency Table for Adolescent Sexuality, Gender Identity, and Attraction at W2.5

Variable	*Counts*	*Percent of Total Sample (77)*
Relationship Status (n = 77)		
Current Relationship	8	10%
Past Relationship	22	29%
Want Relationship	15	19%
Not Interested	32	42%
(Missing)	(2)	(3%)
Gender Expression (n = 77)		
Female	70	94%
Questioning	3	4%
Male	2	3%
Other	2	3%
Sexuality (n = 47)		
Straight	33	43%
Questioning	5	6%
Bisexual	4	5%
Other	3	4%
Gay or Lesbian	2	3%

Table 8 continued

Variable	*Counts*	*Percent of Total Sample (77)*
Attraction (n = 47)		
Only Males	29	38%
Mostly Males	9	12%
Equally Both	4	5%
Mostly Females	3	4%
Unsure	2	3%
Only Females	0	0%

Note: These questions were added to the FSMI to obtain demographic information. 77 participants completed the relationships status and gender identity questions. Due to a coding issue, only 47 participants saw and responded to the sexuality and attraction preference questions.

Relationships between Mating Motivation Measures and Behaviors

To check whether scores on the mate-seeking subscale of the FSMI and the sexual relationships subscale on the K-SRQ related to actual sexual behaviors and experiences, a correlation matrix was created (see Table 9). K-SRQ scores significantly correlated with the number of romantic relationships experienced ($r(28) = .37$, $p = .043$), and with the number of hook-up partners ($r(48) = .50$, $p < .001$). Mate-seeking FSMI scores, however, only correlated with K-SRQ scores ($r(72) = .42$, $p < .001$), but not with number of relationships or hook-up partners (all *p*s > .110).

Next, a one-way analysis of variance (ANOVA) was run to determine whether FSMI scores differed based on whether or not someone was currently in a relationship, previously in a relationship, desired a romantic relationship, or were not interested. See Table 10 for the means and standard deviations of each group. The ANOVA found a significant difference by group ($F(3, 25.9) = 13.78$, $p < .001$) with Tukey post-hoc tests finding significant differences between those currently in a relationship and those who want to be in one ($t(72) = -2.75$, $p = .037$), with those in a relationship scoring lower than those who want to be in one. Scores in the not interested group significantly differed from those who had previously been in a relationship

($t(72) = 4.81$, $p < .001$), and from those who have never been in a relationship but want to be ($t(72) = 5.65$, $p < .001$). Thus, scores on the mate-seeking FSMI are predictably related to adolescent relationship status and desire.

Table 9

Correlation Matrix of Mating Motivation Measures and Romantic Experiences

		FSMI	*K-SRQ*	*Number of Relationships*	*Number of Hook-up Partners*
FSMI	Spearman's rho	—			
	p-value	—			
	N	—			
K-SRQ	Spearman's rho	0.42 ***	—		
	p-value	< .001	—		
	N	74	—		
Number of Relationships	Spearman's rho	0.19	0.37 *	—	
	p-value	0.325	0.043	—	
	N	30	31	—	
Number of Hook-up Partners	Spearman's rho	0.24	0.50 ***	0.49 *	—
	p-value	0.110	< .001	0.025	—
	N	47	48	21	—

Note. * p < .05, ** p < .01, *** p < .001

Table 10

Average FSMI Mate-seeking Scores Grouped by Relationship Status (and Desire)

	N	*Mean*	*SD*
Currently in a relationship	8	3.37	1.00

Table 10 continued

	N	*Mean*	*SD*
Previously in a relationship (not currently)	22	4.21	1.14
Never in a relationship but want to be in one	15	4.66	0.96
Never in a relationship and not interested in one	32	2.78	1.08

Relationships between Pubertal Indices, Romantic Relationships, and Hook-ups

Next, data were explored to determine whether links between pubertal timing or status and sexual behaviors (see Baams et. al., 2014) would replicate in this sample. Binomial logistic regressions tested whether pubertal stage, age of menarche, or T could predict whether or not our participants had ever been in a relationship (yes/no) or had ever hooked-up with someone (yes/no). Table 11 reveals that T level significantly predicted whether or not someone was ever in a relationship ($\beta = 0.61$, $z = 2.00$, $p = .045$, 95% CI [1.03,11.31]), but not whether someone had ever hooked-up ($\beta = 0.92$, $z = 1.41$, $p = .159$). T level also did not predict whether someone was previously in a relationship (n = 22) versus currently in one (n = 8; $\beta = 1.16$, $z = 0.93$, $p = .351$). Figure 9 depicts the relationship between T and whether or not someone has ever been in a romantic relationship. Age of menarche predicted neither romantic relationships nor hook-up experiences, but pubertal stage was a marginally significant predictor of whether or not someone had been in a relationship at $p = .077$).

To explore this association further, Spearman correlations investigated whether pubertal indices related to the *number* of relationships or hook-up partners (see Table 12). While the

Table 11

Binomial Logistic Regression Results

Predictor	*Binomial outcome (yes/no)*	*β*	*z*	*p*
Pubertal Stage	Ever had a romantic relationship	0.76	1.77	.077
	Ever hooked-up with someone	0.81	0.48	.095
Age of Menarche	Ever had a romantic relationship	0.01	0.03	.980
	Ever hooked-up with someone	-0.21	-0.73	.463
Testosterone	Ever had a romantic relationship	0.61	2.00	.045
	Ever hooked-up with someone	0.92	1.41	.159

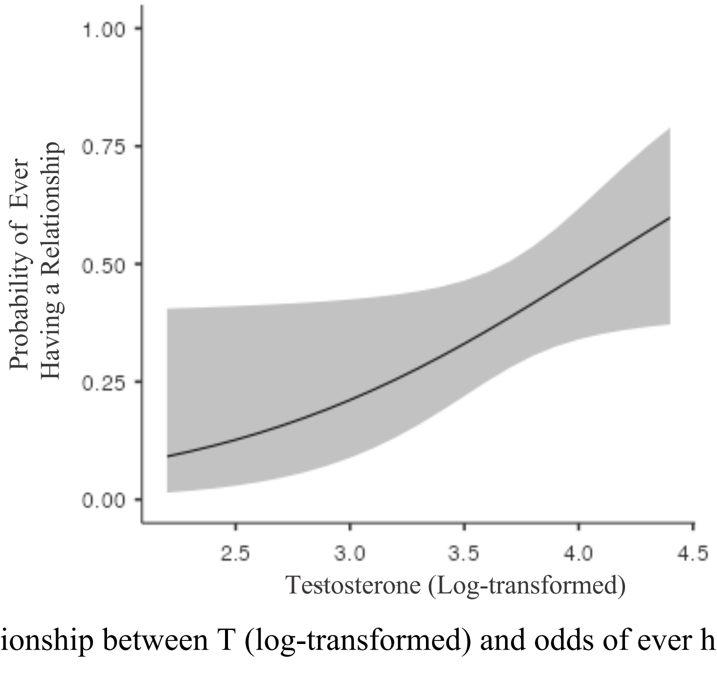


Figure 9. Relationship between T (log-transformed) and odds of ever having been in a romantic relationship.

number of romantic relationships and number of hook-up partners significantly correlated (*r*(19) = .49, *p* = .025), neither number of romantic relationships nor number of partners were related to pubertal status, age of menarche, or T levels (all *p*s > .171).

Next, two independent samples *t*-tests compared K-SRQ and FSMI scores between those who had started their period (n = 60, *M* = 4.27, *SD* = 1.54) and those who had not (n = 15, *M* = 3.22, *SD* = 1.25). Given unequal group sizes, Welch's *t* was used (not assuming equal variances).

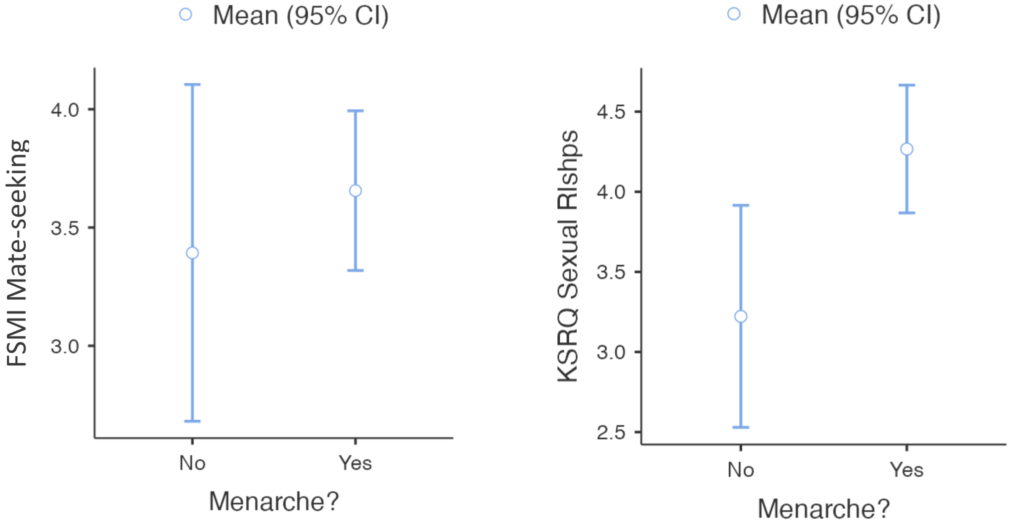
Table 12

Correlation Matrix for Pubertal Indices and Hormones with Romantic Experiences

		Number of Relationships	*Number of Hook-up Partners*	*Pubertal Stage*	*Age of Menarche*	*Testosterone (Log-Transformed)*
Number of Relationships	Spearman's rho	—				
	p-value	—				
	N	—				
Number of Hook-up Partners	Spearman's rho	0.49 *	—			
	p-value	0.025	—			
	N	21	—			
Pubertal Stage	Spearman's rho	-0.09	0.15	—		
	p-value	0.648	0.298	—		
	N	31	48	—		
Age of Menarche	Spearman's rho	-0.07	-0.15	0.02	—	
	p-value	0.739	0.389	0.856	—	
	N	27	37	64	—	
Testosterone (Log-Transformed)	Spearman's rho	0.11	0.13	0.16	0.08	—
	p-value	0.578	0.374	0.171	0.548	—
	N	30	46	74	58	—

Note. * p < .05, ** p < .01, *** p < .001

K-SRQ scores significantly differed depending on whether the participant had started their period (Welch's $t(25.79) = -2.75$, $p = .011$), with those who had started their periods scoring higher than those who had not. No difference was found in the FSMI scores (Welch's $t(20.42) = -0.71$, $p = .485$; See Figure 10).



(a) Plot of means for FSMI mate-seeking subscale, grouped by menarche status

(b) Plot of means for K-SRQ sexual relationships subscale, grouped by menarche status.

Figure 10. Mean plots for FSMI (a) and K-SRQ (b) scores grouped by relationship status

Social Probabilistic Learning Task[1]

First, task validity was assessed by testing whether there were any learning differences depending on task context (mating, neutral, or status). A repeated-measures ANOVA detected no

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[1] Analyses using the SPLT were run twice, once with the full dataset of 70 participants, and then again after removing the nine participants who saw the previous version of the task. Substantively the same results were found,

differences between contexts (*f*(2, 69) = 0.60, *p* = .548; See Figure 11). This indicates that performance was about the same for learning within each context, at the level of the group. However, given the wide range of variability in individual performance (see Table 13) and to be conservative, when assessing predictors of learning in the mating and status contexts, the neutral context was accounted for in each model.

