Review

Facing changes and changing faces in adolescence: A new model for investigating adolescent-specific interactions between pubertal, brain and behavioral development

K. Suzanne Scherf [a,b,*], Marlene Behrmann [c,1], Ronald E. Dahl [d,2]

[a] *Department of Psychology and Social Sciences Research Institute, The Pennsylvania State University, 111 Moore Bldg., University Park, PA 16802, United States*
[b] *Department of Psychology, Center for the Neural Basis of Cognition, Carnegie Mellon University, 115 Mellon Institute, 4400 Forbes Ave., Pittsburgh, PA 15213, United States*
[c] *Baker Hall, Carnegie Mellon University, 5000 Forbes Ave., Pittsburgh, PA 15213, United States*
[d] *Community Health and Human Development and Joint Medical Program, University of California Berkeley, 233 University Hall, Berkeley, CA, United States*

A R T I C L E   I N F O

A B S T R A C T

Adolescence is a time of dramatic physical, cognitive, emotional, and social changes as well as a time for the development of many social–emotional problems. These characteristics raise compelling questions about accompanying neural changes that are unique to this period of development. Here, we propose that studying adolescent-specific changes in *face processing* and its underlying neural circuitry provides an ideal model for addressing these questions. We also use this model to formulate new hypotheses. Specifically, pubertal hormones are likely to increase motivation to master new peer-oriented developmental tasks, which will in turn, instigate the *emergence of new social/affective components of face processing.* We also predict that pubertal hormones have a fundamental impact on the re-organization of neural circuitry supporting face processing and propose, in particular, that, the *functional connectivity,* or temporal synchrony, between regions of the face-processing network will change with the emergence of these new components of face processing in adolescence. Finally, we show how this approach will help reveal why adolescence may be a period of vulnerability in brain development and suggest how it could lead to prevention and intervention strategies that facilitate more adaptive functional interactions between regions within the broader social information processing network.

© 2011 Elsevier Ltd. All rights reserved.

Contents

* Corresponding author. Tel.: +1 814 867 2921.
   E-mail addresses: suzyscherf@psu.edu (K.S. Scherf), behrmann@cmu.edu (M. Behrmann), rondahl@berkeley.edu (R.E. Dahl).
[1] Tel.: +1 412 268 2790.
[2] Tel.: +1 510 643 9063.

1. Introduction

Adolescence is a time of dramatic physical, cognitive, emotional, behavioral, and social changes. In the physical domain, pubertal hormones drive the development of secondary sex characteristics and the emergence of sexual dimorphism, particularly in overall body size and composition, but also in more subtle ways like in the physiognomy of the face (Farkas, 1988). These hormones also launch sexually dimorphic trajectories in brain development and play a role in re-organizing cortical circuitry, particularly the circuitry that supports social behaviors relevant to mate selection and the act of mating (Sisk and Zehr, 2005). In the social arena, adolescents are transitioning into more adult-like social roles that carry higher expectations about their independence and ability to control their own behavior (Dahl, 2004). Peer relations take on new salience as adolescents evaluate and test loyalty and develop a new interest in romantic and sexual relationships (Brown, 2004). Emotions become much more forceful, and learning to regulate them is a challenging developmental task (Dahl and Gunner, 2009; Forbes and Dahl, 2010). Importantly, this period of rapid and complex change toward adult levels of social competence also represents an interval of vulnerability. That is, adolescence is a period during which we see the emergence of many social–emotional problems, including depression, anxiety disorders, bipolar disorder, and a broad range of problem behaviors that are strongly influenced by peer social contexts including risk-taking, alcohol and substance use, aggression, and violence (Gardner and Steinberg, 2005; see Steinberg, 2008).

These characteristics of adolescence raise compelling questions about accompanying neural changes that are unique to this period of development, particularly in terms of the networks that process social information. For example, are there unique changes in brain–behavior correspondences during adolescence? Are such changes directly related to pubertal maturation? Are these changes sexually dimorphic? Do such changes occur specifically in neural networks that support social-information processing, or are they occurring throughout the brain? How are such developmental changes triggered and monitored and/or terminated?

In this paper, we propose that studying adolescent-specific changes in *face processing* and its underlying neural circuitry provides an ideal model for addressing these questions and for understanding adolescence as a unique and even vulnerable developmental period. We use this model to formulate new hypotheses about the functional consequences of social re-orientation toward peers during adolescence and the effects of gonadal hormones on behavior and brain function more generally. Specifically, we propose several new hypotheses, which are represented graphically in Fig. 1.

We argue that the surge of steroidal hormones during the onset of puberty is likely to instigate and causally influence the behavioral and neural basis of face processing, and social information processing more generally, in adolescence (Hypothesis 1 – purple lines in Fig. 1). Specifically, adolescent gonadal hormones are likely to influence motivation to master new developmental tasks, such as developing confiding friendships and romantic relationships with peers. These developmental tasks will, in turn, instigate the *emergence of new social/affective components of face processing* (Hypothesis 2 – blue lines in Fig. 1). For example, we hypothesize that the peer-focused developmental tasks of adolescence will drive attributions and preferences for attractiveness in faces as well as biases in recognition memory for peer, or own-age, faces. Furthermore, we suggest that the increased computational demands of these additional social/affective components of face processing will require a re-organization within the existing face-processing system, which will be manifest as a transient disruption in existing face processing abilities, like identity recognition and emotional expression recognition.

We also predict that the gonadal hormones released during adolescence have a fundamental impact on the re-organization of neural circuitry supporting face processing (as well as social processing, more generally). Specifically, we do not expect to see entirely new neural regions emerge and become incorporated into the existing neural network. Instead, we predict that gonadal hormones will influence a *shift in the balance* among existing visuoperceptual, cognitive, social and affective neural regions supporting face processing (Hypothesis 3 – red lines in Fig. 1). In other words, we hypothesize that the dynamical interactions
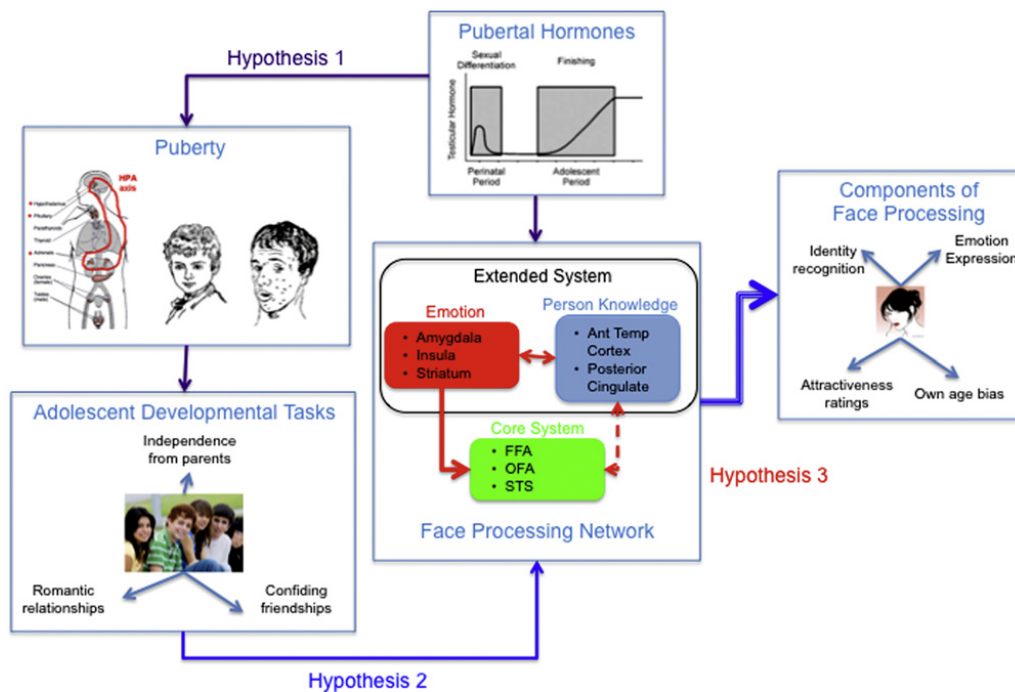
Fig. 1. A schematic representation of the dynamic changes that are predicted to initiate the emergence of new social and affective components of face processing in adolescence (i.e., fine-tuned attractiveness ratings and an own-age bias in identity recognition). In Hypothesis 1 (purple lines), we predict that the pubertal hormones that initiate the development of secondary sex characteristics and sexual dimorphisms in the structure of the face and brain are also are likely to influence motivation to master new developmental tasks, such as developing confiding friendships and romantic relationships with peers. This is manifest in the brain as a modulation in the functioning of limbic circuitry (particularly the amygdala), which induces dynamic changes in the functional organization of many neural circuits that interact with the amygdala, including the face processing system. These developmental tasks will in turn, drive the *emergence of new social/affective components of face processing* (Hypothesis 2 – blue lines). In other words, puberty induces adolescents to be socially and affectively motivated to encode new social information from faces that is related to these developmental tasks, such as the attractiveness, trustworthiness, competence, and social status of a face, particularly for peer-aged faces. Finally, in Hypothesis 3 (red lines), we argue that the dynamical interactions between neural face processing regions are fundamentally altered as a result of the surge of gonadal hormones and the resulting new task demands for face processing. Specifically, the *functional/effective connectivity,* or temporal synchrony, between regions of the face-processing network will change with the emergence of these new components of face processing in adolescence. This re-organization allows for new socially relevant information to be encoded from faces, leading to new components of face processing behavior. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

between face processing regions are fundamentally altered as a result of the surge of gonadal hormones and the resulting new task demands for face processing. Specifically, the *functional connectivity*, or temporal synchrony, between regions of the face-processing network will change with the emergence of these new components of face processing in adolescence.

We begin by demonstrating how face processing is an ideal domain from which to launch an interdisciplinary investigation of developmental changes in the interactions between hormonal, behavioral, and neural, foundations of social-information processing that may be particularly unique to adolescence. Next, we lay out each of our novel hypotheses and review the existing empirical evidence that supports these hypotheses. Finally, we suggest a number of experimental paradigms and potential findings that could launch this approach to better understand the cascade of hormonal, behavioral, and neural interactions that enable more sophisticated social information processing in adolescence, but that may also make adolescence a particularly vulnerable period of development

2. Face processing as a model system in which to study key aspects of adolescent development

2.1. Faces are the pre-eminent social stimulus

In a matter of milliseconds, multiple kinds of information, such as identity, gender, age, and emotional state are seamlessly extracted from face structure, even as faces change dynamically as a function of expression and speech production and vary across many transformations (i.e., changes in lighting, viewpoint, context). Additionally, people use the structure of the face to form impressions about mate potential, social status, intentions, and personality traits, like trustworthiness, approachability, warmth, power, extraversion, aggressiveness, and competence (for review, see Todorov et al., 2008). The social components of face processing have direct relevance in motivating adults' social behavior in terms of selecting mates (Cunningham et al., 1990; Rhodes et al., 2005), motivating sexual behavior and same-sex alliances (Berscheid and Reis, 1998; Berscheid and Walster, 1974; Rhodes et al., 2005), and eliciting personality attributions (Todorov et al., 2008).

2.2. Faces are compelling stimuli to assay the neural basis of social-information processing

Faces have been used to evaluate the neurobiology of emotion (for review see Phillips et al., 2003a,b), emotion expression processing (e.g., Blair et al., 1999; Phillips et al., 1998, 2001), social cognitive reasoning (Pinkham et al., 2008), and the social perception of race (Kubota and Ito, 2007). Face processing is disrupted in many social–emotional disorders (e.g., social anxiety disorder, schizophrenia, bipolar disorder, and autism spectrum disorders) and is a useful index of atypical neural organization of social-information processing (Evans et al., 2008; Kleinhans et al., 2008; Kucharska-Pietura et al., 2005; Marsh and Blair, 2008; Phillips et al., 2003a,b).

The neural basis of face processing requires the integration of a widely distributed network, including a set of "core" and "extended" regions (see Fig. 2; Gobbini and Haxby, 2007; Haxby et al., 2000, 2002) that comprise a functionally connected network (Fairhall and Ishai, 2007; Ishai, 2008; Vuilleumier and Pourtois, 2007). The core regions compute the visuoperceptual and more cognitive aspects face processing and are primarily located in the ventral temporal lobe. They include a lateral region in the inferior occipital cortex ["occipital face area" (OFA); Gauthier et al., 2000], a lateral portion of the posterior fusiform gyrus ["fusiform face area" (FFA); Kanwisher et al., 1997], and the posterior superior temporal sulcus (STS; Hoffman and Haxby, 2000). Although these core regions are strongly implicated in supporting the visuoperceptual and cognitive analysis of faces, they also receive strong inputs from the extended regions, which are implicated in the more social and emotion aspects of face processing (Said et al., 2010, 2011). The extended face processing regions include the amygdala, insula, and medial prefrontal cortex, regions in the anterior paracingulate cortex, and the anterior temporal pole (Gobbini and Haxby, 2007). These extended regions process more changeable aspects of faces, such as facial expressions and associating "person knowledge" with faces, including personal traits, attitudes, mental states, and intentions.

It is important to note that the specific functions ascribed to each region in the face-processing network are general characterizations, which are still contentiously debated (see Kanwisher, 2010; Nestor et al., 2011). An emerging perspective in the literature, and one that we hold, is that modulations in the *interactions among the nodes* in the network produce the seemingly independent components of face processing that have been previously ascribed to individual regions (see Nestor et al., 2011).

Critically, the network of cortical and subcortical regions that support face processing overlap quite extensively with those supporting social information processing more generally (Brothers, 1990; Adolphs, 2001; Nelson et al., 2005; Frith, 2007; Blakemore, 2008). This is especially evident when comparing the Gobbini and Haxby (2007) model of the core and extended face processing regions with the social information processing network (SIPN), a model of the "social brain." Fig. 2 shows both the SIPN and distributed face processing networks and highlights the overlapping regions. The SIPN describes three basic cortical and limbic networks that are implicated in the processing of social stimuli (Nelson et al., 2005). The detection node serves to identify social properties of stimuli and includes posterior regions in the ventral temporal cortex (i.e., fusiform gyrus, inferior occipital cortex, superior temporal sulcus, and temporal poles). Note that the regions in this node, with the exception of the temporal poles, overlap with the "core" regions of Gobbini and Haxby's (2007) model of face processing (see Fig. 2). The affective node, which includes regions that code for approach and avoidance valence (i.e., amygdala, ventral striatum, hypothalamus), functions to imbue social stimuli with affective content and overlaps with the "emotion" face processing regions in the Gobbini and Haxby (2007) model. Importantly, the regions in the affective node are densely innervated by gonadal steroid receptors. Finally, the cognitive-regulatory node, which primarily includes prefrontal regions, regulates and directs the integrated social signal for the purposes of influencing current and future behavior. The overlap between this cognitive-regulatory node and the "person knowledge" regions in the Gobbini and Haxby (2007) model is limited to the overlap between the dorsomedial prefrontal cortex and the anterior paracingulate cortex; regions that are implicated in perceiving the mental state of others (Gallagher and Frith, 2003). This comparison suggests that studying changes in face processing behavior and neural circuitry may serve strategically as a means for understanding changes in the neural networks that processing social information more broadly.

