Exploring the subjective experience and neural correlates of self-conscious emotion processing
in autistic adolescents: Over-reliance on learned social rules during heightened perspective-
taking demands may serve as compensatory strategy for less reflexive mentalizing

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Abstract

Autistic individuals experience a secondary wave of social cognitive challenges during adolescence, which impact interpersonal success (Picci & Scherf, 2015). To better understand these challenges, we investigated the subjective experience and neural correlates of self-conscious emotion (SCE) processing in autistic adolescent males compared to age- and IQ-matched neurotypical (NT) adolescents (ages 11-17). Study I investigated group differences in SCE attributions (the ability to recognize SCEs) and empathic SCEs (the ability/tendency to feel empathic SCEs) and the potential modulatory role of heightened perspective-taking (PT) demands. Furthermore, Study I explored associations between SCE processing, a triad of social cognitive abilities (self-awareness/introspection, perspective-taking/cognitive empathy, and affective empathy), and autistic features. Study II investigated group differences in neural activation patterns recruited during SCE processing and the potential modulatory role of heightened PT demands.

During an MRI scan, participants completed the Self-Conscious Emotions Task (SCET), which featured salient, ecological video clips of adolescents in a singing competition. Videos represented two factors: emotion (embarrassment, pride) and PT demands (low, high). In low PT clips, singers' emotions matched the situational context (singing quality; sing poorly, act embarrassed); in high PT clips, they did not (sing well, act embarrassed). Participants rated how intensely embarrassed and proud each singer felt. They also rated how empathically embarrassed and proud they felt for each singer.

The ASD group recognized SCEs and felt empathic SCEs, and they did so with similar intensity as the NT group. However, the ASD group made atypical emotion attributions when PT demands were high, which more strongly reflected the situational context. Atypical attributions

correlated with greater perspective-taking difficulties, more intense autistic features, and reduced social competence. An over-reliance on contextual cues may reflect a strict adherence to learned social rules, possibly compensating for less reflexive mentalizing, which may underlie real-world interpersonal challenges.

Neuroimaging results support this interpretation. While the ASD and NT groups recruited strikingly similar neural patterns, there were group differences within social cognition regions, visual perception regions, salience regions, and sensorimotor regions, which were modulated by changes in PT demands/the situational context. These findings similarly suggest that greater social norm referencing may serve as a compensatory strategy for less reflexive mentalizing or for difficulties integrating discrepant mental state and contextual information. Implications for intervention are discussed.

Keywords: Autism, self-conscious emotions, social emotions, empathy, perspective-taking, social context, MRI, social cognition, salience

Overview

A recent two-hit model of autism spectrum disorders (ASD) proposes that autistic¹ adolescents experience a critical secondary (post-infancy/early childhood) wave of challenges in social cognition and peer interactions, which are enhanced by accelerated neural maturation and socioaffective changes associated with puberty (Picci & Scherf, 2015). Neurotypical adolescence is accompanied by heightened self-consciousness (Rankin, Lane, Gibbons, & Gerrard, 2004) and enhanced perspective-taking (PT) abilities (Dumontheil, Apperly, & Blakemore, 2010), yet these attributes reportedly develop atypically² in ASD. In particular, self-conscious emotion (SCE) understanding may be altered. Given that adolescence is considered a key period of social reorientation (Nelson, Jarcho, & Guyer, 2016; Nelson, Leibenluft, McClure, & Pine, 2005), acquiring advanced social cognitive abilities and applying them appropriately³ in affective and interpersonal contexts is paramount for developing strong peer relationships and positive mental health outcomes. Relatively little work has explored advanced social cognition in ASD during adolescence. To close this gap, we aimed to characterize the subjective experience and neurobiological substrates of SCE understanding in autistic and neurotypical adolescents.

Self-Conscious Emotions

Emotions can be broadly categorized as basic, nonsocial emotions (e.g., happiness, sadness, anger, fear) or complex, social emotions (e.g., pride, embarrassment, shame, guilt). Nonsocial emotions are believed to promote biological goals and emerge early in life; while social emotions are believed to promote social goals and emerge later in life, coinciding with the acquisition of advanced social cognitive abilities, in particular, self-reflection and perspective-taking (Lewis, 1997). SCEs, a type of social emotion, are elicited by experiencing, inferring, or anticipating others' evaluations of the self, which are informed by internalized social rules and

expectations (Leary, 2007; Lewis, 1995, 1997). SCEs are likely supported by a triad of social cognitive processes: (i) self-awareness, underlying self-consciousness and self-reflection; (ii) other-awareness, underlying mental state attribution; and (iii) social norm-awareness, underlying the identification and adoption of societal standards (Beer, 2007; Jankowski & Takahashi, 2014; Lagattuta & Thompson, 2007). SCEs inform social decision-making and provide feedback on the social appropriateness of one's thoughts and actions (Tangney & Tracy, 2012; Tracy & Robins, 2004a, 2007e). By promoting social acceptance and preventing social rejection, SCEs play an integral role in supporting and maintaining interpersonal relationships (Leary, 2007; Tracy & Robins, 2007e).

Embarrassment. Embarrassment represents inferred negative self-evaluations in response to social norm violations (Miller, 1996). Embarrassment is an emotional response to “normative public deficiencies”, including physical pratfalls or inept performances (Keltner, 1996; Keltner & Buswell, 1997; Tangney, Stuewig, & Mashek, 2007), which include feeling awkward, uncomfortable, or inferior (Parrott & Smith, 1991). Embarrassment is strongly tied to impression management and represents a concern for evoking negative social evaluations or conveying a negative self-image (Miller, 1996; Miller & Tangney, 1994; Parrott & Smith, 1991). Embarrassment serves an appeasement function (Keltner, 1995; Keltner & Buswell, 1997) by signaling one's desire to monitor, hide, or change one's behavior (Tangney et al., 2007). By conveying acknowledgment and regret of one's transgressions, it serves as a “nonverbal apology” and prevents social rejection (Miller, 2007). Embarrassment can be reliably recognized via a combination of facial expressions and body postures (Edelmann & Hampson, 1981a, 1981b; Keltner, 1995; 1996; Miller, 1996). Embarrassed individuals typically avert their gaze, lower and turn away their head, make frequent gaze shifts, display a controlled smile, and cover

their eyes or mouth (Keltner, 1995). They also display nervous body movements, by shifting posture, moving their legs and feet, and using hand gestures (Edelmann & Hampson, 1981a, 1981b).

Pride. Pride represents inferred positive self-evaluations in response to achieving socially-valued goals or exceeding societal standards (Lewis, 1997). Similar to “achievement motivation” (Lewis, 1997; Lewis & Sullivan, 2005), pride is an emotional response to accepting personal responsibility for socially-valued actions, which elicits feelings of efficacy, mastery, or joy (Leary, 2007; Lewis & Sullivan, 2005). Pride reflects status, competence, and achievement (Tracy & Robins, 2004b). It functions to obtain, maintain, and convey social status by signaling one’s deservedness of social acceptance and drawing attention to one’s increased social status (Tracy & Matsumoto, 2008; Tracy & Robins, 2004a; 2007a; 2007b; Tracy, Shariff, & Cheng, 2010; Tracy, Weidman, Cheng, & Martens, 2014). Pride can be reliably recognized via a combination of facial expressions and body postures (Tracy & Robins, 2003, 2004b, 2007c). Proud individuals display a small non-Duchenne smile, tilt their head slightly backward, expand their chest, push their torso outward, and either raise their arms above their head with their hands in fists or place their hands on their hips with their arms akimbo (Tracy & Matsumoto, 2008; Tracy & Robins, 2003, 2004b).

Autism and Adolescence

ASD represents a set of neurodevelopmental disorders characterized in the DSM-V by impaired social communication and social interactions (American Psychiatric Association, 2013). ASD is one of the fastest growing developmental disorders. Prevalence rates have increased almost 120% over the past ten years, representing an estimated 1 in 68 births (Wingate et al., 2014). Despite the growing number of autistic children entering adolescence, relatively

little research has explored this key developmental period. Longitudinal studies suggest that social challenges in ASD persist into adolescence (Anderson, Maye, & Lord, 2011). Compared to neurotypical peers, autistic adolescents experience lower levels of social acceptance and higher levels of social rejection (Symes & Humphrey, 2010). Close to 50% of autistic adolescents never see friends, are never called by friends, and are never invited to social activities, and such interpersonal challenges are proposed to reflect poor social skills (Shattuck et al., 2011). In addition, close to 50% of autistic adolescents are bullied, and peer victimization is associated with worse social skills (Sterzing, Shattuck, Narendorf, Wagner, & Cooper, 2012). These findings converge with research underscoring a link between atypical social skills and interpersonal success in ASD (Orsmond, Krauss, & Seltzer, 2004). Given that adolescence is widely considered a key period of social reorientation (Nelson et al., 2016; Nelson et al., 2005), where peer relationships become more salient and meaningful (O'Brien & Bierman, 1988), it is imperative to study advanced social cognitive abilities in autistic adolescents, to shed light onto the underlying causes of interpersonal challenges and to illuminate possible avenues for intervention. In particular, the ability to identify SCEs conveyed by peers and to respond appropriately may play a key role in interpersonal success.

Autism and Atypical Social Cognition

Autistic individuals show atypicalities across a triad of social cognitive abilities, which overlap with those underlying SCE processing: self-reflection/interoception (self-awareness), Theory of Mind (ToM)/perspective-taking (PT) (other-awareness), and empathy. The “mindblindness” theory postulates that atypical ToM/PT is a core feature of ASD (Baron-Cohen, 1990; Baron-Cohen, Leslie, & Frith, 1985; Frith, 2001). Autistic individuals generally demonstrate attenuated or atypical performance on mental state attribution tasks, including

inferring others' thoughts, intentions, and feelings (Abell, Happe, & Frith, 2000; Baron-Cohen, Wheelwright, Spong, Scahill, & Lawson, 2001; Dziobek et al., 2006; Happé, 1994; Harms, Martin, & Wallace, 2010; Mazza et al., 2014; Wang, Lee, Sigman, & Dapretto, 2006).

Interestingly, ToM/PT deficits may not be as ubiquitous as once believed, particularly in older individuals with higher verbal IQ (Bowler, 1992; Happé, 1995). In such cases, these challenges are typically observed using more nuanced or complex stimuli (Bons et al., 2013; Doi et al., 2013; Golan, Baron-Cohen, Hill, & Golan, 2006; Happé, 1994; 1995), but can be mitigated by providing explicit cues/prompting (Senju, Southgate, White, & Frith, 2009).

Some researchers propose that autistic individuals may also experience difficulties understanding their *own* minds (Lombardo & Baron-Cohen, 2010; Williams, 2010). ASD is associated with atypical self-processing (Henderson et al., 2009; Lombardo, Barnes, Wheelwright, & Baron-Cohen, 2007; Lombardo et al., 2009; Pfeifer et al., 2013; Toichi et al., 2002), and reduced self-awareness is the basis of the “absent self” theory of ASD (Frith, 1989). Some researchers have also linked ASD with alexithymia and poor interoception (Bird & Viding, 2014; Griffin, Lombardo, & Auyeung, 2016; Hill, Berthoz, & Frith, 2004; Lombardo et al., 2007; Patil, Melsbach, Hennig-Fast, & Silani, 2016; Silani et al., 2008), which represents difficulties identifying and describing one's emotions (Bagby, Parker, & Taylor, 2004). A recent theory, that is gaining popularity, proposes that alexithymia may underlie differences in affective processing in ASD, in particular, atypical emotion recognition and empathy (Bird & Cook, 2013; Bird et al., 2010; Cook, Brewer, Shah, & Bird, 2013;). This theory links atypical self-awareness, other-awareness, and empathy in ASD.

ASD has been broadly categorized as an “empathy disorder” (Gillberg, 1992), and researchers often report atypical empathy in ASD (Lombardo et al., 2007). While cognitive

empathy reflects emotional PT abilities (e.g., “I understand what you feel”), affective empathy reflects emotional resonance/affective contagion (e.g., “I feel what you feel”) (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). Despite claims of a global empathy deficit, when cognitive and affective empathy are examined separately, a distinct pattern often emerges. Supporting the “Empathy Imbalance Hypothesis of Autism” (Smith, 2009), autistic individuals often demonstrate attenuated *cognitive* empathy, including atypical performance on mentalizing and emotion recognition tasks and lower PT scores on empathy questionnaires, but intact *affective* empathy, including similar levels of empathic concern on empathy tasks/questionnaires (Dziobek et al., 2008; Jones, Happé, Gilbert, Burnett, & Viding, 2010; Mazza et al., 2014; Rogers, Dziobek, Hassenstab, Wolf, & Convit, 2007; Rueda, Fernández-Berrocal, & Baron-Cohen, 2015; Patil et al., 2016; Schwenck et al., 2012). However, autistic individuals often report heightened personal distress for others (Adler et al., 2015; Dziobek et al., 2008; Lombardo et al., 2007; Patil et al., 2016; Rogers et al., 2007), suggesting empathic hyperarousal. Overall, this cognitive-affective dissociation suggests that autistic individuals may experience difficulties inferring how others feel, similar levels of empathic concern for others, and more intense emotional arousal/distress for others. This pattern may reflect group differences in PT abilities, alexithymic tendencies, and/or anxiety/emotion regulation.

Autism and Atypical Self-Conscious Emotion Processing

As summarized above, reported atypicalities in a triad of social cognitive abilities integral for SCE processing suggest that autistic individuals may also experience difficulties processing SCEs. Research exploring SCE recognition in ASD offers mixed findings. While some studies report that autistic individuals can accurately label SCEs (Adler et al., 2015; Hillier & Allinson, 2002a; Hobson et al., 2006; Tracy et al., 2011; Williams & Happé, 2010); others report impaired

SCE recognition (Heerey et al., 2003; Kasari et al., 2001). Furthermore, some studies report intact but atypical abilities, such as requiring greater time and more frequent prompting to engage in PT (Capps et al., 1992; Hillier & Allinson, 2002a), or offering impoverished justifications for SCE attributions (Hillier & Allinson, 2002a; 2002b). Thus, autistic individuals may recognize the social rules that inform SCEs, but allocate less attention to mental states when inferring SCEs (Hillier & Allinson, 2002a). In support of this interpretation, advanced ToM is associated with enhanced SCE recognition (Heerey et al., 2003) and richer justifications for SCE attributions (Hillier & Allinson, 2002a) in autistic youths.

Little research has explored empathic SCE processing, or feeling SCEs on behalf of others. Autistic adults report feeling either similarly intense (Morita et al., 2012; 2016) or heightened (Adler et al., 2015; Krach et al., 2015) empathic embarrassment. Interestingly, empathic embarrassment may be modulated by the situational context: autistic adults report feeling similar levels of empathic embarrassment as neurotypical peers when targets engage in accidental social norm violations, but reduced empathic embarrassment when targets engage in intentional transgressions (Paulus, Kamp-Becker, & Krach, 2013). Research has not yet uncovered the social cognitive basis for atypical empathic SCE processing in ASD, although heightened empathic embarrassment is linked to increased personal distress (possibly reflecting emotional hyperresponsivity and atypical emotion regulation) (Adler et al., 2015) and elevated empathic tendencies (Paulus et al., 2013). To date, only one study has explored empathic SCEs in autistic children, reporting that they feel similar levels of empathic embarrassment as neurotypical peers for targets in embarrassing situations but offer less rich justifications for emotion attributions (Hillier & Allinson, 2002b). Taken together, autistic individuals may have an intact conceptual understanding of empathic SCEs when framed within the context of

expected outcomes and internalized social rules, but empathic responses may be modulated by PT abilities, empathic tendencies, or the situational context.

Neural Correlates of Self-Conscious Emotion Processing

A review of social emotions highlights three neural networks that potentially underlie SCE processing (Jankowski & Takahashi, 2014). First are cortical midline structures (CMS), associated with self-processing and self-evaluation, including medial prefrontal cortex (mPFC; dorsal, anterior rostral, and ventral regions [dmPFC, armPFC, and vmPFC] and anterior cingulate cortex [ACC]) and medial posterior parietal cortex (mPPC; precuneus [PC], posterior cingulate cortex [PCC], and retrosplenial cortex [RSC]) (Northoff & Bermpohl, 2004; Northoff et al., 2006; Qin & Northoff, 2011). In particular, armPFC and vmPFC support self-referential processing (Denny, Kober, Wager, & Ochsner, 2012) and self-consciousness (Somerville et al., 2013). Second include anterior insula (AI), dorsal anterior cingulate cortex (dACC), and inferior frontal gyrus (IFG), underlying interoception and empathy processing (i.e., emotional resonance and empathic concern) (Fan, Duncan, de Greck, & Northoff, 2011; Lamm, Decety, & Singer, 2011). Third are putative “social brain” regions supporting mental state inference and intention attribution, including mPFC, PC/PCC, posterior superior temporal sulcus (pSTS), temporoparietal junction (TPJ), and anterior temporal lobe (ATL)/temporal pole (TP) (Gallagher et al., 2000; Ruby & Decety, 2004; Young, Cushman, Hauser, & Saxe, 2007). Moral reasoning engages similar cognitive processes as SCE processing, including self-evaluation and social norm referencing, and recruits a frontal-temporal-limbic network, including mPFC, TPJ/pSTS, and ATL (Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Moll, de Oliveira-Souza, & Zahn, 2008; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). ATL may broadly encode abstract social concepts, while frontal-limbic regions may differentially encode social

context and social function (Fontenelle, de Oliveira-Souza, & Moll, 2015; Moll et al., 2008; Zahn et al., 2008).

Embarrassment. Embarrassment is associated with “social brain” regions (mPFC, pSTS/TPJ), supporting mental state inference and social perception; ATL/TP, representing social conceptual knowledge processing (i.e., social standards/rules); and occipital regions, representing salience processing (Berthoz, Armony, Blair, & Dolan, 2002; Krach et al., 2011; Michl et al., 2012; Moll et al., 2007; Takahashi et al., 2004; see Jankowski & Takahashi, 2014 for review.) A seminal study by Takahashi and colleagues (2004) investigated first-person embarrassment using emotion-eliciting sentences. Embarrassment recruited bilateral prefrontal (mPFC, OFC), medial temporal (pSTS, hippocampus), and occipital regions associated with mental state attribution, memory, and emotional salience; and embarrassment ratings correlated positively with pSTS and occipital activity. Compared to guilt, embarrassment recruited greater anterior and medial temporal regions, possibly representing enhanced social conceptual knowledge processing. A replication study revealed bilateral frontal, temporal, and occipital activity, although in more lateral regions (excluding mPFC) (Michl et al., 2012). While no study has investigated the unique neural correlates of SCEs in developmental samples, Burnett and colleagues (2009) broadly studied negative SCEs (first- and third-person embarrassment and guilt, relative to disgust and fear) in adolescents and adults using emotion-eliciting sentences. While both groups recruited armPFC and pSTS/TPJ, adolescents uniquely recruited PC. Adolescents recruited greater armPFC activity, and adults recruited greater ATL/TP activity. These results suggest that negative SCE processing during adolescence may be associated with anterior and posterior CMS, although developmental differences may exist.

Researchers have begun to investigate the neural correlates of empathic embarrassment. Krach and colleagues (Krach et al., 2011; Paulus, Müller-Pinzler, Jansen, Gazzola, & Krach, 2014) studied shared and nonshared empathic embarrassment using drawings of targets in embarrassing situations and manipulated targets' awareness of the social context. Empathic embarrassment broadly recruited social cognition regions (i.e., mPFC, ATL/TP), and affective and empathic pain regions (i.e., AI, ACC). Empathic embarrassment ratings correlated positively with AI and ACC activity, as did trait empathy. Thus, AI and ACC may play key roles in empathic embarrassment, possibly representing emotional resonance of others' pain. Shared empathic embarrassment recruited greater pSTS activity than nonshared empathic embarrassment, which may represent enhanced simulation of emotional states (i.e., emotional contagion). Related research by Melchers and colleagues (2015) explored empathic embarrassment using clips from a reality TV show. Empathic embarrassment recruited inferior frontal, inferior parietal, and medial temporal regions, possibly reflecting mental state attribution and empathic concern, and activity correlated positively with empathic embarrassment ratings.

Broadly, these studies suggest that embarrassment processing may recruit medial prefrontal, temporal, and occipital regions supporting mental state inference, social norm reference, and salience attribution; while empathic embarrassment may additionally recruit limbic regions supporting interoception, emotional resonance, and empathic concern.

Pride. Several studies have investigated pride processing. Takahashi and colleagues (2007) used emotion-eliciting sentences to compare first-person pride and joy. Pride recruited pSTS and ATL/TP, while joy recruited ventral striatum. Compared to joy, pride recruited greater pSTS activity, and pride ratings correlated positively with pSTS activity. These findings may reflect the more social cognitive nature of pride (requiring mental state attribution and social

norm reference) compared to the more hedonic nature of joy. A related study used emotion-eliciting photographs to compare third-person pride and compassion (Simon-Thomas et al., 2011). Pride recruited PCC; and pride, relative to compassion, recruited greater PCC, inferior temporal, parahippocampal, and cerebellar activity. The authors suggested that these neural patterns, combined with the absence of mPFC activity, may represent enhanced self-reflection and autobiographical memory, but not self-appraisal. Research exploring first-person pride via autobiographical memories revealed CMS (dmPFC, PCC, and PC), dlPFC, AI/IFG, striatal, and amygdalar activity (Roth, Kaffenberger, Herwig, & Brühl, 2014). The authors proposed that the recruitment of mPFC and PCC but not pSTS and ATL/TP may reflect self-referential processing and autobiographical memory associated with pride recollection, but not mental state inference.

Broadly, these findings suggest that pride processing may be associated with a temporal-parietal social cognition regions (similar to embarrassment), and the recruitment of medial prefrontal, medial posterior parietal, limbic, and striatal regions may be task-specific, reflecting differences in self-reference/self-appraisal, memory retrieval, and affiliative motivation.