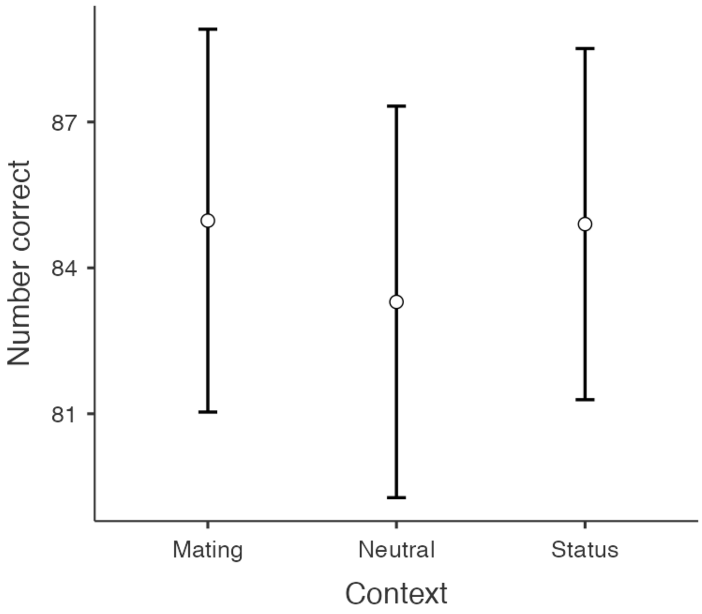

Figure 11. Plot of mean differences between the mating, neutral, and social contexts in the SPLT.

Next, descriptive statistics were gathered (see Table 13) and relationships were explored among the variables to be used in the model explaining SPLT performance. Participants were removed from analysis listwise if they did not complete the SPLT task (*n* = 7). First, my outcome variable counted the number of correct responses in the mating condition of the SPLT, and this data was not normally distributed. Therefore, Spearman rank correlations were used to explore

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in size, direction, and significance of effects – except in one case (which is reported in the text), thus, statistics from the full sample are reported relationships. See Table 14 for a correlation matrix of all variables used in model development, and Figure 12 for a visualization of the correlation matrix. SPLT performance in the mating context was significantly, positively correlated with performance in the neutral context (*r*(68) = .62, *p* <.001), performance in the status context (*r*(68) = .64, *p* < .001), age of menarche (*r*(57) = .40, *p* = .001), and current age (*r*(60) = .29, *p* = .024). Performance in the neutral context and the status context significantly correlated with age of menarche (neutral: *r*(57) = .28, *p* = .034; status: (*r*(57) = .27, *p* = .035). Interestingly, K-SRQ scores were significantly correlated with pubertal status (*r*(73) = .31, *p* = .007), and current age (*r*(73) = .37, *p* = .001). Current age was also correlated with age of menarche (*r*(62) = .34, *p* = .005) and with pubertal stage (*r*(66) = .48, *p* < .001). K-SRQ scores significantly correlated with FSMI scores (*r*(72) = .42, *p* < .001). Finally, T (log transformed) correlated with current age (*r*(73) = .28, *p* = .014).

Table 13

Descriptive Statistics for Variables of Interest

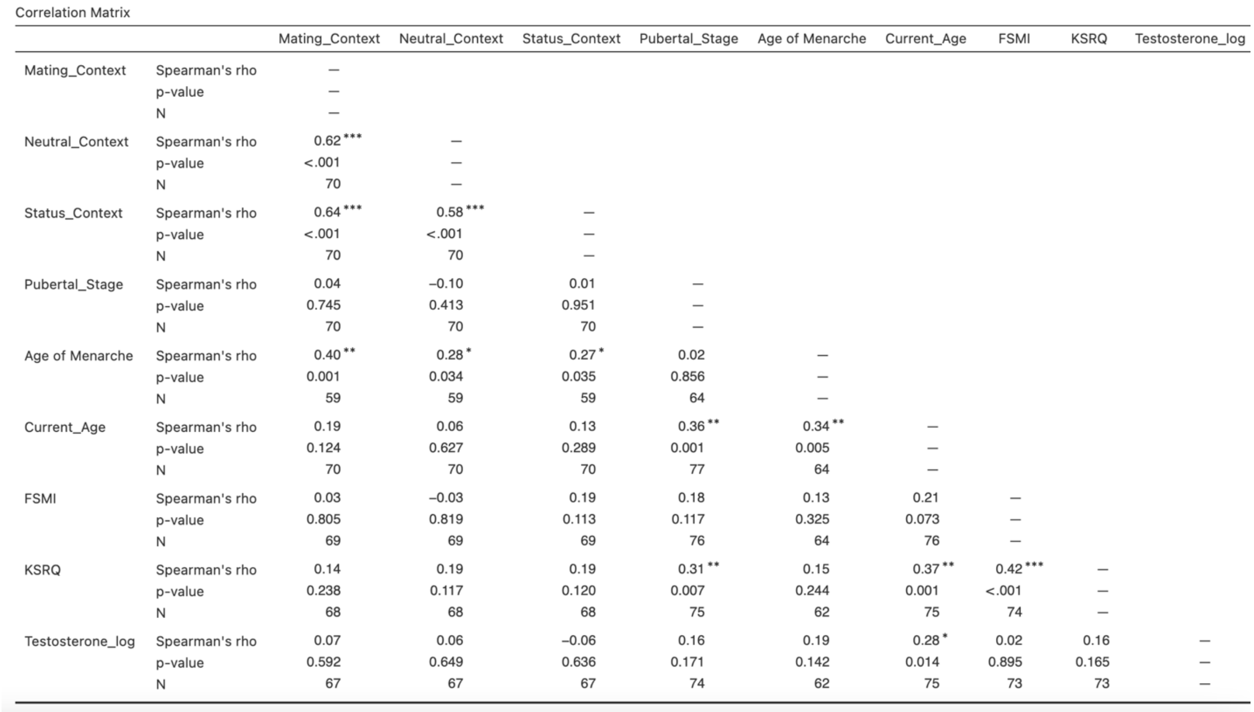
	Age of Menarche	*Puberty Composite*	*FSMI Mate-Seeking*	*K-SRQ Sexual Rlshps*	*Current Age*	*T (Log)*	*SPLT Mating*	*SPLT Neutral*	*SPLT Status*
Mean	12.36	4.13	3.57	4.07	13.58	3.68	84.97	83.30	85.03
St.Dev	1.14	0.63	1.27	1.51	1.09	0.41	16.51	16.88	16.04
Min	9.08	2.50	1	1	11.92	2.27	53	51	55
Max	14.86	5.00	6	7	15.33	4.40	116	115	115

Generalized linear modeling was used to determine the best fitting model, correcting for a poisson distribution as the outcome variable was a count of correct trials. In all models, scores in the neutral condition of the SPLT were used as a control variable. First, main effects of each predictor were explored individually, along with the control variable. Age of menarche (β =

3.03, $t = 1.86$, $p = .067$) and pubertal stage ($\beta = 5.58$, $t = 1.87$, $p = .067$) were marginal predictors of learning about mating cues. All other variables did not predict mating SPLT performance (all $p > .285$) while controlling for performance in the neutral condition. When including both age of menarche and pubertal stage in the model, both were significant predictors

Table 14

Correlation Matrix for Variables Used in Modeling



Correlation Matrix

		Mating_Context	Neutral_Context	Status_Context	Pubertal_Stage	Age of Menarche	Current_Age	FSMI	KSRQ	Testosterone_log
Mating_Context	Spearman's rho	—								
	p-value	—								
	N	—								
Neutral_Context	Spearman's rho	0.62 ***	—							
	p-value	<.001	—							
	N	70	—							
Status_Context	Spearman's rho	0.64 ***	0.58 ***	—						
	p-value	<.001	<.001	—						
	N	70	70	—						
Pubertal_Stage	Spearman's rho	0.04	−0.10	0.01	—					
	p-value	0.745	0.413	0.951	—					
	N	70	70	70	—					
Age of Menarche	Spearman's rho	0.40 **	0.28 *	0.27 *	0.02	—				
	p-value	0.001	0.034	0.035	0.856	—				
	N	59	59	59	64	—				
Current_Age	Spearman's rho	0.19	0.06	0.13	0.36 **	0.34 **	—			
	p-value	0.124	0.627	0.289	0.001	0.005	—			
	N	70	70	70	77	64	—			
FSMI	Spearman's rho	0.03	−0.03	0.19	0.18	0.13	0.21	—		
	p-value	0.805	0.819	0.113	0.117	0.325	0.073	—		
	N	69	69	69	76	64	76	—		
KSRQ	Spearman's rho	0.14	0.19	0.19	0.31 **	0.15	0.37 **	0.42 ***	—	
	p-value	0.238	0.117	0.120	0.007	0.244	0.001	<.001	—	
	N	68	68	68	75	62	75	74	—	
Testosterone_log	Spearman's rho	0.07	0.06	−0.06	0.16	0.19	0.28 *	0.02	0.16	—
	p-value	0.592	0.649	0.636	0.171	0.142	0.014	0.895	0.165	—
	N	67	67	67	74	62	75	73	73	—

of performance in the mating context (age of menarche: $\beta = 3.87$, $t = 2.39$, $p = .019$; pubertal stage: $\beta = 7.11$, $t = 2.40$, $p = .019$) while accounting for the neutral context. An interaction model was tested, but the interaction between age of menarche and pubertal stage was not significant ($p = .238$). The model using age of menarche, pubertal stage, and performance in the neutral condition had the lowest AIC compared to both the individual models (AIC = 656.13). As a final check, performance in the neutral context was removed from the model, and both age of menarche and pubertal stage remained significant predictors ($p's < .04$). A model comparison revealed that the model including the neutral context as a control explained significantly more variance ($\Delta R^2 = .38$, *f*(1, 52) = 36.59, *p* < .001). Thus, the final best fitting model was as follows, with age of menarche (X_1) and pubertal status (X_2) predicting performance in the mating condition of the SPLT (Y_t) controlling for general task learning (X_3):

$$Y_t = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + u_t$$

Follow up analyses found that neither age of menarche (β = 2.73; *t* = 1.69, *p* = .096) nor pubertal stage (β = -2.214; *t* = -0.73, *p* = .471) were significant predictors of performance in the neutral condition in individual models. Similarly, neither age of menarche (β = 2.59; *t* = 1.55, *p* = .126) nor pubertal stage (β = -1.12; *t* = -0.36, *p* = .719) were significant predictors of performance in the neutral context when included together in the model. Age of menarche marginally predicted performance in the status condition alone (β = 2.47; *t* = 1.76, *p* = .08), but became non-significant when accounting for performance in the neutral condition (β = 1.33; *t* = 1.05, *p* = .299). Pubertal stage was not a significant predictor of performance in the status condition either alone or with the neutral context score as a control (all *p*'s < .341). Therefore a model containing both age of menarche and pubertal stage predicting status-learning scores was not tested.

Discussion

This study explored relationships between pubertal indices and romantic experiences/ motivations in early to middle adolescent girls, and also tested whether pubertal, hormonal, or mating-relevant factors influenced learning about mating cues in peers. The first aim of this study was to identify when romantic feelings and behaviors first emerge. The data revealed that romantic experiences were indeed just beginning to emerge in this sample of 12-16 year olds, indicating this a good age range to assess early romantic experiences. This is consistent with other work reporting initial romantic relationship establishment and nascent sexual behaviors (i.e., kissing) during early to middle adolescence (Connolly et al., 2013, Seiffge-Krenke, 2003, Tolman & McClelland, 2011). Scores were higher on the K-SRQ in those who had started their period compared to those who had not. While no similar relationships were found between pubertal indices and FSMI scores, this measure did provide a good indication of whether adolescents were seeking a romantic relationship or not. Further investigation revealed that while T levels (and pubertal stage marginally) predicted whether or not someone had ever been in a romantic relationship, neither T levels nor other pubertal indices related to number of relationships or number of hook-up partners. Finally, it was found that age of menarche and pubertal status were a significant predictors of learning performance when learning about mating cues.