In sum, faces are the pre-eminent social signal from which human adults can form complex social attributions based on a 'quick and dirty' structural analysis of the face (i.e., under 50 ms). Face processing is subserved by a vast network of cortical and subcortical regions that overlap quite extensively with regions implicated in social information processing more generally. Together, these aspects of face processing indicate that it is an ideal model within which to investigate adolescent-specific neuro-maturational development. Furthermore, we expect that this model will provide a unique opportunity to advance understanding of the functional consequences of pubertal hormones on behavior and brain function and structure during adolescence.

In the following sections, we present several novel predictions using this model and review the existing empirical evidence that reflects on the viability of each hypothesis.

3. Hypothesis 1: pubertal hormones launch changes in face processing

We argue that the surge of steroidal hormones during the onset of puberty is likely to instigate and causally influence the behavioral and neural basis of face processing, and social information processing more generally, in adolescence (see Fig. 1). To support this argument, we review evidence for the steroid-dependent sculpting of nervous system *structure* in early development, and subsequent remodeling and refinement of neural circuits by gonadal steroid hormones secreted in adolescence. Importantly, we also show that gonadal hormones specifically
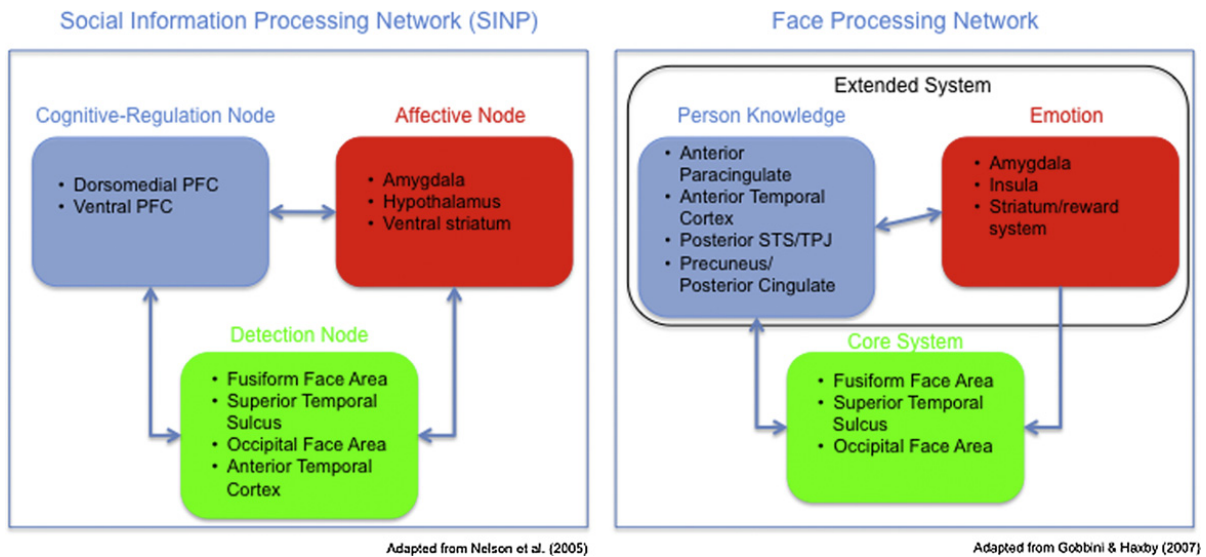
Fig. 2. Schematic drawings of the social information processing network described by Nelson et al. (2005) and the distributed face-processing network summarized by Gobbini and Haxby (2007). Note the similarity in functional organization of the two models, particularly between the detection node of the SIPN and the core face processing system as well as the affective node of the SIPN and the emotion component of the extended face processing network.

influence face processing behavior and its supporting neural circuitry.

3.1. Organizational and activational influences of pubertal hormones

Adolescence begins with the biological changes related to puberty, when the hypo-thalamic–pituitary–gonadal axis becomes activated (for detailed overview of pubertal development, see Buck Louis et al., 2008). The hypothalamus begins pulsing gonadotrophin-releasing hormone, which stimulates the pituitary to release luteinizing hormone (LH) and follicle stimulating hormone (FSH) into the blood. These hormones activate the gonads, which leads to a sharp increase in estrogen in females and testosterone in males. The rising level of estrogen causes breast development and the onset of menstruation in the female and the rising levels of testosterone lead to phallic growth, increased muscle mass, and voice changes in the male. This process exhibits sexually dimorphic developmental trajectories in that it usually begins between the ages of 8 and 14 (mean age of 11) in human females and between ages 9 and 15 in human males (mean age 12). In addition to the HPGA activation, hormones released by the adrenal gland, including DHEA and DHEAS, surge during adolescence. These hormones begin to rise by 6–9 years of age, but continue to increase throughout adolescence and typically peak in the early 20 s. These adrenal hormones are often considered "weak" versions of the sex hormones, but they bind to different receptors in the body, and they contribute to adolescent changes in skin (e.g., acne) and the development of pubic and axillary hair.

Despite the potentially unique and powerful influence of puberty on development, very little is known about the relation between gonadal hormones and neural or behavioral development in humans. There is, however, a large animal literature (primarily in rodents), which suggests

that the elevated secretion of gonadal steroid hormones at puberty has a great impact on the remodeling of cortical and limbic neural circuits and behavior, particularly social behaviors related to mating and reproduction (Sisk and Foster, 2004; Sisk and Zehr, 2005; Schulz and Sisk, 2006). In the animal literature, *organizational* and *activational* effects of gonadal hormonal steroids on the nervous system and behavior are well documented (for review, see Romeo, 2003).

Organizational effects reflect the steroid-dependent sculpting of nervous system *structure* that occurs during sensitive periods of prenatal and early neonatal development in non-human primates and rodents (for review, see Wallen and Baum, 2002). These effects are permanent in that they persist beyond the period of developmental exposure to the hormone, are asymmetric relative to the sexes, and set the stage for subsequent responses to hormones in puberty and adulthood that activate behaviors (Sisk and Zehr, 2005; Schulz and Sisk, 2006; see Fig. 3). However, researchers have begun to identify a second phase of organizational molding of the brain that is triggered by gonadal steroid hormones secreted at puberty (Sisk et al., 2003;
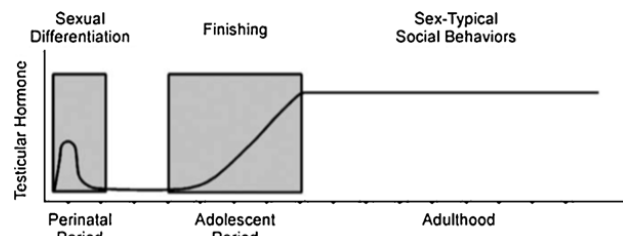

Fig. 3. Two-stage model of social behavior development. Perinatal hormone secretions sexually differentiate behavioral neural circuits and pubertal hormone secretions refine and "finish" these processes during adolescence to allow for the display of sex-typical social behavioral in adulthood.
Figure taken from Schulz and Sisk (2006).

Schulz et al., 2009). The gonadal steroid hormones secreted in adolescence remodel and refine neural circuits (via neurogenesis, apoptosis, growth of axonal projections and axon sprouting, myelination, synaptogenesis, and synapse elimination) to implement long-lasting structural changes in gross morphology and synaptic organization (for review see Sisk and Zehr, 2005). In particular, this second organizational phase of brain development builds on and refines circuits that were initially sexually differentiated during early neural development (Schulz et al., 2009). For example, gonadal steroids influence the addition of *new cells*, including neurons, during puberty that function to maintain and accentuate sexual dimorphisms in the adult brain, like in the medial amygdala, which is larger in male rats (Ahmed et al., 2008).

3.2. Organizational and activational effects of pubertal hormones on face processing in humans

There is compelling evidence that face processing behavior and its underlying neural circuitry are influenced by organizational and activational effects of hormones. First, face-processing behavior is sexually dimorphic. Many studies have reported superior face recognition abilities (Lewin and Herlitz, 2002; Lewin et al., 2001; Herlitz and Yonker, 2002; Rehnman and Herlitz, 2007) as well as superior expression identification (Hampson et al., 2006) in women compared to men. Consistent with these behavioral findings, several studies have reported sex differences in cerebral activation during face processing tasks, which converge on the finding that men tend to be more right lateralized than women (Bourne, 2005; Fiori et al., 2001; Godard and Fiori, 2010; Proverbio et al., 2006). Importantly, these sex differences in face processing do not emerge in adulthood; they are present in infants and children (Cross et al., 1971; Ellis et al., 1973; Feinman and Entwisle, 1976; McClure, 2000; Rehnman and Herlitz, 2006; Temple and Cornish, 1993). This is important when thinking about the potential role of pubertal hormones in re-organizing face processing behavior and neural circuitry in adolescence since this second organizational phase of brain development builds on and refines circuits that were *initially sexually differentiated* during early neural development (Schulz et al., 2009). The findings that sexual dimorphisms exist in face processing behavior across all ages tested, including infants, and in patterns of brain activation in adults provide a strong foundation for arguing that sex hormones play a critical role in the development of this essential component of social information processing.

Second, in populations with neuroendocrine disorders, face processing behavior and neural circuitry is disrupted. For example, women with Turner's syndrome have pervasive face processing deficits and atypical patterns of brain activation during face processing tasks (Lawrence et al., 2003a,b). Turner's syndrome (TS; Turner, 1938) is a genetic disorder in women in which all or part of one X-chromosome is deleted. As a result, TS women are hypogonadal and, therefore, lack the ability to produce estrogen. This syndrome provides the opportunity to study development in the absence of estrogen (or in terms of limited estrogen exposure since many TS women

are treated with estrogen replacement therapy). Skuse and colleagues have reported impaired recognition for both famous and unfamiliar faces and impaired classification of facial expressions, particularly for fear and anger, in TS compared to age-matched control women (Lawrence et al., 2003a,b). Also, TS women are impaired at using the eye region to derive information about emotional state and the mental state/disposition of a person (e.g., shy, anxious, hostile; Lawrence et al., 2003a,b). This pattern of behavioral findings appears to implicate atypical functioning of the amygdala, which is rich in hormone receptors. In fact, TS women exhibit enhanced activation in the right amygdala to fearful faces and less fear-modulated functional connectivity between the amygdala and fusiform gyrus compared to control women (Skuse et al., 2005). In considering the pattern of findings across these studies, the authors suggest that faces carry atypical emotional salience for TS women, which may be due to abnormal amygdala function and may affect the way face representations are learned. This set of findings provides evidence for an influential role of hormones, particularly estrogen, on the early organization of brain systems supporting face processing and social-information processing more generally, and particularly the amygdala and fusiform gyrus.

Third, in adults, natural modulations in hormones influence face-processing behavior and its underlying neural circuitry. During the follicular phase of the menstrual cycle when estrogen levels peak and women are most fertile, women's preferences for symmetry (Little et al., 2007) and sexual dimorphism in male faces (i.e., masculine facial traits) (Johnston et al., 2001; Penton-Voak et al., 1999) is highest. These hormone-behavior relations in women are also reflected in patterns of brain activation (Rupp et al., 2009a,b) and can be altered via dosing of exogenous testosterone (Van Wingen et al., 2010). There are also naturally occurring variations in intrinsic levels of testosterone in men that influence face preferences. For example, Welling and colleagues found a positive association between levels of salivary testosterone and preferences for femininity in women's faces (Welling et al., 2008). Endogenous levels of testosterone in men are also associated with the responsively of the amygdala during facial expression tasks in men (Stanton et al., 2009).

Note that in all the previously described studies, "preferences" in both men and women were derived from the physical structure of a face presented in a static image. The structural analysis of an individual face *necessarily* invokes the core regions of the broader face processing system. Also, the transient changes in estrogen and progesterone in women and testosterone in men that have been linked to changes in face processing behavior and patterns of brain activation are *minute* compared to the surge of estrogen and testosterone that occurs during pubescence. Therefore, these findings of subtle hormonal modulations on the structural analysis of faces in men and women lead to a clear hypothesis that the influx of gonadal hormones during puberty is likely to have a prominent and potentially long-term impact on face processing behavior and neural activation in adolescence. We argue that this effect is manifest in two ways. First, by motivating adolescents to master new developmental tasks related to

developing confiding friendships and romantic relationships with peers and, second by instigating a large-scale re-modeling of the interactions among the neural circuitry supporting social information processing (see Fig. 1).

4. Hypothesis 2: developmental tasks in adolescence instigate new components of face processing

In the social and emotional domains, adolescents evince a dramatic *reorientation* away from parents and toward peers that enhances the primacy of peer interactions. With this dramatic social reorientation emerges an unprecedented drive for acceptance by social peers and hypersensitivity to peer evaluation. Adolescent peer relationships are more elaborate than friendships at any earlier developmental period (for review see Brown, 2004). Peers become a critical source of social support (Brown et al., 1986; Brown and Klute, 2006) as well as the focus of new romantic and sexual interests (see Collins et al., 2009). Adolescents' emotional responses to social stimuli are intensified and are modulated by social contexts involving peers. For example, in the presence of peers, adolescents are more prone to erratic and emotionally influenced behavior, even as they are achieving adult-like competence in many cognitive abilities (Dahl and Spear, 2004).

This social reorientation supports the emergence of social competence and high-quality friendships with peers, two *developmental tasks* that foreshadow the quality of adult relationships (Capaldi et al., 2001). Developmental tasks are salient tasks by which adaptation to life can be judged (Havighurst, 1972; Masten et al., 1995). They are specific to a developmental period and success in mastering these tasks in one ontogenetic period is probabilistically associated with mastery on subsequent developmental tasks in later developmental periods (Roisman et al., 2004). For example, social competence with peers in late adolescence/early adulthood predicts work and romantic competence in young adulthood (Roisman et al., 2004).

In adolescence, there are important social developmental tasks, including acquiring freedom from parental figures, forming confiding friendships with peers, and beginning to form age-appropriate romantic relationships. These tasks lead adolescents to evince a dramatic *reorientation* away from parents and toward peers and enhance the primacy of peer interactions.

We suggest that with the onset of puberty (and, thus, the surge of gonadal hormones), these new developmental tasks and social reorientation toward peers influence the kinds of information that adolescents acquire from faces. In other words, puberty induces adolescents to be socially and affectively motivated to encode new social information from faces that is related to these developmental tasks, such as the attractiveness, trustworthiness, competence, and social status of a face, particularly for peer-aged faces. Importantly, these emerging components of face processing may actually index new competencies in social information processing more generally (see Fig. 1).