Neural Correlates of Self-Conscious Emotion Processing in ASD

Only two neuroimaging studies have investigated SCE processing in ASD. Krach and colleagues (2015) investigated empathic social pain (similar to empathic embarrassment) using images of targets in physically and socially painful situations. Autistic and neurotypical adults recruited similar neural patterns during empathic *physical* pain; however, autistic adults recruited attenuated AI activity (and marginally attenuated ACC activity) during empathic *social* pain, which correlated negatively with autistic symptom severity. Interestingly, empathic social pain ratings correlated positively with AI and ACC activity for neurotypical adults but correlated positively with hippocampal activity for autistic adults. The authors suggested that atypical

empathic social pain processing in ASD may reflect difficulties integrating social rules/expectations with complex contextual demands. Consequently, autistic individuals may experience atypical emotional embodiment of others' social pain (as reflected in reduced AI/ACC activity), which they may compensate for by explicitly referencing and rigidly applying learned social rules (as reflected in increased hippocampal activity).

Pantelis and colleagues (2015) studied social awkwardness (a possible precursor for empathic embarrassment) using clips from a popular TV sitcom. Autistic and neurotypical adults recruited prototypical social cognition regions, including mPFC, TPJ, STS, and PC, as well as OFC and occipital regions; however, autistic adults recruited attenuated TPJ/pSTS activity, which may reflect atypical mentalizing.

Overall, these studies offer preliminary evidence for a relatively intact social cognition network during empathic SCE processing, but atypicalities within select regions supporting emotional awareness/affective embodiment (AI/ACC) and intention attribution (pSTS/TPJ), particularly during complex social situations.

Motivation for the Current Studies

SCE processing plays a key role in interpersonal success, by promoting social acceptance and preventing social rejection (Tracy & Robins, 2007e). Adolescence is an ideal period to investigate the development of SCE understanding. SCEs (particularly embarrassment) are experienced more frequently and more intensely during adolescence (Buss et al., 1979; Miller, 1992), and empathic embarrassment emerges in late childhood (Bennett & Cormack, 1996) and continues to develop throughout adolescence. Advanced social cognitive abilities and their underlying neural correlates mature significantly during adolescence (Blakemore & Choudhury, 2006), which are reflected in increased social and cognitive demands associated with adolescent

interpersonal interactions. Furthermore, peer perceptions and peer relationships become increasingly valued and important (Csikszentmihalyi & Larson, 1984; Nelson et al., 2016). In fact, adolescents' heightened subjective experience of embarrassment (and by extension, other SCEs) may be attributed to enhanced concerns of peer evaluations (Miller, 1992).

Despite age-related reductions in autistic symptoms, approximately 75% of autistic children continue to experience significant social challenges in adolescence and adulthood (Anderson et al., 2011; VanBergeijk, Klin, & Volkmar, 2008). Atypical social cognitive abilities, characteristic of ASD, can significantly impact social interactions and peer relationships; and emotion perception, in particular, is a noted moderator of social skills in ASD (Hudepohl, Robins, King, & Henrich, 2015). Atypical SCE processing may be perceived as diminished social awareness or reduced empathic concern, which may put autistic youths at increased risk for bullying or social exclusion. The current studies aimed to investigate the subjective experience and neural correlates of SCE processing in autistic and neurotypical adolescents, as well as the potential modulatory role of heightened PT demands on group differences, in an effort to shed light onto the real-world interpersonal challenges and to offer possible avenues for intervention.

Aims and Hypotheses

Study I. We investigated the subjective experience of SCE processing in autistic and neurotypical adolescent males using dynamic affective stimuli. We examined group differences in the ability to infer SCEs and to feel empathic SCEs for others, and the potential modulatory role of heightened PT demands. We additionally explored the relationship between SCE processing and a proposed triad of social cognitive abilities (self-awareness/interoception,

PT/cognitive empathy, and affective empathy), as well as autistic features and social competence.

We hypothesized that autistic adolescents would recognize and resonate with SCEs (as reflected in average inferred and empathic SCE ratings); however, group differences would exist, which would be modulated by PT demands. Autistic adolescents would infer less intense SCEs, and group differences would be greater during heightened PT demands. Autistic adolescents would feel similarly intense empathic SCEs, but if group differences did exist, they would feel less intense empathic SCEs during heightened PT demands. SCE processing would be associated with the proposed triad of social cognitive abilities, such that adolescents with reduced self-awareness/interoception, PT/cognitive empathy, and affective empathy would report less intense inferred and empathic SCEs. In addition, adolescents with more intense autistic features and reduced social competence would report less intense inferred and empathic SCEs.

Study II. We investigated the neural correlates of SCE processing recruited by autistic and neurotypical adolescent males. We examined group differences in neural activity recruited during embarrassment and pride processing, and the potential modulatory role of heightened PT demands on group differences. We hypothesized that both autistic and neurotypical adolescents would recruit “social brain” regions associated with mentalizing and social evaluation (CMS, pSTS/TPJ, and ATL/TP) and limbic regions associated with interoception/empathy (AI, IFG, and ACC); however, autistic adolescents would recruit attenuated activity, particularly within “social brain” regions. We hypothesized that PT demands would modulate group differences. While both autistic and neurotypical adolescents would recruit greater “social brain” activity during high, compared to low, PT demands, we hypothesized that group differences would be stronger during high PT demands.

METHODS

Participants

Adolescent males (ages 11-17) were recruited for the study via physical and online flyers and from the University of Oregon's research database. Participants included autistic adolescents (ASD; autism, autism spectrum disorder, Asperger's syndrome, High Functioning Autism, Pervasive Developmental Disorder-Not Otherwise Specified) and one-to-one age-matched (within one year) neurotypical adolescents (NT). Participants were excluded if they had a neurological disorder or FSIQ<75; NT participants were additionally excluded if they had a psychological disorder, including ASD, or if a first-degree relative had ASD (or concern thereof). (See SI for more information on exclusionary criteria.)

Autism diagnosis was confirmed using the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 2000), which is considered gold-standard in the field, in addition to the Social Responsiveness Scale (SRS; Constantino, 2002) and Autism Spectrum Rating Scales (ASRS; Goldstein & Naglieri, 2013), which are more sensitive to milder forms of autism and account for new DSM-V criteria. ASD participants scored within the autism range on all three indices. (See SI for more details on diagnostic criteria.)

Study I included 30 autistic adolescents and 26 neurotypical adolescents. The ASD group ranged from ages 137.90 to 203.80 months (11 years 6 months to 16 years 11 months), with a mean age of 173.97 months (14 years 5 months). The NT group ranged from ages 132.00 to 211.10 months (11 years 0 months to 17 years 7 months), with a mean age of 179.94 months (14 years 8 months). Study II included 27 autistic adolescents and 25 neurotypical adolescents. (Participants in Study II represented a subsample of participants from Study I.) The ASD group ranged from ages 137.90 to 203.80 months (11 years 5 months to 16 years 11 months), with a

mean age of 176.42 months (14 years 8 months). The NT group ranged from ages 133.30 to 211.10 months (11 years 1 month to 17 years 7 months), with a mean age of 178.74 months (14 years 10 months). (See SI for more information on demographics.)

Procedures and Measures

Participants completed up to three appointments: a behavioral appointment, an imaging appointment, and an autism diagnostic appointment. During the behavioral appointment, participants and their parents/guardians completed measures assessing the proposed triad of social cognitive abilities (self-awareness/interoception, PT/cognitive empathy, and affective empathy), autistic features, and social competence. They also completed an IQ test. During the imaging appointment, participants completed an MRI simulation, an MRI scan where they completed the Self-Conscious Emotion Task (SCET), and the Self-Conscious Emotions Rating Task (SCERT). During the autism diagnostic appointment, participants in the ASD group completed the ADOS to confirm their diagnosis.

Social Cognitive Measures. To assess self-awareness/interoception, we used the Revised Self-Consciousness Scale for Children (RSCS-C; Scheier & Carver, 1985) and the Toronto Alexithymia Scale-20 Item (TAS-20; Bagby et al., 1994). We analyzed Public Self-Consciousness and Private Self-Consciousness RSCS-C subscores, and all three TAS-20 subscores: Difficulty Identifying Feelings, Difficulty Describing Feelings, and Externally-Oriented Thinking.

To assess PT abilities, we used the Reading the Mind in the Eyes Task-Child (RMET-C; Baron-Cohen, Wheelwright, Scahill, Lawson, & Spong, 2001) total score, which assesses the ability to infer emotional and mental states from photographs of eyes, and the ToM subscale of the Strange Stories Task-Revised (SS-R; White, Hill, Happé, & Frith, 2009), which assesses the

ability to make mental state attributions, reflecting double-bluffs, white lies, and advanced PT demands.

To assess cognitive and affective empathy, we used the Interpersonal Reactivity Index (IRI; Davis, 1983) and the Basic Empathy Scale (BES; Jolliffe & Farrington, 2006). We assessed cognitive empathy using the Perspective-Taking subscale of the IRI (reflecting the tendency to spontaneously adopt others' psychological point of view), and the Cognitive Empathy subscale of the BES. To assess affective empathy, we used the Empathic Concern subscale of the IRI (reflecting the "other-oriented" tendency to feel sympathy and concern for unfortunate others), the Personal Distress subscale of the IRI (reflecting the "self-oriented" tendency to feel personal anxiety and unease in stressful interpersonal settings), and the Affective Empathy subscale of the BES. Jolliffe and Farrington (2006) argued that the BES and IRI assess distinct empathy constructs. When assessing cognitive empathy, the IRI best reflects the ability and tendency to adopt others' perspectives, while the BES best reflects the ability and tendency to understand others' mental states. When assessing affective empathy, the IRI best reflects the tendency to feel sympathy for others, while the BES best reflects the tendency to emotionally resonate with others.

Autistic Features Measures. Autistic features were assessed using the Social Responsiveness Scale (SRS; Constantino, 2002), the Autism Spectrum Rating Scales (ASRS; Goldstein & Naglieri, 2013), and the Autism Spectrum Quotient-Adolescent (AQ-A; Baron-Cohen, Hoekstra, Knickmeyer, & Wheelwright, 2006). The SRS assesses autism-related social impairments and distinguishes ASD from other psychological disorders. We analyzed all five SRS subscores: Social Awareness, Social Cognition, Social Communication, Social Motivation, and Autistic Mannerisms. The ASRS assesses symptoms and behaviors associated with ASD and

supports diagnostic decision-making and intervention design. We analyzed ASRS total scores (reflecting the tendency to endorse behavioral traits similar to those demonstrated by autistic individuals), and ASRS DSM-V total scores (reflecting symptoms directly related to DSM-V diagnostic criteria). The AQ-A broadly assesses autistic traits, and the AQ-A total score was analyzed. While the ASRS and SRS are frequently used in diagnostic decision-making, the AQ-A is not. Thus, the ASRS and SRS were used as exclusionary criteria, while the AQ-A was not.

Social Competence Measures. To assess social competence, we used the child-reported Social Competence with Peers Questionnaire-Pupil (SCPQ-Pu; Spence, 1995) and the parent-reported Social Competence with Peers Questionnaire-Parent (SCPQ-P; Spence, 1995). We also used two treatment subscales from the ASRS: Peer Socialization (reflecting an attenuated interest and ability to successfully participate in activities that support the development and maintenance of peer relationships) and Social/Emotional Reciprocity (reflecting an attenuated ability to appropriately emotionally respond to others in social situations).

Demographics Measures. To assess generalized intelligence, we used the Weschler Abbreviated Scales of Intelligence-2nd Edition (WASI-II; Wechsler, 2011). We analyzed two-subscale Full Scale IQ scores, reflecting Vocabulary and Matrix Reasoning. To assess pubertal development, we used the male version of the Pubertal Development Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988) and analyzed mean PDS scores (excluding the comparative item). We also used an in-house questionnaire to assess children's ethnicity, parents' education levels, and annual household income.

Self-Conscious Emotions Task. During the MRI scan, participants completed the novel Self-Conscious Emotions Task (SCET), designed to prime SCE processing using dynamic, ecological video stimuli. The SCET was modeled off of a task by Tei and colleagues (2020) and

modified to investigate embarrassment and pride processing in adolescents. Participants were told that they would watch video clips of peers in a singing competition. Singers would have different singing abilities and would feel differently about their performance. Some singers would sing poorly and others would sing well; some singers would feel bad about their singing and others would feel good. Participants were instructed to watch each clip and pay attention to both how the singers sang and how they felt. After each clip, participants used a 4-point Likert scale to rate how embarrassed and proud each singer felt. Clips were 8-12 seconds and featured male and female adolescent actors. Songs were piloted for familiarity, likeability, and likelihood to be sung in a competition. (See SI for more details).

The SCET included 30 clips: 24 emotion clips and 6 neutral clips. Emotion clips portrayed singers singing poorly or well in front of two judges (to prime feelings of social evaluation) and acting embarrassed or proud of their performance. Embarrassment displays included: head tilted downward and to the side, downward eye gaze, hands touching face, shoulders hunched and slumped, and chest narrowed (Keltner, 1995; Keltner & Buswell, 1997). Pride displays included: head tilted upward and back, forward eye gaze, back arched, chest expanded, hands on hips, and a smile (Tracy & Robins, 2004, 2007b). Emotion clips were piloted for singing quality and emotion intensity. (See Figure SI for example stimuli.)

Emotion clips represented two SCE conditions (embarrassment, pride) and two PT conditions (low, high), such that clips varied according to the PT demands required to infer singers' emotional states. In low PT clips, singers conveyed emotions that matched the situational context (i.e., singing quality; e.g., singers sang poorly and acted embarrassed). Thus, participants could infer singers' emotions in low PT clips by either paying attention to singers' affective facial and postural cues or the situational context. In high PT clips, singers conveyed

emotions that did not match the situation context (e.g. singers sang well and acted embarrassed). Thus, participants could only infer singers' emotions in high PT clips by paying attention to singers' affective facial and postural cues, but not the situational context. Neutral clips portrayed actors standing still, displaying neutral facial expressions and body postures, without judges present. Announcers introduced them and instrumental versions of popular songs played in the background. A Gaussian filter blurred and distorted visual information. Neutral clips controlled for low-level visual, auditory, and semantic processing without providing emotional content or priming social evaluation. Thus, the task consisted of five conditions: embarrassment with low PT demands (EmbLo), embarrassment with high PT demands (EmbHi), pride with low PT demands (PrideLo), pride with high PT demands (PrideHi), and neutral emotion (Neutral).

Outside the MRI, participants completed the novel Self-Conscious Emotions Rating Task (SCERT), where they watched the same emotion clips and rated how empathically embarrassed and proud they felt for each singer using the same 4-point Likert scale. (See SI for details.) They also completed a semi-structured interview, where they described which emotion(s) they felt when they watched the emotion clips. (See SI for details). Thus, SCET scores reflected the ability to recognize SCEs, while SCERT scores and interview responses reflected the tendency to feel empathic SCEs.

Data Analysis

Behavioral Data. Behavioral data were analyzed in SPSS. To investigate group differences in the ability to infer SCEs and to feel empathic SCEs, we conducted 2(group: NT, ASD) x 2(emotion: embarrassment, pride) x 2(PT demands: low, high) repeated measures ANOVAs for inferred and empathic SCE ratings, separately. We investigated both congruent and incongruent SCE ratings. Congruent SCE ratings represented inferred or empathic SCEs that

matched singers' conveyed emotions (e.g., rating how embarrassed an embarrassed singer felt, or how empathically embarrassed one felt for an embarrassed singer). Incongruent SCE ratings represent inferred or empathic SCEs that did not match singers' conveyed emotions (e.g., rating how proud an embarrassed singer felt, or how empathically proud one felt for an embarrassed singer). We analyzed interview responses by conducting Pearson chi-square tests to compare group differences in the tendency to feel empathic basic emotions and empathic SCEs. To investigate group differences in social cognitive abilities (self-awareness/interoception, PT/cognitive empathy, and affective empathy), autistic features, and social competence, as well as their relationship with inferred and empathic SCE ratings, we conducted independent samples *t*-tests, correlations, and regressions.

Imaging Data Acquisition. Imaging data were acquired using a Siemens Skyra 3.0 Tesla head-only MRI scanner at the University of Oregon's Lewis Center for Neuroimaging. At the start of the scan, a circle localizer was acquired to allow the prescription of slices in the following scans. A high-resolution T2-weighted structural scan (MP-RAGE; magnetization-prepared rapid-gradient echo sequence) was acquired coplanar to the functional sequence (TR=2500 ms, TE=34 ms, flip angle=7°, matrix size=256 x 256, in-plane resolution=1 x 1 mm, 1 slice, slice thickness=1 mm), and a standard double-echo sequence field map was acquired. Next, participants completed the SCET while blood oxygen-level dependent, echo-planar images (BOLD-EPI; 200 and 203 volumes for the first and second run, respectively) were acquired across the whole brain with a T2*-weighted gradient echo sequence (TR=2000 ms, TE=25 ms, flip angle=90°, matrix size=64 x 64, in-plane resolution=2 x 2 mm, 72 slices, slice thickness=2 mm, interleaved acquisition) along the anterior commissure-posterior commissure (AC-PC) transverse oblique plane, as determined by the midsagittal section, using GRAPPA acceleration

parallel image acquisition ($R=2$). Javascript was used to present stimuli (via back-projection) and to collect participants' responses and reaction times (RTs). Participants used an MRI-compatible button-box to make task-relevant ratings. All participants used a right-handed button box. Three participants were left-handed/ambidextrous; they confirmed they felt comfortable and practiced using a right-handed button-box prior to the MRI scan. Foam padding was used to prevent head movement, and MRI-compatible earbuds were worn to protect hearing and deliver auditory stimuli.

Imaging Data Analysis. Imaging data were preprocessed using Statistical Parametric Mapping (SPM) 12 software (Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB. Images were converted from DICOM to NIfTI format using MRIconvert (<https://lcnj.uoregon.edu/~jolinda/MRIconvert>). Each participant's MP-RAGE was coregistered to SPM's canonical structural template (MNI-152). In cases where coregistration was unsuccessful, modifications were made by manually orienting the coregistered MP-RAGE to the MNI-152 structural template. Voxel displacement maps were calculated for each participant using a double-echo field map (see <https://lcnj.uoregon.edu/kb-articles/kb-0003>) and functional images were realigned and unwarped using participant-specific voxel displacement maps. (One participant was missing a field map. To address this discrepancy, an average of all participants' phase maps was calculated using FSL (FMRIB Software Library). Functional images were unwarped using the average of all participants' phase maps and the specific participant's structural image as inputs for the phase and magnitude maps, respectively.) The realigned and unwarped mean image and functional images were then coregistered to the coregistered MP-RAGE. Each participant's coregistered MP-RAGE was segmented into six tissue types (corresponding to gray matter, white matter, cerebral spinal fluid, bone, skin, and

air/background) and combined to create a DARTEL template, representing all 56 participants. Data were normalized to the DARTEL template and smoothed using a 6 mm full-width, half-maximum (FWHM) isotropic Gaussian kernel. (See SI for imaging data exclusionary criteria.)

First-level, single-subject models were calculated in SPM12. For each participant, condition effects were estimated according to the general linear model, using a canonical hemodynamic response function. An optimal threshold mask representing the average of all participants' combined, binarized, and smoothed gray matter and white matter maps was applied to the data. A 128 second high-pass filter was used to remove low-frequency noise and an autoregressive model, AR(1), was used to estimate temporal autocorrelation. Subject-level models included five regressors of interest (each condition: EmbLo, EmbHi, PrideLo, PrideHi, and Neutral) and seven regressors of no interest (a trash variable representing instructions, two trash variables representing rating blocks for embarrassment and pride, five motion parameters representing: i) and ii) Euclidean distance for translations and rotations, respectively; iii) and iv) their first derivatives; and v) a binary-coded variable marking individual volumes with motion artefacts detected automatically or manually). Planned linear contrasts were created to identify regions where activity was greater for each emotion condition compared to neutral condition (EmbLo>Neutral, EmbHi>Neutral, PrideLo>Neutral, PrideHi>Neutral).

To estimate population effects, whole-brain, group-level models were calculated in AFNI (version 17.1.07) implemented in R (version 3.3.3), given that AFNI's 3dMVM properly accounts for subject-level variance, appropriately models main effects and interaction effects for mixed-design models (including between-subject and within-subject variables), and appropriately analyzes main and interaction effects for groups that have an unequal number of participants. Subject-level contrasts were entered into a 2(group: NT, ASD) x 2(emotion:

embarrassment, pride) x 2(PT demands: low, high) repeated measures ANOVA, and post-hoc *t*-tests and ANOVAs were specified. Results were masked using the same average optimal threshold mask applied at the subject-level. A combined voxel-height and cluster-extent threshold was calculated to control for Type 1 error using Monte Carlo simulations via AFNI's 3dClustSim (version 17.1.07); an $\alpha=0.05$ was achieved via $p<0.001$, $k>30$. Smoothness estimates entered into 3dClustSim represented an average of subject-level spatial autocorrelation function (acf) parameters based on individual subjects' residuals from the group-level model, as calculated by 3dFWHMx using the -acf flag and the average optimal threshold mask.

To investigate significant interaction effects, masks of significant clusters of activity for each group-level contrast of interest (main effect of group, group x emotion interaction effect, group x PT interaction effect, and group x emotion x PT interaction effect) were created using 3dClust. These cluster-specific masks were used to extract average parameter estimates from subject-level contrast maps (representing EmbLo>Neutral, EmbHi>Neutral, PrideLo>Neutral, PrideHi>Neutral) for each participant using 3dmaskave. Parameter estimates were entered into post-hoc *t*-tests in SPSS to explore simple effects. For three-way interactions, we conducted paired *t*-tests for each group to explore the effect of PT demands for each emotion (EmbLo vs EmbHi; PrideLo vs PrideHi), and to explore the effect of emotion for each PT demand level (EmbLo vs PrideLo; EmbHi vs PrideHi).