Aim 1: Characterizing and Exploring Romantic Experiences in Early to Middle Adolescents

The first aim of this chapter was to report and explore romantic experiences in early to middle adolescence, including whether or not they have started participating in romantic relationships or hook-ups, and if so, whether these related to pubertal indices or measures of mating motivation. Given previous evidence that pubertal timing (as assessed by age of menarche and pubertal stage) is associated with romantic and sexual experiences (Baams et al., 2014), it was surprising (and counter to our hypotheses) that those with earlier pubertal timing (i.e., age of menarche) and with more advanced pubertal stage generally did not participate in more romantic relationships and hook-ups compared to others. This contrasts with life history theory, which presumes that early-maturers and fast-maturers represent a “fast” life history strategy, characterized by quicker pacing through sexual development, more frequent sexual encounters, earlier pregnancies, and a greater number of sexual partners compared to on-time or late-maturers (Belsky, 2012). Alternatively, a “slow” life history strategy is represented by later sexual maturity, delayed sexual debut, and prioritizing parental investment in fewer numbers of offspring. Proponents of this theory state that stressful rearing environments (e.g., parental absence, unstable attachments, low socioeconomic status) “code” the body to prioritize quick and frequent reproduction (i.e., greater number of offspring) rather than investing more energy into the quality of offspring. Thus, prior results could be due to differences in early family environments. Indeed, one meta-analysis found support for links between father absence and age of menarche in girls (Webster et al., 2014), and another study found evidence that food scarcity in early development was associated with earlier sexual debuts and earlier pregnancies (Coall & Chisholm, 2003). Therefore, our null findings between pubertal stage and timing and number of romantic relationships or hook-ups may indicate relatively stable rearing environments for this sample. While information about early adverse experiences was collected in the overall TAG study, incorporating it was outside the scope of this dissertation, but presents a promising future direction.

This study did find that levels of T increased the likelihood that the adolescent had ever experienced a romantic relationship. This is consistent with Halpern et al. (1997), which found that T predicted initiation of sexual behaviors in adolescent females, and other studies finding associations between peak T levels and interest in dating in adult women (Gildersleeve et al., 2014; Roney & Simmons, 2013; Thornhill & Gangestad, 2006). This finding also lends support for the estrus model (Jones et al., 2018), which claims that during periods of high T concentrations (such as during the most fertile phase of the menstrual cycle) women experience increased overall sexual motivation.

Associations were also found between pubertal stage and K-SRQ scores, pointing to a positive relationship between pubertal timing and enjoyment of flirting, kissing, or having a crush. However, given strong overlap between pubertal status and age in this dataset, it could be that the relationship between K-SRQ and pubertal indices was not unique to puberty, but rather represented normal maturational processes. This deviation from prior literature is likely due to the limited nature of the instruments used in this project. Previous work parsed sexual behaviors into many different categories, including age of sexual debut, masturbation habits, partnered sexual encounters, and behaviors other than intercourse (e.g., Bearinger et al., 2007; Halpern et al., 1997; Rizzo et al., 2019) while this study included relatively small inventories. Only one question asked about the number of romantic relationships, and another single item asked about the lifetime number of hook-ups. It is probable that assessing a broader scope of adolescent romantic experiences would yield patterns more similar to those seen in previous literature.

Aim2: Social Learning by Context

This study used an updated version of a social probabilistic learning task to investigate whether pubertal indices or mating motivation were related to the salience of mating-relevant cues. It was found that age of menarche and pubertal status predicted performance in the mating context (but not the neutral context) over and above the influence of general task learning. Age of menarche was a marginal, independent predictor of performance in the status condition, but become non-significant when accounting for performance in the neutral condition. In-line with previous work (Baams et al., 2014) pubertal stage effected performance when learning about mating cues such that those at later pubertal stages performed better compared to those in earlier stages. This could represent preliminary evidence that as adolescence progresses across puberty, it becomes easier to learn about mating cues. Furthermore, current age was not a significant predictor, suggesting that this increase in learning performance was not due to normal age-related maturational processes. However, the direction of the effect of age of menarche was opposite of what was expected. It was hypothesized that those with earlier menarche should perform better in the mating context as they would be classified as further along in pubertal development compared to peers who have not started menstruating. Instead, those with a *later* age of menarche tended to perform better in the mating condition compared to those with earlier timing.

One reason for this result may be due to the more rapid pace of development seen in late-developers. In the current study, it was assumed that early developers would reach mating-relevant milestones faster compared to peers. However, there is some evidence suggesting that those who enter puberty later show a relatively faster rate of development compared to early-maturers (Biro et al., 2001; Mendle et al., 2010; Mendle, 2014). Perhaps later-developing adolescents in our sample were experiencing more rapid changes, allowing them more cognitive flexibility with learning about faces. Alternatively (or in addition), it could be that there was something more distracting about mating cues for early-maturers, causing impairment in learning performance relative to the neutral context. This would fit well with prior evidence finding structural changes in the cortical regions of the brain associated with cognitive control (Barbalat et al., 2013; Hare et al., 2009) and pubertal hormone influences on social-processing, including face interpretation (e.g., Cservenka et al., 2015; Nelson et al., 2016). Therefore, it could be that early-maturers had a harder time inhibiting distractions in the mate-relevant condition. Perhaps mating-relevant cues elicited some emotional response that impaired performance in early-maturers compared to late-maturers.

However, given the overall lack of learning differences by social context, it is also possible that that mating and status information was simply not more salient to adolescents than the neutral cues. While prior work found differences in learning rate based on social versus non-social information (Flournoy, 2018), perhaps the neutral cues used in the current task were also interpreted as social information, and therefore equally salient as the other cues. Nelson et al.'s (2005; 2016) social reorientation hypothesis proposes that adolescents become much more interested in information about their peers compared to earlier ages. Thus, it could be that *any* information about the peer faces used in the task was equally important. Indeed, learning that someone has siblings and/or likes swimming could elicit thoughts about the adolescent swimming with the peer in the image or engaging in social interactions with their siblings. This would explain the overall lack of learning differences by context category.

Finally, the lack of relationships between baseline T and task performance or mating motivation indices is surprising given animal models where T influences learning about mating behaviors (e.g., Dahl et al., 2018; Doupe & Kuhl, 1999; Fawcett & Frankenhuis, 2015; Marler et al., 1987; Templeton et al., 2012). In these previous models, however, T exposure in-utero and during puberty related to distant behavioral effects, sometimes emerging later in adolescence or adulthood. This is consistent with the organizational–activational hypothesis, which proposes that hormone concentrations during gestation organize neural circuitry that is later activated by pubertal hormone fluctuations (Wallen, 2015). It could be that effects of T across puberty influence mating motivation in later adolescence rather than in early or middle adolescence, and that daily T levels simply do not influence differences in mating cognition. Similar to the previous chapter in this dissertation, measurement error could be an issue when detecting relatively small levels of T as ELISA kits can be unreliable for very small T concentrations (Meta & Anderson, 2016).

Of course, another plausible conclusion is that T does not influence mating cognition or behaviors in adolescent girls. Previous work has detected T influences in boys (e.g., Halpern et al., 1997, 1998) but results for adolescent girls is mixed. Some researchers have found that, rather than testosterone, estradiol and progesterone are linked with sexual desire and behaviour in females. However, the direction of the association differed by hormone: estradiol correlated with an increase in sexual desire while progesterone associated with declines in sexual motivation (Rupp & Wallen, 2007). Furthermore, with the estrus model of female mating strategies proposing fluctuations in sexual desire across the menstrual cycle, both T and estradiol are at their highest during the ovulatory window, when fertility is highest. Therefore, changes in mating psychology could actually be related to estradiol in girls rather than T.

Limitations & Future Directions

This study had several methodological limitations that likely impacted results. First, the sample size could have been too small, as recruitment was halted when the COVID-19 pandemic forced lab closures. Particularly given the small sample size of this dataset in terms of number of relationships or hook-up partners, (n = 31 for relationships; n = 48 for number of partners), additional data is needed to improve confidence in study findings.

Second, the measures of mating motivation turned out not to be robust indicators of actual mating behaviors, suggesting mating motivation may not have as much influence on behaviors as initially proposed, or that these were poor measures of mating motivation for the current sample. For example, one could desire a romantic partner, but not have the confidence or opportunity to engage in behaviors towards that goal. A more comprehensive inventory of sexual thoughts, fantasies, desires, and variable sexual behaviors (i.e., including light kissing versus making out, touching versus oral sex, anal sex, etc.) might better elucidate relationships between pubertal indices and mating motivation. Finally, the social probabilistic learning task may not be a robust measure of individual differences in motives, so future work should seek to develop a task that more accurately represents underlying social motives.

Interestingly, this sample included substantial variability in terms of both sexual and gender identity. It could be that results found here are impacted by the relatively high proportion of non-heterosexual/non-gender-conforming participants compared to previous work. While future work could use a more homogenized sample, this would not accurately reflect the gender and sexual preferences in this stage of life. According to Erikson's (1950) stage model of development, adolescence as a time of intense identity exploration. The variability in sexual and gender identity during this window could represent a time of identity exploration specifically within the mating context. It will be important for future researchers to explore the more nuanced sexual identities of modern youth, and how more variable romantic experiences impact health and wellbeing into adulthood.

Conclusion

This study provides evidence that romantic-related motivations and behaviors begin to emerge during early to middle adolescence. Evidence of how these attitudes and experiences relate to pubertal indices is mixed. Mating cues did not improve social learning performance, but it was influenced by age of menarche and pubertal status, such that those with earlier age of menarche showing some impairment in this context compared to on-time and later-maturers, while adolescents who are more advanced in pubertal development perform better on the mate-learning task. Overall, early to middle adolescence represents a key point in development where dating and romantic behaviors emerge. Future work is needed to investigate the interrelationships between cognitive, behavioral, and environmental influences on romantic development across adolescence.

CHAPTER V

GENERAL DISCUSSION

Romantic and sexual experiences represent key milestones across adolescent development. From the first “crush” to the first kiss to the first sexual encounter, each experience is seen as fundamentally transformative, propelling one away from childhood and towards more adult-like roles, behaviors, and responsibilities. However, much emphasis is placed on the behavior itself rather than the underlying cognitive, social, and affective features of adolescent sexuality. Furthermore, many investigators have focused on the risk-taking aspects of sexual experiences, viewing them as inept, confused, and innately dangerous (Schalet, 2004; Fortenberry, 2013). Indeed, this “risk-taking” perspective has dominated sex education narratives across America, with many adults feeling the need to suppress (or control) adolescent sexuality. Relatively fewer studies examine the more positive influences romantic relationships can have on an adolescent’s self-esteem (Meier & Allen, 2008), feelings of connectedness (Montgomery, 2005), and general wellbeing (Gómez-López, 2019). However, more researchers have recently endorsed romantic and sexual activities in youth as normative developmental tasks that can influence healthy relationships dynamics into adulthood (e.g., Dahl et al., 2018; Suleiman et al., 2017). While adolescent sexual behavior is not without its risks (similar to adult sexual behaviors), it is important to also view this period as a central aspect of the adolescent experience.