This hypothesis draws from Dynamic Systems (DS) theories of developmental change (e.g., Smith and Thelen, 2003; Thelen and Smith, 1994; Smith, 2005; Van Geert, 1994). In our view, face-processing abilities go through periods of relative stability and instability as development proceeds and environmental demands induce new developmental tasks. Thus, face-processing abilities *self-organize* as developmental tasks change. In DS theories, *self-organization* is a process through which higher-order components of development emerge through recursive interactions from simpler components to spontaneously induce new developmental outcomes. Lewis (2000) articulated several characteristics of self-organizing systems in DS theories. First, they permit true novelty in developmental outcomes. Second, new outcomes *emerge* during periods of phase transitions; points of instability in the system when old patterns break down and new ones appear. Third, these transitions are global and abrupt, indicating that new outcomes require the cooperation of all existing system components and that they appear discontinuously. As a result, small effects can strongly influence development during these transition phases. Finally, self-organizing systems are exquisitely sensitive to aspects of their environments because of their propensity for feedback and coupling with other systems. It is with these principles in mind that we argue that adolescent-specific developmental tasks instigate a period of relative instability in the existing face processing system that develops in pre-pubertal children. Importantly, this instability leads to abrupt change and re-organization to accommodate the new task demands and, thus, new components of face processing. In this way, the dynamics of face processing abilities are embedded in the dynamics of broader developmental tasks/demands.

A strong empirical evaluation of our hypothesis will require large-scale cross-sectional and longitudinal studies of multiple aspects of face processing behavior from childhood through early adulthood. While this work is currently non-existent, there are some promising results indicating that social components of face processing related to the developmental tasks of adolescence are emerging and becoming much more fine-tuned during adolescence. We review this evidence below.

4.1. Developmental changes in attractiveness ratings of faces

We argue that the new motivation to develop romantic relationships in adolescence will dramatically influence adolescents' ability to encode and rate attractiveness (or mate potential) from the structure of a face and that this ability will track with the progression of puberty. While there is very little work evaluating any social components of face processing (e.g., attractiveness, trustworthiness, status, competence) in children and adolescents, there is some evidence to support our claim, which indicates that adult-like processing of attractiveness in faces becomes more fine-tuned, stronger, and more consistent during adolescence.

In adults, averageness, symmetry, and sexual dimorphism influence judgments of facial attractiveness (for review see Rhodes, 2006). For example, adults rate faces in which the features occupy average locations on the face

with respect to the norm or prototype as more attractive (Geldart et al., 1999). Twelve-year-olds, but not 9-year-olds, also show this sensitivity when making judgments about attractiveness (Cooper et al., 2006). This finding represents a fine-tuning in the perception of attractiveness from late childhood to early adolescence. Both 12- and 9-year-olds find faces with high features (small forehead, large chin) to be less attractive than those with average features; however, 9-year-olds rate faces with low features (high forehead, small chin) and average features to be equally attractive. Twelve-year-olds, like adults, find faces with average features to be the most attractive. In another study, the direction and strength of children's, adolescents', and adults' attractiveness ratings for faces were evaluated (Kissler and Bäuml, 2000). Interestingly, when rating adult women's faces, all three age groups were indistinguishable in the direction and strength of their attractiveness ratings. However, when rating peer faces, children's and adolescents' ratings were less discriminating and weaker than were those of the adults, indicating that there may be a transition in the qualitative nature of the attractiveness ratings, particularly for peer faces, in adolescence. Finally, the consistency in attractiveness ratings across individuals increases from ages 5 to 8 (Cavior and Lombardi, 1973) and from preadolescence to adolescence (Saxton et al., 2006). Together, these findings suggest that the ability to encode and process facial attractiveness becomes more specific and more consistent across individuals during the transition from late childhood to early adolescence when pubertal hormones are increasing dramatically.

This is not to say that infants and children show no ability to encode or rate attractiveness from the structure of a face. In fact, there is some evidence that infants discriminate between faces that adults report as attractive versus unattractive (Langlois et al., 1987; Samuels and Ewy, 1985). However, more recent studies have suggested that infants' discriminations reflect novelty detection rather than aesthetic preferences and that averageness and symmetry do not influence infants' face preferences in they same way they do adults' (Rhodes et al., 2002). Instead, we argue that there are measurable quantitative and qualitative changes in the ability to encode attractiveness from the structure of a face in adolescence and that these changes are likely to be closely related to the developmental progression of puberty, an indication of the levels of intrinsic gonadal hormones.

Only one study, to our knowledge, has linked this developmental transition in attractiveness ratings to pubertal development in adolescents. Saxton and colleagues tested the facial attractiveness ratings of over 300 adolescents aged 11 to 15 on facial stimuli of age-matched individuals (Saxton et al., 2009). Younger adolescents (approximately age 11) were less sensitive to averageness, femininity, and symmetry when making judgments of male faces than were older adolescents (approximately 13 years). They were also less sensitive to averageness, but not femininity or symmetry, when judging female faces. Among boys, increased pubertal development (when controlling for age) corresponded to a lower proportion of feminized male faces selected as more attractive. The authors did not observe any relation

between pubertal status and sensitivity to averageness, femininity, or symmetry when judging either male or female faces in the adolescent girls after controlling for age. In sum, these findings indicate that sensitivity to the dimensions that affect adults' judgments of facial attractiveness increases specifically during adolescence and with more advanced pubertal status, particularly in boys, when adolescents judge age-matched peer faces.

Although adolescents may be more motivated to encode the attractiveness of peer faces as a result of their emerging developmental tasks, this may be an especially difficult process given that their own faces undergo important and dramatic biological changes with puberty; they become more sexually dimorphic (Enlow, 1990; Enlow and Hans, 1996; Farkas, 1988). Males develop more prominent jaws, cheekbones, brow ridges, and facial hair. Females develop fuller lips. Adolescents' own faces are changing, as are the faces of their peers. This may require them to consistently update their cognitive representations of individual peer faces and of face averages. So, in addition to increasing in specificity for attractiveness, adolescents' representations of *face identity* may be changing dramatically as well. This leads to our second hypothesis about how social reorientation in adolescence affects new components of face processing.

4.2. Emergence of an own-age bias in face recognition

We argue that the ability to recognize individual peer faces improves dramatically in adolescence, due to the social reorientation toward peers, which leads to the emergence of an own-age bias in face processing (i.e., superior recognition abilities for own- and compared to other-age faces). Several studies have reported an own-age bias in face recognition in adults (Anastasi and Rhodes, 2006; Bäckman, 1991; Fulton and Bartlett, 1991; Perfect and Moon, 2003; Wright and Stroud, 2002). In other words, across several different kinds of face processing tasks with unfamiliar faces (e.g., identifying a perpetrator from a lineup following observation of a video crime scene, old/new recognition tasks), adults seem to exhibit better recognition for faces within their own age group compared to both younger and older faces.

Importantly, there is very little consistency in the pattern of results with children and adolescents. This may be due to limitations in the experimental protocols. To our knowledge, only two developmental studies evaluated recognition memory skills for same-age peer faces in children and adults. In support of our hypotheses, both of these studies failed to find a strong own-age bias in preadolescent children. For example, Chung (1997) tested 7–12-year-old children and adults in a recognition memory task with faces from both age groups and only found evidence for an own-age bias in the adults. There was no own-age bias in the children's recognition memory performance.

Similarly, Anastasi and Rhodes (2005) tested children (ages 5–8 years) and older adults (ages 55–89 years) in an old/new recognition memory task for faces from four different age groups (5–8 years, 18–25 years, 35–45 years, and 55–75 years). In the learning phase of the experiment, participants had to categorize the faces into one of

these four age groups. In the subsequent recognition task where participants had to individuate the faces, the children exhibited no clear own-age bias. Instead, they showed superior recognition performance for both peer and older adult faces compared to recognition of young adult faces. In contrast, the older adults exhibited a strong own-age bias in their accuracy to recognize the oldest faces compared to all other age groups. These findings indicate that the own-age bias in preadolescent children is much less robust than in adults, and there are no data tracking the developmental progression of such a bias across adolescence. We predict that an own-age bias in face recognition does not emerge until social re-orienting begins in early adolescence (which could be measured as a relative change in proportion of time spent with parents to that spent with peers) and may not stabilize until early adulthood when the physical changes in face physiognomy, initiated by pubertal hormones, have stabilized.

Although there is very little work that speaks to this prediction, future studies evaluating adolescent-specific changes in these social components of face processing (e.g., attractiveness, trustworthiness, status, competence) and in the own-age bias may provide a unique opportunity to understand how developmental tasks influence the emergence of qualitatively new kinds of social-information processing and, furthermore, how the adolescent brain re-organizes to accommodate these changes. Importantly, these changes in face processing and functional organization of the underlying neural circuitry should also be related to various measures of hormonal changes as well (e.g., hormonal assay, Tanner staging).

4.3. Functional consequences of accommodating new components of face processing

Another prediction from our new model of adolescent-specific changes in social-information processing (see Fig. 1) is that the increased computational demands of the new social/affective components of face processing that emerge as a result of adolescent-specific developmental tasks will require a re-organization within the existing face-processing system. Again, drawing on DS theories of developmental change, we suggest that this re-organization will be manifest behaviorally initially as a *disruption* in existing face processing abilities, like identity recognition and emotional expression recognition, to accommodate the new task demands of face processing in adolescence. Next, we review the evidence suggesting a long developmental trajectory for face processing abilities that does appear to be disrupted in early adolescence.

There is a wealth of data suggesting that face-processing abilities continue to develop through and beyond adolescence. Although infants have early proclivities for face processing (e.g., De Haan and Nelson, 1999; Farroni et al., 2005; Johnson, 2005) and even very young children exhibit some of the behavioral markers of adult-like face processing (e.g., Crookes and McKone, 2009), studies investigating face processing abilities of older children and adolescents suggest that both *emotional expression* recognition and *identity* recognition abilities develop long into adolescence.

Surprisingly, explicit recognition of emotional expressions emerges slowly during childhood and may even be delayed compared to recognition of the verbal labels for the expressions (Camaras and Allison, 1985). Explicit memory for emotional expressions improves from late childhood through adolescence (Pine et al., 2004), particularly for fear, anger, and disgust (Herba and Phillips, 2004; Herba et al., 2006; Thomas et al., 2007). Also, the ability to match a visual image of a facial expression with a verbal label for the expression develops into early adolescence, particularly for the expressions of fear, disgust, and anger (Durand et al., 2007). Furthermore, it is not until middle childhood that individuals become fairly accurate at identifying conflicting or mixed emotional expressions and understanding display rules (Brown and Dunn, 1996).

Similarly, the ability to recognize *face identity* follows a delayed developmental trajectory even beyond adolescence (Carey and Diamond, 1977; Carey et al., 1980; Diamond et al., 1983; Ellis et al., 1973; Flin, 1985; Mondloch et al., 2004; O'Hearn et al., 2010). Importantly, these results have been reported across a wide range of recognition tasks. For example, using an old/new recognition memory paradigm, Carey and Diamond (1977) provided some of the first evidence that children continue to show large improvements in their abilities to recognize unfamiliar faces until 12 years of age. Importantly, these results were contrasted with adult-like performance in unfamiliar house (Carey and Diamond, 1977) and shoe (Teunisse and de Gelder, 2003) recognition and in other visuospatial tasks (e.g., Embedded Figures Task; Diamond et al., 1983) in early childhood and adolescence.

In a series of tasks requiring same/different judgments, Maurer and colleagues showed that children's (i.e., 8-year-olds) abilities to discriminate the identity of two faces is not as sensitive as are adults', particularly when the faces differ in configural properties (Maurer et al., 2002; Mondloch et al., 2002). In a more recent paper using a sequential-matching version of the same task, these researchers found that even 10-year-old children are not as sensitive as are adults in their abilities to discriminate facial identity even when the faces only differ in the shape of the features, but not the spacing among the features (Mondloch et al., 2010). Golarai et al. (2010) tested adolescents (ages 12–16 years) and young adults in an old/new recognition memory paradigm for faces, scenes, and objects as well as in the Benton Facial Recognition task. Adolescents were consistently less accurate than were adults in the face, but not in the scenes or the object, recognition memory tasks.

Very recently, several groups have investigated developmental changes in face recognition abilities across a much more extensive age range from childhood through early and later adulthood. O'Hearn et al. (2010) studied face recognition abilities in both typically developing children (ages 9–12 years), adolescents (ages 13–17), and young adults (ages 18–29 years) as well as in those with autism using the Cambridge Face Memory Task (CFMT). They reported dramatic improvements in face recognition performance across the entire age range in the typically developing individuals. Similarly, Germine et al. (2011) tested identity recognition abilities using the CFMT in more than 60,000 participants ranging in age from 10 to 70 years.

Across a series of three experiments, they consistently found that the peak age of performance for face recognition was approximately 30 years of age, which was contrasted with a peak age of performance of 23 years for inverted face and word recognition.

Of greatest relevance for the current paper, there is evidence that the developmental trajectory of face expression and identity recognition abilities is actually *temporarily disrupted* during adolescence, especially during puberty (Carey et al., 1980; Diamond and Carey, 1986; Diamond et al., 1983; Flin, 1980). In a study of 210 children and adolescents (8–16 years), Diamond and colleagues identified a stasis in face identity recognition, with an actual decline in performance at age 12 (Diamond et al., 1983). In two follow-up studies, they evaluated the contribution of pubertal status to performance differences on the same face identity task in more than 200 girls ages 10–14 years. They measured pubertal status with height/weight ratios and with Tanner staging. The height/weight ratio indexes the drop in proportion of body weight that is lean (i.e., increase in percent body fat) that occurs in adolescence and can accurately predict the age at menarche. Tanner staging requires a physical examination and rates the degree of pubic hair and breast development in girls. Across both studies, the authors found that girls in the midst of pubertal change make more errors in the face identity task than do pre- or post-pubescent girls (Diamond et al., 1983). They argued that this temporary developmental disruption appears to be specific to faces since performance on another visuospatial task, the Embedded Figures Task, was not related to pubertal status.

More recently, a large-scale study of approximately 500 participants ages 6–16 years found a similar developmental trajectory and plateau in adolescence (Lawrence et al., 2008). Lawrence et al. (2008) reported a linear improvement in face recognition skills (as assessed using the Warrington Recognition Memory for Faces test) from ages 6 to 10 years, followed by a plateau in performance from ages 10 to 13 years, and later by additional improvement from ages 13 to 16 years. In this same study, performance on emotion classification tasks correlated with face recognition performance across the age range.