Given that prior studies have only explored SCE processing during low PT demands (and ASD studies have only explored embarrassment during low PT demands; EmbLo>Neutral), we additionally conducted independent samples *t*-tests to investigate group differences for each emotion condition (NT vs ASD EmbLo>Neutral, EmbHi>Neutral, PrideLo>Neutral, PrideHi>Neutral), as well as for each emotion during high relative to low PT demands, to

investigate the modulatory role of heightened PT demands (NT vs ASD EmbHi>Neutral vs EmbLo>Neutral, PrideHi>Neutral vs PrideLo>Neutral). Results were considered significant at $p \leq 0.05$ (uncorrected), and marginally significant at $p \leq 0.06$ (uncorrected).

We also conducted complementary ROI analyses. Significant clusters from the intercept that represented *a priori* regions of interest were used as ROIs. Parameter estimates were similarly extracted from masks representing these clusters and entered into 2(group: NT, ASD) x 2(emotion: embarrassment, pride) x 2(PT demands: low, high) repeated measures ANOVAs and analyzed in SPSS. Results were considered significant at $p \leq 0.05$ (uncorrected), and marginally significant at $p \leq 0.06$ (uncorrected). Post-hoc analyses were conducted to explore main effects and interaction effects using the same analysis plan as mentioned above. We also conducted independent samples *t*-test to explore group differences in activity within each ROI during each emotion condition (NT vs ASD: EmbLo>Neutral, EmbHi>Neutral, PrideLo>Neutral, PrideHi>Neutral), regardless if a significant main or interaction effect was observed. Anatomical labels were determined via visual inspection and confirmed with AFNI's automated labeling program.

In addition, we conducted two 2(emotion: embarrassment, pride) x 2(PT demands: low, high) repeated measures ANOVAs for the NT and ASD groups, separately. Combined voxel-height and cluster-extent thresholds were calculated to control for Type 1 error using Monte Carlo simulations via AFNI's 3dClustSim (version 17.1.07); an $\alpha=0.05$ was achieved via $p < 0.001$, $k=45$ and $k=46$, for NT and ASD groups, respectively. Parameter estimates were extracted from masks representing significant clusters and analyzed in SPSS. Results were considered significant at $p \leq 0.05$ (uncorrected), and marginally significant at $p \leq 0.06$ (uncorrected).

This project was pre-registered on the Open Science Framework, <https://osf.io/skg8h>.

STUDY I RESULTS: THE SUBJECTIVE EXPERIENCE OF SCES

SCE Processing

SCE processing was assessed in two ways: the ability to infer SCEs experienced by others, and the ability/tendency to feel empathic SCEs on behalf of others. Inferred SCEs were assessed using the SCET, and empathic SCEs were assessed using the SCERT. During the SCET and SCERT, participants made both embarrassment and pride ratings, regardless of the emotion being conveyed. Thus, participants made *congruent* SCE ratings, which matched the emotion the singer conveyed, and *incongruent* SCE ratings, which did not match the emotion the singer conveyed. When describing the results, the emotion included in the label represents the emotion the singer conveyed. For example, if a participant observed a singer singing poorly and acting embarrassed, inferred *congruent* embarrassment ratings represent evaluations of how *embarrassed* (congruent emotion) the *embarrassed* (conveyed emotion) singer felt; inferred *incongruent* embarrassment ratings represent evaluations of how *proud* (incongruent emotion) the *embarrassed* (conveyed emotion) singer felt. Similarly, empathic *congruent* embarrassment ratings represent how empathically *embarrassed* (congruent emotion) the participant felt for the *embarrassed* (conveyed emotion) singer; and empathic *incongruent* embarrassment ratings represent how empathically *proud* (incongruent emotion) the participant felt for the *embarrassed* (conveyed emotion) singer. Clips represented either low or high PT demands. In low PT clips, singers conveyed emotions that matched the situational context (i.e., singing quality; e.g., singers sang poorly and acted embarrassed, like the example above). In high PT clips, singers conveyed emotions that did not match the situational context (e.g., singers sang well and acted embarrassed). Thus, inferred *congruent* embarrassment ratings during *low PT* demands represent

evaluations of how *embarrassed* (congruent emotion) the *embarrassed* (conveyed emotion) singer felt when (s)he sang *poorly* (low PT); while inferred *congruent* embarrassment ratings during *high PT* demands represent evaluations of how *embarrassed* (congruent emotion) the *embarrassed* (conveyed emotion) singer felt when (s)he sang *well* (high PT); and inferred *incongruent* embarrassment ratings during *high PT* demands represent evaluations of how *proud* (incongruent emotion) the *embarrassed* (conveyed emotion) singer felt when (s)he sang *well* (high PT). (See Table 1 for mean inferred and empathic SCE ratings for each group.)

Table 1.
Group Comparisons of Mean Self-Conscious Emotion Ratings

Rating Type	Group	N	M (SD)			
			EmbLo	EmbHi	PrideLo	PrideHi
Inferred Congruent	NT	26	2.58 (0.34)	2.31 (0.34)	2.61 (0.25)	2.20 (0.40)
	ASD	30	2.62 (0.30)	2.22 (0.48)	2.69 (0.35)	2.15 (0.54)
Inferred Incongruent	NT	26	0.60 (0.36)	1.03 (0.51)	0.34 (0.27)	0.61 (0.27)
	ASD	30	0.58 (0.39)	1.09 (0.57)	0.51 (0.38)	1.04 (0.62)
Empathic Congruent	NT	26	1.56 (1.01)	1.01 (0.76)	1.83 (0.79)	0.76 (0.62)
	ASD	29	1.76 (0.88)	1.16 (0.87)	2.00 (0.79)	1.08 (0.72)
Empathic Incongruent	NT	26	0.63 (0.63)	1.44 (0.70)	0.35 (0.55)	1.46 (0.84)
	ASD	29	0.74 (0.74)	1.29 (0.76)	0.34 (0.48)	1.16 (0.88)

Note. One ASD participant was missing SCERT data (empathic emotion ratings). ASD=autism spectrum disorder; EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; NT=neurotypical; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands; PT=perspective-taking.

Inferred Congruent SCEs. Results for inferred congruent SCE ratings revealed a main effect of PT demands, $F(1,54)=107.97, p<0.001$; and an emotion by PT demands interaction effect, $F(1,54)=4.16, p=0.046$. Participants inferred more intense congruent SCEs when PT demands were low compared to high (e.g., they inferred greater embarrassment when singers sang poorly and acted embarrassed than when singers sang well and acted embarrassed), $t(55)=10.37, p<0.001$. This pattern held for both embarrassment, $t(55)=7.01, p<0.001$; and pride,

$t(55)=8.65, p<0.001$. Thus, the ASD and NT groups inferred similarly intense congruent SCEs, which were similarly impacted by PT demands. (See Table 1 and Figure 1.)

Figure 1.

Group Comparisons of Mean Inferred Congruent and Incongruent SCE Ratings

Panel A. Inferred congruent SCE ratings. *Panel B.* Inferred incongruent SCE ratings. ASD=autism spectrum disorder; NT=neurotypical; PT=perspective-taking demands.

Inferred Incongruent SCEs. Results for inferred incongruent SCE ratings revealed a main effect of group, $F(1,54)=4.49, p=0.039$; a main effect of emotion, $F(1,54)=7.10, p=0.010$; a main effect of PT demands, $F(1,54)=114.09, p<0.001$; and a group by PT demands interaction effect, $F(1,54)=4.29, p=0.043$. The main effect of group revealed that broadly, the ASD group inferred more intense incongruent SCEs than the NT group, $t(54)=-2.12, p=0.039$. The main effect of emotion revealed that participants inferred more intense incongruent embarrassment than incongruent pride (e.g., participants inferred more intense pride when singers acted embarrassed than embarrassment when singers acted proud), $t(55)=2.49, p=0.016$. The main effect of PT demands revealed that participants broadly inferred more intense incongruent SCEs during high compared to low PT demands (e.g., they inferred more intense pride when singers sang well and acted embarrassed than when singers sang poorly and acted embarrassed), $t(55)=-10.55, p<0.001$. The group by PT demands interaction effect revealed that both groups inferred

more intense incongruent SCEs during high compared to low PT demands (e.g., groups inferred more intense pride when singers sang well and acted embarrassed than when singers sang poorly and acted embarrassed), $t(25)=-7.45, p<0.001$ for the NT group; and $t(28)=-6.91, p<0.001$ for the ASD group. When PT demands were low, both groups inferred similarly intense incongruent SCEs; however, when PT demands were high, the ASD group inferred more intense incongruent SCEs, $t(54)=-2.36, p=0.022$, (e.g., groups inferred similarly intense pride for singers who sang poorly and acted embarrassed, but the ASD group inferred more intense pride for singers who sang well and acted embarrassed). Thus, the ASD group inferred more intense incongruent SCEs, which was driven by heightened PT demands. (See Table 1, Figure 1.)

Group Comparison of Inferred Congruent and Inferred Incongruent SCEs. Group differences in inferred incongruent SCE ratings prompted an exploratory analysis investigating potential group differences in the intensity of inferred congruent SCE ratings relative to inferred incongruent SCE ratings. Difference scores between inferred congruent SCE ratings and inferred incongruent SCE ratings were calculated for each clip and averaged across emotion conditions (e.g., EmbLo, EmbHi, PrideLo, PrideHi) for each participant. Low difference scores represented more similar intensity ratings for congruent and incongruent SCEs, while high difference scores represented less similar intensity ratings. Average difference scores were entered into a 2(group) x 2(emotion) x 2(PT demands) repeated measures ANOVA. There was a main effect of PT demands, $F(1,54)=157.00, p<0.001$; qualified by a group by PT demands interaction effect, $F(1,54)=4.96, p=0.030$. Difference scores were greater when PT demands were low compared to high, $t(55)=12.29, p<0.001$. This pattern held for the NT group, $t(25)=7.22, p<0.001$; and the ASD group, $t(29)=10.49, p<0.001$. When PT demands were low, groups endorsed similarly intense difference scores, $t(54)=0.18, ns$; however, when PT demands were high, the NT group

endorsed more intense difference scores than the ASD group, $t(54)=2.08$, $p=0.042$. Thus, when PT demands were high, the ASD group provided more similar intensity ratings for congruent and incongruent SCEs than the NT group.

Empathic Congruent SCEs. Results for empathic congruent SCE ratings revealed a main effect of PT demands, $F(1,53)=109.71$, $p<0.001$; qualified by an emotion by PT demands interaction effect, $F(1,53)=2.39$, $p<0.001$. Participants felt more intense empathic congruent SCEs when PT demands were low relative to high, $t(54)=10.62$, $p<0.001$; this pattern was observed for empathic congruent embarrassment, $t(54)=8.34$, $p<0.001$; and empathic congruent pride, $t(54)=9.51$, $p<0.001$. When PT demands were low, participants felt more intense empathic congruent pride than embarrassment (e.g., they felt more intense pride for singers who sang well and acted proud than they felt embarrassment for singers who sang poorly and acted embarrassed), $t(54)=-2.62$, $p=0.011$. However, when PT demands were high, participants felt similarly intense empathic congruent embarrassment and pride (e.g., they felt similarly intense embarrassment for singers who sang well and acted embarrassed as they felt pride for singers who sang poorly and acted proud). Thus, the ASD and NT groups felt similarly intense empathic congruent SCEs, which were similarly impacted by PT demands. (See Table 1, Figure 2.)

Figure 2.*Group Comparisons of Mean Empathic Congruent and Incongruent SCE Ratings*

Panel A. Empathic congruent SCE ratings. *Panel B.* Empathic incongruent SCE ratings. ASD=autism spectrum disorder; NT=neurotypical; PT=perspective-taking demands.

Empathic Incongruent SCEs. Results for empathic incongruent SCE ratings revealed a main effect of PT demands, $F(1,53)=110.58, p<0.001$; qualified by an emotion by PT demands interaction effect, $F(1,53)=9.10, p=0.004$. Participants felt more intense empathic incongruent emotions when PT demands were high relative to low, $t(54)=-10.23, p<0.001$; this pattern was observed for empathic incongruent embarrassment (e.g., they felt more intense pride for singers who sang well and acted embarrassed than for singers who sang poorly and acted embarrassed), $t(54)=-8.20, p<0.001$; and empathic incongruent pride (e.g., they felt more intense embarrassment for singers who sang poorly and acted proud than for singers who sang well and acted proud), $t(54)=-9.44, p<0.001$. When PT demands were low, participants felt more intense empathic incongruent embarrassment than pride (e.g., they felt more intense pride for singers who sang poorly and acted embarrassed than they felt embarrassment for singers who sang well and acted proud), $t(54)=3.18, p=0.002$. When PT demands were high, participants felt similarly intense empathic incongruent embarrassment and pride (e.g., they felt similarly intense pride for singers who sang well and acted embarrassed as they felt embarrassment for singers who sang

poorly and acted proud). Thus, the ASD and NT groups felt similarly intense empathic incongruent SCEs, which were similarly impacted by PT demands. (See Table 1, Figure 2.)

Interview Responses. In addition to investigating group differences in inferred and empathic SCE intensity ratings, we also explored group differences in the tendency to broadly feel empathic emotions for singers based on their performance. There were no group differences in the tendency to feel basic, nonsocial emotions (e.g., feel bad), $X^2(1)=0.42$, *ns*; nor SCEs (e.g., feel embarrassed), $X^2(1)=0.29$, *ns*, for singers who sang poorly. There were also no group differences in the tendency to feel basic, nonsocial emotions (e.g., feel good), $X^2(1)=0.42$, *ns*; nor SCEs (e.g., feel proud), $X^2(1)=0.28$, *ns*, for singers who sang well. These findings converge with results from the empathic SCE intensity ratings analyses.

Group Comparisons of Behavioral Measures

Social Cognitive Abilities. The ASD group reported reduced self-awareness/interoception. (See Table 2.) Specifically, they reported lower Public Self-Consciousness and lower Private Self-Consciousness scores on the RSCS-C. They also reported elevated Alexithymia scores on the TAS-20, reflecting higher scores on the Difficulty Describing One's Own Feelings and Externally-Oriented Thinking subscales.

The ASD group reported reduced PT/cognitive empathy, representing attenuated mentalizing abilities and reduced real-world PT tendencies. (See Table 2.) While there were no group differences on task-based measures (RMET-C, SS-R), the ASD group scored lower on both self-report questionnaires (BES, IRI). The Cognitive Empathy subscale of the BES represents the ability and tendency to understand other people's mental states and is associated with PT skills and ToM. The Perspective-Taking subscale of the IRI represents the ability and tendency to adopt other people's point of view, thus representing cognitive empathy. The ASD

group reported lower Cognitive Empathy scores on the BES, representing attenuated mental state understanding, and marginally lower PT tendencies on the IRI.

In contrast, the ASD and NT groups reported similar levels of affective empathy. (See Table 2.) Groups scored similarly on the Affective Empathy subscale of the BES (representing emotional resonance), and the Empathic Concern and Personal Distress subscales of the IRI (representing “other-oriented” sympathy and “self-oriented” personal anxiety, respectively).

Autism Features. The ASD group reported more intense autistic features and greater difficulties in social awareness, social cognition, social communication, and social motivation, as reflected by higher total SRS, total ASRS, total ASRS DSM-V, and AQ-A scores. (See Table 2.)

Social Competence. The ASD group reported lower levels of social competence, as reflected by child- and parent-reported SCPQ-Pu and SCPQ-P total scores, and Peer Socialization and Social/Emotional Responsivity subscores on the ASRS. (See Table 2.)

Table 2.
Group Comparisons of Behavioral Measures

Measure	Group	N	M (SD)	T Statistic
Public Self-Consciousness (RSCS-C)	NT	26	30.58 (7.08)	$t(54)=2.49, p=0.016^*$
	ASD	30	25.08 (9.14)	
Private Self-Consciousness (RSCS-C)	NT	26	42.31 (5.52)	$t(54)=2.26, p=0.028^*$
	ASD	30	38.66 (6.43)	
Difficulty Describing Feelings (TAS-20)	NT	26	13.81 (3.41)	$t(53)=-2.16, p=0.035^*$
	ASD	29	16.10 (4.35)	
Difficulty Identifying Feelings (TAS-20)	NT	26	16.42 (3.73)	$t(53)=-1.71, ns$
	ASD	29	18.74 (5.95)	
Externally Oriented Feelings (TAS-20)	NT	26	20.50 (3.82)	$t(53)=-2.57, p=0.013^*$
	ASD	29	23.60 (4.97)	
	ASD	29	58.45 (12.58)	
Theory of Mind (RMET-C)	NT	26	20.54 (2.69)	$t(54)=1.55, ns$
	ASD	30	19.33 (3.08)	
Theory of Mind (SS-R)	NT	26	13.42 (2.23)	$t(54)=1.53, ns$
	ASD	30	12.33 (2.97)	
Perspective-Taking (IRI)	NT	26	15.46 (2.66)	$t(54)=1.93, p=0.059^\dagger$
	ASD	30	13.93 (3.18)	
Empathic Concern (IRI)	NT	26	13.49 (2.30)	$t(54)=0.23, ns$
	ASD	30	13.32 (3.22)	
Personal Distress (IRI)	NT	26	14.19 (2.73)	$t(54)=-0.27, ns$
	ASD	30	14.43 (3.64)	
Cognitive Empathy (BES)	NT	26	36.73 (3.19)	$t(53)=4.57, p<0.001^{**}$
	ASD	29	31.69 (4.74)	
Affective Empathy (BES)	NT	25	36.96 (5.72)	$t(52)=1.07, ns$
	ASD	29	34.86 (8.25)	
Autism Social Impairment (SRS)	NT	26	44.88 (4.69)	$t(54)=-18.32, p<0.001^{**}$
	ASD	30	81.53 (9.21)	
Autism Symptomatology (ASRS)	NT	26	44.58 (6.20)	$t(53)=-15.20, p<0.001^{**}$
	ASD	29	67.45 (4.94)	
DSM-V Autism Symptomatology (ASRS)	NT	26	45.12 (6.96)	$t(53)=-14.00, p<0.001^{**}$
	ASD	29	70.62 (6.57)	
Autistic Traits (AQ-A)	NT	25	11.05 (4.92)	$t(53)=-14.53, p<0.001^{**}$
	ASD	30	34.46 (6.69)	
Social Competence (SCPQ-Pu)	NT	26	15.23 (3.69)	$t(54)=6.82, p<0.001^{**}$
	ASD	30	8.80 (3.37)	
Social Competence (SCPQ-P)	NT	26	15.38 (4.23)	$t(54)=9.68, p<0.001^{**}$

	ASD	30	4.83 (3.92)	
Peer Socialization (ASRS)	NT	26	45.35 (7.05)	$t(53)=-14.11, p<0.001^{**}$
	ASD	29	71.62 (6.75)	
Social/Emotional Reciprocity (ASRS)	NT	26	44.69 (7.66)	$t(53)=-11.64, p<0.001^{**}$
	ASD	29	66.28 (6.07)	

Note. AQ-A=Autism Spectrum Quotient-Adolescent; ASD=autism spectrum disorder; ASRS=Autism Spectrum Rating Scales; BES=Basic Empathy Scale; DSM-V=Diagnostic Statistical Manual-5th Edition; IRI=Interpersonal Reactivity Index; NT=neurotypical; RMET-C=Reading the Mind in the Eyes-Child; RSCS-C=Revised Self-Consciousness Scale-Child; SCPQ-Pu=Social Competence with Peers Questionnaire-Pupil; SCPQ-P=Social Competence with Peers Questionnaire-Parent; SRS=Social Responsiveness Scale; SS-R=Strange Stories Task-Revised; TAS-20=Toronto Alexithymia Scale-20 Item.

† $p<0.06$; * $p<0.05$; ** $p<0.005$

Correlational Analyses

Social Cognitive Abilities. Inferred congruent SCE ratings did not correlate with social cognitive abilities. However, inferred incongruent SCE ratings correlated negatively with ToM scores on the SS-R. (See Table 3.) This pattern held when PT demands were high, $r(54)=-0.34$, $p=0.011$; but not low, $r(54)=-0.10$, *ns*; although differences between the two correlations were not significant ($Z=-1.31$, *ns*).

Empathic congruent SCE ratings correlated positively with Affective Empathy scores on the BES. (See Table 3.) This pattern held when PT demands were low, $r(51)=0.32$, $p=0.021$; and high, $r(51)=0.32$, $p=0.018$. In addition, empathic incongruent SCE ratings correlated positively with Affective Empathy scores on the BES. (See Table S3.) This pattern held when PT demands were low, $r(51)=0.28$, $p=0.042$; and high, $r(51)=0.40$, $p=0.003$.

Table 3.*Correlations Between Mean SCE Ratings and Social Cognitive Measures*

Measure	Inferred Congruent	Inferred Incongruent	Empathic Congruent	Empathic Incongruent
Public Self-Consciousness (RSCS-C)	-0.08	0.04	-0.03	0.19
Private Self-Consciousness (RSCS-C)	-0.07	0.10	0.13	0.21
Difficulty Describing Feelings (TAS-20)	0.11	-0.08	-0.07	-0.20
Difficulty Identifying Feelings (TAS-20)	0.08	-0.04	0.02	-0.06
Externally Oriented Feeling (TAS-20)	0.02	0.18	0.14	0.01
Theory of Mind (RMET-C)	-0.18	-0.07	-0.06	-0.12
Theory of Mind (SS-R)	0.07	-0.27*	-0.13	-0.01
Perspective-Taking (IRI)	0.06	-0.15	-0.12	0.08
Empathic Concern (IRI)	0.10	-0.12	-0.15	-0.01
Personal Distress (IRI)	-0.08	0.12	0.19	0.12
Cognitive Empathy (BES)	0.05	-0.22	-0.04	0.20
Affective Empathy (BES)	-0.06	-0.20	0.34*	0.41**

Note. BES=Basic Empathy Scale; IRI=Interpersonal Reactivity Index; RSCS-C=Revised Self-Consciousness Scale-Child; RMET-C=Reading the Mind in the Eyes-Child; SS-R=Strange Stories Task-Revised; TAS-20=Toronto Alexithymia Scale-20 Item.

df range: 51-54; * $p < 0.05$; ** $p < 0.005$

Autistic Features. Inferred congruent SCE ratings did not correlate with autistic features. However, inferred incongruent SCE ratings correlated positively with SRS scores. (See Table 4.) This pattern held when PT demands were high, $r(54)=0.35$, $p=0.009$; but not low, $r(54)=0.19$, ns ; although differences were not significant ($Z=0.89$, ns). Neither empathic congruent nor empathic incongruent SCE ratings correlated with autistic features.