It is clear that a substantive shift in social cognition occurs across puberty. Rising hormones at puberty regulate structural and functional growth in brain regions that support social processing, leading to more nuanced understanding of social dynamics (Blakemore, 2008; Blakemore & Mills, 2014; Vijayakumar et al., 2018). While normative social-perceptual processes begin to develop early in life, specialization occurs in adolescence specifically attuned to more complex social contexts. For example, increases in sensation-seeking, reward-processing, and mentalizing capacities occur during puberty that emphasize peer interaction as highly salient sources of key information (Nelson et al., 2016). Distinct from childhood, peer interactions take on a whole new meaning during adolescence, when youth start to experience romantic feelings and attitudes for the first time (Connolly et al., 2014; Seiffge-Krenke, 2003). Thus, it is likely that cognitive, social, and affective changes across this phase of development prepare the adolescent to learn and master these new types of interactions.

Mating Behaviors and Motivations

Data presented in this dissertation characterizes the emergence of romantic attitudes and experiences in early to middle adolescence. Among our sample of 12-16 year olds (reported in chapter IV), youth are just beginning to explore romantic relationships, and report enjoyment of mating behaviors such as flirting or kissing. By middle adolescence (reported in chapter III), more than 70% participants had either been in a romantic relationship or desired one. This follows patterns found in previous literature, finding early relationship formation beginning as soon as 10 years old (Seiffge-Krenke, 2003), and first dates, hook-ups, and intercourse occurring prior to graduating high school (Connolly et al., 2014). While much research on the development of sexuality investigates this using retrospective accounts (i.e., Collins et al., 2003; Demir et al., 2010; Gómez-López, 2019), the current sample has been tracked across pubertal development and early adolescence, getting more real-time accounts of these experiences.

A major goal of the current dissertation was to explore the development of underlying mating motivation associated with emerging romantic behaviors. Assessing mating motivation primarily relied on two inventories: the Fundamental Social Motives Inventory (mate-seeking subscale; FSMI, Neel et al., 2015) and the Kid's version of the Social Rewards Questionnaire (sexual relationships subscale; K-SRQ, Foulkes et al., 2017). While related under the broad category of mating relationships, it was found that these two scales measured distinct aspects of mating cognition. The FSMI focused primarily on the desire to be in a romantic partnership while the K-SRQ assessed enjoyment of particular interactions, including flirting, kissing, or having a crush on someone).

Face validity for each scale was high, however no underlying factor structure was identified for combining them. Across both chapters, scores on the mate-seeking subscale of the FSMI were significantly different between those who were currently in a relationship (or not interested in seeking one) and those who stated interest in finding one. Thus, higher scores on this scale truly represented desire for a romantic partnership. Similarly, scores on the K-SRQ seemed to accurately reflect interest in romantic or flirtatious interactions, as they correlated with number of romantic relationships, desire to be in a romantic relationship, and number of hook-up partners in chapter IV. However, chapter III showed that together, these measures did not map onto a single factor. Indeed, one can enjoy romantic experiences without specifically desiring a partnered relationship, and one can desire a romantic relationship but not enjoy flirtatious interactions. Furthermore, these subscales contained only a limited number of items, missing a wider perspective of adolescent romantic experiences. Future work should develop more detailed inventories to investigate early adolescent thoughts, desires, attitudes, and curiosity about romantic or sexual contexts, and incorporate both environmental and biological influences.

Pubertal Stage, Pubertal Timing, and Mating Behaviors

Associations between puberty and sexual behaviors has been well researched. Previous work has found links between pubertal timing, pubertal stage, and initiation of sexual interactions where earlier pubertal timing and pubertal status associated with earlier sexual behaviors (Baams et al., 2014). This link makes sense according to life history theory (Belsky, 2012; Wenner et al., 2013), where early puberty represented a “fast” strategy, devoting energetic resources to procreating early and often. In evolutionary terms, this fast strategy would be advantageous in unstable, harsh environments, given the higher probability of mortality. In this type of environment, reproducing early and having more offspring increases the likelihood of one’s gene pool making it to the next generation. Alternatively, a slower life history trajectory is typical of resource-rich environments, where organisms have more time and energy to devote to child-rearing, and ultimately have an extended youth period and have fewer offspring. While humans as a species represent a slower-paced life history strategy compared to other animals, it has recently been proposed that a similar kind of divergence can be seen in adolescents. Specifically, those who grow up in relatively unstable rearing environments (e.g., father absence, food scarcity, low socioeconomic status) reach menarche earlier and have sexual intercourse or get pregnant at earlier ages compared to peers (Hochberg & Konner, 2020; Kaplan & Gangestad, 2015; Wenner et al., 2013).

Consistent with previous work, chapter IV revealed marginally significant links between (1) age of menarche and number of romantic relationships, and (2) between pubertal status and ever having a romantic relationship. However, results did not reach statistical significance and so interpretation of this work should be cautious. Further, chapter III did not find any significant correlations between pubertal timing or stage with number of romantic relationships. Methodological considerations could have led to these results, given the small sample sizes, and limited assessment questions. Additionally, both studies were impacted by the COVID-19 pandemic, which limited opportunities for engaging in these romantic interactions. However, a strength of this dissertation is that we investigated this sample at the age where these behaviors are first emerging, indicating potential for cognitive desires to be present without enacting the behaviors yet. Thus, this was the right age to capture the potential underlying motivations of mating prior to initiation of any sexual behaviors.

Pubertal Stage, Pubertal Timing, and Mating Motivation

Pubertal Stage

One focus of this dissertation was to examine the motivational aspects of mating that likely precede enacting any sexual behaviors - such as interest in finding a romantic partner, and enjoyment of flirting or kissing. Specifically, it was hypothesized that mating motivation would be positively related to pubertal stage, and that later pubertal stage would improve learning about mating cues in peer faces. Results were mixed as chapter III found no links between pubertal stage with measures of mating motivation, while chapter IV found that later pubertal status did significantly relate to interest in kissing, flirting, or having a crush on someone. This difference could be due to the disruption caused by the COVID-19 pandemic. Some participants used in chapter III (n = 43) responded to surveys during the pandemic (between March 2020 and September 2021), and studies have indicated that sexual desire decreased among adolescents and young adults (Stavridou et al., 2021; Wignall et al., 2021) due to fear of contracting COVID-19. Alternatively, most participants in chapter IV (n = 75) responded to questionnaires prior to February 2020, thus the link between pubertal stage and enjoyment of flirting behaviors was found. This result also coincides with marginal links between pubertal stage and ever having a romantic relationship or hooking-up found in chapter IV, and with links in previous literature (Baams et al., 2014). Thus, as one progresses through puberty, romantic cognitions and behaviors begin to emerge.

Age of Menarche

It was also predicted that age of menarche would have a negative relationship with mating motivation (such that earlier menarche would be associated with greater mating motivation). Chapter III revealed no links between age of menarche and measures of mating motivation. While chapter IV found that enjoyment of kissing, flirting, or having a crush on someone significantly correlated with age of menarche, it was discovered that an *older* age of menarche (later menarche) was associated with increased enjoyment of these activities. Further, an older age of menarche significantly predicted performance on a social learning task using mating cues when controlling for general task learning. This opposes previous work finding links between an earlier age of menarche and sexual desire (Sýkorová & Flegr, 2021), and between earlier age of menarche and sexual behaviors (Baams et al., 2014). One reason for these findings could be due to general maturational processes. In chapter IV, participant's current age correlated relatively strongly with both age of menarche and K-SRQ scores, so this third variable may explain the relationship. As one gets older they tend to become more interested in sexual behaviors or in finding romantic partners. Previous work has also found that age of menarche correlates with current age, particularly when the average age of menarche for the sample is low (Aryeetey et al., 2011; Koprowski et al., 2001). Given the average age of menarche in this sample was 11.82 while the current age ranged from approximately 12 - 15 years old, perhaps the variance in mating motivation was due to chronological age progression rather than the age of menarche. There is also the possibility of participants in both samples misremembering or misreporting the exact timing of menarche, which could also skew findings, although this is less likely in our largely prospective approach. Overall, findings in this dissertation point out that previous links between age of menarche and adolescent sexuality may be more nuanced than previously thought.

Testosterone and Mating Motivation

Another central aspect of this dissertation was exploring the impact of T on mating motivation and mating behaviors. It was hypothesized that T was a mechanism via which puberty would ignite interest in dating and romantic activities. However, chapter III found no associations between T changes, current T, and mating motivation or behaviors, and chapter IV revealed that current levels of T did not influence performance on learning about mating cues. Although T showed linear progression with pubertal stage (chapter III) and current levels of T indicated an increased likelihood of ever having been in a romantic partnership (chapter IV), T's impact on mating motivation was not detected.

The null results connecting current T concentration (either in the past month or on the same day as testing) with mating motivation was surprising. Consistent with the biosocial model, T has previously been found to be a causal factor for sexuality in adolescent girls (Halpern et al., 1997; Udry et al., 1986), and T has also been used as a treatment for female sexual dysfunction, improving sex drive and arousal in adult women (Khera, 2015). Furthermore, T has been linked with mating behaviors in several animal models (e.g., Fawcett & Frankenhuis, 2015; Marler et al., 1987; Templeton et al., 2012). Given much previous work did not assess cognitive underpinnings of sexual behaviors, perhaps T initiates sexual behaviors irrespective of sexual desire. It could be that other reproductive hormones - like estradiol and progesterone - initiate motivation to engage in romantic interactions while T correlates to the actual behaviors. Future work should identify associations between estradiol and progesterone with mating motivation.

There are also methodological considerations to be made for the studies in this dissertation that could have led to these null findings. First, the sample sizes in both chapters were relatively small, and included some diversity in terms of sexual identity and gender expression. It could be that hormonal relationships with mating motivation are more variable depending on the subject's sexual orientation or gender identity. Animal models and most work in humans only investigate T relationships in heterosexual male-female pairings. Given some evidence of T associations with sexual orientation (Hines, 2011; Neave et al., 1999) and gender expression (Nakamura et al., 2012) it could be that the samples used in this dissertation show more nuanced relationships between T and mating motivation. It will be important for future research to include more diverse sexual and gender identities in their samples when identifying links between reproductive hormones and mating motivation.

Furthermore, the method of T assessment used in this dissertation could have influenced results. In chapter III, saliva samples for half of the subjects have yet to be assayed at the time of this writing. Due to COVID-19 and relocation of the wet lab, hormonal assays for the TAG project have been stalled. Further, ELISA kits were used to measure T concentrations, and there is some evidence that these types of assays may not be sensitive enough to detect differences in subjects with low levels of testosterone, as found in young, adolescent girls (Kushnir et al., 2010; Welker et al., 2016). Therefore, these measurement errors could have impacted study findings.

Conclusion

This dissertation explored the development of mating motivation in early to middle adolescence, and investigated whether T or other pubertal indices played a role in these emerging romantic ideations and behaviors. It adds to the literature characterizing the normative trajectory of romantic experiences at the time when they first appear. This dissertation also presents preliminary evidence that age of menarche may have a more nuanced relationship with emerging motivations and behaviors than previously thought, with an older age of menarche predicting increased enjoyment of flirting, kissing, or having a crush on someone, and predicting number of romantic relationships. Furthermore, evidence from chapter IV indicates that age of menarche influences learning about mating-relevant cues, with late-maturers performing better on the task. However, neither changes in T nor current levels of T were related to the development of mating motivation as assessed in this dissertation. It will be important for future work to include more diverse samples in research on emerging mating psychology, include other reproductive hormones when exploring relationships in young girls, and include a broader range of sexual thoughts, desires, and attitudes when assessing early sexual development. Furthermore, future work should elucidate the biological, social, and cultural influences on adolescent mating psychology and identify how early thoughts and experiences impact sexual health into adulthood. Adolescence represents a sensitive window of opportunity where learning about dating and mating interactions - including associated emotions, thoughts, and motivations - may have a lasting impact on future health and wellbeing.