There is also evidence that some aspects of emotion expression processing abilities are disrupted during adolescence. McGivern et al. (2002) found a developmental disruption (slowing reaction time) in expression recognition during the approximate ages of the onset of puberty (11–12 years) in a task in which participants made a yes/no decision about the emotion expressed in a face, a word, or a face/word combination. Emotion expression recognition improved from 13 to 14 years of age and stabilized by the age of 15. These results are very consistent with the timing of the disruption in unfamiliar face recognition originally reported by Carey and colleagues (Carey and Diamond, 1977; Diamond et al., 1983) and Lawrence et al. (2008).

Carey and colleagues suggested that this adolescent-specific disruption in face processing skills may be directly related to pubertal changes via hormonal changes that influence the neural substrate for face processing. Recent developmental neuroimaging findings support the notion that the neural substrate for face processing emerges slowly over the course of childhood and adolescence, and does not reach mature levels until early adulthood. However, the contribution of hormonal changes to this late-developing neural circuitry has yet to be investigated, which we will discuss in the final section of the paper.

5. Hypothesis 3: re-organization of the neural circuitry supporting face processing during adolescence

In our model, we predict that the gonadal hormones released during adolescence have a fundamental impact on the re-organization of neural circuitry supporting face processing. Specifically, we predict that gonadal hormones will influence a *shift in the balance* among existing visuoperceptual, cognitive, social and affective neural regions supporting face processing. In other words, we hypothesize that the dynamical interactions between face processing regions are fundamentally altered as a result of the surge of gonadal hormones and the resulting new task demands for face processing. Specifically, the *functional/effective connectivity,* or temporal synchrony, between regions of the face-processing network will change with the emergence of these new components of face processing in adolescence (see Fig. 1).

In this section, we review the evidence indicating that regions within the face processing system are undergoing both structural and functional development through, and even beyond, adolescence. Of particular relevance to our hypotheses, there are only a small number of studies investigating functional connectivity within the face-processing system with a focus on adolescence. However, the scant evidence suggests that it is likely that the functional relation between the core and extended regions is changing, as are the structural connections among these regions in adolescence.

5.1. Structural changes to the face processing network in adolescence

Recall that gonadal steroid hormones secreted in adolescence remodel and refine neural circuits to implement long-lasting *structural* changes in gross morphology and synaptic organization (for review, see Sisk and Zehr, 2005). Therefore, evidence that regions in the face processing system (as well as the connections between these regions) are undergoing important structural change during adolescence supports our prediction that gonadal hormones secreted in adolescence could physically remodel and refine the neural circuits of social information processing in fundamental ways.

There is a wealth of evidence showing that regions in all of the face-processing/SIPN nodes exhibit impressive structural changes in adolescence and that the developmental trajectories of these regions are often sexually dimorphic. The presence of sexual dimorphisms suggests that the gonadal steroidal hormones released during neonatal development and then again during puberty directly affect brain development, a notion that has been well researched in the animal literature (for review see Sisk and Zehr, 2005).

Although some of these sexual dimorphisms are present in the neonatal brain (Gilmore et al., 2007), many of the sex differences in brain structure emerge in early adolescence (Giedd and Lenroot, 2006; Goldstein et al., 1999; Sowell et al., 1999) and become more divergent as males and females approach adulthood (see Lenroot and Giedd, 2010).

Interestingly, even the SIPN detection node exhibits a slow developmental trajectory in that it peaks in total grey matter volume in late adolescence (age 16; Giedd et al., 1999). Also, there is sexual dimorphism in the detection node in the size (grey matter volume) of the left fusiform gyrus and right temporal pole (Witte et al., 2010). Within the SIPN affective node, subcortical structures exhibit age-related sexually dimorphic developmental changes in grey matter (GM) volume. Regionally, the basal ganglia and limbic structures show the most consistent morphological sex differences in adolescence. In particular, the caudate nucleus and hippocampus are proportionally larger in adolescent females, whereas the amygdala is proportionally larger in males (for review, see Lenroot and Giedd, 2010). This is especially interesting given that the amygdala is dense with estrogen and androgen receptors whereas the hippocampus is dense with estrogen receptors. Finally, in the SIPN cognitive regulatory node, the GM volume in the entire frontal lobe appears to peak in early adolescence, with girls exhibiting a peak at age 11 and boys exhibiting a peak a bit later at age 12 (Giedd et al., 1999). More specifically, cortical thickness in the dorsomedial prefrontal cortex and the anterior paracingulate regions of the SIPN and face processing models that have been the focus of this paper peak between the ages of 11 and 12 years (Shaw et al., 2008). Interestingly, the magnitude of some of these regional differences in adults, particularly in anterior temporal (detection) regions, is correlated with levels of circulating sex hormones (Witte et al., 2010). Importantly, since the SIPN functions as a distributed network, developmental changes in the structure of one node are likely to influence the interactive dynamics among nodes, which can lead to a functional re-organization of the entire network.

Critically, there is emerging evidence in human adolescents suggesting a *direct impact* of steroid hormones on the organization of the developing brain, particularly in the regions described in the face processing and SIPN networks. For example, sexually dimorphic amygdala and hippocampal volumes (part of the affective node) in 8–15-year-old girls and boys are related to pubertal development as well as to circulating levels of sex hormones (Neufang et al., 2009). More specifically, in both sexes, GM volume in the amygdala decreases with more advanced stages of puberty and higher testosterone levels, whereas GM volume in the hippocampus increases with more advanced stages of puberty and testosterone levels. Also, in girls, GM volumes in the medial temporal lobe (part of the detection node) are positively related to estrogen levels. Similarly, in a slightly older sample of 10–15 year old girls, circulating estradiol levels were related to GM volume in the right middle frontal gyrus (cognitive detection node) as well as inferior temporal and middle occipital gyri (detection node) (Peper et al., 2009).

In addition to affecting the development of individual regions within the SIPN, sex hormones, and testosterone in particular, influence the integrity of the white matter (WM) tracts connecting these regions. In a longitudinal study, Chura and colleagues found a relation between prenatal testosterone exposure (measured in utero) and subsequent rightward asymmetry in a posterior subsection of the corpus callosum, which projects mainly to parietal and superior temporal areas (detection node), in young adolescent boys (mean age 9.5; Chura et al., 2010). In two studies with adolescent girls and boys (ages 12–18), age-related increases in WM volume throughout the brain were much stronger in boys than in girls, suggesting sexual dimorphism in WM growth during adolescence (Perrin et al., 2008, 2009). Finally, in the boys there was a positive association between this global WM volume and circulating testosterone levels (Perrin et al., 2008) and between pubertal stage and WM volume separately in the frontal, parietal, temporal, and occipital lobes (Perrin et al., 2009).

In sum, many of the regions (as well as the connections between these regions) implicated in social information processing as spelled out in the SIPN model and in face processing, more specifically, are undergoing important structural changes in adolescence. Critically, many of these developmental changes exhibit sexual dimorphism, which is an indication of the influence of both organizational and activational effects of gonadal hormones on these regions. Evidence of these activational effects is just beginning to be shown, particularly in the amygdala and medial temporal lobes (extended face processing regions and detection and affective nodes in the SIPN). Although very little is known in general about how to relate changes in brain structure to changes in brain function and/or behavior, these findings lend evidence to support our hypotheses that pubertal hormones influence (and may instigate) important changes in the neural circuitry supporting social information and face processing.

5.2. Functional changes to the face processing network in adolescence

In addition to adolescent-specific changes in the structural regions and connections between regions in the SIPN and face processing networks, developmental brain imaging studies also converge on the finding that adolescence is critical for the functional development of the core face processing regions and the functional interactions between them. For example, several fMRI studies indicate that children younger than 8 years of age, as a group, do not consistently activate the FFA (see Fig. 4) and that FFA activation continues to mature through adolescence (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007, 2010; Joseph et al., 2010; Passarotti et al., 2003, 2007; Peelen et al., 2009; Scherf et al., 2007). In one recent fMRI experiment conducted with children (ages 5–8), adolescents (ages 11–14), and adults (ages 20–23), participants viewed naturalistic, real-time movies of unfamiliar faces, buildings, navigation through open fields, and objects in a blocked fMRI paradigm (Scherf et al., 2007). Scherf and colleagues found adult-like face-related activation in the right, but not left, hemisphere core face-processing regions
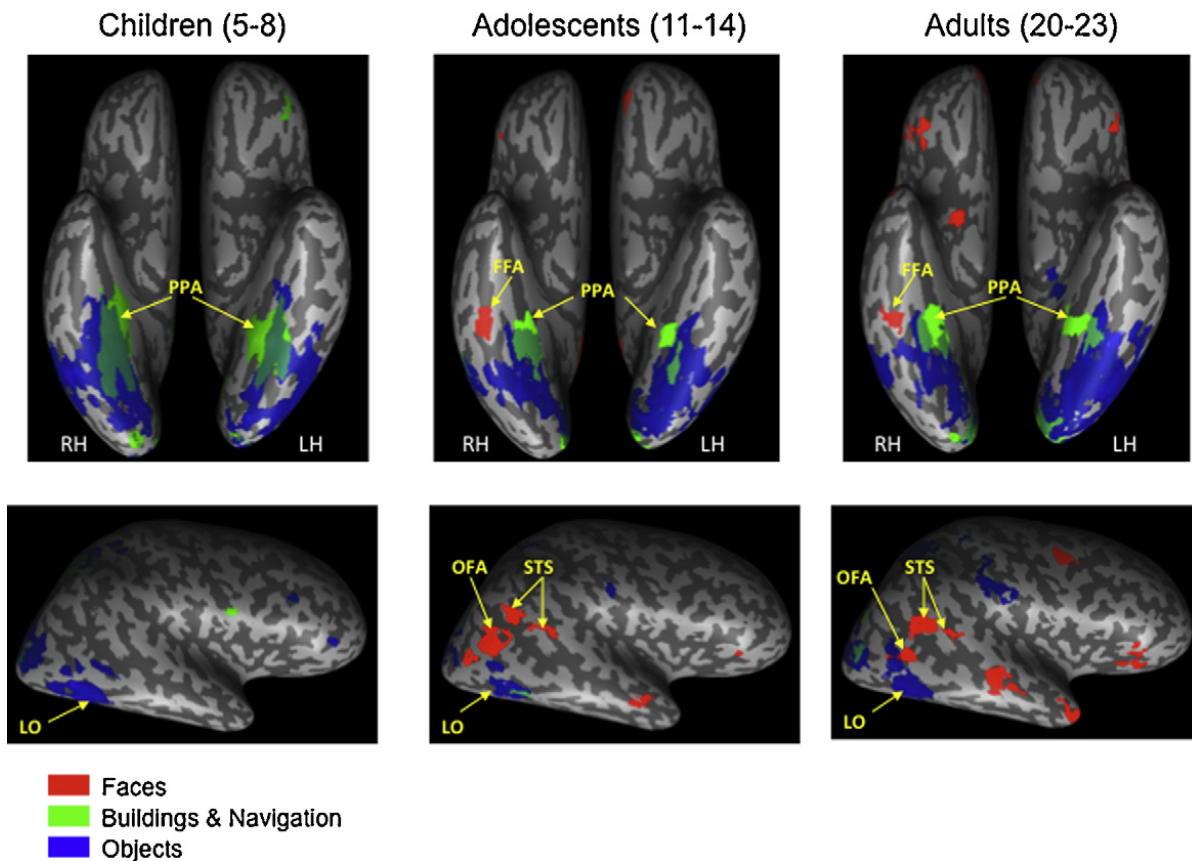
Fig. 4. Topography of face-, place-, and object-related regions in separate groups of children, adolescents, and adults projected onto a representative inflated brain. All three age groups exhibit indistinguishable topography for the place- and object-related regions. Only adults and adolescents exhibited consistent activation in the core face processing regions of the right hemisphere (FFA, OFA, STS). Only adults exhibited activation in these same core face processing regions in the left hemisphere. Neither children nor adolescents exhibited the same patterns of activation in the extended regions of the face processing network (anterior temporal lobes and prefrontal regions).
Taken from Scherf et al. (2007).

(OFA, FFA, STS) in adolescents (see Fig. 4). There was no group-level face-related activation in the right or left hemisphere for the children. Importantly, when the regions were identified within each individual participant, there was a linear relation between the size/volume of the face-processing regions and age. This result has been replicated and extended in other recent studies (Golarai et al., 2007, 2010; Scherf et al., 2011), indicating that the core face processing regions continue to exhibit ongoing development in adolescence. Interestingly, in contrast to the volume, the magnitude of selectivity within these regions appears to be more adult-like earlier in development (Cantlon et al., 2011; Pelphrey et al., 2009), particularly when the regions are identified in each participant individually (Scherf et al., 2007, 2011).

In addition to the growing size of the core face-processing regions, the nature of the computations within these regions appears to be changing in adolescence as well. In a follow-up study, Scherf et al. (2011) investigated whether the nature of the representations that adolescents compute for individual faces within the FFA are similarly fine-grained as are adults'. They used an fMRI-adaptation paradigm to evaluate the nature of the face representations being computed in the fusiform gyrus in children,

adolescents, and adults. The fMRI-adaptation paradigm (Grill-Spector and Malach, 2001) exploits the fact that repeated presentations of the same stimulus leads to a reduction in the magnitude of the BOLD response compared with consecutive presentations of different stimuli. Scherf and colleagues presented participants with blocks of different and identical faces and houses, and measured the degree of face- or house-specific adaptation that occurred in the FFA (and in other regions of ventral cortex) in each group. Only adults exhibited the strong attenuation in the BOLD signal during blocks of identical compared to different faces in the right and left FFA, reflecting a strong role for each region in representing individual faces. Adolescents only exhibited this pattern in the left FFA and children showed no adaptation whatsoever (see Fig. 5). These results suggest that the nature of the representations being computed in these regions is still developing long into adolescence.