Table 4.
Correlations Between Mean SCE Ratings and Autistic Features/Traits Measures

Measure	Inferred Congruent	Inferred Incongruent	Empathic Congruent	Empathic Incongruent
Autism Social Impairment (SRS)	-.06	.32*	.11	-.10
Autism Symptomatology (ASRS)	-.11	.24	.13	-.15
DSM-V Autism Symptomatology (ASRS)	-.11	.23	.11	-.17
Autistic Traits (AQ-A)	-.00	.20	.11	-.14

Note. AQ-A=Autism Spectrum Quotient-Adolescent; ASRS=Autism Spectrum Rating Scales; DSM-V=Diagnostic Statistical Manual-5th Edition; SRS=Social Responsiveness Scale.

df range: 52-54; * $p<0.05$; ** $p<0.001$

Social Competence. Neither inferred congruent, inferred incongruent, nor empathic congruent SCE ratings correlated with social competence. However, empathic incongruent SCE ratings correlated positively with SCPQ-Pu scores (reflecting participants' self-evaluations of their own social competence), $r(53)=0.32$, $p=0.019$. (See Table 5.) This pattern held when PT demands were high, $r(54)=0.30$, $p=0.028$; but not low, $r(54)=0.24$, ns ; although differences were not significant ($Z=0.33$, ns). Interestingly, SCPQ-P scores (reflecting parents' evaluations of their children's social competence) correlated negatively with inferred incongruent SCE ratings

when PT demands were high, $r(54)=-0.31$, $p=0.021$; but not low, $r(54)=-0.07$, ns ; although differences were not significant ($Z=-1.29$, ns).

Table 5.

Correlations Between Mean SCE Ratings and Social Competence Measures

Measure	Inferred Congruent	Inferred Incongruent	Empathic Congruent	Empathic Incongruent
Social Competence (SCPQ-Pu)	.05	-.22	.03	.32*
Social Competence (SCPQ-P)	.07	-.24	-.14	.13
Peer Socialization (ASRS)	-.09	.23	.16	-.14
Social/Emotional Reciprocity (ASRS)	-.12	.23	.11	-.12

Note. ASRS=Autism Spectrum Rating Scales; SCPQ-Pu=Social Competence with Peers Questionnaire-Pupil; SCPQ-P=Social Competence with Peers Questionnaire-Parent.

df range: 52-54; * $p<0.05$; ** $p<0.001$

Regression Analyses

We also conducted separate step-wise regression analyses for each SCE condition, with variables representing the proposed triad of social cognitive abilities, as well as group and age, as predictors. Given high multicollinearity between group and measures of autistic features, the later were not included in the models. Broadly, results from the regression analyses replicated results from the correlational analyses. Most notably, ToM scores on the SS-R was a significant predictor of inferred incongruent SCE ratings during high PT demands, $\beta=-0.33$, $t(51)=-2.50$, $p=0.016$, and the overall model fit was $R^2=0.11$, $F(1,51)=6.23$, $p=0.016$. Group was a marginally significant predictor, $\beta=0.26$, $t(51)=1.96$, $p=0.055$, and thus, not included in the model.

In addition, Affective Empathy scores on the BES were significant predictors of empathic congruent and incongruent SCE ratings during low and high PT demands. Specifically, for empathic congruent SCE ratings during low PT demands, Affective Empathy scores on the BES was a significant predictor, $\beta=0.32$, $t(50)=2.35$, $p=0.023$, and the overall model fit was $R^2=0.10$, $F(1,50)=5.52$, $p=0.023$. Public Self-Consciousness scores on the RSCS-C were a marginally significant predictor, $\beta=-0.27$, $t(50)=-1.98$, $p=0.053$, and thus, not included in the model. For empathic congruent SCE ratings during high PT demands, Affective Empathy scores on the BES was a significant predictor, $\beta=0.36$, $t(49)=2.74$, $p=0.008$, and group was also a significant predictor, $\beta=0.28$, $t(49)=2.14$, $p=0.037$. The overall model fit was $R^2=0.18$, $F(2,49)=5.35$, $p=0.008$. For empathic incongruent SCE ratings during low PT demands, Affective Empathy score on the BES was a significant predictor, $\beta=0.28$, $t(50)=2.04$, $p=0.046$, and the overall model fit was $R^2=0.08$, $F(1,50)=4.18$, $p=0.046$. For empathic incongruent SCE ratings during high PT demands, Affective Empathy score on the BES was a significant predictor, $\beta=0.39$, $t(50)=3.03$, $p=0.004$, and the overall model fit was $R^2=0.16$, $F(1,50)=9.17$, $p=0.004$.

Furthermore, for inferred incongruent SCE ratings during low PT demands, BES Affective Empathy scores were a significant predictor, $\beta=-0.31$, $t(51)=-2.31$, $p=0.025$, and the overall model fit was $R^2=0.09$, $F(1,51)=5.31$, $p=0.025$. Age was a marginally significant predictor, $\beta=-0.26$, $t(1,50)=-1.99$, $p=0.053$, and thus, not included in the model. No step-wise regression models fit our data for inferred congruent SCE ratings during low PT demands or high PT demands, and there were no marginally significant predictors.

STUDY I DISCUSSION: THE SUBJECTIVE EXPERIENCE OF SCES

The goal of Study I was to investigate the subjective experience of SCE processing in autistic adolescent males with average/above average IQ, relative to age- and IQ-matched neurotypical adolescents. We explored group differences in the intensity of inferred and empathic SCE ratings, as well as the modulatory role of heightened PT demands. Broadly, autistic adolescents demonstrated an intact ability to recognize SCEs and to feel empathic SCEs for others, and they did so with similar intensity as neurotypical adolescents; however, they made atypical emotional inferences when PT demands were high. Social cognitive challenges, in particular, difficulties inferring mental states, may underlie atypical SCE processing in ASD, which may, in turn, impact real-world social interactions and interpersonal success.

SCE Attributions

Inferred Congruent SCEs. Our findings demonstrate that autistic adolescents can both *identify* SCEs and *recognize their intensity* to a similar degree as neurotypical peers. Given that participants made Likert ratings and not binary responses (e.g., positive/negative, yes/no), a lack of group differences in inferred congruent SCE ratings cannot be attributed to autistic adolescents performing at chance or relying on low-level valence attributions. These results converge with reports of intact emotion recognition abilities in “high-functioning” autistic youth (e.g., Capps et al., 1992; Heerey et al., 2003). While ASD has historically been associated with impaired emotion recognition abilities (Hobson, 1986), our findings support theories which suggest that challenges may be driven by lower verbal intelligence or developmental delays in younger children (Bowler, 1992; Buitelaar, van der Wees, Swaab-Barneveld, & van der Gaag, 1999; Happé, 1995; Golan et al., 2006; Teunisse & de Gelder, 2001) and may not accurately represent the capabilities of older adolescents and adults with higher verbal intelligence.

Comparing paradigm designs may enhance our understanding of emotion recognition abilities in ASD, as well as potentially clarify inconsistencies within the literature. Prior studies have predominantly used static stimuli, particularly photographs of eyes, to explore emotion recognition in ASD. While this approach allows researchers to pinpoint which types of cues are critical for performing distinct tasks, it may inadvertently introduce a group-specific handicap that is not experienced outside of a laboratory setting. While neurotypical individuals generally reference eye regions to make emotion attributions (Klin et al., 2002), autistic individuals often demonstrate an aversion (or reduced sensitivity) to direct eye contact, as represented by more frequent gaze shifts away from, and shorter gaze fixations on, eye regions (Bons et al., 2013; Kliemann, Dziobek, Hatri, Steimke, & Heekeren, 2010; Klin et al., 2002).

In contrast, body/postural cues may be more salient in ASD. Autistic individuals display longer gaze fixations on body regions than eye regions (Klin et al., 2002; Speer, Cook, McMahon, & Clark, 2007); and autistic and neurotypical individuals demonstrate equivalent recognition of nonsocial emotions when referencing photographs of bodies compared to eyes (Peterson, Slaughter, & Brownell, 2015). Thus, frequently used unimodal tasks (particularly those that capitalize on static images of eyes) may fail to accurately represent real-world social interactions and may unintentionally “stack the cards” against autistic individuals (Kliemann et al., 2010). In contrast, the SCET provides multimodal affective information, including facial, gestural, body/postural, and speech/prosodic cues. This is particularly valuable for studying SCEs, which rely heavily on body/postural cues, and which cannot be identified via facial cues alone (Beer & Keltner, 2004). Thus, the current study may be better positioned to investigate real-world emotion recognition abilities and challenges in autistic adolescents.

Our findings shed light onto the broader emotion processing capabilities of autistic youths. A lack of group differences in inferred congruent SCE ratings suggests that autistic adolescents can appropriately select salient affective cues from facial expressions, body postures, and prosody to infer emotional states, which converges with prior reports that autistic individuals use affective information from multiple sources during emotion recognition (Loveland et al., 1997). These findings suggest that when viewing targets conveying high-intensity SCEs, autistic adolescents may not require explicit instructions (or additional prompting) to direct their attention to salient cues. These results also suggest that autistic adolescents can identify salient affective cues even when they are embedded within more complex, dynamic scenes. By requiring participants to identify and process multiple, dynamic affective cues, this study offers a more ecologically-valid design that more accurately simulates real-world social interactions.

Of particular significance, our findings suggest that intact emotion recognition abilities in ASD extend beyond basic, nonsocial emotions to include more complex, social emotions. While a small number of studies have explored (and generally report intact) SCE recognition in ASD, conclusions have often been based on the recognition of one stimulus (Heerey et al., 2003; Williams & Happé, 2010). Two prior studies explored SCEs using more diverse stimuli. Tracy and colleagues (2011) found that autistic adolescents recognize pride in photographs; however, they only reported the presence or absence of an emotion, not its intensity. Adler and colleagues (2015) found that autistic individuals recognize embarrassment in videos and make similarly intense emotional inferences as neurotypical peers; however, only adults were studied. Our findings suggest that successful SCE recognition extends to autistic adolescents and reflects the ability to both label and recognize the intensity of negatively- and positively-valenced SCEs.

A key aim of Study I was to explore how PT demands influence potential group differences in SCE attributions. Across groups, participants inferred less intense congruent SCEs when PT demands were high. Surprisingly, autistic and neurotypical adolescents inferred similarly intense SCEs during low and high PT demands, despite reports of pervasive ToM impairments in ASD (Baron-Cohen, 1990; Baron-Cohen et al., 1985; Frith, 2001). This suggests that autistic and neurotypical adolescents are similarly impacted by changes in PT demands when making congruent SCE attributions, perhaps because high-intensity affective cues (such as those provided in the SCET) are equally salient to autistic and neurotypical adolescents.

Inferred Incongruent SCEs. Participants rated how intensely embarrassed and proud each singer felt, regardless of the emotion the singer conveyed. Thus, participants made both *congruent* SCE attributions (e.g., rating how intensely embarrassed an embarrassed singer felt) and *incongruent* SCE attributions (e.g., rating how intensely proud an embarrassed singer felt). This design is strikingly different from most emotion recognition tasks, where participants only evaluate conveyed emotions (i.e., congruent SCE attributions). Consequently, by exploring incongruent SCE attributions, this design affords a more nuanced investigation of SCEs. Across groups, participants inferred more intense incongruent SCEs when PT demands were high, but autistic adolescents were more strongly impacted by changes in PT demands. While autistic adolescents inferred similarly intense incongruent SCEs as neurotypical peers when PT demands were low, they inferred more intense incongruent SCEs when PT demands were high.

Broadly speaking, our findings suggest that autistic adolescents are differentially impacted by changes in PT demands during SCE processing, although perhaps not in the way one might initially expect. While autistic and neurotypical adolescents inferred similarly intense *congruent* SCEs during both low and high PT demands, autistic adolescents inferred more

intense *incongruent* SCEs during high PT demands. Taken together, this suggests that autistic adolescents are as capable of identifying high-intensity congruent SCEs as neurotypical adolescents; however, when PT demands are elevated, they may *additionally* infer more intense incongruent SCEs, which targets may not convey/experience. Thus, during high PT demands, the emotional inferences of autistic adolescents may be more complex and multifaceted. This unique pattern of results may shed light on how autistic individuals can pass explicit emotion recognition tasks in laboratory settings (when they are only required to make *congruent* SCE attributions), yet report emotion processing difficulties and interpersonal challenges in the real-world (when they may make inappropriate *incongruent* SCE attributions).

Although this study was designed to explore the impact of differential PT demands on SCE processing, an alternative framework may suggest that it explores the impact of the situational context on SCE processing. Thus, clips with low PT demands may represent instances when singers' emotional reactions match the situational context (i.e., singers act embarrassed when they sing poorly), while clips with high PT demands may represent instances when singers' emotional reactions do not match the situational context (i.e., singers act embarrassed when they sing well). Consequently, an alternative interpretation of the results is that autistic and neurotypical adolescents may be similarly impacted by the situational context when they make *congruent* SCE attributions; however, autistic adolescents may be more strongly impacted by the situational context when they make *incongruent* SCE attributions. Specifically, autistic adolescents may be more likely to infer that targets feel emotions that reflect the situational context (or how they expect/believe targets *should* feel), even if targets do not convey these emotions. Thus, the emotion attributions of autistic individuals may be the product of intact

emotion recognition abilities, in addition to personal expectations of situationally-appropriate reactions, possibly based on learned social scripts.

Potential Difficulties Prioritizing/Integrating Affective Information

Our findings suggest that autistic adolescents can appropriately recognize affective facial, postural, and/or prosodic cues. This is evidenced by similarly intense congruent SCE ratings made by autistic and neurotypical adolescents, as well as by successful performance on a popular emotion recognition task, the RMET-C. However, group differences in incongruent SCE ratings, cognitive empathy scores, and social competence scores; and correlations between more intense incongruent SCE ratings, reduced mental state understanding, and lower social competence, suggest that autistic adolescents may experience difficulties integrating and interpreting diverse, conflicting cues during SCE processing. These difficulties may, in turn, contribute to real-world interpersonal challenges. We propose that neurotypical adolescents prioritize making mental state attributions via affective cues (e.g., from facial expressions, body postures, or prosody), while autistic adolescents prioritize making contextual inferences, based on learned social rules and generalized social scripts, possibly to compensate for less reflexive mentalizing.

Research investigating nonsocial emotion processing lends support for a “contextual bias” in ASD, but only when affective cues conflict. Autistic youths can identify nonsocial emotions as accurately as neurotypical peers during a speech comprehension task but show a “contextual bias” when presented with discrepant prosodic and contextual cues (Le Sourn-Bissaoui, Aguert, Girard, Chevreuil, & Laval, 2013). The authors proposed that group differences may represent atypical inferential strategies, particularly when integrating affective information from multiple cues. Our findings support and extend this interpretation by

suggesting that a “contextual bias” for weighing and integrating discrepant information extends to social emotion processing and may be the source of interpersonal challenges in ASD.

Social cognition research similarly suggests that autistic individuals adopt a rule-based strategy to compensate for less reflexive mentalizing. Baez and colleagues (2012) argued that social cognitive challenges in autistic adults may represent difficulties integrating contextual and mental state information (targets’ intentions), and autistic adults may reference abstract social rules to compensate. Moral reasoning research lends further support. Autistic and neurotypical adults similarly evaluate the social permissibility of intentional harms; however, autistic adults judge accidental harms (when intentions and outcomes are discrepant) as less permissible (Moran et al., 2011). This suggests that when presented with conflicting information, neurotypical adults rely more strongly on targets’ intentions, while autistic adults rely more strongly on situational outcomes. Research by Zalla and colleagues (2011) similarly suggests that autistic adults show an over-reliance on learned social rules and an under-reliance on inferred intentions/affective responses, possibly to compensate for reduced cognitive empathy.

Interestingly, Baron-Cohen (1991) argued that autistic individuals experience greater difficulty identifying emotions that are the consequence of beliefs, compared to situations. This underscores the potential modulatory role of mentalizing abilities in atypical emotion processing in ASD. In the current study, autistic adolescents made similar SCE attributions as neurotypical adolescents when singers conveyed emotions that matched the situational context (situation-based emotions); however, they made atypical SCE attributions when singers conveyed emotions that did not match the situational context and instead reflected singers’ evaluations of their own performance (belief-based emotions). These findings further underscore how PT difficulties and strict rule adherence may lead to atypical emotion processing in ASD.

Empathic SCEs

We also investigated empathic SCEs. Autistic adolescents reported feeling both negatively-valenced (embarrassment) and positively-valenced (pride) empathic SCEs, and they reported feeling similarly intense empathic *congruent* and empathic *incongruent* SCEs as neurotypical peers. Interestingly, autistic and neurotypical adolescents were similarly impacted by changes in PT demands. Across groups, participants felt less intense empathic congruent SCEs when PT demands were high, and they felt less intense empathic incongruent SCEs when PT demands were low. These results suggest that autistic adolescents engage in similar empathic SCE processing as neurotypical peers, which converge with reports of similarly intense affective empathy (particularly empathic concern) in ASD and neurotypical development (Dziobek et al., 2008; Rogers et al., 2007; Rueda et al., 2015).

Only two studies have explicitly investigated empathic SCE processing in ASD. Similar to our findings, autistic and neurotypical adults reported feeling similarly intense empathic embarrassment for drawings of targets who made accidental social norm violations and were aware of their transgressions (similar to embarrassment clips with low PT demands), as well as for targets who made accidental social norm violations and were unaware of their transgressions (similar to embarrassment clips with high PT demands) (Paulus et al., 2013). However, autistic adults reported feeling more intense empathic embarrassment than neurotypical adults for videos of targets performing embarrassing tasks (Alder et al., 2015).

One possible explanation for these discrepant findings is that empathic embarrassment reflects distinct affective processes across studies. Alder and colleagues (2015) reported that empathic embarrassment ratings correlated positively with personal distress scores for autistic adults, which suggests that these ratings may more accurately reflect physiological arousal, while

empathic SCE ratings in the current study may more accurately reflect emotional simulation/resonance. Differences between the premises of these two tasks support this interpretation. Participants in Adler and colleagues' (2015) study were aware that targets were required to perform embarrassing actions as part of the study (and participants had recently performed the same embarrassing actions themselves). Thus, viewing these targets likely evoked feelings of personal distress. In contrast, participants in our study were led to believe that targets were competing in a singing competition (and participants had not been asked to sing themselves), which may have elicited affective simulation. Alternatively, a lack of group differences may represent a developmental trend, such that autistic adults feel more intense empathic SCEs than neurotypical adults, while autistic and neurotypical adolescents feel similarly intense empathic SCEs. However, Paulus and colleagues (2013) reported that autistic adolescents and adults feel similarly intense empathic SCEs, which does not support this alternative explanation. Cross-sectional research comparing adolescents and adults, and longitudinal research tracking developmental changes from pre-adolescence to adulthood will be key in exploring this theory.

Role of Underlying Social Cognitive Abilities

We also investigated the role of social cognitive abilities in adolescents' capacity to infer SCEs and to feel empathic SCEs. We hypothesized that autistic adolescents would demonstrate atypical social cognitive abilities, which would underlie group differences in SCE processing. As expected, autistic adolescents reported attenuated self-awareness/interoception, as represented by reduced self-consciousness and greater alexithymic tendencies, which converge with prior findings (Griffin et al., 2016; Patil et al., 2016; Silani et al., 2008). They also reported reduced PT and cognitive empathy, similar to past research (Castelli et al., 2002; Dziobek et al., 2008;

Happé, 1994). However, there were no group differences in PT task performance (e.g., RMET-C and SS-R). This pattern of results resembles findings from the executive functioning literature, where autistic children perform well on experimental tasks but report real-world challenges (Geurts, Corbett, & Solomon, 2009; Kenworthy, Yerys, Anthony, & Wallace, 2008).

There were no group differences in affective empathy, such that autistic and neurotypical adolescents reported feeling similar levels of empathic concern, personal distress, and emotional resonance. In general, autistic adults report similar levels of empathic concern, but heightened levels of personal distress (Dziobek et al., 2008; Patil et al., 2016; Rogers et al., 2007). Thus, developmental differences may exist, such that autistic and neurotypical individuals, regardless of age, feel equivalent empathic concern, yet autistic adults feel greater personal distress. Future research should test this theory. Our results also converge with reports of attenuated cognitive empathy but equivalent affective empathy in autistic adults (Dziobek et al., 2008; Rogers et al., 2007), suggesting that a similar cognitive/affective empathy distinction may exist in adolescents.

Contrary to our expectations, social cognitive abilities neither predicted nor correlated with inferred congruent SCE ratings, such that ToM/PT difficulties were not associated with less intense congruent SCE attributions. One possible explanation is that the ability to recognize emotional expressions (e.g., from photographs or videos) may function independent of PT skills, while the ability to cognitively infer emotional states (e.g., from short vignettes) may rely more strongly on cognitive empathy skills. Research using vignettes to study embarrassment found that autistic children offer less appropriate justifications for SCE attributions compared to neurotypical peers, and impoverished justifications are associated with attenuated ToM (Hillier & Allinson, 2002a). An alternative explanation is that our results reflect ceiling effects. The SCET uses high-intensity stimuli, and autistic and neurotypical adolescents reported, on average,

medium to high intensity ratings for congruent SCEs. Thus, the SCET may not be sufficiently sensitive to explore more nuanced group differences, and thus, may be unable to detect associations between affective inferential abilities and social cognitive skills, if a relationship exists. Future studies should test this theory using more subtle/ambiguous stimuli.