REFERENCES

Acevedo, B. P., & Aron, A. P. (2014). ‘Romantic love, pair-bonding, and the dopaminergic reward system’. In *Mechanisms of Social Connection: From Brain to Group*, edited by M. Mikulincer & P. R. Shaver. American Psychological Association.

Acevedo, B. P., Aron, A., Fisher, H. E., & Brown, L. L. (2012). Neural correlates of long-term intense romantic love. *Social Cognitive and Affective Neuroscience, 7*(2), 145–159.

Apicella, C. L., & Dreber, A. (2015). Sex differences in competitiveness: Hunter-gatherer women and girls compete less in gender-neutral and male-centric tasks. *Adaptive Human Behavior and Physiology, 1*(3), 247–269.

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. *Journal of Neurophysiology, 94*(1), 327–337.

Aryeetey, R., Ashinyo, A., & Adjuik, M. (2011). Age of menarche among basic level school girls in Madina, Accra. *African Journal of Reproductive Health, 15*(3), 113-121.

Ballonoff Suleiman, A., Johnson, M., Shirtcliff, E. A., & Galván, A. (2015). School-based sex education and neuroscience: What we know about sex, romance, marriage, and adolescent brain development. *Journal of School Health, 85*(8), 567-574.

Barbalat, G., Bazargani, N., & Blakemore, S.J. (2013). The influence of prior expectations on emotional face perception in adolescence. *Cerebral Cortex 23*(7), 1542–1551.

Barendse, M., Vijayakumar, N., Byrne, M. L., Flannery, J., Cheng, T. W., Flournoy, J. C., Nelson, B. W., Cosme, D., Mobasser, A., Chavez, S., Hval, L., Brady, B., Nadel, H., Helzer, A., Shirtcliff, E., Allen, N. B., & Pfeifer, J. H. (2019). *Study protocol: Transitions in Adolescent Girls (TAG)* [Preprint]. PsyArXiv. https://doi.org/10.31234/osf.io/pvsbw

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The ‘Reading the mind in the eyes’ test revised version: A study with normal adults, and adults with asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry, and Allied Discipline,s 42*(2), 241–251.

Barrett, J. C., & Marshall, J. (1969). The risk of conception on different days of the menstrual cycle. *Population Studies, 23*(3), 455–461.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1-48. https://doi:10.18637/jss.v067.i01.

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*(9568), 1220–1231.

Beauregard, M., Courtemanche, J., Paquette, V., & St-Pierre, É. L. (2009). The neural basis of unconditional love. *Psychiatry Research: Neuroimaging, 172*(2), 93–98.

Becker, J.B., Arnold, A.P., Berkley, K.J., Blaustein, J.D., Eckel, L.A., Hampson, E., Herman, J.P., Marts, S., Sadee, W., Steiner, M., Taylor, J., Young, E. (2005). Strategies and methods for research on sex differences in brain and behavior. *Endocrinology, 146,* 1650–1673.

Bellizzi, S., Ali, M. M., & Cleland, J. (2019). Long-term trends in reproductive behavior among young women in four countries, 1995–2009. *Journal of Adolescent Health, 64*(2), 201–210.

Belsky, J. (2012). The development of human reproductive strategies: Progress and prospects. *Current Directions in Psychological Science, 21*, 310–316.

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development, 62,* 647–670. https://doi.org/10.2307/1131166

Beltz, A. M., Corley, R. P. Bricker, J. B., Wadsworth, S. J., Berenbaum, S. A. (2014). Modeling pubertal timing and tempo and examining links to behavior problems. *Developmental Psychology, 50*(2), 2715 - 2726.

Bercovitch, F. B. (1991). Social stratification, social strategies, and reproductive success in primates. *Ethology and Sociobiology, 12*(4), 315–333.

Blakemore, S.-J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience, 9*(4), 267–277.

Blakemore, S.-J., & Mills, K. L. (2014). Is adolescence a sensitive period for sociocultural processing?. *Annual Review of Psychology, 65*(1), 187–207.

Blakemore, S.-J., & Robbins, T. W. (2012). Decision-making in the adolescent brain. *Nature Neuroscience, 15*(9), 1184–1191.

Blakemore, S.-J., den Ouden, H., Choudhury, S., & Frith, C. (2007). Adolescent development of the neural circuitry for thinking about intentions. *Social Cognitive and Affective Neuroscience, 2*(2), 130–139.

Bolling, D. Z., Pelphrey, K. A., & Wyk, B. C. V. (2016). Unlike adults, children and adolescents show predominantly increased neural activation to social exclusion by members of the opposite gender. *Social Neuroscience, 11*(5), 475–486.

Bolling, D. Z., Pitskel, N. B., Deen, B., Crowley, M. J., Mayes, L. C., & Pelphrey, K. A. (2011). Development of neural systems for processing social exclusion from childhood to adolescence. *Developmental Science 14*(6), 1431–1444.

Booth, A., Granger, D. A., Mazur, A., & Kivlighan, K. T. (2006). Testosterone and social behavior. *Social Forces, 85*(1), 167–191.

Bos, P. A., Panksepp, J., Bluthé, R.-M., & van Honk, J. (2012). Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: A review of single administration studies. *Frontiers in Neuroendocrinology, 33*(1), 17–35.

Braams, B. R., Duijvenvoorde, A. C. K., van Peper, J. S., & Crone, E. A. (2015). Longitudinal changes in adolescent risk-taking: A comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *Journal of Neuroscience, 35*(18), 7226–7238.

Braams, B. R., van Leijenhorst, L., & Crone, E. A. (2014). Risks, rewards, and the developing brain in childhood and adolescence. In *The Neuroscience of Risky Decision Making*, edited by V. F. Reyna & V. Zayas. American Psychological Association.

Bradshaw, C. P., Goldweber, A., Fishbein, D., & Greenberg, M. T. (2012). Infusing Developmental Neuroscience Into School-based Preventive Interventions: Implications and Future Directions. *Journal of Adolescent Health*, *51*(2, Supplement), S41–S47. https://doi.org/10.1016/j.jadohealth.2012.04.020

Brown B.B., Feiring C., Furman W. (1999). Missing The Love Boat: Why Researchers Have Shied Away from Adolescent Romance. In: Furman W., Brown B.B., Feiring C., editors. *Cambridge Studies in Social and Emotional Development. The Development of Romantic Relationships in Adolescence,* Cambridge University Press; New York, NY, USA, pp. 1–16.

Brumbaugh, C. C., & Fraley, R. C. (2006). The evolution of attachment in romantic relationships. Dynamics of romantic love: Attachment, caregiving, and sex, ed. M. Mikulincer & GS Goodman, 71-101.

Burke, A. R., McCormick, C. M., Pellis, S. M., & Lukkes, J. L. (2017). Impact of adolescent social experiences on behavior and neural circuits implicated in mental illnesses. *Neuroscience & Biobehavioral Reviews, 76,* 280–300.

Burnett, S., Bault, N., Coricelli, G., & Blakemore, S.-J. (2010). Adolescents' heightened risk-seeking in a probabilistic gambling task. *Cognitive Development, 25*(2), 183–196.

Burnham, T. C. (2007). High-testosterone men reject low ultimatum game offers. *Proceedings of the Royal Society B: Biological Sciences, 274*(1623), 2327–2330.

Burrow, A. L., & Rainone, N. (2017). How many likes did I get?: Purpose moderates links between positive social media feedback and self-esteem. *Journal of Experimental Social Psychology, 69*, 232–236.

Burrows, C. A., Laird, A. R., & Uddin, L. Q. (2016). Functional connectivity of brain regions for self- and other-evaluation in children, adolescents and adults with autism. *Developmental Science, 19*(4), 564–580.

Buster, J. E., Kingsberg, S. A., Aguirre, O., Brown, C., Breaux, J. G., Buch, A., Rodenberg, C.A., Wekselman, K. & Casson, P. (2005). Testosterone patch for low sexual desire in surgically menopausal women: A randomized trial. *Obstetrics & Gynecology, 105*(5), 944-952.

Campbell, B. C., Dreber, A., Apicella, C. L., Eisenberg, D. T. A., Gray, P. B., Little, A. C., Lum, J. K. (2010). Testosterone exposure, dopaminergic reward, and sensation-seeking in young men. *Physiology & Behavior, 99*(4), 451–456.

Cardoos, S. L., Suleiman, A. B., Johnson, M., van den Bos, W., Hinshaw, S. P., & Dahl, R. E. (2017). Social status strategy in early adolescent girls: Testosterone and value-based decision making. *Psychoneuroendocrinology.* doi:10.1016/j.psyneuen.2017.03.013

Carter, R. M., Macinnes, J. J., Huettel, S. A., & Adcock, R. A. (2009). Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. *Frontiers in Behavioral Neuroscience, 3*, 21-28.

Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology, 66*(1), 295–319.

Casey, B. J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review, 28*(1), 62–77.

Centers for Disease Control and Prevention (CDC). (2017, June 22). Over Half of U.S. Teens Have Had Sexual Intercourse by Age 18, New Report Shows. https://www.cdc.gov/nchs/pressroom/nchs_press_releases/2017/201706_NSFG.htm

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: Peer influence on risk taking. *Developmental Science, 14*(2), F1–F10.

Cheng, T. W., Vijayakumar, N., Flournoy, J. C., Macks, Z. O., de Peake, S. J., Flannery, J. E., Pfeifer, J. H. (2019). Feeling left out or just surprised? Neural correlates of social exclusion and over-inclusion in adolescence. *Biology Review, 52*(4), 934-940.

Coall, D. A., & Chisholm, J. S. (2003). Evolutionary perspectives on pregnancy: maternal age at menarche and infant birth weight. *Social science & medicine, 57*(10), 1771-1781.

Cohen Kadosh, K., Cohen Kadosh, R., Dick, F., & Johnson, M. H. (2011). Developmental changes in effective connectivity in the emerging core face network. *Cerebral Cortex, 21*(6), 1389–1394.

Cohen Kadosh, K., Johnson, M. H., Dick, F., Cohen Kadosh, R., & Blakemore, S.-J., 2013. Effects of age, task performance, and structural brain development on face processing. *Cerebral Cortex, 23*(7), 1630–1642.

Collins W.A., Welsh D.P., Furman W. (2009). Adolescent Romantic Relationships. *Annual Review in Psychology, 60,* 631–652. doi: 10.1146/annurev.psych.60.110707.163459.

Connolly J., McIsaac C., Shulman S., Wincentak K., Joly L., Heifetz M., Bravo V. (2014) Development of Romantic Relationships in Adolescence and Emerging Adulthood: Implications for Community Mental Health. *Canadian Journal of Communication and Mental Health, 33,* 7–19. doi: 10.7870/cjcmh-2014-002

Connolly, J., Nguyen, H. N., Pepler, D., Craig, W., & Jiang, D. (2013). Developmental trajectories of romantic stages and associations with problem behaviours during adolescence. *Journal of adolescence, 36*(6), 1013-1024.

Cooper, J. C., Dunne, S., Furey, T., & O'Doherty, J. P. (2014). The role of the posterior temporal and medial prefrontal cortices in mediating learning from romantic interest and rejection. *Cerebral Cortex, 24*(9), 2502–2511.

Cornwell, R. E., Law Smith, M. J., Boothroyd, L. G., Moore, F. R., Davis, H. P., Stirrat, M., Perrett, D. I. (2006). Reproductive strategy, sexual development and attraction to facial characteristics. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2143–2154.

Cservenka, A., Stroup, M. L., Etkin, A., & Nagel, B. J. (2015). The effects of age, sex, and hormones on emotional conflict-related brain response during adolescence. *Brain and Cognition, 99*, 135–150.