Beyond the core regions, adolescence is a critical time for the functional development of the extended face-processing regions, and, particularly, the amygdala. Researchers investigating developmental changes in the neural basis of emotion expression processing overwhelmingly use fearful faces as stimuli in passive viewing tasks,
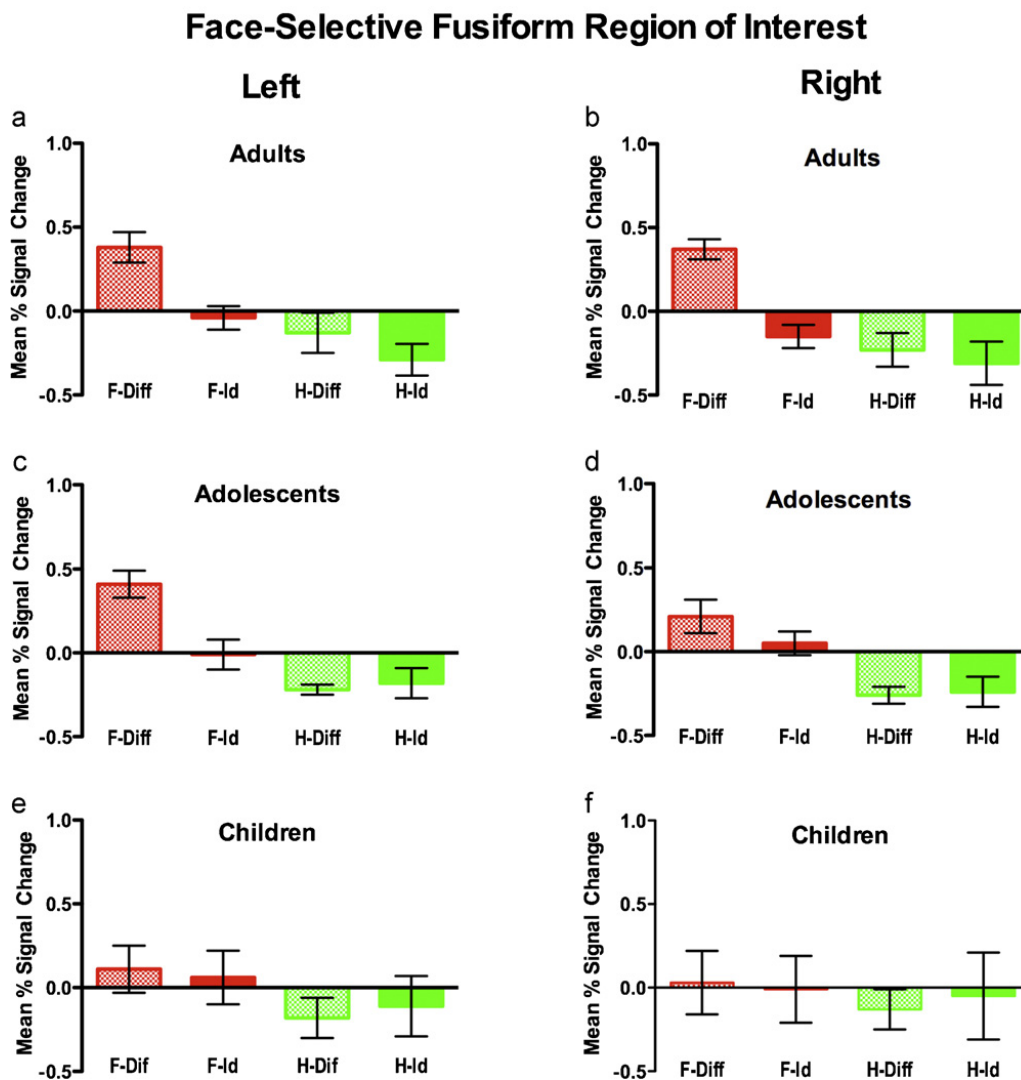
Face-Selective Fusiform Region of Interest

Fig. 5. Results from an fMRI-adaptation study in which children, adolescents, and adults observed images of different and identical faces and houses. Only adults exhibited bilateral adaptation for faces and not houses in the individually defined fusiform face selective regions. Adolescents only exhibited this adult-like pattern in the left fusiform and children failed to exhibit significant face-selective adaptation in either the right or the left fusiform gryus. These findings indicate that even though this core face processing region is exhibiting some degree of functional maturity in adolescence, the nature of the representations being computed in these regions is still developing into adulthood.
Taken from Scherf et al. (2011).

which are particularly effective at activating the amygdala in adults (Morris et al., 1998; Whalen et al., 1998). In these studies, researchers have described a u-shaped pattern of functional development in the amygdala with increasing activation through adolescence (Baird et al., 1999; Hare et al., 2008) and an age-related decline in activation from adolescence to adulthood (Guyer et al., 2008; Monk et al., 2003). There is also evidence of a qualitative shift in amygdala function from late childhood to adulthood in amygdala function such that children show greater activation to neutral faces and adults show enhanced activation to fearful faces (Thomas et al., 2001).

There are also a small number of studies indicating that there are impressive, quantitative as well as qualitative changes within the extended face-processing regions in adolescence[3]. For example, Somerville et al. (2010) tested children, adolescents, and adults in a go/no-go task with happy and calm faces. They found a linear increase in impulse control (i.e., ability to withhold responses on no-go trails) to the calm faces across the three age groups, which correlated with prefrontal activation. However, they reported a nonlinear *reduction* in impulse control in the

---

[3] There is extensive work evaluating developmental changes in the functional properties of regions within the emotion/affective and person knowledge/cognitive-regulatory nodes of the SIPN model. However, the overwhelming majority of this work does *not* employ faces as stimuli. As a result, reviewing this evidence is beyond the scope of this paper. Importantly, this work is largely consistent with the findings we report from studies using faces as stimuli (see Burnett et al., 2011).

adolescents in response to the happy faces, which was coupled with a relative increase in activation of the ventral striatum.

5.3. Changes in functional connectivity between regions in face processing network in adolescence

There are a handful of cutting-edge fMRI studies that are beginning to evaluate developmental differences in the functional connectivity among regions implicated in face processing. Only one study to date has evaluated the functional connectivity among the set of core face processing regions (i.e., OFA, FFA, STS). Cohen Kadosh and colleagues (2011) used dynamic causal modeling to evaluate the directional flow of functional connectivity among the three core face processing regions as children (7–8 years of age), young adolescents (10–11 years of age), and young adults (25 years of age) completed target detection tasks. The authors reported that the basic patterns of connectivity among these three regions was similar across all three age groups (i.e., two separate pathways from OFA to FFA and OFA to STS); however, the connectivity between OFA and FFA was weaker in the two younger groups and was virtually non-existent between the OFA and STS in the youngest group. Most importantly, there was no modulation of the connectivity among these regions by the task demands in either of the developmental groups. Adults were the only group to show enhanced connectivity between the OFA and FG during a face identity target detection task, and enhanced connectivity between the OFA and STS during the emotional expression target detection task. The authors interpreted their findings to suggest that the functional connections within the core face-processing network are limited by the continued development of the specialization within each of these regions, which is consistent with the findings of Scherf et al. (2011). These findings indicate that the functional coordination among the core face processing regions is still emerging in early adolescence.

The majority of the functional connectivity studies have evaluated connectivity within the extended face processing regions/affective node of social information processing. In a study evaluating individual differences in amygdala function in adolescents with bi-polar disorder, Rich et al. (2008) investigated the functional connectivity between the amygdala and the fusiform gyrus as participants viewed fearful faces. They reported reduced functional connectivity between the left amygdala and right fusiform in adolescents with biopolar disorder compared to age-matched controls. Since this study compared differences *within* age-matched groups, it cannot speak to *age-related changes* in such functional connectivity per se. However, Guyer and colleagues compared the extent of functional connectivity between the amygdala and hippocampus in typically developing adolescents and adults during viewing of fearful faces (Guyer et al., 2008). They reported decreased connectivity between these regions in the adolescents compared to the adults. Although the hippocampus is not traditionally considered a critical component of the face-processing network, the authors argued that stronger amygdala–hippocampal connectivity in adults might reflect maturation in learning or

habituation to facial expressions. Finally, Hare et al. (2008) reported reduced functional connectivity between the amygdala and the ventral prefrontal cortex in adolescents, particularly those with higher anxiety, than children and adults during and emotional expression go/no-go task (Liang et al., 2010). These findings indicate that functional connectivity supporting face processing, especially with the amygdala, may be weak, changing, and even vulnerable in adolescence. This is especially interesting in light of the findings in adults that the amygdala is largely implicated in supporting the very social components of face processing (Winston et al., 2007; Baron et al., 2010; Liang et al., 2010) that we suggest are emerging in adolescence as a result of new developmental tasks.

To summarize, the existing evidence suggests that neither the core nor the extended (to the extent that they have been evaluated) face-processing regions in the ventral temporal lobe are entirely functionally mature by adolescence. The extended regions, particularly the amygdala, exhibit prolonged development into early adulthood. Although there is very little connectivity evidence to draw upon, it seems likely that the functional relation between the core and extended regions is changing dramatically in adolescence, particularly as a function of the particular task demands (e.g., face versus expression identification). All of these findings lend support to our hypotheses that there is a functional re-organization among regions supporting face processing in adolescence. However, unlike in the work on structural development of these regions, there is no data to reflect on the relative influence of pubertal hormones on this process of functional re-organization and maturation of regions in the face processing (and SIPN) networks.

6. Putting the plan into action: studying unique interactions between pubertal, brain and behavioral development in adolescence

To review, we have argued for the following hypotheses and include a brief summary of the existing data that support the hypotheses:

(1) The surge of steroidal hormones during the onset of puberty is likely to influence motivation to master adolescent-specific developmental tasks, which will, in turn, instigate the *emergence of new social/affective components of face processing*, including, attributions and preferences for attractiveness in faces as well as biases in recognition memory for peer, or own-age, faces.
  - Sensitivity to the dimensions of facial attractiveness increases during adolescence and with more advanced pubertal status, particularly in boys.
  - The own-age bias in preadolescent children is much less robust than in adults, and, unfortunately, there are no data tracking the developmental progression of such a bias across adolescence or attempting to relate this bias to pubertal development.
(2) The increased computational demands of these additional components of face processing will require a re-organization within the existing face-processing system, which will be manifest as a disruption in

existing face processing abilities, like identity recognition and emotional expression recognition.

- Both *emotional expression* recognition and *identity* recognition abilities develop long into adolescence.
- The developmental trajectory of face expression and identity recognition abilities appears to be *temporarily disrupted* during adolescence, especially during puberty.

(3) Pubertal hormones have a fundamental impact on the re-organization of neural circuitry supporting face processing.

- Neither the core nor the extended face-processing regions in the ventral temporal lobe are entirely functionally mature by adolescence.
- Although there is very little connectivity evidence to draw upon, it seems likely that the functional relation between the core and extended regions is changing dramatically in adolescence, particularly as a function of the particular task demands (e.g., face versus expression identification).
- There are no studies investigating the relation between pubertal development and development of the functional connections between regions supporting face processing, and social information processing more generally.

Given that there is little to no existing direct evidence to reflect on the viability of our hypothesis about pubertal hormones and the shift in functional and effective connectivity between the extended and core regions of the face-processing network (detection and affective nodes in the SIPN), we would like to suggest a number of experimental paradigms and potential findings that could specifically evaluate our hypotheses.

We argue that the functional properties of the network will change by leveraging stronger inputs from the affective and cognitive regulatory (i.e., prefrontal) regions. For example, in adults, the amygdala is reportedly involved in sensing the value of social stimuli, and has been specifically implicated in evaluating the reward value of faces (as indexed by facial attractiveness; Winston et al., 2007). We predict that, during adolescence, stronger inputs from affective regions (e.g., amygdala) that support new social components of face processing (e.g., ratings of attractiveness, trustworthiness, status) may disrupt the existing coordination among visuoperceptual and cognitive components that support other more perceptual and cognitive aspects of face processing like identity recognition. This would be reflected in changes in the functional coupling of the patterns of activation between these regions during more social versus cognitive components of face processing.

Furthermore, we suggest that the amygdala is an ideal region upon which to focus our hypotheses about the emergence of new social components of face processing during adolescence and changes in the neural networks supporting these new abilities. As described previously, the amygdala is rich with estrogen and androgen receptors and exhibits sexual dimorphism in its structural development. Also, the functional profile of the amygdala and its functional connections to other social-information

processing regions is changing dramatically during adolescence (e.g., Killgore and Yurgelun-Todd, 2010; Vasa et al., 2011) and in a sexually dimorphic way (Zuo et al., 2010). For example, sex differences in amygdala responses to fearful and threatening faces begin to emerge in the transition from adolescence to adulthood (Killgore et al., 2001; McClure et al., 2004). Importantly, in adults, activation in the amygdala is positively associated with the very social dimensions of face processing that we predict emerge in adolescence, such as competence ratings, as well as with objective real-world measures of social competence (Rule et al., 2011).

These findings are especially interesting in light of the evidence that the amygdala is part of a sub-cortical system that receives rapid (<100 ms) low-spatial-frequency information about faces (and potentially other visual objects) that is sufficient to develop a course or "quick and dirty" representation of a face and that can modulate face processing in the fusiform gyrus through direct feedback connections (Vuilleumier and Pourtois, 2007). Evaluating whether and how adolescent-specific developmental changes in amygdala function influence other parts of the face-processing network (e.g., the fusiform gyrus, OFA, and STS) may provide a unique opportunity to evaluate whether and how functional re-organization among regions in the distributed face processing network is accomplished as new components of face processing come online in adolescence.

One specific prediction is that there may be a dramatic change in the nature of the face-related computations and feedback provided by the amygdala to the fusiform gyrus during adolescence. This potentially new or enhanced kind of input to the fusiform from the amygdala could modulate the nature of the computations in the fusiform as well, resulting in a snowball effect that alters the functioning of the entire face-processing network. Future studies investigating modulations in the functional connectivity between the amygdala and fusiform gyrus as children, adolescents, and adults view faces that vary with respect to emotional expression and/or any of the social dimensions we have discussed (e.g., attractiveness, trustworthiness) may help characterize adolescent-specific re-organizations in brain networks that support more sophisticated social-information processing. Additionally, tracking hormonal changes separately from age-related changes in these kinds of studies will facilitate a better understanding of the functional consequences of pubertal hormones on the functional re-organization of these neural networks.

This approach may also be particularly useful for understanding how adolescence may be a period of vulnerability in brain development, particularly with respect to key aspects of social cognitive development. In particular, we envision that a natural disruption in the dynamics of the face-processing network is required to allow for the re-organization that we are predicting, and this natural disruption may provide a unique opportunity for an atypical re-organization to emerge.

To explain this prediction, we draw upon the notion of self-organized learning as explained in many neural network models (see Johnson and Munakata, 2005; Munakata and McClelland, 2003). Self-organized learning is a

process of forming representations that capture important aspects of environmental structure and that occurs based on patterns of simultaneous activation among processing units. Self-organized learning has been modeled extensively with connectionist neural networks that learn a set of real-valued weights on connections among neuron-like processing units, which support the generation of appropriate, context-sensitive, conditional expectations (see McClelland et al., 2010; Munakata and McClelland, 2003). Learning and development in these models are driven by experience and occur through small, non-linear changes in the connection weights. Importantly, processing in connectionist models is highly interactive, which, under many conditions, leads them to settle to attractor states, or states in which the connection weights are very stable and resistant to change. These attractor states provide for fast, efficient, and accurate performance as long as the inputs/environmental structure stay the same. However, when the environmental structure changes, learning can only proceed once the attractor state is disrupted. As a result, there is a period of network instability until the connection weights are re-established to accommodate the new inputs.