Interestingly, PT abilities both correlated with and predicted inferred *incongruent* SCE ratings, but only when PT demands were high. Thus, when contextual and affective cues were discrepant (e.g., singers sang poorly but acted proud), adolescents with attenuated ToM inferred more intense incongruent SCEs (e.g., inferred more intense embarrassment), which reflected the situational context. These findings are novel, as prior studies only investigated congruent SCEs. The results suggest that reduced cognitive empathy may underlie atypical SCE attributions in ASD, such that when presented with discrepant contextual and affective cues, adolescents with attenuated ToM abilities may rely more strongly on contextual information to make emotion attributions. Importantly, ToM difficulties were not associated with inferring less intense *congruent* SCEs, but instead, more intense *incongruent* SCEs. A possible explanation is that when PT demands are high, autistic adolescents compensate for atypical mentalizing by relying more strongly on learned rules/social scripts (e.g., people who perform poorly feel embarrassed). In support of this theory, research suggests that autistic adults adopt rule-based strategies during nonsocial emotion recognition tasks (Rutherford & McIntosh, 2007) and may reference social knowledge to compensate for social cognitive difficulties (Baez et al., 2012).

Affective empathy both correlated with and predicted empathic SCE ratings. This suggests that adolescents who tend to feel greater empathy not only resonate more strongly with conveyed emotions (empathic *congruent* SCEs), but also feel more intense vicarious emotions based on the situational context (empathic *incongruent* SCEs), even if targets do not convey

these emotions. Thus, empathic SCEs may be a function of general empathy processing in both autistic and neurotypical adolescents. Interestingly, PT abilities/cognitive empathy neither correlated with nor predicted empathic SCE ratings, suggesting that the tendency to feel empathic SCEs may not be associated with the ability or tendency to adopt other people's perspectives. Given reports of intact affective empathy but reduced cognitive empathy in ASD, it perhaps should not be surprising that these two processes appear independent here.

The "alexithymia hypothesis" posits that atypical emotion recognition and empathy in ASD may be driven by elevated alexithymia, above and beyond the influence of autistic features (Bird & Cook, 2013). Autistic and neurotypical adults matched on alexithymia severity demonstrate similar sensitivity for recognizing nonsocial emotional facial expressions; and alexithymic tendencies, but not autistic traits, predict reduced sensitivity (Cook et al., 2013). Relatedly, autistic adults show reduced recognition of nonsocial emotional vocalizations compared to neurotypical adults, which correlates with more severe alexithymia across groups (Heaton et al., 2012). Our study revealed group differences in autistic features and alexithymia; however, more intense inferred incongruent SCE ratings were associated with more intense autism-related social challenges, but not alexithymia. These findings converge with research linking alexithymic traits with atypical emotional resonance, but linking autistic traits with atypical cognitive PT (Lockwood, Bird, Bridge, & Viding, 2013). Thus, atypical SCE processing in the current study appears to be driven by autism-specific social challenges, not general interoceptive impairments, which does not support the "alexithymia hypothesis".

Although purely speculative, correlations between inferred incongruent SCE ratings and SRS scores, but neither ASRS nor AQ-A scores, may shed further light onto the underlying causes of atypical SCE processing in ASD. While the SRS measures autism-relevant social

challenges (i.e., poor social awareness, social cognition, social communication, and social motivation), the ASRS and AQ-A more broadly measure autistic behaviors, mannerisms, and traits. Thus, our findings suggest that atypical SCE processing in ASD may be related to real-world social difficulties, and more intense incongruent SCE attributions may be the consequence of engaging in compensatory strategies aimed at addressing these challenges.

Strengths, Limitations, and Future Directions

This study has several strengths. First, it used dynamic emotional stimuli, which provided multimodal (i.e., facial, postural, and prosodic) affective information. Relative to static stimuli, dynamic stimuli are more ecologically-valid, more closely resemble real-world emotion expressions (particularly SCEs), and enhance emotion recognition (Krumhuber et al., 2013; Wehrle et al., 2000). Second, a singing competition is inherently evaluative, and adolescents are familiar with the general standards used to evaluate performances. Third, by featuring adolescent singers, this study used more developmentally-appropriate stimuli. Peer relevance increases substantially during adolescence (Nelson et al., 2016); thus, age-matched targets may be more motivationally salient. In addition, children and adults recognize age-matched faces with better accuracy and discriminability (Rhodes & Anastasi, 2012). Fourth, SCEs rely heavily on body/postural cues and cannot be identified from facial cues alone. Thus, using stimuli that featured both facial and postural/gestural cues was essential.

This study also has several limitations. The SCET featured high-intensity affective stimuli to enhance recognition rates and neural activity; however, reduced task demands may have resulted in ceiling effects, which may have limited our ability to detect more nuanced group differences. Future research could use less intense and less prototypical stimuli or could reduce allotted response times. Participants could also identify SCEs by either selecting from multiple

labels (similar to the RMET-C) or by generating their own, as well as justify their ratings by discussing what cognitive, affective, or contextual features they prioritized. In prior studies, autistic children demonstrated similar emotion recognition rates as neurotypical peers, but offered less appropriate justifications (Hillier & Allinson, 2002a, 2002b). Therefore, exploring *how* autistic youths make emotion attributions may be informative. Finally, replication studies with larger sample sizes will be helpful, as our sample size was designed with the pragmatic and financial constraints of an MRI study.

Implications for Intervention

Our results demonstrate that autistic adolescents can appropriately recognize high-intensity affective facial, postural, and/or prosodic cues to make SCE attributions; nevertheless, they frequently experience real-world interpersonal challenges. One explanation for these seemingly inconsistent findings is that autistic youths may have difficulty applying affective knowledge to novel social contexts. This interpretation converges with the “Weak Central Coherence Theory” (Frith, 1989), which proposes that autistic individuals have a local processing bias that hinders generalizing across contexts (Plaisted, 2001; Vermeulen, 2015). Relatedly, the “Weak Central Coherence Theory” (Frith, 1989) and the “Reduced Generalization Theory” (Plaisted, 2001) may tentatively explain group differences in incongruent SCE attributions. Autistic individuals often demonstrate a strict adherence to rules, even when they are contextually inappropriate (Klinger & Dawson, 2001). Thus, autistic adolescents may have rigidly followed learned social rules (e.g., people who perform well feel proud) when PT demands were high, and thus made atypical emotional inferences. Assuming that autistic adolescents have intact emotion recognition abilities, as our study reveals, these findings suggest that more intensive emotion recognition training may not be beneficial, as autistic adolescents

have already learned how to identify and process salient affective cues. Instead, autistic youths may benefit more from practicing applying this knowledge to novel social situations, such as via role-play. Another avenue for intervention involves teaching autistic adolescents the necessity of differentially weighting affective and contextual cues, particularly when they are discrepant. Finally, intervention programs should use diverse stimuli (not just high-intensity, prototypical exemplars) as testing criteria, to promote broader generalization of emotion recognition skills.

STUDY II RESULTS: THE NEURAL CORRELATES OF SCES

We investigated neural activation patterns recruited by autistic and neurotypical adolescents during SCE processing and the modulatory role of heightened PT demands. First, we investigated neural activation patterns for the NT and ASD groups, separately. We reported activity associated with the intercept, which represented activity during SCE processing for each group, collapsed across emotion type and PT demands, and controlling for low-level visual, auditory, and semantic processes. We also reported significant main effects and interaction effects for each group. Second, we compared neural activation patterns between the NT and ASD groups. We conducted whole-brain analyses and reported activity associated with the intercept, significant main effects and interaction effects, and significant contrasts of interest. We also conducted complementary ROI analyses.

Whole Brain Analyses for NT Group

Results from the 2(emotion) x 2(PT demands) repeated measures ANOVA for the NT group revealed a main effect of emotion, a main effect of PT demands, and an emotion by PT demands interaction effect. (See Figure 3 and Table 6.)

Figure 3.*Intercept for NT and ASD Groups, Separately*

Panel A. Intercept for NT group. *Panel B.* Intercept for ASD group.

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 45$ and $k = 46$ for NT and ASD groups, respectively. ASD=autism spectrum disorder; NT=neurotypical.

Table 6.*Neural Activity During Self-Conscious Emotion Processing for the NT Group*

Contrast	Hemisphere	Region	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>F</i>
Intercept	Bilateral	Lingual gyrus (ext. cuneus, calcarine gyrus, middle occipital gyrus, middle temporal gyrus, angular gyrus)	8476	-12	-78	-12	100
	Right	Middle temporal gyrus (BA 37; ext. middle occipital gyrus, superior occipital gyrus, inferior occipital gyrus, lingual gyrus, inferior temporal gyrus, fusiform gyrus)	3007	48	-66	4	100
	Left	Inferior occipital gyrus (ext. lingual gyrus, calcarine gyrus, middle occipital gyrus)	2195	-24	-102	-8	100
	Left	Supramarginal gyrus (BA 40; ext. inferior parietal lobe, postcentral gyrus, Rolandic operculum)	688	-62	-24	40	53.33
	Bilateral	Posterior cingulate cortex (BA 31/7; ext. precuneus)	527	-8	-34	34	66.23
	Left	Middle temporal gyrus (BA 37/21; ext. inferior temporal gyrus)	517	-60	-46	-12	57.16
	Left	Middle temporal gyrus (BA 21/22; ext. superior temporal gyrus/Heschl's gyrus)	411	-58	-8	-10	93.60
	Right	Angular gyrus (BA 7/39)	324	48	-64	26	33.05
	Right	Precentral gyrus (BA 6)	254	52	4	48	87.52
	Right	Supplementary motor area (BA 6)	221	6	10	66	79.77
	Left	Superior frontal gyrus/precentral gyrus (BA 6)	169	-20	-10	70	75.76
	Right	Supramarginal gyrus (BA 40)	167	60	-34	20	60.55
	Left	Postcentral gyrus (BA 5; ext. superior parietal lobe)	158	-22	-42	66	59.75
	Left	Supplementary motor area/middle cingulate cortex (BA 24)	150	8	2	52	40.36
	Left	Fusiform gyrus (BA 37)	148	-42	-50	-18	56.18
	Right	Heschl's gyrus (BA 41)	139	52	-18	8	42.14
	Left	Precentral gyrus (BA 6)	118	-50	-2	54	45.93
	Right	Inferior temporal gyrus (BA 20)	114	42	-2	-46	25.85
		Medial prefrontal cortex (BA 9/10)	110	4	60	18	23.62
	Right	Middle temporal gyrus (BA 21)	92	50	-10	-18	55.12
	Left	Cerebellum	78	30	-62	-54	46.14
	Right	Supplementary motor area (BA 6)	70	8	-20	62	38.59
	Left	Precentral gyrus (BA 4)	53	-34	-20	46	38.94
	Left	Middle frontal gyrus (BA 9/6)	52	-40	12	50	27.76
	Left	Cerebellum	48	-32	-62	-24	28.74

Main Effect of Emotion	Right	Lingual gyrus (ext. calcarine gyrus, middle occipital gyrus, middle temporal gyrus)	1559	16	-86	-8	60.5
	Left	Middle occipital gyrus	938	-50	-76	10	59.38
	Left	Superior temporal gyrus/supramarginal gyrus (BA 41)	81	-44	-38	16	33.71
	Right	Superior temporal gyrus (BA 22)	80	50	-12	2	38.68
	Left	Superior temporal gyrus (BA 22)	76	-46	-16	0	35.95
	Right	Superior temporal gyrus/inferior parietal lobe (BA 13/40)	46	56	-38	24	24.91
Main Effect of PT Demands	Right	Middle temporal gyrus (BA 19)	292	42	-66	2	51.43
	Right	Lingual gyrus (ext. calcarine gyrus)	198	18	-88	-8	56.29
	Left	Middle occipital gyrus	89	-50	-78	6	46.1
Emotion x PT Demands	Left	Precentral gyrus (BA 4/6; ext. postcentral gyrus)	148	-22	-22	60	33.1
	Left	Calcarine gyrus (ext. cuneus)	85	-2	-96	10	26.9
	Right	Precentral gyrus (BA 6)	72	40	-10	38	33.83
	Right	Postcentral gyrus (BA 4/6; ext. precentral gyrus)	51	62	0	24	28.52
	Left	Postcentral gyrus (BA 4/6)	46	-44	-12	42	24.07
	Right	Inferior parietal lobe (BA 40)	45	26	-54	50	20.14

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 45$. BA=putative Brodmann Area; ext.= extending into; NT=neurotypical; PT=perspective-taking.

Intercept. The intercept revealed frontal activity within medial prefrontal cortex, left middle frontal gyrus, left superior frontal gyrus, bilateral precentral gyrus, left postcentral gyrus, and bilateral supplementary motor area; limbic activity within right inferior frontal gyrus; parietal activity within bilateral posterior cingulate cortex, bilateral precuneus, and bilateral inferior parietal lobe (including bilateral angular gyrus and supramarginal gyrus); temporal activity within bilateral inferior temporal gyrus, bilateral fusiform gyrus, bilateral middle temporal gyrus, and bilateral superior temporal gyrus/Heschl's gyrus; occipital activity within bilateral lingual gyrus, bilateral calcarine gyrus, bilateral cuneus, bilateral inferior occipital gyrus, bilateral middle occipital gyrus, and right superior occipital gyrus; as well as activity within middle cingulate cortex and left cerebellum.

Main Effect of Emotion. The main effect of emotion revealed activity within bilateral superior temporal/inferior parietal and occipital regions. During embarrassment clips, the NT group recruited greater activity within right superior temporal gyrus/inferior parietal lobe, right lingual gyrus, and left middle occipital gyrus. During pride clips, the NT group recruited greater activity within left superior temporal gyrus/supramarginal gyrus and bilateral superior temporal gyrus.

Main Effect of PT Demands. The main effect of PT demands revealed activity within right middle temporal gyrus and bilateral occipital regions. During low PT demands, the NT group recruited greater activity within left lingual gyrus. During high PT demands, the NT group recruited greater activity within bilateral middle temporal gyrus.

Emotion x PT Demands Interaction Effect. The emotion by PT demands interaction effect revealed activity within bilateral somatosensory regions, right inferior parietal lobe, and left occipital regions.

Left precentral gyrus. There was an emotion by PT demands interaction effect within left precentral gyrus extending into postcentral gyrus, $F(1,24)=37.56, p<0.001$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-3.48, p=0.002$; but greater activity during pride clips with low, relative to high, PT demands, $t(24)=3.32, p=0.003$. During low PT demands, the NT group recruited greater activity for pride clips, $t(24)=-4.52, p<0.001$; but during high PT demands, they recruited greater activity for embarrassment clips, $t(24)=2.16, p=0.041$.

Right precentral gyrus. There was an emotion by PT demands interaction effect within right precentral gyrus, $F(1,24)=32.07, p<0.001$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-2.77, p=0.011$; but greater

activity during pride clips with low, relative to high, PT demands, $t(24)=6.07$, $p<0.001$. During low PT demands, the NT group recruited greater activity for pride clips, $t(24)=-5.65$, $p<0.001$; but during high PT demands, the NT group recruited greater activity for embarrassment clips, $t(24)=2.22$, $p=0.036$.

Left postcentral gyrus. There was an emotion by PT demands interaction effect within left postcentral gyrus, $F(1,24)=30.65$, $p<0.001$. The NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-1.76$, ns ; but greater activity during pride clips with low, relative to high, PT demands, $t(24)=5.20$, $p<0.001$. During low PT demands, the NT group recruited greater activity for pride clips, $t(24)=-6.30$, $p<0.001$; but during high PT demands, the NT group recruited similar activity for embarrassment and pride clips, $t(24)=1.11$, ns .

Right postcentral gyrus There was an emotion by PT demands interaction effect within right postcentral gyrus extending into precentral gyrus, $F(1,24)=30.85$, $p<0.001$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-3.49$, $p=0.002$; but greater activity during pride clips with low, relative to high, PT demands, $t(24)=4.29$, $p<0.001$. During low PT demands, the NT group recruited greater activity for pride clips, $t(24)=-3.84$, $p=0.001$; but during high PT demands, the NT group recruited greater activity for embarrassment clips, $t(24)=4.22$, $p<0.001$.

Right inferior parietal lobe. There was an emotion by PT demands interaction effect within right inferior parietal lobe, $F(1,24)=21.45$, $p<0.001$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-5.43$, $p<0.001$; but similar activity during pride clips with low and high PT demands, $t(24)=1.40$, ns . During low PT demands, the NT group recruited similar activity for embarrassment and pride

clips, $t(24)=-1.21$, ns ; but during high PT demands, the NT group recruited greater activity for embarrassment clips, $t(24)=4.59$, $p<0.001$.

Left calcarine gyrus. There was an emotion by PT demands interaction effect within left calcarine gyrus extending into cuneus, $F(1,24)=46.37$, $p<0.001$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-5.69$, $p<0.001$; but greater activity during pride clips with low, relative to high, PT demands, $t(24)=2.64$, $p=0.014$. During low PT demands, the NT group recruited greater activity for pride clips, $t(24)=-2.10$, $p=0.046$; but during high PT demands, the NT group recruited greater activity for embarrassment clips, $t(24)=4.91$, $p<0.001$.

Whole Brain Analyses for ASD Group

Results from the 2(emotion) x 2(PT demands) repeated measures ANOVA for the ASD group revealed a main effect of emotion and a main effect of PT demands. There was no emotion by PT demands interaction. (See Figure 3 and Table 7.)

Table 7.*Neural Activity During Self-Conscious Emotion Processing for the ASD Group*

Contrast	Hemisphere	Region	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>F</i>
Intercept	Bilateral	Lingual gyrus (ext. calcarine gyrus, cuneus, precuneus)	3740	-10	-74	-8	86.00
	Right	Middle temporal gyrus (BA 37; ext. inferior temporal gyrus, fusiform gyrus, lingual gyrus, cerebellum)	2973	54	-66	2	100
	Left	Inferior occipital gyrus (ext. lingual gyrus, middle occipital gyrus)	2407	-28	94	-12	100
	Left	Middle temporal gyrus (BA 37; ext. inferior temporal gyrus)	843	-60	-46	-8	80.66
	Right	Angular gyrus (BA 7)	831	44	-62	28	60.48
	Right	Middle temporal gyrus/inferior temporal gyrus (BA 21/20)	611	62	-34	-16	60.51
	Left	Angular gyrus (BA 7/40)	503	-38	-80	44	49.30
	Bilateral	Posterior cingulate cortex/precuneus (BA 31)	386	-2	-46	38	51.54
	Right	Supramarginal gyrus (BA 40)	264	60	-28	22	47.35
	Left	Middle temporal gyrus (BA 21)	254	-52	-4	-18	55.59
	Left	Middle frontal gyrus/precentral gyrus (BA 6/4)	236	50	0	52	52.70
		Dorsal anterior cingulate cortex (BA 32)	198	-6	28	30	65.11
	Bilateral	Middle cingulate cortex (BA 24)	175	-6	2	46	26.24
	Left	Precentral gyrus (BA 6)	130	-50	-4	54	78.27
	Right	Supplementary motor area (BA 6)	126	8	4	74	40.23
	Left	Precentral gyrus (BA 6)	121	-22	-18	68	25.63
	Right	Superior frontal gyrus (BA 8)	111	26	26	50	29.91
	Right	Middle frontal gyrus (BA 46)	104	36	42	8	28.76
	Right	Caudate	86	12	22	4	42.73
	Right	Heschl's gyrus (BA 41/42)	84	52	-18	10	30.30
	Left	Cerebellum	78	-26	-64	-26	40.79
	Left	Cerebellum	74	-18	-66	-50	33.59
	Right	Rolandic operculum/inferior frontal gyrus (BA 22/47)	63	54	10	0	27.38
	Right	Inferior frontal gyrus (BA 9)	60	44	10	24	32.77
	Right	Inferior frontal gyrus (BA 9)	56	40	16	36	26.13
	Left	Precentral gyrus (BA 4)	56	-38	-14	56	28.72
	Right	Anterior insula (BA 13/45/47)	49	36	24	4	27.17
	Right	Middle temporal gyrus (BA 21)	46	54	-8	-18	25.00
Main Effect of Emotion	Right	Lingual gyrus (ext. calcarine gyrus, superior occipital gyrus, cuneus, middle temporal gyrus, inferior temporal gyrus, fusiform gyrus)	3141	18	-86	-8	99.02

	Left	Middle occipital gyrus (ext. inferior occipital gyrus, middle temporal gyrus)	1358	-26	94	10	83.08
	Right	Inferior parietal lobe/superior parietal lobe (BA 7/40)	354	26	-54	52	40.59
	Left	Superior parietal lobe (BA 7; ext. inferior parietal lobe)	213	-24	-60	54	34.85
	Left	Middle occipital gyrus (ext. superior occipital gyrus)	183	-26	-72	28	50.44
	Left	Superior temporal gyrus (BA 41/42)	103	-58	-16	6	34.02
	Right	Cuneus	58	20	-82	46	26.65
	Left	Middle occipital gyrus	56	-10	-104	4	26.77
Main Effect of PT Demands	Right	Middle temporal gyrus (BA 37/39; ext. middle occipital gyrus, inferior occipital gyrus)	854	48	-64	4	76.48
	Left	Calcarine gyrus (ext. middle occipital gyrus, superior occipital gyrus)	309	6	-94	8	40.70
	Left	Middle frontal gyrus (BA 9)	149	-42	30	36	32.38
	Left	Middle occipital gyrus/middle temporal gyrus (BA 19/37)	128	-48	-74	4	32.84
	Left	Inferior parietal lobe/angular gyrus (BA 40/7)	114	-40	-52	48	31.60
	Left	Cerebellum	100	-16	-84	-32	29.29
	Right	Lingual gyrus	67	28	-92	-16	31.72
	Left	Calcarine gyrus	62	-6	-98	4	35.98
	Left	Inferior occipital gyrus	48	-40	-74	-6	43.90
		Dorsal medial prefrontal cortex (BA 8)	46	4	36	54	27.97
Emotion x PT Demands		-	-	-	-	-	-

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 46$. ASD=autism spectrum disorder; BA=putative Brodmann Area; ext.= extending into; PT=perspective-taking.