Dahl, R. E., Allen, N. B., Wilbrecht, L., & Suleiman, A. B. (2018). Importance of investing in adolescence from a developmental science perspective. *Nature, 554*(7693), 441-450.

Davey, C. G., Yücel, M., & Allen, N. B. (2008). The emergence of depression in adolescence: Development of the prefrontal cortex and the representation of reward. *Neuroscience & Biobehavioral Reviews, 32*(1), 1–19.

Dawson, P., & Guare, R. (2018). Executive Skills in Children and Adolescents: A Practical Guide to Assessment and Intervention, Guilford Press.

De Backer, C., Farinpour, L., & Braeckman, J. (2007). Mating intelligence in personal ads: do people care about mental traits, and do self-advertised traits match opposite-sex preferences? Mating intelligence: theoretical, experimental, and differential perspectives (pp. 77–102). Lawrence Erlbaum Associates.

Demir, M. (2010). Close Relationships and Happiness among Emerging Adults. *Journal of Happiness Studies 11,* 293–313.

Dixson, B. J. W., Blake, K. R., Denson, T. F., Gooda-Vossos, A., O'Dean, S. M., Sulikowski, D., Brooks, R. C. (2018). The role of mating context and fecundability in women's preferences for men's facial masculinity and beardedness. *Psychoneuroendocrinology 93,* 90–102.

Donaldson, S.H. & Mills K. (2021). Development of Social Cognition in Adolescence and the Importance of Mating. In Ferguson, H.J., Brunsdon, V., & Bradford, E. (Eds.), *The Cognitive Basis of Social Interaction across the Lifespan.* Oxford University Press, Oxford, UK.

Doupe, A. J. & Kuhl, P. K. (1999). Birdsong and human speech: common themes and mechanisms, *Annual Review in Neuroscience, 22,* 567–631.

Dreher, J.-C., Dunne, S., Pazderska, A., Frodl, T., Nolan, J. J., & O'Doherty, J. P. (2016). Testosterone causes both prosocial and antisocial status-enhancing behaviors in human males. *Proceedings of the National Academy of Sciences of the United States of America, 113*(41), 11633–11638.

Dumontheil, I., Hillebrandt, H., Apperly, I. A., & Blakemore, S.-J. (2012). Developmental differences in the control of action selection by social information. *Journal of Cognitive Neuroscience, 24*(10), 2080–2095.

Dumontheil, I., Küster, O., Apperly, I. A., & Blakemore, S.-J. (2010). Taking perspective into account in a communicative task. *NeuroImage 52*(4), 1574–1583.

Durante, K. M., Griskevicius, V., Simpson, J. A., Cantú, S. M., & Li, N. P. (2012). Ovulation leads women to perceive sexy cads as good dads. *Journal of Personality and Social Psychology, 103*(2), 292–305.

Eder, D., (1985). The cycle of popularity: Interpersonal relations among female adolescents. *Sociology of Education, 58*(3), 154–165.

Eder, D., & Kinney, D. A. (1995). The effect of middle school extracurricular activities on adolescents' popularity and peer status. *Youth & Society, 26*(3), 298–324.

Eisenegger, C., Haushofer, J., & Fehr, E. (2011). The role of testosterone in social interaction. *Trends in Cognitive Sciences, 15*(6), 263–271.

Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., & Wilson, D. S. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. *Developmental Psychology, 48*(3), 598–623.

Ember, C. R., Ember, M., & Peregrine, P. N. (2014). Human Culture: Highlights of Cultural Anthropology. Pearson.

Ember, C. R., Pitek, E., & Ringen, E. J. (2017). Adolescence. In *Explaining Human Culture,* edited by C. R. Ember, Human Relations Area Files. https://hraf.yale.edu/teach-ehraf/adolescence/

Erikson, E. H. (1950). *Childhood and Society.* New York, NY: Norton.

Ewing, S. W. F., Houck, J. M., & Bryan, A. D. (2015). Neural activation during response inhibition is associated with adolescents' frequency of risky sex and substance use. *Addictive Behaviors, 44,* 80–87.

Fawcett, T. W. & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in development. *Frontiers in Zoology, 12,* S3.

Fett, A.-K. J., Shergill, S. S., Gromann, P. M., Dumontheil, I., Blakemore, S.-J., Yakub, F., & Krabbendam, L. (2014). Trust and social reciprocity in adolescence—A matter of perspective-taking. *Journal of Adolescence, 37(*2), 175–184.

Flournoy, J.C. (2018). *Adolescent social motives: measurement and implications*. Doctoral dissertation, University of Oregon.

Fincham F.D., Cui M., (2011). Romantic Relationships in Emerging Adulthood. Cambridge University Press; Cambridge, UK.

Fitzhugh, B. (2003). The evolution of complex hunter-gatherers. In *The Evolution of Complex Hunter-Gatherers*, pp. 1–10. Springer.

Fox, J., & Anderegg, C. (2014). Romantic relationship stages and social networking sites: Uncertainty reduction strategies and perceived relational norms on Facebook. *Cyberpsychology, Behavior, and Social Networking, 17*(11), 685-691.

Forbes, E. E., & Dahl, R. E. (2010). Pubertal development and behavior: Hormonal activation of social and motivational tendencies. *Brain and cognition, 72*(1), 66-72. doi:10.1016/j.bandc.2009.10.007

Foulkes, L., Neumann, C. S., Roberts, R., McCrory, E., & Viding, E. (2017). Social Reward Questionnaire—Adolescent Version and its association with callous–unemotional traits. *Royal Society Open Science*, *4*(4), 160991. https://doi.org/10.1098/rsos.160991

Foulkes, L., Viding, E., McCrory, E., & Neumann, C. S. (2014). Social Reward Questionnaire (SRQ): Development and validation. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.00201

Frith, U., & Frith, C. (2010). The social brain: Allowing humans to boldly go where no other species has been. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1537), 165–176.

Madison H Fung, Brittany K Taylor, Michaela R Frenzel, Jacob A Eastman, Yu-Ping Wang, Vince D Calhoun, Julia M Stephen, Tony W Wilson, Pubertal Testosterone Tracks the Developmental Trajectory of Neural Oscillatory Activity Serving Visuospatial Processing, *Cerebral Cortex,* Volume 30, Issue 11, November 2020, Pages 5960–5971, https://doi.org/10.1093/cercor/bhaa169

Furman W., & Collibee C. (2014). A Matter of Timing: Developmental Theories of Romantic Involvement and Psychosocial Adjustment. *Developmental Psychopathology, 26,* 1149–1160. doi: 10.1017/S0954579414000182.

Furman, D., Hejblum, B. P., Simon, N., Jojic, V., Dekker, C. L., Thiébaut, R., & Davis, M. M. (2014). Systems analysis of sex differences reveals an immunosuppressive role for testosterone in the response to influenza vaccination. *Proceedings of the National Academy of Sciences, 111*(2), 869–874.

Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society B: Biological Sciences, 275*(1638), 991-1000.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010). Fertility in the cycle predicts women's interest in sexual opportunism. *Evolution and Human Behavior, 31*(6), 400-411.

Garcia, N. V., & Scherf, K. S. (2015). Emerging sensitivity to socially complex expressions: a unique role for adolescence? *Child Development Perspectives 9*(2), 84–90.

Gardner, M., & Steinberg, L. (2005). Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: An experimental study. Developmental Psychology, 41(4), 625.

Geher, G., & Kaufman, S.B. (2011). Mating intelligence. In *The Cambridge Handbook of Intelligence*, pp. 603–620. Cambridge University Press.

Geher, G., Miller, G., & Murphy, J. (2008). Mating intelligence: Toward an evolutionarily informed construct. In *Mating Intelligence: Sex, Relationships, and the Mind's Reproductive System* (G. Geher, G. Miller, Eds.), pp. 3–34. Psychology Press.

Gómez-López M, Viejo C, Ortega-Ruiz R. (2019). Well-Being and Romantic Relationships: A Systematic Review in Adolescence and Emerging Adulthood. *International Journal of Environmental Research and Public Health, 16*(13), 2415. doi: 10.3390/ijerph16132415. PMID: 31284670; PMCID: PMC6650954.

Gray, P. B., Chapman, J. F., Burnham, T. C., McIntyre, M. H., Lipson, S. F., & Ellison, P. T., (2004). Human male pair bonding and testosterone. *Human Nature, 15*(2), 119–131.

Gunther Moor, B., Op de Macks, Z. A., Güroğlu, B., Rombouts, S. A. R. B., Van der Molen, M. W., & Crone, E. A. (2012). Neurodevelopmental changes of reading the mind in the eyes. *Social Cognitive and Affective Neuroscience, 7*(1), 44–52.

Halpern, C. T., Udry, J. R., & Suchindran, C. (1997). Testosterone predicts initiation of coitus in adolescent females. *Psychosomatic Medicine, 59*(2), 161.

Halpern, C. T., Udry, R., & Suchindran, C. (1998). Monthly measures of salivary testosterone predict sexual activity in adolescent males. *Archives of Sexual Behavior, 27*(5), 445–465.

Harden, K. P., Mann, F. D., Grotzinger, A. D., Patterson, M. W., Steinberg, L., Tackett, J. L., & Tucker-Drob, E. M. (2018). Developmental differences in reward sensitivity and sensation seeking in adolescence: Testing sex-specific associations with gonadal hormones and pubertal development. *Journal of Personality and Social Psychology, 115*(1), 161–178.

Hare, T. A., Camerer, C. F., & Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. *Science, 324*(5927), 646–648.

Haselton, M.G., & Buss, D.M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology, 78*(1), 81–91.

Heck, A.L., Handa, R.J. (2019). Sex differences in the hypothalamic–pituitary–adrenal axis' response to stress: an important role for gonadal hormones. *Neuropsychopharmacology 44,* 45–58. https://doi.org/10.1038/s41386-018-0167-9

Herting, M. M., Gautam, P., Spielberg, J. M., Dahl, R. E., & Sowell, E. R. (2015). A longitudinal study: Changes in cortical thickness and surface area during pubertal maturation. *PLoS One, 10*(3), e0119774.

Hines, M. (2011). Prenatal endocrine influences on sexual orientation and on sexually differentiated childhood behavior. *Frontiers in Neuroendocrinology, 32*(2), 170-182.

Hochberg, Z. E., & Konner, M. (2020). Emerging adulthood, a pre-adult life-history stage. *Frontiers in endocrinology, 10,* 918.

Hopcroft, R. L. (2006). Sex, status, and reproductive success in the contemporary United States. *Evolution and Human Behavior, 27*(2), 104–120.

Jazaieri, H., Morrison, A. S., Goldin, P. R., & Gross, J. J. (2014). The role of emotion and emotion regulation in social anxiety disorder. *Current Psychiatry Reports, 17*(1), 531.

Johnston, L., Arden, K., Macrae, C. N., & Grace, R. C. (2003). The need for speed: The menstrual cycle and person construal. *Social Cognition, 21*(2), 89–100.

Jones, B. C., Hahn, A. C., & De Bruine, L. M. (2019). Ovulation, sex hormones, and women's mating psychology. *Trends in Cognitive Sciences, 23*(1), 51–62.

Judd, H. L., & Yen, S. S. (1973). Serum androstenedione and testosterone levels during the menstrual cycle. *Journal of Clinical Endocrinology and Metabolism, 36*(3), 475–481.

Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolutionary psychology. In *Handbook of Evolutionary Psychology*, edited by D. M. Buss, pp. 68–95. John Wiley & Sons.

Khera, M. (2015). Testosterone therapy for female sexual dysfunction. *Sexual Medicine Reviews,* 3(3), 137-144.