Using this model, we suggest that the functional re-organization of brain circuitry that is instigated by the new demands on face processing in adolescence may require a period of instability in the functional relationships among component regions in the neural network supporting face processing behavior. In other words, the stability of existing connections/interactions among nodes in this neural network may need to be disrupted, perhaps even substantially, so as to allow for new interactions to be established that accommodate new task demands. During this period of instability, individual differences in the magnitude of inputs, particularly from affective and regulatory regions, may have a profound effect in the formation of new functional interactions within the network. Furthermore, a period of instability may provide a context for laying down atypical interactions between nodes, as appears to be the case in individuals with anxiety disorder who exhibit atypical interactions between the amygdala and prefrontal regulatory regions (e.g., Campbell-Sills et al., 2011). Identifying potential periods of instability in network interactions and understanding whether these periods provide a context for abnormal functional organization of these networks could have a profound impact on our understanding of the development of many social-emotional problems and domains of problem behaviors (e.g., substance abuse and risk taking) that emerge in adolescence.

Finally, this kind of work might lead to prevention and intervention strategies that facilitate more adaptive functional interactions between regions within the broader social information-processing network. For example, many of our predictions focus on the increased affective inputs to the face-processing system, particularly from the amygdala, during adolescence. Importantly, many of the social–emotional problems that tend to emerge in adolescence (i.e., depression, anxiety disorders, bipolar disorder) have measurable impact in the functional and structural profile of the amygdalae and its connections with other regions (e.g., Blair et al., 2011; Cullen et al., 2010; Monk et al., 2008a, 2008b). However, none of this work, to our knowledge, has systematically evaluated the potential role of pubertal hormones in either instigating these social–emotional problems or in modulating functional interactions between the amygdala and other regions of the SIPN or face-processing networks. Findings from the program of research that we are proposing may help understand whether medication interventions to alter the timing of puberty could be useful for individuals at risk for developing these social–emotional disorders during adolescence. Perhaps an even more fruitful translational approach of this work will be in the form of behavioral interventions that are designed to influence the strength of particular functional pathways between nodes of the face-processing network. For example, atypical amygdala functioning might be avoided or minimized by enhancing the functional connections between the amygdala and the cognitive-regulatory/prefrontal regions, particularly in adolescents at risk for developing social–emotional disorders. Thus, a deeper and more mechanistic understanding of adolescent-specific interactions between pubertal, brain, and behavioral development may provide insights into the timing and targets for learning experiences or behavioral therapies that could alter the trajectories of these interactions.

7. Important considerations for investigating adolescent-specific interactions between pubertal, brain, and behavioral development

Going forward with this approach will require a keen sensitivity to several issues, including the need to evaluate the effects of sex steroids and/or pubertal status *independently* from chronological age. This is an important concern for two reasons. First, the correlation between age and pubertal status differs between males and females; such that females tend to be at more advanced stages of pubertal status at a younger age than are males. In other words, age-matched boys and girls may be at very different stages of pubertal development. Second, there are likely to be age-related changes in brain (and behavioral) development that are independent from and occurring in parallel with puberty-related changes.

Only one study, to our knowledge, has attempted to dissociate age- and puberty-related changes in brain development. Bramen et al. (2011) matched adolescents in a very limited age range (boys range 11.7–14.0 years and girls range 10.8–13.5 years) on pubertal status and evaluated whether sex-differences in the volumetric measurements in the medial temporal lobe (amygdala, hippocampus), thalamus, and basal ganglia are driven by sex differences in puberty-related maturation. The authors reported that sex differences in the right hippocampus, bilateral amygdala, and cortical grey matter were greater in more sexually mature adolescents, with volumes rising in boys and declining in girls when evaluated as a function of sexual maturity. Interestingly, there were no such age-independent, puberty-related changes in the caudate nuclei. This important set of findings illustrates (1) evidence that there are puberty-specific, age-independent

effects on the structural development of regions strongly implicated in social-information and face processing in human adolescents, and (2) that puberty and age-related effects on structural brain development are dissociable and need to be considered independently.

A second relevant issue will be to compare the developmental trajectories of these dynamic interactions between hormonal, brain, and behavioral development under a variety of task and stimulus conditions. Our hypotheses are specific to emerging social/affective components of face processing in adolescence and the resulting modulation of functional connectivity among neural regions supporting face processing. Recall, we predict that there are disruptions to existing visuoperceptual/cognitive components of face processing as the nature of the underlying representations change to accommodate the emerging social/affective components of face processing. As a result, it will be essential to evaluate the profile of functional connections and the potential influence of pubertal hormones on these connections as adolescents engage in tasks that emphasize either the visuoperceptual, cognitive, affective or social components of face processing *separately*. It will be important to evaluate these connectivity profiles as independently as possible given that we predict vastly different developmental trajectories (e.g., disruption or plateau versus some function of increasing refinement) for the visuoperceptual/cognitive versus social/affective components of face processing in adolescence.

A related issue is the need to evaluate the profile of functional connections and the potential influence of pubertal hormones on these connections for other classes of visual stimuli, in addition to faces. We argue that faces are the preeminent social stimulus and that the developmental tasks of adolescence that induce new components of social information processing are fundamentally social and affective in nature. Therefore, it will be important to establish that these same adolescent-specific changes in face processing are not evident for the processing of non-social visual stimuli, including those that require similar visuoperceptual and/or cognitive processing strategies (e.g., configural processing).

A third important issue will be to consider whether and how these dynamic interactions between hormonal, brain, and behavioral development may unfold differently in adolescents developing a sexual minority identity. This is especially important in light of findings of differences in the magnitude of sexual dimorphisms in the structure, function, and functional connectivity of particular brain regions in heterosexual and homosexual men and women. For example, there are large-scale differences in the asymmetry of hemispheric volumes such that heterosexual men and homosexual women exhibit larger right hemisphere volumes, whereas the hemispheric volumes are symmetrical in homosexual men and heterosexual women (Savic and Lindström, 2008). Of particular relevance for the current paper, the functional connections from the amygdala, as measured during resting state, are differentially organized depending on sexual orientation (Savic and Lindström, 2008). Finally, one study addressed the impact of sexual preference on facial attractiveness ratings and profiles of neural activation. Kranz and Ishai

(2006) reported that regardless of gender or sexual orientation, homosexual and heterosexual men and women rated the attractiveness of male and female faces similarly. Furthermore, similar patterns of activation were found in all participants in response to both male and female faces in core face processing regions (bilateral FFA, OFA, and STS), limbic regions (bilateral amygdala, caudate nuclei), and prefrontal regions (bilateral inferior frontal gyrus, orbitofrontal cortex). However, they also reported an interaction between the gender of the stimulus faces and the sexual preference of the participants in both the thalamus and the orbitofrontal cortex. They concluded that these findings suggest that sexual preference can modulate face-related activation, particularly in the reward circuitry. Together, these findings indicate that sexual orientation and gender will be important factors to consider in a program of research investigating developmental interactions between hormones, neural circuitry, and behavior in adolescence. Unfortunately, none of the existing work has been conducted in adolescents, which makes it very difficult to speculate about how the developmental trajectories and/or interactions between hormones, neural circuitry, and behavior will differ or not for adolescents developing with a minority sexual identity.

8. Conclusions

To summarize, a primary goal of understanding adolescence as a unique developmental period of brain reorganization must include investigations of the influence of puberty-specific aspects of neurobehavioral development. We suggest that the surge of gonadal hormones in adolescence has a profound impact on the development of face processing behaviors (i.e., new social components of face processing) and underlying brain circuitry. Future studies investigating developmental changes in identity recognition, own-age bias, emotional expression categorization and recognition, and social components of face processing that include measures of pubertal status via Tanner staging and/or hormonal assay will have a unique opportunity to evaluate whether and how the onset of gonadal hormones fundamentally influences reorganization in the dynamics of widely distributed cortical networks and brain–behavior relations that are specific to adolescence. Such studies could also provide a template for understanding sexual dimorphisms in functional and structural brain development and its relation to behavioral development. Given the strong asymmetries in the distribution of sex in disorders of social information processing (e.g., autism and ADHD exhibit high male:female ratios but anxiety and depression exhibit low male:female ratios), it will be essential to have a model in which to evaluate sexual dimorphisms in typical brain and behavioral development so as to understand vulnerabilities in these potentially sexually dimorphic developmental trajectories. Finally, this approach may provide critical information about how hormone-dependent and age-related/hormone-independent processes contribute separately to developmental changes in social-information processing that make adolescence a unique and potentially vulnerable period of development for social and emotional

learning, in ways that can be targeted for early intervention/prevention.

References

Adolphs, R., 2001. The neurobiology of social cognition. Current Opinion in Neurobiology 11 (2), 231–239.

Ahmed, E., Zehr, J., Schulz, K., Lorenz, B., DonCarlos, L., Sisk, C., 2008. Pubertal hormones modulate the addition of new cells to sexually dimorphic brain regions. Nature Neuroscience 11, 995–997.

Anastasi, J., Rhodes, M.G., 2005. An own-age bias in face recognition for children and older adults. Psychonomic Bulletin & Review 12, 1043–1047.

Anastasi, J., Rhodes, M., 2006. Evidence for an own-age bias in face recognition. North American Journal of Psychology 8 (2), 237–252.

Aylward, E.H., Park, J.E., Field, K.M., Parsons, A.C., Richards, T.L., Cramer, S.C., Meltzoff, A.N., 2005. Brain activation during face perception: evidence of a developmental change. Journal of Cognitive Neuroscience 17, 308–319.

Baird, A.A., Gruber, S.A., Fein, D.A., Maas, L.C., Steingard, R.J., et al., 1999. Functional magnetic neuroimaging of facial affect recognition in children and adolescence. Journal of the American Academy of Child and Adolescent Psychiatry 38, 195–199.

Bäckman, L., 1991. Recognition memory across the adult life span: the role of prior knowledge. Memory & Cognition 19, 63–71.

Baron, S.G., Gobbini, M.I., Engell, A.D., Todorov, A., 2010. Amygdala and dorsomedial prefrontal cortex responses to appearance-based and behavior-based person impressions. Social Cognitive and Affective Neuroscience, doi:10.1093/scan/nsq086.

Berscheid, E., Reis, H.T., 1998. Attraction and close relationships. In: Gilbert, D.T., Fiske, S.T., Lindzey, G. (Eds.), The Handbook of Social Psychology. , 4th ed. Oxford University Press, New York/London, pp. 193–281.

Berscheid, E., Walster, E., 1974. Physical attractiveness. Advances in Experimental Social Psychology 7, 157–215.

Blair, K.S., Geraci, M., Korelitz, K., Otero, M., Towbin, K., Ernst, M., et al., 2011. The pathology of social phobia is independent of developmental changes in face processing. The American Journal of Psychiatry, doi:10.1176/appi.ajp.2011.10121740.

Blair, R.J., Morris, J.S., Frith, C.D., Perrett, D.I., Dolan, R.J., 1999. Dissociable neural responses to facial expressions of sadness and anger. Brain 122, 883–893.

Blakemore, S.J., 2008. The social brain in adolescence. Nature Neuroscience 9, 267–277.

Bourne, V.J., 2005. Lateralized processing of positive facial emotion: sex differences in strength of hemispheric dominance. Neuropsychologia 43 (6), 953–956.

Bramen, J., Hranilovich, J., Dahl, R., Forbes, E., Chen, J., Toga, A., et al., 2011. Puberty influences medial temporal lobe and cortical gray matter maturation differently in boys than girls matched for sexual maturity. Cerebral Cortex 21, 636–646.

Brothers, L., 1990. The neural basis of primate social communication. Motivation and Emotion 14 (2), 81–91.

Brown, B.B., 2004. Adolescents' relationships with peers. In: Lerner, R.M., Steinberg, L. (Eds.), Handbook of Adolescent Psychology, 2nd ed. Wiley, Hoboken, NJ, pp. 363–394.

Brown, B.B., Eicher, S.A., Petrie, S., 1986. The importance of peer group ("crowd") affiliation in adolescence. Journal of Adolescence 9, 73–96.

Brown, B.B., Klute, C., 2006. Friendships, cliques, and crowds. In: Adams, G.R., Bersonsky, M.D. (Eds.), Blackwell Handbook of Adolescence. Blackwell Publishing, Oxford, UK, pp. 330–348.

Brown, J.R., Dunn, J., 1996. Continuities in emotion understanding from three to six years. Child Development 67, 789–802.

Buck Louis, G.M., Gray Jr., L.E., Marcus, M., Ojeda, S.R., Pescovitz, O.H., Witchel, S.F., et al., 2008. Environmental factors and puberty timing: expert panel research needs. Pediatrics 121 (Suppl. 3), S192–S207.

Burnett, S., Sebastian, C., Cohen Kadosh, K., Blakemore, S.J., 2011. The social brain in adolescence: evidence from functional magnetic resonance imaging and behavioural studies. Neuroscience and Biobehavioral Reviews 35 (8), 1654–1664.

Camaras, L.A., Allison, K., 1985. Children's understanding of emotional facial expressions and verbal labels. Journal of Nonverbal Behavior 9, 84–94.

Campbell-Sills, L., Simmons, A.N., Lovero, K.L., Rochlin, A.A., Paulus, M.P., Stein, M.B., 2011. Functioning of neural systems supporting emotion regulation in anxiety-prone individuals. Neuroimage 54, 689–696.

Capaldi, D., Dishion, T., SToolmiller, M., Yoerger, K., 2001. Aggression toward female partners by at-risk young men: the contribution of male adolescent friendships. Developmental Psychology 37 (1), 61–73.

Cantlon, J.F., Pinel, P., Dehaene, S., Pelphrey, K.A., 2011. Cortical representations of symbols, objects, and faces are pruned back during early childhood. Cerebral Cortex 21 (1), 191–199.

Carey, S., Diamond, R., 1977. From piecemeal to configurational representation of faces. Science 195 (4275), 312–314.

Carey, S., Diamond, R., Woods, B., 1980. Development of face recognition: a maturational component? Developmental Psychology 16, 257–269.

Cavior, N., Lombardi, P.A., 1973. Developmental aspects of judgments of physical attractiveness in children. Developmental Psychology 8, 67–71.

Chung, M.S., 1997. Face recognition: effects of age of subjects and age of stimulus faces. Korean Journal of Developmental Psychology 10, 167–176.

Chura, L., Lombardo, M., Ashwin, E., Auyeung, B., Chakrabarti, B., Bullmore, E., Baron-Cohen, S., 2010. Organizational effects of fetal testosterone on human corpus callosum size and asymmetry. Psychoneuroendocrinology 35 (1), 122–132.

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 (New York, N.Y.: 1991), doi:10.1093/cercor/bhq215.

Collins, W.A., Welsh, D.P., Furman, W., 2009. Adolescent romantic relationships. Annual Review of Psychology 60, 631–652.

Cooper, P.A., Geldart, S.S., Mondloch, C.J., Maurer, D., 2006. Developmental changes in perceptions of attractiveness: a role of experience? Developmental Science 9, 530–543.