Intercept. The intercept revealed frontal activity within bilateral middle frontal gyrus, right superior frontal gyrus, bilateral precentral gyrus, and right supplementary motor area; limbic activity within right anterior insula, right inferior frontal gyrus, dorsal anterior cingulate cortex, and middle cingulate cortex; striatal activity within right caudate; parietal activity within bilateral posterior cingulate cortex, bilateral precuneus, right supramarginal gyrus, and bilateral angular gyrus; temporal activity within bilateral inferior temporal gyrus, right fusiform gyrus,

bilateral middle temporal gyrus, and right Heschl's gyrus; occipital activity within bilateral lingual gyrus, bilateral calcarine gyrus, bilateral cuneus, bilateral inferior occipital gyrus, and left middle occipital; as well as bilateral cerebellar activity.

Main Effect of Emotion. The main effect of emotion revealed activity within left superior temporal gyrus, left superior parietal lobe/inferior parietal lobe, and bilateral occipital regions. During embarrassment clips, the ASD group recruited greater activity within left superior parietal lobe extending into inferior parietal lobe, right inferior parietal lobe/superior temporal gyrus, right cuneus, right lingual gyrus, left middle occipital gyrus, left middle occipital gyrus extending into inferior occipital gyrus and middle temporal gyrus, and left middle occipital gyrus extending into superior occipital gyrus. During pride clips, the ASD group recruited greater activity within left superior temporal gyrus.

Main Effect of PT Demands. The main effect of PT demands revealed activity within right dorsal medial prefrontal cortex, left middle frontal gyrus, left inferior parietal lobe/angular gyrus, bilateral middle temporal gyrus, and bilateral occipital regions. During high PT demands, the ASD group recruited greater activity within dorsal medial prefrontal cortex, left middle frontal gyrus, left inferior parietal lobe/angular gyrus, right middle temporal gyrus extending into middle and inferior occipital gyri, right lingual gyrus, left calcarine gyrus, left calcarine gyrus extending into middle occipital gyrus and superior occipital gyrus, left inferior occipital gyrus, left middle occipital gyrus, and left cerebellum. The ASD group did not recruit greater activity in any region during low PT demands.

Whole Brain Analyses for All Participants

Results from the 2(group) x 2(emotion) x 2(PT demands) repeated measures ANOVA revealed a main effect of emotion, a main effect of PT demands, as well as two-way and three-way interaction effects. (See Figures 4 and 5 and Tables 8 and 9.)

Figure 4.
Intercept During Self-Conscious Emotion Processing

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$.

Table 8.*Intercept during Self-Conscious Emotion Processing, Collapsed Across Groups*

Hemisphere	Region	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>F</i>
Bilateral	Lingual gyrus (ext. bilateral cuneus, calcarine gyrus, precuneus, middle occipital gyrus, angular gyrus, posterior cingulate cortex)	12231	-10	-80	-12	100
Right	Middle occipital gyrus (ext. inferior occipital gyrus, inferior temporal gyrus, middle temporal gyrus, fusiform gyrus, cerebellum)	4601	44	-76	-4	100
Left	Inferior occipital gyrus (ext. middle occipital gyrus, fusiform gyrus, cerebellum)	3922	-30	-90	-12	100
Left	Middle temporal gyrus (ext. superior temporal gyrus/Heschl's gyrus, inferior parietal lobe, precentral gyrus, postcentral gyrus, inferior parietal lobe, supramarginal gyrus)	3443	-60	-46	-10	100
Right	Transverse temporal gyrus/Heschl's gyrus (ext. inferior temporal gyrus, superior temporal gyrus)	1603	54	-18	10	62.63
Right	Angular gyrus	1519	40	-70	44	60.18
Left	Precentral gyrus (BA 6; ext. supplementary motor area, middle cingulate cortex)	1037	-18	-12	68	49.70
Right	Inferior frontal gyrus (BA 47/45/13 ext. anterior insula)	869	48	24	0	33.02
Left	Middle frontal gyrus (BA 6; ext. precentral gyrus)	488	-40	10	48	41.91
Right	Superior temporal gyrus/supramarginal gyrus (BA 40)	466	60	-32	20	78.87
Right	Precentral gyrus (BA 6; ext. middle frontal gyrus)	425	54	0	48	100
Right	Supplementary motor area (BA 6)	368	6	10	66	92.97
Left	Precentral gyrus (BA 6)	316	-50	-2	54	92.96
Left	Postcentral gyrus (BA 5; ext. superior parietal lobe, precuneus)	299	-20	-42	66	45.65
Right	Inferior temporal gyrus (BA 20; ext. fusiform gyrus)	272	42	-4	-46	50.76
Right	Medial prefrontal cortex (BA 9/10; ext. dorsal medial prefrontal cortex)	262	4	58	14	28.93
Right	Superior frontal gyrus (BA 8; ext. middle frontal gyrus)	252	28	24	50	26.79
Left	Dorsal anterior cingulate cortex (BA 32; ext. dorsal medial prefrontal cortex)	226	-8	28	30	49.75
Left	Cerebellum	191	-30	-62	-54	60.48
Right	Caudate	182	12	22	4	43.32
Right	Inferior parietal lobe (BA 7/40; ext. superior parietal lobe)	172	30	-48	54	36.09
Left	Orbitofrontal cortex/ventral medial prefrontal cortex (BA 11/25)	135	-4	30	-14	28.24
Left	Postcentral gyrus (BA 4; ext. precentral gyrus)	114	-58	-2	20	40.10

Left	Supramarginal gyrus/superior temporal gyrus (BA 13)	112	-46	-38	24	41.96
Right	Superior frontal gyrus (BA 6)	97	20	-16	64	32.18
Right	Supplementary motor cortex (BA 6)	93	8	-20	62	30.19
Right	Postcentral gyrus (BA 6; ext. precentral gyrus)	91	62	2	20	35.63
Right	Postcentral gyrus (BA 4)	89	58	-12	36	26/92
Left	Inferior frontal gyrus (BA 47)	77	-34	20	-16	31.64
Left	Anterior insula (BA 13/47)	73	-42	12	-6	34.95
Left	Cerebellum	67	-12	-92	-36	26.12
Right	Middle frontal gyrus (BA 9)	57	40	18	36	24.82
Left	Inferior frontal gyrus (BA 11/47)	51	-36	34	-14	36.77
Right	Thalamus	48	4	-10	12	39.27
Left	Orbitofrontal cortex (rectal gyrus; BA 11)	47	-2	40	-26	20.05
Left	Posterior insula (BA 13)	34	-34	-18	6	24.33
Left	Temporal pole (BA 38)	33	-44	14	-20	38.06
Left	Inferior frontal gyrus (BA 47)	32	-38	28	2	22.90
Left	Caudate	32	-16	4	22	27.08
Left	Hippocampus	31	16	-4	-16	34.43
Right	Inferior frontal gyrus (BA 9)	30	44	8	26	18.32

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$. Bolded clusters represent *a priori* regions of interest that were selected as ROIs for further analysis. BA=putative Brodmann Area; ext.= extending into.

Table 9.

Neural Activity during Self-Conscious Emotion Processing as Modulated by Group, Emotion, and Perspective-Taking Demands

Contrast	Hemisphere	Region	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>F</i>
Main Effect of Group	-	-	-	-	-	-	-
Main Effect of Emotion	Bilateral	Lingual gyrus (ext. bilateral calcarine gyrus, inferior occipital gyrus, middle occipital gyrus, middle temporal gyrus, fusiform gyrus, superior occipital gyrus)	7855	18	-86	-8	100
	Right	Inferior parietal lobe/precuneus (BA 7; ext. superior parietal lobe, postcentral gyrus)	765	26	-54	52	35.85
	Left	Superior temporal gyrus (BA 41)	498	-56	-16	6	50.29
	Right	Superior temporal gyrus (BA 22/42; ext. Heschl's gyrus)	213	58	-14	8	31.7
	Left	Inferior parietal lobe/precuneus (BA 7; ext. superior parietal lobe)	184	-26	-52	52	29.89
	Right	Supramarginal gyrus (BA 40; ext. superior temporal gyrus)	90	58	-40	28	32.84
	Right	Superior frontal gyrus (BA 9/8)	85	24	40	38	24.87
	Right	Cerebellum	41	48	-74	-34	20.48
	Right	Supplementary motor area (BA 6)	36	12	10	66	21.79
	Right	Precentral gyrus (BA 6)	30	32	-2	46	18.79
Main Effect of PT Demands	Right	Middle temporal gyrus/middle occipital gyrus (BA 37/19)	1006	52	-70	2	91.56
	Left	Middle temporal gyrus/middle occipital gyrus (BA 19)	341	-46	-74	4	60.5
	Right	Inferior parietal lobe/superior parietal lobe (BA 40)	300	42	-52	42	22.53
	Left	Inferior parietal lobe (BA 40)	211	-36	-50	48	33.95
	Right	Middle frontal gyrus (BA 46)	155	42	32	20	29.03
	Right	Fusiform gyrus (BA 37)	151	42	-52	18	43.25
	Right	Middle frontal gyrus (BA 8)	139	38	32	50	28.00
	Right	Lingual gyrus	130	18	-88	-6	63.41

	Right	Precuneus (BA 7)	122	8	-78	50	24.86
	Right	Cuneus	121	8	-96	8	51.16
	Left	Cuneus	117	-4	-98	6	35.91
	Left		84	-40	28	42	27.09
		Middle frontal gyrus (BA 9)					
	Right	Middle occipital gyrus	57	28	-90	14	24.34
	Right	Superior parietal lobe (BA 7)	51	20	-68	60	20.57
	Left	Fusiform gyrus	37	-34	-74	-16	23.01
	Left	Lingual gyrus	36	-14	-86	0	22.99
	Right	Lingual gyrus	33	22	-96	-16	17.43
Group x Emotion	Left	Inferior parietal lobe (BA 40)	47	-52	-48	50	25.04
	Left	Cerebellum	94	-22	-82	-32	24.55
Group x PT	Left	Fusiform gyrus (BA 19)	50	-28	-74	-8	26.61
Demands	Right	Lingual gyrus	48	20	-86	-12	22.16
	Right	Inferior occipital gyrus	34	42	-74	-2	24.28
	Left	Middle occipital gyrus	176	-36	-90	2	26.92
Emotion x PT	Left	Cerebellum	83	-26	-82	-38	34.68
Demands	Left	Calcarine gyrus	62	-4	-100	6	30.3
	Right	Middle occipital gyrus	44	29	-86	12	24.21
	Right	Precentral gyrus (BA 4)	80	20	-28	60	21.85
	Left	Middle cingulate	39	-4	-36	52	18.76
Group x Emotion		cortex/paracentral lobe (BA					
x PT Demands		5)					
	Left	Cerebellum	32	-46	-74	-32	21.16
	Left	Precentral gyrus (BA 4)	30	-22	22	58	27.98

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$. BA=putative Brodmann Area; ext.= extending into; PT=perspective-taking.

Figure 5.

Interaction Effects Between Group, Emotion, and Perspective-Taking Demands During Self-Conscious Emotion Processing

Panel A. Group x PT Demands interaction effect within left fusiform gyrus (not shown: left cerebellum, right lingual gyrus, and right inferior occipital gyrus). *Panel B.* Group x Emotion interaction effect within left inferior parietal lobe. *Panel C.* Group x Emotion x PT Demands interaction effect within left and right precentral gyrus (not shown: left middle cingulate cortex/paracentral lobe, left cerebellum).

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$. PT=perspective-taking.

Intercept. The intercept revealed frontal activity within dorsal medial prefrontal cortex, medial prefrontal cortex, ventral medial prefrontal cortex, orbitofrontal cortex/rectal gyrus, bilateral middle frontal gyrus, bilateral superior frontal gyrus, and bilateral precentral gyrus/postcentral gyrus; limbic activity within bilateral inferior frontal gyrus, bilateral anterior insula, left posterior insula, dorsal and subgenual anterior cingulate cortex, middle cingulate cortex, and right thalamus; striatal activity within bilateral caudate; parietal activity within left posterior cingulate cortex, bilateral precuneus, bilateral inferior parietal lobe (including bilateral supramarginal gyrus and left angular gyrus), and bilateral superior parietal lobe; temporal activity within right amygdala, bilateral fusiform gyrus, left hippocampus, right inferior temporal gyrus, left temporal pole, bilateral middle temporal gyrus, bilateral superior temporal gyrus, and right transverse temporal gyrus (Heschl's gyrus); occipital activity within bilateral lingual gyrus,

bilateral calcarine gyrus, bilateral cuneus, bilateral inferior occipital gyrus, and bilateral middle occipital gyrus; as well as left cerebellar activity. (See Figure 4 and Table 8.)

Main Effect of Emotion. The main effect of emotion revealed activity within right middle frontal gyrus (precentral gyrus and supplementary motor area), right superior frontal gyrus, bilateral inferior parietal lobe, right supramarginal gyrus, bilateral superior temporal gyrus, bilateral occipital cortex, and right cerebellum. During embarrassment clips, participants recruited greater activity within right precentral gyrus, right supplementary motor area, left inferior parietal lobe, right inferior parietal lobe, right supramarginal gyrus, and bilateral lingual gyrus. During pride clips, participants recruited greater activity within left superior frontal gyrus, bilateral superior temporal gyrus, and right cerebellum.

Main Effect of PT Demands. The main effect of PT demands revealed activity within right middle frontal gyrus, right superior parietal lobe (including precuneus), left inferior parietal lobe, right fusiform gyrus, and bilateral occipital cortices. During low PT demands, participants recruited greater activity within bilateral lingual gyrus. During high PT demands, participants recruited greater activity within left middle frontal gyrus, right middle frontal gyrus, bilateral inferior parietal lobe, right precuneus, right superior parietal lobe, bilateral middle temporal gyri, bilateral fusiform gyrus, left lingual gyrus (more posterior than the two clusters recruited during low PT demands), left cuneus, right cuneus, and right middle occipital gyrus.

Group x Emotion Interaction Effect. The group by emotion interaction effect revealed activity within left inferior parietal lobe, $F(1,50)=20.60$, $p<0.001$. Groups recruited similar activity during embarrassment clips, $t(50)=-1.40$, ns ; and pride clips, $t(50)=1.59$, ns . The NT group recruited greater activity during pride, relative to embarrassment, clips, $t(24)=-4.38$,

$p < 0.001$; while the ASD group recruited similar activity during embarrassment and pride clips, $t(26) = 1.88$, *ns*.

Group x PT Demands Interaction Effect. The group by PT demands interaction effect revealed activity within left fusiform gyrus, bilateral occipital regions, and left cerebellum.

Left fusiform gyrus. There was a group by PT demands interaction effect within left fusiform gyrus, $F(1,50) = 26.27$, $p < 0.001$. The NT and ASD groups recruited similar activity during low PT demands, $t(50) = -0.29$, *ns*; however, the ASD group recruited greater activity than the NT group during high PT demands, $t(50) = -2.58$, $p = 0.013$. The NT group recruited greater activity during low, relative to high, PT demands, $t(24) = 3.01$, $p = 0.006$; while the ASD group recruited greater activity during high, relative to low, PT demands, $t(26) = -4.45$, $p < 0.001$.

Left lingual gyrus. There was a group by PT demands interaction effect within left lingual gyrus, $F(1,50) = 24.58$, $p < 0.001$. The NT and ASD groups recruited similar activity during low PT demands, $t(50) = 1.84$, *ns*; and high PT demands, $t(50) = -0.25$, *ns*. The NT group recruited greater activity during low, relative to high, PT demands, $t(24) = 4.82$, $p < 0.001$; while the ASD group recruited similar activity during low and high PT demands, $t(26) = -1.95$, *ns*.

Right inferior occipital gyrus. There was a group by PT demands interaction effect within right inferior occipital gyrus, $F(1,50) = 28.32$, $p < 0.001$. The NT and ASD groups recruited similar activity during low PT demands, $t(50) = -0.17$, *ns*; however, the ASD group recruited marginally greater activity than the NT group during high PT demands, $t(50) = -2.01$, $p = 0.052$. The NT group recruited similar activity during low and high PT demands, $t(24) = 0.24$, *ns*; while the ASD group recruited greater activity during high, relative to low, PT demands, $t(26) = -6.87$, $p < 0.001$.

Left cerebellum. There was a group by PT demands interaction effect within left cerebellum, $F(1,50)=26.91, p<0.001$. The NT and ASD groups recruited similar activity during low PT demands, $t(50)=0.76, ns$; while the ASD group recruited marginally greater activity than the NT group during high PT demands, $t(50)=-5.26, p=0.057$. The NT group recruited greater activity during low, relative to high, PT demands, $t(24)=2.36, p=0.027$; while the ASD group recruited greater activity during high, relative to low, PT demands, $t(26)=-5.26, p<0.001$.

Emotion x PT Demands Interaction Effect. There was an emotion by PT demands interaction effect within bilateral occipital regions and left cerebellum.

Left calcarine gyrus. There was an emotion by PT demands interaction effect within left calcarine gyrus, $F(1,51)=32.80, p<0.001$. Participants recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(51)=-6.33, p<0.001$; but recruited similar activity during pride clips with low and high PT demands, $t(51)=1.74, ns$. When PT demands were low, participants recruited similar activity for embarrassment and pride clips, $t(51)=1.68, ns$; however, when PT demands were high, participants recruited greater activity during embarrassment, relative to pride, clips, $t(51)=6.57, p<0.001$.

Left middle occipital gyrus. There was an emotion by PT demands interaction effect within left middle occipital gyrus, $F(1,51)=25.60, p<0.001$. Participants recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(51)=-4.35, p<0.001$; but recruited greater activity during pride clips with low, relative to high, PT demands, $t(51)=2.37, p=0.022$. Participants recruited greater activity during embarrassment, relative to pride, clips when PT demands were low, $t(51)=2.51, p=0.015$; and high, $t(51)=8.56, p<0.001$.

Right middle occipital gyrus. There was an emotion by PT demands interaction effect within right middle occipital gyrus, $F(1,51)=23.06, p<0.001$. Participants recruited greater

activity during embarrassment clips with high, relative to low, PT demands, $t(51)=-4.97$, $p<0.001$; but recruited similar activity during pride clips with low and high PT demands, $t(51)=1.21$, *ns*. Participants recruited greater activity during embarrassment, relative to pride, clips when PT demands were low, $t(51)=2.84$, $p=0.006$; and high, $t(51)=9.68$, $p<0.001$.

Left cerebellum. There was an emotion by PT demands interaction effect within left cerebellum, $F(1,51)=28.64$, $p<0.001$. Participants recruited greater activity during embarrassment clips with low, relative to high, PT demands, $t(51)=3.56$, $p=0.001$; but recruited greater activity during pride clips with high, relative to low, PT demands, $t(51)=-3.55$, $p=0.001$. When PT demands were low, participants recruited greater activity during embarrassment, relative to pride, clips, $t(51)=2.81$, $p=0.007$; but when PT demands were high, participants recruited greater activity for pride, relative to embarrassment, clips, $t(51)=-5.31$, $p<0.001$.

Group x Emotion x PT Demands Interaction Effect. There was a three-way interaction effect within bilateral precentral gyrus, left paracentral lobe/middle cingulate cortex, and left cerebellum.

Left precentral gyrus. There was a three-way interaction effect within left precentral gyrus, $F(1,50)=29.70$, $p<0.001$. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50)=-0.91$, *ns*; and during embarrassment clips with high PT demands, $t(50)=0.86$, *ns*. The NT group recruited greater activity than the ASD group during pride clips with low PT demands, $t(50)=2.21$, $p=0.032$; however, the NT and ASD groups recruited similar activity during pride clips with high PT demands, $t(50)=-1.44$, *ns*.

Within-group comparisons revealed that the NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-0.01$, *ns*; and during pride clips with low and high PT demands, $t(24)=-1.38$, *ns*. When PT demands were low, the NT group recruited

greater activity during pride, relative to embarrassment, clips, $t(24)=-4.18$, $p<0.001$; however, when PT demands were high, the NT group recruited similar activity during embarrassment and pride clips, $t(24)=1.85$, *ns*. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=-0.94$, *ns*; and during pride clips with low and high PT demands, $t(26)=0.15$, *ns*. The ASD group recruited similar activity during embarrassment and pride clips with low PT demands, $t(26)=1.01$, *ns*; and high PT demands, $t(26)=-1.84$, *ns*.

Right precentral gyrus. There was a three-way interaction effect within right precentral gyrus, $F(1,50)=26.25$, $p<0.001$. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50)=-0.38$, *ns*; but the NT group recruited greater activity than the ASD group during embarrassment clips with high PT demands, $t(50)=2.23$, $p=0.030$. The NT group recruited greater activity than the ASD group during pride clips with low PT demands, $t(50)=2.53$, $p=0.015$; but the NT and ASD groups recruited similar activity during pride clips with high PT demands, $t(50)=-1.04$, *ns*.

Within-group comparisons revealed that the NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-3.04$, $p=0.006$; and recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=2.79$, $p=0.010$. When PT demands were low, the NT group recruited greater activity during pride, relative to embarrassment, clips, $t(24)=-2.84$, $p=0.009$; however, when PT demands were high, the NT group recruited greater activity during embarrassment, relative to pride, clips, $t(24)=2.54$, $p=0.018$. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=1.10$, *ns*; but recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-2.80$, $p=0.009$. When PT demands were low, the ASD group recruited similar activity during embarrassment and pride clips, $t(26)=1.59$, *ns*; however, when

PT demands were high, the ASD group recruited greater activity during pride, relative to embarrassment, clips, $t(26)=-2.09$, $p=0.047$.

Left paracentral lobe/middle cingulate cortex. There was a three-way interaction effect within left paracentral lobe/middle cingulate cortex; $F(1,50)=21.54$, $p<0.001$. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50)=-1.16$, ns ; and during embarrassment clips with high PT demands, $t(50)=1.88$, ns . The NT group recruited greater activity than the ASD group during pride clips with low PT demands, $t(50)=2.23$, $p=0.030$; however, the NT and ASD groups recruited similar activity during pride clips with high PT demands, $t(50)=-0.91$, ns .