Kilford, E. J., Garrett, E., & Blakemore, S.-J. (2016). The development of social cognition in adolescence: An integrated perspective. *Neuroscience & Biobehavioral Reviews, 70*, 106–120.

Knutson, B., & Greer, S. M. (2008). Anticipatory affect: Neural correlates and consequences for choice. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363 (*1511), 3771–3786.

Koprowski, C., Coates, R. J., & Bernstein, L. (2001). Ability of young women to recall past body size and age at menarche. *Obesity research, 9*(8), 478-485.

Kushnir, M. M., Blamires, T., Rockwood, A. L., Roberts, W. L., Yue, B., Erdogan, E. & Meikle, A. W. (2010). Liquid chromatography–tandem mass spectrometry assay for androstenedione, dehydroepiandrosterone, and testosterone with pediatric and adult reference intervals. *Clinical Chemistry, 56*(7), 1138-1147.

Kyriazos, T. A. (2018). Applied Psychometrics: Sample Size and Sample Power Considerations in Factor Analysis (EFA, CFA) and SEM in General. *Psychology*, *09*(08), 2207. https://doi.org/10.4236/psych.2018.98126

Lee, Y., Dennis, S. (2013). Influences on the onset and tempo of puberty in human beings and implications for adolescent psychological development. *Hormones & Behavior, 64,* 250-261.

Li, N.P., van Vugt, M., & Colarelli, S.M. (2018). The evolutionary mismatch hypothesis: Implications for psychological science. *Current Directions in Psychological Science, 27*(1), 38–44.

Lindberg, L. D., Firestein, L., & Beavin, C. (2021). Trends in US adolescent sexual behavior and contraceptive use, 2006-2019. *Contraception: X,* 3, 100064.

Little, A. C. (2015). Attraction and human mating. In *Evolutionary Perspectives on Social Psychology,* edited by V. Zeigler-Hill et al., Springer International Publishing.

Little, A. C., & Jones, B. C. (2012). Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context. *Psychoneuroendocrinology, 37*(7), 999–1008.

Lobmaier, J. S., Bobst, C., & Probst, F., (2016). Can women detect cues to ovulation in other women's faces? *Biology Letters, 12*(1), 63-68.

Lombardo, M. V., Ashwin, E., Auyeung, B., Chakrabarti, B., Lai, M.-C., Taylor, K., & Baron-Cohen, S. (2012). Fetal programming effects of testosterone on the reward system and behavioral approach tendencies in humans. *Biological Psychiatry, 72*(10), 839–847.

Lu, S., McKenna, S. E., Cologer-Clifford, A., Nau, E. A., & Simon, N. G. (1998). Androgen receptor in mouse brain: sex differences and similarities in autoregulation. *Endocrinology 139*(4), 1594–1601.

Manani, P., & Sharma, S. (2013). Self esteem and suicidal ideation: A correlational study. *MIER Journal of Educational Studies Trends & Practices,* 75-83.

Maner, J. K., Gailliot, M. T., & DeWall, C. N. (2007). Adaptive attentional attunement: Evidence for mating-related perceptual bias. *Evolution and Human Behavior, 28*(1), 28-36.

Mansfield, C. F., & Wosnitza, M. (2010). Motivation goals during adolescence: A cross-sectional perspective. *Issues in Educational Research, 20*(2), 149–165.

Marler, P., Peters, S. & Wingfield, J. (1987). Correlations between song acquisition, song production, and plasma levels of testosterone and estradiol in sparrows. *Journal of Neurobiology, 18,* 531–548.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences, 21*(3), 353–363.

McCormick, E. M., & Telzer, E. H. (2016). Adaptive adolescent flexibility: Neurodevelopment of Decision-making and learning in a risky context. *Journal of Cognitive Neuroscience, 29*(3), 413–423.

McIver, T. A., Bosma, R. L., Goegan, S., Sandre, A., Klassen, J., Chiarella, J., & Craig, W. (2019). Functional connectivity across social inclusion and exclusion is related to peer victimization and depressive symptoms in young adults. *Journal of Affective Disorders, 253,* 366–375.

McRae, K., Gross, J. J., Weber, J., Robertson, E. R., Sokol-Hessner, P., Ray, R. D., & Ochsner, K. N. (2012). The development of emotion regulation: An fMRI study of cognitive reappraisal in children, adolescents and young adults. *Social Cognitive and Affective Neuroscience, 7*(1), 11–22.

Meier, A.; Allen, G. (2008). Intimate Relationship Development During the Transition to Adulthood: Differences by Social Class. *New Directions in Childhood and Adolescence. 2008,* 25–39

Mendle, J., Harden, K. P., Brooks-Gunn, J., & Graber, J. A. (2012). Peer relationships and depressive symptomatology in boys at puberty. *Developmental Psychology, 48*(2), 429–435.

Mills, K. L., Dumontheil, I., Speekenbrink, M., & Blakemore, S. J. (2015). Multitasking during social interactions in adolescence and early adulthood. *Royal Society Open Science, 2*(11), 150117.

Mills, K. L., Lalonde, F., Clasen, L. S., Giedd, J. N., & Blakemore, S.-J. (2014). Developmental changes in the structure of the social brain in late childhood and adolescence. *Social Cognitive and Affective Neuroscience, 9*(1), 123–131.

Monk, C. S., McClure, E. B., Nelson, E. E., Zarahn, E., Bilder, R. M., Leibenluft, E., & Pine, D. S. (2003). Adolescent immaturity in attention-related brain engagement to emotional facial expressions. *NeuroImage, 20*(1), 420–428.

Montgomery, M.J. (2005). Psychosocial Intimacy and Identity: From Early Adolescence to Emerging Adulthood. *Journal of Adolescent Research, 20,* 346–374.

Morris, N. M., & Udry, J. R. (1980). Validation of a self-administered instrument to assess stage of adolescent development. *Journal of Youth and Adolescence*, *9*(3), 271–280. https://doi.org/10.1007/BF02088471

Nakamura, A., Watanabe, M., Sugimoto, M., Sako, T., Mahmood, S., Kaku, H., ... & Kumon, H. (2012). Dose-response analysis of testosterone replacement therapy in patients with female to male gender identity disorder. *Endocrine Journal,* 12-0319.

Neave, N., Menaged, M., & Weightman, D. R. (1999). Sex differences in cognition: the role of testosterone and sexual orientation. *Brain and Cognition, 41*(3), 245-262.

Neel, R., Kenrick, D. T., White, A. E., & Neuberg, S. L. (2015). Individual Differences in Fundamental Social Motives. *Journal of Personality and Social Psychology*, No Pagination Specified. https://doi.org/10.1037/pspp0000068

Nelson, E. E., Jarcho, J. M., & Guyer, A. E. (2016). Social re-orientation and brain development: An expanded and updated view. *Developmental Cognitive Neuroscience, 17,* 118–127.

Nelson, E. E., Leibenluft, E., McClure, E. B., & Pine, D. S. (2005). The social re-orientation of adolescence: A neuroscience perspective on the process and its relation to psychopathology. *Psychological Medicine, 35*(2), 163–174.

Ojanen, T., & Nostrand, F. V. (2014). Social goals, aggression, peer preference, and popularity: Longitudinal links during middle school. *Developmental Psychology, 50*(8), 2134–2143.

Olson, I. R., McCoy, D., Klobusicky, E., & Ross, L. A. (2013). Social cognition and the anterior temporal lobes: A review and theoretical framework. *Social Cognitive and Affective Neuroscience, 8*(2), 123–133.

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. *Journal of Sexual Medicine, 7*(11), 3541–3552.

Overgaauw, S., van Duijvenvoorde, A. C. K., Gunther Moor, B., & Crone, E. A. (2015). A longitudinal analysis of neural regions involved in reading the mind in the eyes. *Social Cognitive and Affective Neuroscience, 10*(5), 619–627.

Patton, G. C., Coffey, C., Cappa, C., Currie, D., Riley, L., Gore, F., & Ferguson, J. (2012). Health of the world's adolescents: A synthesis of internationally comparable data. *Lancet, 379*(9826), 1665–1675.

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.

Penke, L., & Asendorpf, J. B. (2008). Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of Personality and Social Psychology, 95*, 1113-1135.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience, 16*(10), 1706–1716.

Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior, 25*(4), 229–241.

Peper, J. S., Brouwer, R. M., van Leeuwen, M., Schnack, H. G., Boomsma, D. I., Kahn, R. S., & Hulshoff Pol, H. E. (2010). HPG-axis hormones during puberty: A study on the association with hypothalamic and pituitary volumes. *Psychoneuroendocrinology, 35*(1), 133–140.

Pessoa, L. (2009). How do emotion and motivation direct executive control?. *Trends in cognitive sciences, 13*(4), 160–166.

Peters, M., Simmons, L. W., & Rhodes, G. (2009). Preferences across the menstrual cycle for masculinity and symmetry in photographs of male faces and bodies. *PLoS One, 4*(1), e4138.

Pfeifer, J. H., & Allen, N. B. (2016). The audacity of specificity: Moving adolescent developmental neuroscience towards more powerful scientific paradigms and translatable models. *Developmental Cognitive Neuroscience, 17,* 131–137.

Pfeifer, J. H., Masten, C. L., Moore III, 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.

Pfeifer, J. H., Kahn, L. E., Merchant, J. S., Peake, S. J., Veroude, K., Masten, C. L., & Dapretto, M. (2013). Longitudinal change in the neural bases of adolescent social self-evaluations: Effects of age and pubertal development. *Journal of Neuroscience, 33*(17), 7415–7419.

Phoenix, C.H., Goy, R.W., Gerall, A.A., Young, W.C. (1959). Organizing action of prenatally administered testosterone propionate on the tissues mediating mating behavior in the female guinea pig. *Endocrinology, 65*, 369–382.

Platt, B., Kadosh, K. C., & Lau, J. Y. F. (2013). The role of peer rejection in adolescent depression. *Depression and Anxiety, 30*(9), 809–821.

Prastika, D., & Hasanah, I. (2022). Adolescent Sexual Behavior In The Era Of The Industrial Revolution 4.0. *Jurnal Kebidanan Dan Kesehatan Tradisional*, 1-10. https://doi.org/10.37341/jkkt.v0i0.301

Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*(1431), 435–445.

Puts, D. (2016). Human sexual selection. *Current Opinion in Psychology, 7,* 28–32.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health?. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*(1), S93–S95.

Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., & Petrie, M. (2004). Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(5), S270–S272.

Rizzo, C. J., Collibee, C., Nugent, N. R., & Armey, M. F. (2019). Let's get digital: Understanding adolescent romantic relationships using naturalistic assessments of digital communication. *Child development perspectives, 13*(2), 104-109.

Rodriguez-Llanes, J.M., Verbeke, G., & Finlayson, C. (2009). Reproductive benefits of high social status in male macaques (Macaca). *Animal Behaviour, 78*(3), 643–649.

Romeo, R. D., Schulz, K. M., Nelson, A. L., Menard, T. A., & Sisk, C. L. (2003). Testosterone, puberty, and the pattern of male aggression in Syrian hamsters. *Developmental Psychobiology, 43*(2), 102–108.

Roney, J. R., & Simmons, Z. L. (2013). Hormonal predictors of sexual motivation in natural menstrual cycles. *Hormones and Behavior, 63*(4), 636–645.

Roney, J. R., Simmons, Z. L., & Gray, P. B. (2011). Changes in estradiol predict within-women shifts in attraction to facial cues of men's testosterone. *Psychoneuroendocrinology, 36*(5), 742–749.