Crookes, K., McKone, E., 2009. Early maturity of face recognition: No childhood development of holistic processing, novel face encoding, or face-space. Cognition 111 (2), 219–247, doi:10.1016/j.cognition.2009.02.004.

Cross, J.F., Cross, J., Daly, J., 1971. Sex, race, age, and beauty as factors in recognition of faces. Perception and Psychophysics 10, 393–396.

Cullen, K.R., Klimes-Dougan, B., Muetzel, R., Mueller, B.A., Camchong, J., Houri, et al., 2010. Altered white matter microstructure in adolescents with major depression: a preliminary study. Journal of the American Academy of Child and Adolescent Psychiatry 49 (2), pp. 173–183.e1.

Cunningham, M.R., Barbee, A.P., Pike, C.L., 1990. What do women want? Facial metric assessment of multiple motives in the perception of male facial physical attractiveness. Journal of Personality and Social Psychology 59, 61–72.

Dahl, R.E., 2004. Adolescent brain development: a period of vulnerabilities and opportunities. Keynote address. Annals of the New York Academy of Sciences 1021, 1–22.

Dahl, R.E., Gunner, M.R., 2009. Heightened stress responsivity and emotional reactivity during pubertal maturation: implications for psychopathology. Development and Psychopathology 21, 1–6.

Dahl, R., Spear, L.P., 2004. Adolescent brain development. Annals of the New York Academy of Sciences 1021, 1–22.

De Haan, M., Nelson, C.A., 1999. Discrimination and categorization of facial expressions of emotion during infancy. In: Slater, A. (Ed.), Perceptual Development: Visual, Auditory, and Speech Perception in Infancy. Psychology Press, pp. 287–310.

Diamond, R., Carey, S., Black, K.J., 1983. Genetic influences on the development of spatial skills during adolescence. Cognition 13, 167–185.

Diamond, R., Carey, S., 1986. Why faces are and are not special: an effect of expertise. Journal of Experimental Psychology: General 115, 107–117.

Durand, K., Gallay, M., Seigneuric, A., Robichon, F., Baudouin, J.Y., 2007. The development of facial emotion recognition: the role of configural information. Journal of Experimental Child Psychology 97 (1), 14–27.

Ellis, H.D., Shepard, J., Bruce, A., 1973. The effects of age and sex on adolescents' recognition of faces. Journal of Genetic Psychology 123, 173–174.

Enlow, D.H., 1990. Facial Growth. W.B. Saunders Company, Philadelphia, PA.

Enlow, D.H., Hans, M.G., 1996. Essentials of Facial Growth. W.B. Saunders Company, Philadelphia, PA.

Evans, K.C., Wright, C.I., Wedig, M.M., Gold, A.L., Pollack, M.H., Rauch, S.L., 2008. A functional MRI study of amygdala responses to angry schematic faces in social anxiety disorder. Depression and Anxiety 25, 496–505.

Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. Cerebral Cortex 17 (10), 2400–2406.

Farkas, L.G., 1988. Age- and sex-related changes in facial proportions. In: Farkas, L.G., Munro, I.R. (Eds.), Anthropometric Proportions in Medicine. Thomas, Springfield, IL, pp. 29–56.

Farroni, T., Johnson, M.H., Menon, E., Zulian, L., Faraguna, D., Csibra, G., 2005. Newborns' preference for face-relevant stimuli: effects of contrast polarity. Proceedings of the National Academy of Sciences of the United States of America 102 (47), 17245–17250.

Feinman, S., Entwisle, D., 1976. Children's ability to recognize other children's faces. Child Development 47 (2), 506–510.

Fiori, N., Chaby, L., George, N., 2001. Gender differences in the neural bases of face processing and recognition: two ERP studies. International Journal of Psychophysiology 41, 231.

Flin, R.H., 1980. Age effects in children's memory for unfamiliar faces. Developmental Psychology 16 (4), 373–374.

Flin, R.H., 1985. Development of face recognition: an encoding switch? British Journal of Psychology 76 (Pt 1), 123–134.

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.

Frith, C.D., 2007. The social brain? Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 362 (1480), 671.

Fulton, A., Bartlett, J.C., 1991. Young and old faces in young and old heads: the factor of age in face recognition. Psychology & Aging 6, 623–630.

Gallagher, H.L., Frith, C.D., 2003. Functional imaging of theory of mind. Trends in Cognitive Sciences 7 (2), 77–83.

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, 625–635.

Gathers, A.D., Bhatt, R., Corbly, C.R., Farley, A.B., Joseph, J.E., 2004. Developmental shifts in cortical loci for face and object recognition. Neuroreport 15 (10), 1549–1553.

Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform "face area" is part of a network that processes faces at the individual level. Journal of Cognitive Neuroscience 12, 495–504.

Geldart, S., Maurer, D., Henderson, H., 1999. Effects of the height of internal features of faces on adults' aesthetic ratings and 5-month-olds' looking times. Perception 28, 839–850.

Germine, L.T., Duchaine, B., Nakayama, K., 2011. Where cognitive development and aging meet: face learning ability peaks after age 30. Cognition 118 (2), 201–210.

Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., et al., 1999. Brain development during childhood and adolescence: a longitudinal MRI study. Nature Neuroscience 2 (10), 861–863.

Giedd, J., Lenroot, R., 2006. Brain development in children and adolescents: insights from anatomical magnetic resonance imaging. Neuroscience and Biobehavioral Reviews 30 (6), 718–729.

Gilmore, J., Lin, W., Prastawa, M., Looney, C., Vetsa, Y., Knickmeyer, R., Evans, D., Smith, J.K., Hamer, R., Lieberman, J., 2007. Regional gray matter growth, sexual dimorphism, and cerebral asymmetry in the neonatal brain. The Journal of Neuroscience 27 (6), 1255–1260.

Gobbini, M.I., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. Neuropsychologia 45, 32–41.

Godard, O., Fiori, N., 2010. Sex differences in face processing: are women less lateralized and faster than men? Brain and Cognition 73 (3), 167–175.

Golarai, G., Liberman, A., Yoon, J. M.D., Grill-Spector, K., 2010. Differential development of the ventral visual cortex extends through adolescence. Frontiers in Human Neuroscience, doi:10.3389/neuro.09.080.2009.

Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D., et al., 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. Nature Neuroscience 10, 512–522.

Goldstein, J., Goodman, J., Seidman, L., Kennedy, D., Makris, N., Lee, H., Tourville, J., Caviness, V., Faraone, S., Tsuang, M., 1999. Cortical abnormalities in schizophrenia identified by structural magnetic resonance imaging. Archive of General Psychiatry 56, 537–547.

Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychologica (Amsterdam) 107 (1–3), 293–321.

Guyer, A.E., Monk, C.S., McClure-Tone, E.B., Nelson, E.E., Roberson-Nay, R., Adler, A.D., Fromm, S.J., Leibenluft, E., Pine, D.S., Ernst, M., 2008. A developmental examination of amygdala response to facial expressions. Journal of Cognitive Neuroscience 20, 1565–1582.

Hampson, E., van Anders, S., Mullin, L., 2006. A female advantage in the recognition of emotional facial expressions: test of an evolutionary hypothesis. Evolution and Human Behavior 27 (6), 401–416.

Hare, T.A., Tottenham, N., Galvan, A., Voss, H.U., Glover, G.H., Casey, B.J., 2008. Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. Biological Psychiatry 63 (10), 927–934.

Havighurst, R.J., 1972. Developmental Tasks and Education, 3rd ed. McKay, New York (1st ed. 1948).

Haxby, J.V., Hoffman, E., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends in Cognitive Science 4 (6), 223–232.

Haxby, J.V., Hoffman, E., Gobbini, M.I., 2002. Human neural systems for face recognition and social communication. Biological Psychiatry 51, 59–67.

Herba, C., Landau, A., Russell, T., Ecker, C., Phillips, M., 2006. The development of emotion-processing in children: effects of age, emotion, and intensity. Journal of Child of Psychology and Psychiatry 11, 1098–1106.

Herba, C., Phillips, M., 2004. Annotation: development of facial expression recognition from childhood to adolescence: behavioral and neurological perspectives. Journal of Child Psychology and Psychiatry 45, 1185–1198.

Herlitz, A., Yonker, J.E., 2002. Sex differences in episodic memory: the influence of intelligence. Journal of Clinical and Experimental Neuropsychology 24, 107–114.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nature Neuroscience 3 (1), 80–84.

Ishai, A., 2008. Let's face it: it's a cortical network. Neuroimage 40, 415–419.

Johnson, M., 2005. Subcortical face processing. Nature Reviews Neuroscience 6 (10), 766–774.

Johnson, M.H., Munakata, Y., 2005. Processes of change in brain and cognitive development. Trends in Cognitive Science 9 (3), 152–158.

Johnston, V.S., Hagel, R., Franklin, M., Fink, B., Grammar, K., 2001. Male facial attractiveness: evidence for a hormone-mediated adaptive design. Evolution and Human Behavior 22, 251–267.

Joseph, J.E., Gathers, A.D., Bhatt, R., 2010. Progressive and regressive developmental changes in neural substrates for face processing: testing specific predictions of the Interactive Specialization account. Developmental Science 16, 487–502.

Kanwisher, N., 2010. Functional specificity in the human brain: a window into the functional architecture of the mind. Proceedings of the National Academy of Sciences of the United States of America 107 (25), 11163.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. Journal of Neuroscience 17 (11), 4302–4311.

Killgore, W.D., Oki, M., Yurgelun-Todd, D.A., 2001. Sex-specific developmental changes in amygdala responses to affective faces. Neuroreport 12, 427–433.

Killgore, W., Yurgelun-Todd, D., 2010. Cerebral correlates of amygdala responses during non-conscious perception facial affect in adolescent and pre-adolescent children. Cognitive Neuroscience 1, 33–43.

Kissler, J., Bäuml, K.H., 2000. Effects of the beholder's age on the perception of facial attractiveness. Acta Psychologica 104, 145–166.

Kleinhans, N.M., Richards, T., Sterling, L., Stegbauer, K.C., Mahurin, R., Johnson, L.C., et al., 2008. Abnormal functional connectivity in autism spectrum disorders during face processing. Brain 131, 1000–1012.

Kranz, F., Ishai, A., 2006. Face perception is modulated by sexual preference. Current Biology 16 (1), 63–68.

Kubota, J.T., Ito, T.A., 2007. Multiple cues in social perception: the time course of processing race and facial expression. Journal of Experimental Social Psychology 43, 738–752.

Kucharska-Pietura, K., David, A.A., Phillips, M.L., 2005. Perception of facial and vocal affect by people with schizophrenia in early and late stages of illness. British Journal of Psychiatry 187, 523–528.

Langlois, J.H., Roggman, L.A., Casey, R.J., Ritter, J.M., Reiser-Danner, L.A., Jenkins, V.Y., 1987. Infant preferences for attractive faces: rudiments of a stereotype? Developmental Psychology 23, 363–369.

Lawrence, K., Bernstein, D., Pearson, R., Mandy, W., Campbell, R., Skuse, D., 2008. Changing abilities in recognition of unfamiliar face photographs through childhood and adolescence: performance on a test of non-verbal immediate memory (Warrington RMF) from 6 to 16 years. Journal of Neuropsychology 2, 27–45.

Lawrence, K., Kuntsi, J., Coleman, M., Campbell, R., Skuse, D., 2003a. Face and emotion recognition deficits in Turner Syndrome: a possible role for s-linked genes in amygdala development. Neuropsychology 17, 39–49.

Lawrence, K., Campbell, R., Swettenham, J., Terstegge, J., Akers, R., Coleman, M., Skuse, D., 2003b. Interpreting gaze in Turner syndrome: impaired sensitivity to intention and emotion, but preservation of social cueing. Neuropsychologia 41, 894–905.

Lenroot, R., Giedd, J., 2010. Sex differences in the adolescent brain. Brain and Cognition 72 (1), 46–55.

Lewin, C., Wolgers, G., Herlitz, A., 2001. Sex differences favoring women in verbal but not in visuospatial episodic memory. Neuropsychology 15, 165–173.

Lewin, C., Herlitz, A., 2002. Sex differences in face recognition: women's faces make a difference. Brain and Cognition 50, 121–128.

Lewis, M., 2000. The promise of dynamic systems approaches for an integrated account of human development. Child Development 71 (1), 36–43.

Liang, X., Zebrowitz, L.A., Zhang, Y., 2010. Neural activation in the "reward circuit" shows a nonlinear response to facial attractiveness. Society for Neuroscience 5 (3), 320–334.

Little, A.A., Jones, B.C., Burt, D.M., Perrett, D.I., 2007. Preferences for symmetry in faces changes across the menstrual cycle. Biological Psychiatry 76, 209–216.

Marsh, A.A., Blair, R.J., 2008. Deficits in facial affect recognition among antisocial populations: a meta-analysis. Neuroscience and Biobehavioral Reviews 32, 454–465.

Masten, A.S., Coatsworth, J.D., Neemann, J., Gest, S.D., Tellegen, A., Garmezy, N., 1995. The structure and coherence of competence from childhood through adolescence. Child Development 66, 1635–1659.

Maurer, D., Grand, R., Mondloch, C., 2002. The many faces of configural processing. Trends in Cognitive Sciences 6 (6), 255–260.

McClelland, J., Botvinick, M., Noelle, D., Plaut, D., Rogers, T., Seidenberg, M., Smith, L., 2010. Letting structure emerge: connectionist and dynamical systems approaches to cognition. Trends in Cognitive Sciences 14 (8), 348–356.

McClure, E.B., 2000. A meta-analytic review of sex differences in facial expression processing and their development in infants, children, and adolescents. Psychological Bulletin 126, 424–453.

McClure, E.B., Monk, C.S., Nelson, E.E., Zarahn, E., Leibenluft, E., Bilder, R.M., Charney, D.S., Ernst, M., Pine, D., 2004. A developmental examination of gender differences in brain engagement during evaluation of threat. Biological Psychiatry 55, 1047–1055.

McGivern, R.F., Andersen, J., Byrd, D., Mutter, K.L., Reilly, J., 2002. Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. Brain and Cognition 50, 73–89.

Mondloch, C.J., Dobson, K.S., Parsons, J., Mauer, D., 2004. Why 8-year-olds cannot tell the difference between Steve Martin and Paul Newman: factors contributing to the slow development of sensitivity to the spacing of facial features. Journal of Experimental Child Psychology 89, 159–181.

Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. Perception 31 (5), 553–566.

Mondloch, C.J., Robbins, R., Maurer, D., 2010. Discrimination of facial features by adults, 10-year-olds, and cataract-reversal patients. Perception 39 (2), 184–194.

Monk, C.S., McClure, E.B., Nelson, E.E., Zarahn, E., Bilder, R.M., Leibenluft, E., et al., 2003. Adolescent immaturity in attention-related brain engagement to emotion facial expressions. Neuroimage 20, 420–428.