Within-group comparisons revealed that the NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-3.12$, $p=0.005$; but similar activity during pride clips with low and high PT demands, $t(24)=1.78$, ns . When PT demands were low, the NT group recruited greater activity during pride, relative to embarrassment, clips, $t(24)=-3.07$, $p=0.005$; however, when PT demands were high, the NT group recruited similar activity during embarrassment and pride clips, $t(24)=1.08$, ns . The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(50)=1.89$, ns ; but recruited greater activity during pride clips with high, relative to low, PT demands, $t(50)=-3.68$, $p=0.001$. When PT demands were low, the ASD group recruited greater activity during embarrassment, relative to pride, clips, $t(26)=2.50$, $p=0.019$; however, when PT demands were high, the ASD group recruited greater activity during pride, relative to embarrassment, clips, $t(26)=-2.62$, $p=0.014$.

Left cerebellum. There was a three-way interaction effect within left cerebellum, $F(1,50)=22.12$, $p<0.001$. The ASD group recruited greater activity than the NT group during

embarrassment clips with low PT demands, $t(50)=-2.63, p=0.011$; but the NT and ASD groups recruited similar activity during embarrassment clips with high PT demands, $t(50)=-0.42, ns$. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=1.62, ns$; however, the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.06, p=0.044$.

Within-group comparisons revealed that the NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-1.84, ns$; but recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=3.11, p=0.005$. When PT demands were low, the NT group recruited greater activity during pride, relative to embarrassment, clips, $t(24)=-4.12, p<0.001$; however, when PT demands were high, the NT group recruited similar activity during embarrassment and pride clips, $t(24)=0.05, ns$. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=1.46, ns$; but recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-3.12, p=0.004$. When PT demands were low, the ASD group recruited similar activity during embarrassment and pride clips, $t(26)=1.80, ns$; however, when PT demands were high, the ASD group recruited greater activity during pride, relative to embarrassment, clips, $t(26)=-3.29, p=0.003$.

Specific Contrasts of Interest. Given that prior research has only explored embarrassment processing in autistic individuals during low PT demands, we separately investigated group differences for each contrast of interest. (See Figure 6 and Table 10.) There were group differences within right postcentral gyrus and right anterior insula when comparing activity during embarrassment clips with high, relative to low, PT demands ((EmbHi>Neutral) vs (EmbLo>Neutral)). There were also group differences within right inferior temporal gyrus and

right middle occipital gyrus during pride clips with low PT demands (PrideLo>Neutral). In addition, there were group differences within dorsal anterior cingulate cortex, left inferior parietal lobe, bilateral cuneus, left lingual gyrus, and bilateral cerebellum when comparing activity during pride clips with high, relative to low, PT demands ((PrideHi>Neutral) vs (PrideLo>Neutral)). No other contrasts yielded significant group differences.

Figure 6.

Group Comparisons of Interest During Self-Conscious Emotion Processing

Panel A. NT vs ASD ((EmbHi>Neutral) vs (EmbLo>Neutral)) within right anterior insula and right postcentral gyrus. *Panel B.* NT vs ASD (PrideLo>Neutral) within right inferior temporal gyrus (not shown: right middle occipital gyrus). *Panel C.* NT vs ASD ((PrideHi>Neutral) vs (PrideLo>Neutral)) within dorsal anterior cingulate cortex, left cuneus, and left cerebellum (not shown: left superior parietal lobe, right cuneus/precuneus, right lingual gyrus, and right cerebellum).

Note. Voxel-height and cluster-extent thresholds of $p<0.001$ and $k=30$. ASD=autism spectrum disorder; EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; NT=neurotypical; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands; PT=perspective-taking.

Table 10.*Group Comparisons of Interest during Self-Conscious Emotion Processing*

Contrast	Hemisphere	Region	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>
NT vs ASD (EmbLo>Neutral)	-	-	-	-	-	-	-
NT vs ASD (EmbHi>Neutral)	-	-	-	-	-	-	-
NT vs ASD	Right	Postcentral gyrus (BA 2)	47	46	-32	50	22.55
((EmbHi>Neutral) vs (EmbLo>Neutral))	Right	Anterior insula (BA 13)	30	44	0	6	22.08
NT vs ASD	Right	Inferior temporal gyrus (BA 20)	40	54	-34	-22	4.34
(PrideLo>Neutral)	Right	Middle occipital gyrus	37	34	-94	4	4.55
NT vs ASD (PrideHi>Neutral)	-	-	-	-	-	-	-
	Left	Superior parietal lobe (BA 7)	97	-34	-70	48	19.66
	Right	Cerebellum	86	8	-80	-34	21.22
NT vs ASD	Right	Lingual gyrus	73	10	-58	-4	32.35
((PrideHi>Neutral) vs (PrideLo>Neutral))	Left	Cuneus	72	0	-76	18	17.8
		Dorsal anterior cingulate cortex (BA 9)	47	-2	34	36	20.15
	Left	Cerebellum	43	-46	-72	-32	24.12
	Right	Cuneus (ext. precuneus)	30	20	-74	20	19.06

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$. ASD=autism spectrum disorder; BA=putative Brodmann Area; EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; NT=neurotypical; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands; PT=perspective-taking.

NT vs ASD (EmbHi>Neutral vs EmbLo>Neutral). When comparing activity during embarrassment clips with high, relative to low, PT demands, there were group differences within right postcentral gyrus and right anterior insula.

Right postcentral gyrus. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50) = -1.92$, *ns*; and during embarrassment clips with high PT demands, $t(50) = 1.06$, *ns*. The NT group recruited greater activity during embarrassment

clips with high, relative to low PT demands, $t(24)=-6.44, p<0.001$; while the ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=-0.04, ns$.

Right anterior insula. The ASD group recruited greater activity than the NT group during embarrassment clips with low PT demands, $t(50)=-2.38, p=0.021$; while the NT and ASD groups recruited similar activity during embarrassment clips with high PT demands, $t(50)=1.88, ns$. The NT group recruited greater activity during embarrassment clips with high, relative to low, PT demands, $t(24)=-4.80, p<0.001$; while the ASD group recruited greater activity during embarrassment clips with low, relative to high, PT demands, $t(26)=3.52, p=0.002$.

NT vs ASD (PrideLo>Neutral). When comparing activity during pride clips with low PT demands, there were group differences within right posterior inferior temporal gyrus (anterior to the preoccipital notch) and right middle occipital gyrus. The NT group recruited greater activity than the ASD group during pride clips with low PT demands within both right posterior inferior temporal gyrus, $t(50)=5.64, p<0.001$, and right middle occipital gyrus, $t(50)=4.89, p<0.001$.

NT vs ASD (PrideHi>Neutral vs PrideLo>Neutral). When comparing activity during pride clips with high, relative to low, PT demands, there were group differences within dorsal anterior cingulate cortex, left superior parietal lobe, right lingual gyrus, bilateral cuneus, and bilateral cerebellum.

Dorsal anterior cingulate cortex. The NT group recruited greater activity than the ASD group during pride clips with low PT demands, $t(50)=2.04, p=0.046$; while the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.06, p=0.045$. The NT group recruited marginally greater activity during pride clips with low,

relative to high, PT demands, $t(24)=2.03$, $p=0.054$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-4.72$, $p<0.001$.

Left superior parietal lobe. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=1.89$, *ns*; however, the ASD group recruited marginally greater activity than the NT group during pride clips with high PT demands, $t(50)=-1.93$, $p=0.060$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=2.76$, $p=0.011$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-3.86$, $p=0.001$.

Right lingual gyrus. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=0.60$, *ns*; however, the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.70$, $p=0.009$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=5.00$, $p<0.001$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-4.15$, $p<0.001$.

Left cuneus. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=0.10$, *ns*; however, the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.82$, $p=0.007$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=3.27$, $p=0.003$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-3.61$, $p=0.001$.

Right cuneus (extending into precuneus). The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=0.86$, *ns*; however, the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-$

2.71, $p=0.009$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=3.17$, $p=0.004$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-4.12$, $p<0.001$.

Left cerebellum. The NT group recruited greater activity than the ASD group during pride clips with low PT demands, $t(50)=2.07$, $p=0.044$; while the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.43$, $p=0.019$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=2.77$, $p=0.011$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-4.35$, $p<0.001$.

Right cerebellum. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=1.79$, ns ; however, the ASD group recruited greater activity than the NT group during pride clips with high PT demands, $t(50)=-2.81$, $p=0.007$. The NT group recruited greater activity during pride clips with low, relative to high, PT demands, $t(24)=3.19$, $p=0.004$; while the ASD group recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-4.76$, $p<0.001$.

Regions of Interest Analyses

As described above, the intercept represented activity broadly recruited during SCE processing, collapsed across groups, emotions, and PT demands, and controlling for low-level visual, auditory, and semantic processes. Ten clusters from the intercept, which represented *a priori* regions of interest (ROIs), were selected for further analysis. These ROIs represented clusters within: i) medial prefrontal cortex (BA 9/10) extending into dorsal medial prefrontal cortex; ii) dorsal anterior cingulate cortex (BA 32) extending into dorsal medial prefrontal cortex; iii) orbitofrontal cortex/ventral medial prefrontal cortex (BA 11/25); iv) orbitofrontal

cortex (BA 11); v) left inferior frontal gyrus (BA 11/47); vi and vii) left inferior frontal gyrus (BA 47); viii) right inferior frontal gyrus (BA 45/47/13, extending into right anterior insula); ix) left anterior insula (BA 13/47); and x) left temporal pole (BA 38). Significant main effects, interaction effects, and group differences between specific conditions (i.e., EmbLo, EmbHi, PrideLo, PrideHi), were reported. When necessary, analyses were corrected for unequal variances. (See Figure 7 and bolded clusters in Table 8.)

Figure 7.
Intercept ROIs During Self-Conscious Emotion Processing

Note. Voxel-height and cluster-extent thresholds of $p < 0.001$ and $k = 30$.

Medial Prefrontal Cortex (BA 9/10). There were no main effects nor interaction effects within a cluster peaking in anterior rostral aspects of medial prefrontal cortex and extending into dorsal medial prefrontal cortex. However, the NT group recruited greater activity than the ASD group during embarrassment clips with low PT demands, $t(50) = 2.23$, $p = 0.030$.

Dorsal Anterior Cingulate Cortex (BA 32). There was a three-way interaction effect within a cluster peaking in dorsal anterior cingulate cortex and extending into dorsal medial prefrontal cortex, $F(1,50) = 4.78$, $p = 0.033$. The ASD group recruited greater activity than the NT group during embarrassment clips with low PT demands, $t(50) = -2.01$, $p = 0.050$; but the NT and

ASD groups recruited similar activity during embarrassment clips with high PT demands, $t(50)=-0.74$, *ns*. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=0.22$, *ns*; but the ASD group recruited marginally greater activity than the NT group during pride clips with high PT demands, $t(50)=-1.95$, $p=0.056$.

Within-group comparisons revealed that the NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-1.60$, *ns*; and during pride clips with low and high PT demands, $t(24)=0.56$, *ns*. When PT demands were low, the NT group recruited greater activity during pride, relative to embarrassment, clips, $t(24)=-2.56$, $p=0.017$. When PT demands were high, the NT group recruited similar activity during embarrassment and pride clips, $t(24)=-0.00$, *ns*. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=-0.07$, *ns*; but recruited greater activity during pride clips with high, relative to low, PT demands, $t(26)=-3.01$, $p=0.006$. The ASD group recruited similar activity during embarrassment and pride clips when PT demands were low, $t(26)=0.58$, *ns*; and during embarrassment and pride clips when PT demands were high, $t(26)=-1.76$, *ns*.

Orbitofrontal Cortex/Ventral Medial Prefrontal Cortex (BA 11/25). There was a main effect of emotion within a cluster representing orbitofrontal cortex/ventral medial prefrontal cortex, $F(1,50)=8.97$, $p=0.004$, qualified by an emotion by PT demands interaction effect, $F(1,50)=8.97$, $p=0.004$. Participants recruited similar activity during embarrassment clips with low and high PT demands, $t(51)=-1.65$, *ns*; but recruited greater activity during pride clips with low, relative to high, PT demands, $t(51)=2.67$, $p=0.010$. When PT demands were low, participants recruited greater activity during pride, relative to embarrassment, clips, $t(51)=-3.86$, $p<0.001$; but when PT demands were high, participants recruited similar activity during embarrassment and pride clips, $t(51)=0.56$, *ns*.

Orbitofrontal Cortex (Rectal Gyrus; BA 11). There were no main effects nor interaction effects within a second cluster representing orbitofrontal cortex (rectal gyrus).

Left Inferior Frontal Gyrus (BA 11/47). There was a main effect of emotion within a cluster representing left inferior frontal gyrus, $F(1, 50)=5.71$, $p=0.021$, such that participants recruited greater activity during pride clips.

Left Inferior Frontal Gyrus (BA 47). There was a marginally significant main effect of PT demands within a second cluster representing left inferior frontal gyrus, $F(1,50)=3.72$, $p=0.059$, such that participants recruited marginally greater activity when PT demands were high.

Left Inferior Frontal Gyrus (BA 47). There were no main effects nor interaction effects within a third cluster representing left inferior frontal gyrus.

Right Inferior Frontal Gyrus (BA 45/47/13). There was a three-way interaction effect within a cluster representing right inferior frontal gyrus extending into right anterior insula, $F(1,50)=4.09$, $p=0.048$. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50)=-0.86$, *ns*; and high PT demands, $t(50)=0.28$, *ns*. The NT and ASD groups also recruited similar activity during pride clips with low PT demands, $t(50)=0.80$, *ns*; and high PT demands, $t(50)=-1.01$, *ns*.

Within-group comparisons revealed that the NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-0.41$, *ns*; and during pride clips with low and high PT demands, $t(24)=0.52$, *ns*. The NT group recruited similar activity during embarrassment and pride clips when PT demands were low, $t(24)=-0.08$, *ns*; and high, $t(24)=0.84$, *ns*. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=1.17$, *ns*; but recruited marginally greater activity during pride clips

with high, relative to low, PT demands, $t(26)=-2.01$, $p=0.055$. The ASD group recruited similar activity during embarrassment and pride clips when PT demands were low, $t(26)=1.92$ *ns*; and high, $t(26)=-1.13$, *ns*.

Left Anterior Insula (BA 13/47). There was a three-way interaction effect within a cluster representing left anterior insula, $F(1,50)=4.25$, $p=0.044$. The NT and ASD groups recruited similar activity during embarrassment clips with low PT demands, $t(50)=-1.33$, *ns*; and high PT demands, $t(50)=0.21$, *ns*. The NT and ASD groups recruited similar activity during pride clips with low PT demands, $t(50)=0.13$, *ns*; and high PT demands, $t(50)=-1.60$, *ns*.

Within-group comparisons revealed that the NT group recruited similar activity during embarrassment clips with low and high PT demands, $t(24)=-0.26$, *ns*; and during pride clips with low and high PT demands, $t(24)=1.92$, *ns*. The NT group recruited similar activity during embarrassment and pride clips when PT demands were low, $t(24)=-1.16$, *ns*; and high, $t(24)=1.14$, *ns*. The ASD group recruited similar activity during embarrassment clips with low and high PT demands, $t(26)=1.59$, *ns*; and during pride clips with low and high PT demands, $t(26)=-0.36$, *ns*. The ASD group recruited similar activity during embarrassment and pride clips when PT demands were low, $t(26)=0.94$, *ns*; and high, $t(26)=-1.04$, *ns*.

Left Temporal Pole (BA 38). There was a marginally significant group by PT demands interaction effect within a cluster representing left temporal pole, $F(1,50)=3.72$, $p=0.059$. The NT and ASD groups recruited similar activity when PT demands were low, $t(50)=-0.63$, *ns*; however, the ASD group recruited greater activity than the NT group when PT demands were high, $t(50)=-2.40$, $p=0.020$. Furthermore, the ASD group recruited greater activity than NT group during pride clips with high PT demands, $t(50)=-2.67$, $p=0.010$.

Within-group comparisons revealed that the NT group recruited similar activity during clips with low and high PT demands, $t(24)=1.57$, *ns*. The ASD group also recruited similar activity during clips with low and high PT demands, $t(246)=-1.11$, *ns*.

STUDY II DISCUSSION: THE NEURAL CORRELATES OF SCES

The goal of Study II was to investigate neural activation patterns recruited by autistic adolescent males with average/above average IQ, relative to age- and IQ-matched neurotypical adolescents, during SCE processing, and to explore the potential modulatory role of heightened PT demands. Broadly, autistic and neurotypical adolescents recruited strikingly similar neural patterns; however, results revealed several noteworthy group differences within regions implicated in social cognition, visual perception, salience processing, and sensorimotor processing, which were modulated by heightened PT demands/changes in the situational context.

Neural Activity Associated with Self-Conscious Emotion Processing

Before comparing group differences in neural activation patterns, we first investigated brain regions broadly involved in SCE processing. The intercept represented an interaction between SCEs and neutral emotion, averaged across emotion types and PT demand levels, and collapsed across groups. Thus, it broadly reflected activity associated with SCE processing (such as activity subserving affective inference, mental state attribution, social conceptual knowledge processing, and empathy), while controlling for low-level visual, auditory, and semantic processes. Adolescents recruited activity within medial prefrontal; middle and superior prefrontal; somatosensory; limbic; striatal; medial, inferior, and superior parietal; medial, inferior, middle, and superior temporal; occipital; and cerebellar regions. These neural patterns strongly resembled activity recruited during relevant cognitive and affective processes, including emotional facial processing, emotional prosody perception, and moral cognition. Emotion facial

processing is associated with prefrontal, limbic, temporoparietal, occipitotemporal, and cerebellar activity, including amygdala, fusiform gyrus, insula, inferior frontal gyrus, superior temporal sulcus, orbitofrontal cortex, and occipital cortex, which are believed to subserve facial identification; biological motion; and emotional salience, arousal, and valuation (Adolphs, 2002a, 2002b; Fusar-Poli et al., 2009; Trautmann et al., 2009). Emotional prosody perception is supported by superior temporal gyrus (Heschl's gyrus/transverse temporal gyrus), as well as medial prefrontal cortex, premotor cortex, insula, and inferior frontal gyrus (Alba-Ferrara, Hausmann, Mitchell, & Weis, 2011; Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Rosenblau, Kleinman, Dziobek, & Heekeren, 2017; Witteman, Van Heuven, & Schiller, 2012). Moral cognition and moral emotion processing recruit medial prefrontal cortex, dorsolateral prefrontal cortex, orbitofrontal cortex/ventral medial prefrontal cortex, superior temporal sulcus, temporal pole, and amygdala (Moll et al., 2005; 2008). Interestingly, these neural patterns also resembled activity within regions implicated in recognizing and evaluating the contextual appropriateness of SCEs, including temporal pole, fusiform gyrus, precentral gyrus, and inferior and middle occipital regions (Caillaud et al., 2019). Taken together, these results serve as proof of concept that the SCET successfully recruited robust activity associated with visual and auditory emotion processing and social norm evaluation. Furthermore, these results suggest that any group differences in neural recruitment reflect group differences in SCE processing strategies and the modulatory roles of emotion type and PT demands.

When separately investigating group-specific neural patterns, autistic and neurotypical adolescents recruited activity from similar regions, including middle and superior prefrontal; somatosensory; limbic; medial and inferior parietal; inferior and middle temporal; occipital; and cerebellar regions. These results suggest that SCE processing in ASD and neurotypical

development are broadly supported by similar brain regions, although groups may demonstrate quantitative differences that are modulated by emotion type and PT demands.

Group Differences in Neural Activity Associated with Self-Conscious Emotion Processing

The goal of Study II was to compare group differences in neural patterns during SCE processing, and to explore the potential modulatory role of heightened PT demands. Results did not reveal a main effect of group, suggesting that autistic adolescents do not broadly overactivate or underactivate specific brain regions during SCE processing. However, interaction effects highlight the modulatory roles of emotion type and PT demands on group differences in neural recruitment. SCE research has predominantly investigated embarrassment processing during low PT demands (e.g., when targets act embarrassed in embarrassing situations). Thus, the generalizability of past findings may be limited. The wider scope of the current study has the potential to enhance our understanding of SCE processing in ASD. Interestingly, the majority of group differences were observed when PT demands were high (i.e., when targets conveyed emotions that did not match the situational context, such as when targets acted proud in embarrassing situations). Group differences were observed within regions associated with social cognition (cortical midline structures and cerebellar extensions), visual perception (occipital-temporal structures, including fusiform gyrus), salience processing (anterior insula and dorsal anterior cingulate cortex), and sensorimotor processing (precentral gyrus, postcentral gyrus, and paracentral lobe). Thus, the current findings may offer a more nuanced understanding of the neural basis of SCE processing in ASD, and may shed light onto differential cognitive strategies adopted by autistic youths.

Social Cognition Regions. The social cognition network represents a set of cortical midline structures (particularly medial prefrontal cortex, temporal pole, superior temporal sulcus,

and temporoparietal junction), which aid in understanding others, including the ability to infer mental and emotional states (Blakemore, 2008; Castelli, Happé, Frith, & Frith, 2000; Frith & Frith, 2003; Gallagher et al., 2000; Saxe & Kanwisher, 2003). ASD is often associated with atypical recruitment of the social cognition network, which researchers have interpreted as reflecting poor ToM and PT abilities (Castelli et al., 2002; Frith, 2001; White, Frith, Rellecke, Al-Noor, & Gilbert, 2014). In the current study, autistic and neurotypical adolescents displayed differential recruitment of social cognition regions during SCE processing, which was driven by changes in PT demands. Converging with previous findings, autistic adolescents demonstrated hypoactivation when PT demands were low (i.e., when targets conveyed emotions that matched the situational context), particularly during embarrassment processing. In addition, autistic adolescents demonstrated hyperactivation when PT demands were high (i.e., when targets conveyed emotions that did *not* match the situational context), particularly during pride processing. Group differences were observed within medial prefrontal cortex, temporal pole, and cerebellum, a proposed extension of the social cognition network.