Rooker, K., Gavrilets, S. (2020). On the evolution of sexual receptivity in female primates. *Scientific Reports, 10*, 1-12. https://www.nature.com/articles/s41598-020-68338-y.pdf

Rowe, R., Maughan, B., Worthman, C. M., Costello, E. J., & Angold, A. (2004). Testosterone, antisocial behavior, and social dominance in boys: Pubertal development and biosocial interaction. *Biological Psychiatry, 55*(5), 546–552.

Rubia, K., Smith, A. B., Woolley, J., Nosarti, C., Heyman, I., Taylor, E., & Brammer, M. (2006). Progressive increase of frontostriatal brain activation from childhood to adulthood during event related tasks of cognitive control. *Human Brain Mapping, 27*(12), 973–993.

Rupp, H. A., & Wallen, K. (2007). Relationship between testosterone and interest in sexual stimuli: The effect of experience. *Hormones and Behavior, 52*(5), 581–589.

Sawyer, S. M., Azzopardi, P. S., Wickremarathne, D., & Patton, G. C. (2018). The age of adolescence. *The Lancet Child & Adolescent Health, 2*(3), 223-228.

Saxton, T. K., DeBruine, L., Jones, B., Little, A., Roberts, S. (2009). Face and voice attractiveness judgments change during adolescence. *Evolution and Human Behavior, 30,* 398–408.

Schlegel, A., & Barry III, H. (1991). Adolescence: An Anthropological Inquiry. Free Press.

Schulz, K. M., & Sisk, C. L. (2016). The organizing actions of adolescent gonadal steroid hormones on brain and behavioral development. *Neuroscience & Biobehavioral Reviews, 70,* 148–158.

Sebastian, C. L., Fontaine, N. M. G., Bird, G., Blakemore, S.-J., De Brito, S. A., McCrory, E. J. P., & Viding, E. (2012). Neural processing associated with cognitive and affective Theory of Mind in adolescents and adults. *Social Cognitive and Affective Neuroscience, 7*(1), 53–63.

Seiffge-Krenke, I. (2003). Testing theories of romantic development from adolescence to young adulthood: Evidence of a developmental sequence. *International Journal of Behavioral Development, 27*(6), 519-531.

Shirtcliff, E. A., Dahl, R. E., & Pollak, S. D. (2009). Pubertal Development: Correspondence between hormonal and physical development. *Child Development*, *80*(2), 327–337. https://doi.org/10.1111/j.1467-8624.2009.01263.x

Shulman S., Davila J., Shachar-Shapira L. (2011). Assessing Romantic Competence among Older Adolescents. *Journal of Adolescence, 34,* 397–406. doi: 10.1016/j.adolescence.2010.08.002.

Silvers, J. A., McRae, K., Gabrieli, J. D. E., Gross, J. J., Remy, K. A., & Ochsner, K. N. (2012). Age-related differences in emotional reactivity, regulation, and rejection sensitivity in adolescence. *Emotion, 12*(6), 1235.

Silvers, J. A., Insel, C., Powers, A., Franz, P., Helion, C., Martin, R. E., & Ochsner, K. N. (2017). VlPFC–vmPFC–amygdala interactions underlie age-related differences in cognitive regulation of emotion. *Cerebral Cortex, 27*(7), 3502–3514.

Simon R.W., Barrett A.E. (2010). Nonmarital Romantic Relationships and Mental Health in Early Adulthood: Does the Association Differ for Women and Men? *Journal of Health and Social Behaviors, 51,* 168–182. doi: 10.1177/0022146510372343.

Sisk, C. L., & Foster, D. L. (2004). The neural basis of puberty and adolescence. *Nature Neuroscience, 7*(10), 1040–1047.

Sisk, C. L., & Zehr, J. L. (2005). Pubertal hormones organize the adolescent brain and behavior. *Frontiers in Neuroendocrinology, 26*(3), 163–174.

Sýkorová, K., & Flegr, J. (2021). Faster life history strategy manifests itself by lower age at menarche, higher sexual desire, and earlier reproduction in people with worse health. *Scientific reports, 11*(1), 1-18.

Smith, A. R., Chein, J., & Steinberg, L. (2014). Peers increase adolescent risk taking even when the probabilities of negative outcomes are known. *Developmental Psychology, 50*(5), 1564.

Smith, A. R., Steinberg, L., Strang, N., & Chein, J. (2015). Age differences in the impact of peers on adolescents' and adults' neural response to reward. *Developmental Cognitive Neuroscience, 11,* 75–82.

Somerville, L. H., Jones, R. M., Ruberry, E. J., Dyke, J. P., Glover, G., & Casey, B. J. (2013). The medial prefrontal cortex and the emergence of self-conscious emotion in adolescence. *Psychological Science, 24*(8), 1554–1562.

Spielberg, J. M., Olino, T. M., Forbes, E. E., & Dahl, R. E. (2014). Exciting fear in adolescence: Does pubertal development alter threat processing? *Developmental Cognitive Neuroscience, 8*, 86–95.

Stavridou, A., Samiakou, C., Kourti, A., Tsiorou, S., Panagouli, E., Thirios, A. & Tsitsika, A. (2021). Sexual activity in adolescents and young adults through COVID-19 pandemic. Children, 8(7), 577.

Steinberg, L. (2010). A dual systems model of adolescent risk-taking. *Journal of the International Society for Developmental Psychobiology, 52*(3), 216–224.

Suleiman, A. B., Galván, A., Harden, K. P., & Dahl, R. E. (2017). Becoming a sexual being: The 'elephant in the room' of adolescent brain development. *Developmental Cognitive Neuroscience, 25,* 209–220.

Symeonidou, I., Dumontheil, I., Chow, W.-Y., & Breheny, R. (2016). Development of online use of theory of mind during adolescence: An eye-tracking study. *Journal of Experimental Child Psychology, 149*, 81–97.

Templeton, C. N., Burt, J. M., Campbell, S. E., Lent, K., Brenowitz, E. A., & Beecher, M. D. (2012). Immediate and long-term effects of testosterone on song plasticity and learning in juvenile song sparrows. *Behavioural processes, 90*(2), 254-260.

Tolman, D.L., McClelland, S.I. (2011). Normative sexuality development in adolescence: a decade in review, 2000–2009. *Journal of Research on Adolescence*, *21* (1), 242-255. 10.1111/j.1532-7795.2010.00726.x

U.S. Census Bureau (2020). Selected Housing Characteristics 2011 - 2020. Retrieved from: https://data.census.gov/cedsci/table?q=United%20States&table=DP05&tid=ACSDP1Y2017.DP05&g=0100000US&lastDisplayedRow=29&vintage=2017&layer=state&cid=DP05_0001E

van den Berg, Y. H. M., Burk, W. J., & Cillessen, A. H. N. (2019). The functions of aggression in gaining, maintaining, and losing popularity during adolescence: A multiple-cohort design. *Developmental Psychology, 55*(10), 2159.

van den Bos, W., & Eppinger, B. (2016). Developing developmental cognitive neuroscience: From agenda setting to hypothesis testing. *Developmental Cognitive Neuroscience, 17*, 138–144.

van den Bos, W., Cohen, M. X., Kahnt, T., & Crone, E. A. (2012). Striatum-medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning. *Cerebral Cortex, 22*(6), 1247–1255.

van den Bos, W., van Dijk, E., Westenberg, M., Rombouts, S. A. R. B., & Crone, E. A. (2011). Changing brains, changing perspectives: The neurocognitive development of reciprocity. *Psychological Science, 22*(1), 60–70.

van den Broek, N., Deutz, M. H. F., Schoneveld, E. A., Burk, W. J., & Cillessen, A. H. N. (2016). Behavioral correlates of prioritizing popularity in adolescence. *Journal of Youth and Adolescence, 45*(12), 2444–2454.

van Honk, J., Schutter, D. J. L. G., Hermans, E. J., Putman, P., Tuiten, A., & Koppeschaar, H. (2004). Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. *Psychoneuroendocrinology, 29*(7), 937–943.

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.

Victor, E. C., & Hariri, A. R. (2016). A neuroscience perspective on sexual risk behavior in adolescence and emerging adulthood. *Development and Psychopathology, 28*(2), 471–487.

Vijayakumar, N., Cheng, T. W., & Pfeifer, J. H. (2017). Neural correlates of social exclusion across ages: A coordinate-based meta-analysis of functional MRI studies. *NeuroImage, 153,* 359–368.

Vijayakumar, N., Op de Macks, Z., Shirtcliff, E. A., & Pfeifer, J. H. (2018). Puberty and the human brain: Insights into adolescent development. *Neuroscience & Biobehavioral Reviews, 92*, 417–436.

Vijayakumar, N., Shirtcliff, E. A., Byrne, M. L., Mills, K., Cheng, T. W., Mobasser, A., Flannery, J., Nelson, B., Flournoy, J., Wang, W., Allen, N., & Pfeifer, J. (2019). *Pubertal hormones and brain structure: Exploring the value of hair assays*. PsyArXiv. https://doi.org/10.31234/osf.io/btf4y

Wallen, Kim. (2015). The Organizational Hypothesis: Reflections on the 50th anniversary of the publication of Phoenix, Goy, Geral, and Young (1959). *Hormones and Behavior* 561.

Wang, A. T., Lee, S. S., Sigman, M., & Dapretto, M. (2006). Neural basis of irony comprehension in children with autism: The role of prosody and context. *Brain: A Journal of Neurology, 129*(4), 932–943.

Webster G.D., Graber, J.A., Gesselman, A.N, Crosier, B.S., Schember, T.O. (2014) A Life History Theory of Father Absence and Menarche: A Meta-Analysis. *Evolutionary Psychology.* doi:10.1177/147470491401200202

Welker, K. M., Lassetter, B., Brandes, C. M., Prasad, S., Koop, D. R., & Mehta, P. H. (2016). A comparison of salivary testosterone measurement using immunoassays and tandem mass spectrometry. *Psychoneuroendocrinology, 71,* 180-188.

Wenner, C. J., Bianchi, J., Figueredo, A. J., Rushton, J.P ., & Jacobs, W. J. (2013). Life history theory and social deviance: The mediating role of executive function. *Intelligence, 41*(2), 102–113.

Wierenga LM, Bos MGN, Schreuders E, Vd Kamp F, Peper JS, Tamnes CK, Crone EA. (2018). Unraveling age, puberty and testosterone effects on subcortical brain development across adolescence. *Psychoneuroendocrinology. 91,* 105-114. doi: 10.1016/j.psyneuen.2018.02.034. Epub 2018 Mar 8. PMID: 29547741.

Wignall, L., Portch, E., McCormack, M., Owens, R., Cascalheira, C. J., Attard-Johnson, J., & Cole, T. (2021). Changes in sexual desire and behaviors among UK young adults during social lockdown due to COVID-19. *The Journal of Sex Research, 58*(8), 976-985.

Wingfield, J. C., Hegner, R. E., Dufty, Alfred M., & Ball, G. F. (1990). The ‘Challenge Hypothesis’: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist, 136*(6), 829–846.

Wirth, M. M., & Schultheiss, O. C. (2007). Basal testosterone moderates responses to anger faces in humans. *Physiology & Behavior, 90*(2–3), 496–505.

Wlodarski, R., & Dunbar, R. I. M. (2014). The effects of romantic love on mentalising abilities. Review of General Psychology, 18(4), 313–321.

Xie, X., Mulej Bratec, S., Schmid, G., Meng, C., Doll, A., Wohlschläger, A., & Sorg, C. (2016). How do you make me feel better? Social cognitive emotion regulation and the default mode network. *NeuroImage, 134,* 270–280.

Yurgelun-Todd, D. A., & Killgore, W. D. S. (2006). Fear-related activity in the prefrontal cortex increases with age during adolescence: A preliminary fMRI study. *Neuroscience Letters. 406*(3), 194–199.