Monk, C.S., Klein, R.G., Telzer, E.H., Schroth, E.A., Mannuzza, S., Moulton III, J.L., et al., 2008a. Amygdala and nucleus accumbens activation to emotional facial expressions in children and adolescents at risk for major depression. American Journal of Psychiatry 165 (1), 90.

Monk, C.S., Telzer, E.H., Mogg, K., Bradley, B.P., Mai, X., Louro, H.M., Chen, G., McClure-Tone, E.B., Ernst, M., Pine, D., 2008b. Amygdala and ventrolateral prefrontal cortex activation to masked angry faces in children and adolescents with generalized anxiety disorder. Archives of General Psychiatry 65, 568–576.

Morris, J.S., Friston, K.J., Büchel, C., Frith, C.D., Young, A.W., Calder, A.J., Dolan, R.J., 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. Brain 121, 47–57.

Munakata, Y., McClelland, J.L., 2003. Connectionist models of development. Developmental Science 6 (4), 413–429.

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, 163–174.

Nestor, A., Plaut, D.C., Behrmann, M., 2011. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. Proceedings of the National Academy of Sciences of the United States of America 108 (24), 9998–10003.

Neufang, S., Specht, K., Hausmann, M., Gunturkun, O., Herpertz-Dahlmann, B., Fink, G., Konrad, K., 2009. Sex differences and the impact of steroid hormones on the developing human brain. Cerebral Cortex 19 (2), 464–473.

O'Hearn, K., Schroer, E., Minshew, N., Luna, B., 2010. Lack of developmental improvement on a face memory task during adolescence in autism. Neuropsychologia, doi:10.1016/j.neuropsychologia.2010.08.024.

Passarotti, A.M., Paul, B.M., Bussiere, J.R., Buxton, R.B., Wong, E., Stiles, J., 2003. The development of face and location processing: an fMRI study. Developmental Science 6 (1), 100–117.

Passarotti, A.M., Smith, J., DeLano, M., Huang, J., 2007. Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. Neuroimage 34, 1708–1722.

Peelen, M.V., Glaser, B., Vuilleumier, P., Eliez, S., 2009. Differential development of selectivity for faces and bodies in the fusiform gyrus. Developmental Science 12 (6), F16–F25.

Pelphrey, K.A., Lopez, J., Morris, J.P., 2009. Developmental continuity and change in responses to social and nonsocial categories in human extrastriate visual cortex. Frontiers in Human Neuroscience 3, 25.

Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, L.K., Minamisawa, R., 1999. Menstrual cycle alters face preference. Nature 399, 741–742.

Peper, J., Brouwer, R., Schnack, H., van Baal, G.C., Leeuwen, M., van den Berg, S.M., Delemarre-Van de Waal, H., Boomsma, D., Kahn, R., Hulshoff Pol, H., 2009. Sex steroid and brain structure in pubertal boys and girls. Psychoneuroendocrinology 34 (3), 332–342.

Perfect, T.J., Moon, H., 2003. The own-age effect in face recognition. In: Duncan, J., Phillips, L., McLeod, P. (Eds.), Measuring the Mind: Speed, Control, and Age. Oxford University Press, Oxford, pp. 317–340.

Perrin, J., Herve, P., Leonard, G., Perron, M., Pike, G., Pitiot, A., et al., 2008. Growth of white matter in the adolescent brain: role of testosterone and androgen receptor. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience 28 (38), 9519–9524.

Perrin, J., Leonard, G., Perron, M., Pike, G., Pitiot, A., Richer, L., et al., 2009. Sex differences in the growth of white matter during adolescence. Neuroimage 45 (4), 1055–1066.

Phillips, M.L., Bullmore, E.T., Howard, R., Woodruff, P.W., Wright, I.C., Williams, S.C., Simmons, A., Andrew, C., Brammer, M., David, A.A., 1998. Investigation of facial recognition memory and happy and sad facial expression perception: an fMRI study. Psychiatry Research 83, 127–138.

Phillips, M.L., Drevets, W.C., Rauch, S.L., Lane, R., 2003a. Neurobiology of emotion perception I: the neural basis of normal emotion perception. Biological Psychiatry 54, 504–514.

Phillips, M.L., Drevets, W.C., Rauch, S.L., Lane, R., 2003b. Neurobiology of emotion perception II: implications for major psychiatric disorders. Biological Psychiatry 54, 515–528.

Phillips, M.L., Medford, N., Young, A.W., Williams, L., Williams, S.C., Bullmore, E.T., Gray, J.A., Brammer, M.J., 2001. Time course of left and right amygdalar responses to fearful facial expressions. Human Brain Mapping 12, 193–202.

Pine, D.S., Lissek, S., Klein, R.G., Mannuzza, S., Moulton, J.L., Guardino, M., Woldehawariat, G., 2004. Face-memory and emotion: association with major depression in children and adolescents. Journal of Child Psychology and Psychiatry 45, 1199–1208.

Pinkham, A.E., Hopfinger, J.B., Pelphreym, K.A., Piven, J., Penn, D.L., 2008. Neural bases for impaired social cognition in schizophrenia and autism spectrum disorders. Schizophrenia Research 99, 164–175.

Proverbio, A., Brignone, V., Matarazzo, S., Del Zotto, M., Zani, A., 2006. Gender differences in hemispheric asymmetry for face processing. Neuroscience 7 (44), 1–10.

Rehnman, J., Herlitz, A., 2006. Higher face recognition ability in girls: magnified by own-sex and own-ethnicity bias. Memory 14 (3), 289–296.

Rehnman, J., Herlitz, A., 2007. Women remember more faces than men do. Acta Psychologica (Amsterdam) 124, 344–355.

Rich, B.A., Fromm, S.J., Berghorst, L.H., Dickstein, D.P., Brotman, M.A., Pine, D.S., Leibenluft, E., 2008. Neural connectivity in children with bipolar disorder: impairment in the face emotion processing circuit. Journal of Child Psychology and Psychiatry 49, 88–96.

Rhodes, G., Geedes, K., Jeffery, L., Dziurawiec, S., Clark, A., 2002. Are average and symmetric faces attractive to infants? Discrimination and looking preferences. Perception 31, 315–321.

Rhodes, G., Simmons, L.W., Peters, M., 2005. Attractiveness and sexual behavior: does attractiveness enhance mating success? Evolution and Human Behavior 26, 186–201.

Rhodes, G., 2006. The evolutionary psychology of facial beauty. Annual Review of Psychology 57, 199–226.

Roisman, G.I., MAsten, A.S., Coatsworth, D., Tellegen, A., 2004. Salient and emerging developmental tasks in the transition to adulthood. Child Development 75, 123–133.

Romeo, R.D., 2003. Puberty, a period of both organizational and activational effects of steroid hormones of neurobehavioral development. Journal of Neuroendocrinology 15, 1185–1192.

Rule, N.O., Moran, J.M., Freeman, J.B., Whitfield-Gabrielli, S., Gabrielli, J.D.E., Ambady, N., 2011. Face value: amygdala response reflects the validity of first impressions. Neuroimage 54, 734–741.

Rupp, H.A., James, T.W., Ketterson, E.D., Sengelaub, D.R., Janssen, E., Heiman, J.R., 2009a. Neural activation in the orbitofrontal cortex in response to males faces increases during the follicular phase. Hormones and Behavior 56, 66–72.

Rupp, H.A., James, T.W., Ketterson, E.D., Sengelaub, D.R., Janssen, E., Heiman, J.R., 2009b. Neural activation in women in response to masculinized male faces: medication by hormones and psychosexual factors. Evolution and Human Behavior 30, 1–10.

Said, C.P., Dotsch, R., Todorov, A., 2010. The amygdala and FFA track both social and non-social face dimensions. Neuropsychologia 48, 3596–3605.

Said, C.P., Haxby, J.V., Todorov, A., 2011. Brain systems for assessing the affective value of faces. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 366 (1571), 1660–1670.

Samuels, C.A., Ewy, R., 1985. Aesthetic perception of faces during infancy. British Journal of Developmental Psychology 3, 221–228.

Saxton, T.K., Caryl, P.G., Roberts, S.C., 2006. Vocal and facial attractiveness judgments of children, adolescents and adults: the ontogeny of mate choice. Ethology 112, 1179–1185.

Saxton, T.K., Debruine, L.M., Jones, B.C., Little, A.C., Roberts, C., 2009. Face and voice attractiveness judgments change during adolescence. Evolution and Human Behavior 30, 398–408.

Scherf, K.S., Behrmann, M., Humphreys, K., Luna, B., 2007. Visual category-selectivity for faces, places, and objects emerges along different developmental trajectories. Developmental Science 10 (4), F15–F30.

Scherf, K.S., Luna, B., Avidan, G., Behrmann, M., 2011. 'What' precedes 'which': developmental neural tuning in face- and place-related cortex. Cerebral Cortex, doi:10.1093/cercor/bhq269.

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

Schulz, K.M., Sisk, C.L., 2006. Pubertal hormones, the adolescent brain, and the maturation of social behaviors: lessons from the Syrian hamster. Molecular and Cellular Endocrinology 254–255, 120–126.

Schulz, K.M., Molenda-Figueira, H.A., Sisk, C.L., 2009. Back to the future: the organizational–activational hypothesis adapted to puberty and adolescence. Hormones and Behavior 55 (5), 597–604.

Shaw, P., Kabani, N., Lerch, J., Eckstrand, K., Lenroot, R., Gogtay, N., et al., 2008. Neurodevelopmental trajectories of the human cerebral cortex. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience 28 (14), 3586–3594.

Sisk, C.L., Schulz, K.M., Zehr, J.L., 2003. Puberty: a finishing school for male social behavior. Annals of the New York Academy of Sciences 1007, 189–198.

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

Skuse, D.H., Morris, J.S., Dolan, R.J., 2005. Functional dissociation of amygdala-modulated arousal and cognitive appraisal, in Turner syndrome. Brain 128, 2084–2096.

Savic, I., Lindström, P., 2008. PET and MRI show differences in cerebral asymmetry and functional connectivity between homo- and heterosexual subjects. Proceedings of the National Academy of Sciences of the United States of America 105 (27), 9403–9408.

Smith, L.B., 2005. Self-organizing processes in learning to learn words: development is not induction. In: Nelson, C.A. (Ed.), New perspectives on learning and development: Minnesota Symposium on Child Psychology, vol. 28. Academic Press, New York, pp. 1–32.

Smith, L., Thelen, E., 2003. Development as a dynamic system. Trends in Cognitive Sciences 7 (8), 343–348.

Somerville, L.H., Jones, R.M., Casey, B.J., 2010. A time of change: behavioral and neural correlates of adolescent sensitivity to appetitive and aversive environmental cues. Brain and Cognition 72 (1), 124–133.

Sowell, E.R., Thompson, P.M., Holmes, C.J., Batth, R., Jernigan, T.L., Toga, A.W., 1999. Localizing age-related changes in brain structure between childhood and adolescence using statistical parametric mapping. Neuroimage 9, 587–597.

Stanton, S.J., Wirth, M.M., Waugh, C.E., Schultheiss, O.C., 2009. Endogenous testosterone levels are associated with amygdala and ventromedial prefrontal cortex responses to anger faces in men but not women. Biological Psychiatry 81, 118–122.

Steinberg, L., 2008. A social neuroscience perspective on adolescent risk-taking. Developmental Review 28, 78–106.

Temple, C.M., Cornish, P.J., 1993. Recognition memory for words and faces in school children: a female advantage for words. British Journal of Developmental Psychology 11, 421–426.

Thelen, E., Smith, L.B., 1994. A Dynamic Systems Approach to the Development of Cognition and Action. Bradford/MIT Press, Cambridge, MA.

Thomas, K.M., Drevets, W.C., Whalen, P.J., Eccard, C.H., Dahl, R.E., Ryan, N.D., Casey, B.J., 2001. Amygdala response to facial expressions in children and adults. Biological Psychiatry 49, 309–316.

Thomas, L.A., de Bellis, M.D., Graham, R., LaBar, K., 2007. Development of emotional facial recognition in late childhood and adolescence. Developmental Science 10, 547–558.

Todorov, A., Said, C.P., Engell, A.D., Oosterhof, N.N., 2008. Understanding evaluation of faces on social dimensions. Trends in Cognitive Sciences 12, 455–460.

Teunisse, J.P., de Gelder, B., 2003. Face processing in adolescents with autistic disorder: the inversion and composite effects. Brain and Cognition 52, 285–294.

Turner, H., 1938. A syndrome of infantilism, congenital webbed neck, and cubitus valgus. Endocrinology 23, 566–574.

Van Geert, P., 1994. Dynamic Systems of Development: Change between Complexity and Chaos. Prentice Hall/Harvester Wheatsheaf, New York.

Van Wingen, G., Mattern, C., Verkes, R.J., Buitelaar, J., Fernáandez, G., 2010. Testosterone reduces amygdala-orbitofrontal cortex coupling. Psychoneuroendocrinology 35, 105–113.

Vasa, R.A., Pine, D.S., Thorn, J.M., Nelson, T.E., Spinelli, S., Nelson, E., et al., 2011. Enhanced right amygdala activity in adolescents during encoding of positively-valenced pictures. Developmental Cognitive Neuroscience 1, 88–89.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.

Wallen, K., Baum, M.J., 2002. Masculinazation and defeminazation in altricial and precocial mammals: comparative aspects of steroid hormone action. In: Pfaff, D.W., Arnold, A.P., Etgen, A.M., Fahrbach, S.E., Rubins, R.T. (Eds.), Hormones, Brain, and Behavior, vol. 4. Amsterdam, Elsevier, pp. 385–423.

Welling, L.L.M., Jones, B.C., DeBruine, L.M., Smith, F.G., Feinberg, D.R., Little, A.C., 2008. Men report stronger attraction to femininity in women's faces when their testosterone levels are high. Hormones and Behavior 54, 703–708.

Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., Jenike, M.A., 1998. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. Journal of Neuroscience 18, 411–418.

Winston, J.S., O'Doherty, J., Kilner, J.M., Perrett, D.I., Dolan, R.J., 2007. Brain systems for assessing facial attractiveness. Neuropsychologia 45, 195–206.

Witte, A., Savli, M., Holik, A., Kasper, S., Lanzenberger, R., 2010. Regional sex differences in grey matter volume are associated with sex hormones in the young adult human brain. Neuroimage 49 (2), 1205–1212.

Wright, D.B., Stroud, J.N., 2002. Age differences in lineup identification accuracy: people are better with their own age. Law and Human Behavior 26, 641–654.

Zuo, X., Kelly, C., Di Martino, A., Mennes, M., Margulies, D.S., Bangaru, S., 2010. Growing together and growing apart: regional sex differences in the lifespan developmental trajectories of functional homotopy. Journal of Neuroscience 30, 15034–15043.