Medial Prefrontal Cortex. A highly-studied region within the social cognition network is medial prefrontal cortex, which is believed to support mental state attribution and intention inference (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Castelli et al., 2000; Gallagher et al., 2000; Van Overwalle, 2011). Of particular relevance, medial prefrontal cortex is associated with feelings of self-consciousness (Somerville et al., 2013), and is implicated in embarrassment processing (Berthoz et al., 2002; Takahashi et al., 2004) and, to a lesser extent, pride processing (Gilead, Katzir, Eyal, & Liberman, 2016; Roth et al., 2014; but see Takahashi et al., 2007). Thus, medial prefrontal cortex may support adopting others' perspectives or referencing others' mental states, especially during self-evaluation. Autistic individuals demonstrate medial prefrontal

hypoactivity during mental state attribution (Castelli et al., 2002; Happé et al., 1996; O’Nions et al., 2014; Wang, Lee, Sigman, & Dapretto, 2007), self-other referential processing (Lombardo & Baron-Cohen, 2010; Pfeifer et al., 2013), and emotion processing (Kana, Patriquin, Black, Channell, & Wicker, 2016), which converge with reports of atypical mentalizing in ASD.

Results from the current study converge with previous findings. Autistic adolescents recruited reduced medial prefrontal activity during SCE processing, although this pattern was only observed during embarrassment processing when PT demands were low (e.g., when targets sang well and acted embarrassed). As summarized above, previous research investigating mentalizing abilities has typically required participants to make mental or emotional state attributions that match the situational context (similar to the low PT demands condition). Thus, the current findings demonstrate that medial prefrontal hypoactivation in ASD may extend to more complex SCE processing but may be limited to instances when PT demands are low (when individuals must infer mental or emotional states that match the situational context).

Temporal Pole. Another key region of the social cognition network is anterior temporal lobe/temporal pole, which is implicated in abstract social contextual knowledge processing (Moll et al., 2008; Zahn et al., 2007; 2008). This region plays an important role in moral reasoning and SCE evaluation, when participants must reference abstract social norms/rules to evaluate the moral permissibility or social appropriateness of specific actions. Neurotypical adults recruit temporal pole when evaluating both intentional and unintentional social norm violations (Berthoz et al., 2002). Temporal pole is also recruited during SCE evaluations, including during embarrassment, guilt, and pride processing (Takahashi et al., 2004; Zahn et al., 2007). Temporal pole is associated with decoding SCEs, when participants identify if emotional expressions are congruent or incongruent with the situational context (Caillaud et al., 2019). This suggests that

temporal pole is involved in norm-based social evaluations but may not be critical for mentalizing. In support of this distinction, research investigating irony processing (which requires contextualized mental state inference) has distinguished the role of temporal pole, which is believed to support the assessment of the social context, from medial prefrontal cortex, which is believed to support intention attribution (Wakusawa et al., 2007). Particularly relevant, autistic children recruit greater temporal pole activity when attending to affective prosodic cues during irony processing, compared to neurotypical children, which the authors suggested reflect a compensatory strategy for less reflexive mentalizing, particularly when engaging in more explicit inferential tasks (Wang et al., 2006).

In the current study, autistic adolescents recruited greater temporal pole activity than neurotypical peers during SCE processing when PT demands were high, particularly during pride processing (i.e., when targets acted proud but sang poorly). Framed within the context of past findings, temporal pole hyperactivation may reflect greater social conceptual knowledge processing, particularly when presented with discrepant affective and contextual cues, to determine if emotional expressions are contextually and socially appropriate. Thus, when PT demands are high and targets express contextually-inappropriate pride, autistic adolescents may recruit greater activity from regions implicated in social norm referencing. This interpretation converges with findings from Study I (as well as previous research) to suggest that autistic individuals may engage in greater social norm referencing during complex emotion attribution, perhaps to compensate for less reflexive mentalizing or difficulties integrating discrepant mental state and contextual information (Baez et al., 2012; Zalla et al., 2011).

Cerebellum. Cerebellum is a proposed extension of the social cognition network.

Although this region is most readily associated with motor coordination, recent research supports

its role in higher-order social cognition, including emotion perception, emotion recognition, and emotion regulation (Adamaszek et al., 2014; 2017; Clausi et al., 2017). Schmahmann (1998) proposed that cerebellum is responsible for coordinating cognitive and affective processes, and cerebellar dysfunction is linked with cognitive and emotional atypicalities, including atypical social communication, executive dysfunction, and language delays (Hoche, Guell, Sherman, Vangel, & Schmahmann, 2016; Schmahmann, 1998; Schmahmann & Sherman, 1998), which are commonly reported in ASD. A large-scale meta-analysis of over 350 social cognition studies offers empirical support for the distinct role of cerebellum in “higher abstraction mentalizing”, but not mirroring or mentalizing (Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014). Thus, cerebellar activity, similar to temporal pole activity, may indirectly support social cognition via abstract social conceptual knowledge processing.

In the current study, group differences in cerebellar recruitment were modulated by PT demands, particularly during pride processing. Autistic adolescents showed cerebellar hypoactivity during pride processing when PT demands were low (when targets conveyed emotions that matched the situational context), but cerebellar hyperactivity during pride processing when PT demands were high (when targets conveyed emotions that did not match the situational context). This pattern of hypoactivation during low PT demands and hyperactivation during high PT demands mirrors the aforementioned neural patterns observed within the prototypical social cognition network (i.e., medial prefrontal cortex and temporal pole), as well as lends further support for an association between ASD and cerebellar atypicalities (Wang, Kloth, & Badura, 2014). A possible interpretation is that autistic adolescents may engage in greater higher-level abstraction mentalizing (as reflected by cerebellar hyperactivity) when they observe targets conveying emotions that conflict with observed contextual cues. Supporting this

interpretation, Schmahmann (1998) proposed that cerebellum promotes contextually-appropriate behaviors and monitors incongruencies between intended and observed outcomes. An alternative, although not mutually-exclusive, interpretation is based on research linking cerebellar activity with multisensory integration (Ronconi et al., 2017; Wang et al., 2014). Accordingly, cerebellar hyperactivity when PT demands are high (when targets convey contextually-discrepant emotions) may represent more effortful integration of multimodal cues.

Integration of Results Across the Social Cognition Network. Taken together, results from the current study extend past findings by suggesting that autistic individuals do not demonstrate global hypoactivation of the social cognition network; instead, activity may be differentially modulated by changes in PT demands. These neural patterns may reflect different cognitive strategies adopted by autistic youths during emotion attribution. When PT demands are low, autistic adolescents demonstrate hypoactivation of the social cognition network, perhaps representing less reflexive mentalizing; however, when PT demands are high, they demonstrate hyperactivation of this network and its extensions, perhaps representing a greater need to access social conceptual knowledge when integrating discrepant affective and contextual cues.

Visual Perception Regions. Results also revealed group differences within occipital-temporal regions, including fusiform gyrus, inferior temporal gyrus, lingual gyrus, cuneus, and inferior and middle occipital cortices, which are implicated in visual perception. Similar to neural patterns observed within the social cognition network, group differences in occipital-temporal recruitment were modulated by PT demands, particularly during pride processing. Autistic adolescents demonstrated hypoactivation when PT demands were low, but hyperactivation when PT demands were high. Within-group comparisons offered converging

evidence. Autistic adolescents recruited greater activity when PT demands were high, while neurotypical adolescents recruited greater activity when PT demands were low.

Occipital and posterior temporal regions play key roles in visual perception (Haxby, Hoffman, & Gobbini, 2000), particularly when evaluating social and affective stimuli (Adolphs, 2002a). While fusiform gyrus is most commonly associated with emotional facial processing (Kanwisher & Yovel, 2006), it is also implicated in emotional body processing (De Gelder, 2006; Peelen & Downing, 2005). Meanwhile, lateral occipital-temporal regions may be selective for bodies (Downing, Jiang, Shuman, & Kanwisher, 2001), and inferior and middle occipital regions may be particularly important for recognizing body and postural cues during SCE decoding (Caillaud et al., 2019). Autistic individuals commonly demonstrate hypoactivation within fusiform gyrus and occipital cortices during facial processing (Pierce, Müller, Ambrose, Allen, & Courchesne, 2001). This includes during emotion recognition and affective empathy tasks that use decontextualized static photographs of faces (Greimel et al., 2010; Hall, Doyle, Goldberg, West, & Szatmari, 2010; Hubl et al., 2003); decontextualized animated photographs of faces (Sato, Toichi, Uono, & Kochiyama, 2012); and static photographs of faces paired with matching prosodic voices (Hall, Szechtman, & Nahmias, 2003). However, prior studies were limited to only using tasks with low PT demands. Findings from the current study both confirm and extend past research by suggesting that autistic individuals may demonstrate attenuated visual attention during SCE processing when PT demands are low (Dichter, 2012), but heightened visual attention when PT demands are high, which may serve as a compensatory strategy for less reflexive mentalizing. Our findings cannot dissociate if enhanced occipital-temporal recruitment reflects greater attention to facial features, body postures, or more effortful visual search, in general. However, a lack of group differences within posterior superior temporal

sulcus, a region implicated in biological motion (Allison, Puce, & McCarthy, 2000) and perceptual atypicalities in ASD (Pelphrey, Adolphs, & Morris, 2004), suggests that group differences may reflect atypical feature detection when integrating discrepant visual affective and contextual information, and not atypical intention attribution according to changes in facial (e.g., eye gaze) and body cues (Allison et al., 2000; Haxby et al., 2000).

Salience Regions. Neuroimaging research has defined an intrinsically-connected salience network, with hubs located within anterior insula and dorsal anterior cingulate cortex (Menon & Uddin, 2010; Seeley et al., 2007). This network is believed to integrate sensory, affective, and cognitive cues, and to detect and highlight stimuli that are self-relevant, emotionally-arousing, or novel (Menon, 2015). Anterior insula is implicated in interoceptive-awareness, visceral arousal, salience detection, and attention to/integration of multisensory information (Craig, 2009; Critchley, Wiens, Rotshtein, & Dolan, 2004; Immordino-Yang, McColl, Damasio, & Damasio, 2009; Nelson et al., 2010); while dorsal anterior cingulate cortex is implicated in response selection and conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Of particular relevance, anterior insula and dorsal anterior cingulate cortex are posited to play key roles in empathy processing (Bernhardt & Singer, 2012; Fan et al., 2011), including empathy for physical pain (Singer et al., 2004), social pain (Masten, Morelli, & Eisenberger, 2011), embarrassment (Krach et al., 2015); disgust (Deen, Pitskel, & Pelphrey, 2010; Jabbi, Swart, & Keysers, 2007); and enjoyment (Jabbi et al., 2007).

Researchers have linked ASD with atypical salience network function (Di Martino et al., 2009; Uddin & Menon, 2009), which has been suggested to underlie autistic symptomatology (Uddin et al., 2013). Researchers have been particularly interested in exploring group differences in empathy processing, in an effort to better understand interpersonal challenges in ASD.

However, findings have been mixed, including insular hyperactivation (Gu et al., 2015), hypoactivation (Krach et al., 2015; Morita et al., 2012; 2016), and no group differences (Klapwijk et al., 2016; Pantelis et al., 2015), which may reflect the modulatory role of the situational context in salience network recruitment.

In support of this theory, the current study revealed three-way interactions within bilateral dorsal anterior insula and dorsal anterior cingulate cortex, highlighting the interacting, modulatory roles of group, emotion type, and PT demands in the recruitment of salience network activity during SCE processing. Two key patterns emerged. First, autistic adolescents recruited greater anterior insular activity than neurotypical adolescents during embarrassment processing when PT demands were low. In addition, autistic adolescents recruited greater dorsal anterior cingulate activity during embarrassment processing when PT demands were low. Thus, autistic adolescents demonstrated salience network hyperactivation when they observed targets acting embarrassed in embarrassing situations.

Second, autistic adolescents recruited greater dorsal anterior cingulate activity than neurotypical adolescents during pride processing when PT demands were high. In contrast, neurotypical adolescents recruited greater dorsal anterior cingulate activity during pride processing when PT demands were low. Thus, autistic adolescents demonstrated salience network hyperactivation when they observed targets acting proud in embarrassing situations, but hypoactivation when they observed targets acting proud in pride-evoking situations.

Within-group comparisons revealed similar patterns. Autistic adolescents recruited greater salience network activity during embarrassment processing when PT demands were low, and during pride processing when PT demands were high. In contrast, neurotypical adolescents

recruited greater activity during embarrassment processing when PT demands were high, and during pride processing when PT demands were low.

Broadly, these findings suggest that autistic adolescents recruit greater salience network activity not only when they observe embarrassed targets in embarrassing situations, but also when observe proud targets in embarrassing situations. This suggests that the embarrassing context (more so than the expression of embarrassment) may drive salience network hyperactivation in ASD. Consequently, group differences in salience network recruitment appear to be driven by changes in the situational context, such that autistic adolescents recruit greater activity during embarrassing situations (when they expect embarrassment/failure), but reduced activity during pride-evoking situations (when they expect pride/success).

There are several possible interpretations for these differential neural patterns. First, autistic adolescents might find embarrassing situations more emotionally distressing. Thus, salience network hyperactivation may reflect heightened affective arousal. This interpretation coincides with findings from behavioral research showing that autistic individuals have an increased tendency to feel personal distress on behalf of others (Adler et al., 2015; Dziobek et al., 2008; Lombardo et al., 2007; Patil et al., 2016; Rogers et al., 2007). Particularly relevant to this interpretation, Gu and colleagues (2015) reported that autistic adults experience heightened autonomic arousal and neural responsivity during empathic physical pain processing, including elevated skin conductance, anterior insular hyperactivity, and anterior insular hyperconnectivity (which the authors interpreted as a failure to inhibit). Autistic adults also demonstrate a stronger correlation between elevated skin conductance and anterior insular hyperactivity, which may suggest a stronger relationship between autonomic and affective arousal during empathy for pain. Findings from the current study extend prior research by suggesting that autistic

adolescents may not only experience heightened affective arousal when they *directly* observe others in pain, but also when they observe others in situations that would *typically elicit* these feelings (regardless if targets convey these emotions or not). Thus, atypical anterior insula recruitment may underlie atypical empathy processing, given its proposed role in contextualized, interoceptive predictions (Gu et al., 2015). Autistic individuals may be hypersensitive to these signals and/or fail to inhibit them (Gu et al., 2015). Consequently, they may be more strongly influenced by the situational context during affective inference, particularly when making embarrassment attributions, which may evoke affective hyperarousal.

A second possible interpretation is that salience network hyperactivation during embarrassing situations may reflect hypersensitivity to rule violations in ASD. This interpretation is supported by research linking anterior insula to attention allocation (Menon & Uddin, 2010) and dorsal anterior cingulate cortex to conflict monitoring (Botvinick et al., 2001). During the SCET, participants were told that they would watch clips of singers performing in a singing competition. Thus, an implicit rule of this task is that singers should sing well. Framed with this context, autistic adolescents may have perceived singers who sang poorly as having violated this rule. Autistic children, adolescents, and adults recruit greater anterior insular and dorsal anterior cingulate activity when they observe social and nonsocial rule violations (Bolling et al., 2011; Dichter, Felder, & Bodfish, 2009). Given that autistic individuals commonly demonstrate a strict adherence to rule-following (Zalla et al., 2011), the current findings may suggest that autistic youths allocate greater attention to detecting rule violations, which may modulate neural responsivity during social interactions.

A third possible interpretation is that embarrassing situations may be relatively more salient and personally-relevant to autistic adolescents, while pride-evoking situations may be

relatively more salient and personally-relevant to neurotypical adolescents. Autistic youths experience greater peer rejection and bullying, while neurotypical youths experience greater peer acceptance and social support (Symes & Humphrey, 2010). Despite documented mentalizing difficulties, autistic youths offer personal accounts of being excluded by peers, which suggest that they are both cognizant of and distressed by negative social interactions (Ochs, Kremer-Sadlik, Solomon, & Sirota, 2001). Relatedly, autistic adults experience greater proneness to feeling shame, compared to neurotypical adults (Davidson, Vanegas, & Hilvert, 2017). Thus, in the current study, salience network hyperactivity during embarrassing situations may represent heightened awareness or perceived importance, which may reflect a history of social exclusion/social rejection in ASD.

Sensorimotor Regions. Results also revealed three-way interactions within lateral frontal and parietal regions, including precentral gyrus, postcentral gyrus, and paracentral lobe/middle cingulate cortex. These patterns highlight the interacting, modulatory roles of group, emotion type, and PT demands in the recruitment of somatosensory and motor regions during SCE processing. Neurotypical adolescents recruited greater sensorimotor activity than autistic adolescents during pride processing when PT demands were low (when targets sang well and acted proud), as well as during embarrassment processing when PT demands were high (when targets sang well and acted embarrassed). This suggests that neurotypical adolescents recruit greater sensorimotor activity than autistic adolescents during pride-evoking situations. Within-group comparisons revealed converging patterns. Neurotypical adolescents recruited greater activity when targets sang well compared to when they sang poorly (regardless of the emotion conveyed), while autistic adolescents recruited greater activity when targets sang poorly

compared to when they sang well (regardless of the emotion conveyed). Thus, group differences in sensorimotor recruitment appear to have been modulated by the situational context.

Somatosensory and premotor/motor regions are broadly implicated in bottom-up information processing, such as low-level sensory and motor simulation during facial perception (Zaki, Weber, & Ochsner, 2012). These regions may serve as sensory afferents and motor efferents to anterior insula and anterior cingulate cortex within a larger salience network (Uddin & Menon, 2009). Research investigating empathic pain processing highlight distinct sensory and affective-motivational components of a putative pain matrix, which are supported by sensorimotor regions and anterior insula/anterior cingulate cortex, respectively (Avenanti, Buetti, Galati, & Aglioti, 2005; Han et al., 2009; Lamm et al., 2011). Thus, group differences in sensorimotor recruitment during SCE processing may represent atypical sensorimotor resonance.

It is worth noting that sensorimotor regions reported in the current study are not part of the putative mirror neuron system (i.e., inferior frontal gyrus and inferior parietal lobule), which supports affective empathy through action observation and motor simulation (Van Overwalle & Baetens, 2009). Research suggests that sensorimotor activity during empathic pain processing represents visual processing of sensorimotor cues, and not the explicit mirroring of somatosensory states (Lamm et al., 2011). Thus, in the current study, group differences in sensorimotor recruitment may reflect enhanced processing of contextual cues that are uniquely salient for each group (pride-relevant cues for neurotypical adolescents and embarrassment-relevant cues for autistic adolescents), which, in turn, may be associated with group differences in empathy processing.

Absence of Group Differences within Amygdala and Temporoparietal Junction

The current study did not detect group differences within amygdala or temporoparietal junction, two regions associated with social cognition. Amygdala is broadly implicated in emotion processing and may be particularly responsive to emotional valence (Breiter et al., 1996). While a popular theory of autism proposes that amygdala dysfunction may underlie social cognitive challenges (Baron-Cohen et al., 2000), studies investigating personal and empathic embarrassment in autistic adults have not detected group differences in amygdala activity (Krach et al., 2015; Morita et al., 2012; 2016; Pantelis et al., 2015). One possible explanation is that amygdala may play a more critical role in basic, nonsocial emotion processing than in complex, social emotion processing (including SCE attribution and empathic SCEs). In support of this interpretation, Schultz (2005) argued that amygdala supports early-stage, automatic emotion processing, such as signaling affective arousal and emotional salience, while higher-level cortical structures support more advanced emotional inference. Thus, the current findings suggest that autistic adolescents may have intact foundational emotion recognition abilities, as reflected in similar amygdalar recruitment as neurotypical peers, but atypical advanced social cognitive abilities, as reflected in enhanced temporal pole and cerebellar recruitment. Findings from Study I support this interpretation.

The current study did not detect group differences within temporoparietal junction. Temporoparietal junction is proposed to play a critical role in social cognition and ToM (Saxe & Kanwisher, 2003), and dysfunction is associated with atypical social cognition in ASD (Lombardo, Chakrabarti, Bullmore, Baron-Cohen, & Consortium, 2011). One possible explanation for a lack of group differences relates to differences in paradigm design. Studies that reported group differences in temporoparietal junction used tasks that required complex social reasoning and cognitive inference, such as reading vignettes describing social norm violations,

inferring targets' intentions, and then using this information to make moral evaluations (Berthoz et al., 2002; Young et al., 2007). In comparison, the SCET required less cognitive inference and greater affect recognition, by requiring participants to identify affective facial and postural cues and then using this information to make emotion attributions. In support of this interpretation, research by Caillaud and colleagues (2003) highlight the role of temporal parietal junction in SCE reasoning (i.e., cognitive inference) but not SCE decoding (i.e., emotion recognition.) Thus, ASD may not be characterized by global temporoparietal junction dysfunction, and group differences may be task-specific, modulated by cognitive inferential demands.

Strengths, Limitations, and Future Directions

This study is associated with several strengths. First, neuroimaging research investigating emotion processing predominantly used static photographic stimuli. In comparison, the current study used dynamic video stimuli, which is more engaging and may evoke more robust neural activity (Trautmann et al., 2009). Second, past neuroimaging studies generally used simplified stimuli (such as images of only eyes). Thus, past results may reflect the engagement of only one type of cognitive strategy (limited by the task design). In comparison, the SCET featured complex video stimuli which provided diverse, multisensory, affective cues, including eye gaze, facial expressions, body postures, and prosody. Thus, the current findings may more accurately represent the multiple, concurrent strategies that are likely adopted during real-world social interactions. Third, most neuroimaging studies investigating empathy processing used photographs of body parts in pain (e.g., a hand being pricked by a needle or hit with a hammer), which limited the generalizability of these findings to empathic *physical* pain. To date, only one study has investigated empathy for *social* pain in autistic individuals, using drawings of targets in stereotypically embarrassing social situations (Krach et al., 2011). The current study built off

past research by investigating more realistic and implicit empathic social pain processing using video clips that in some ways more closely resemble real-world social interactions with peers. This study also extended prior research that only investigated SCE processing in autistic adults to include autistic youths.

Despite these advantages, this study is associated with several limitations. First, the SCET featured multimodal stimuli that provided multiple affective cues. While these stimuli may be more ecologically-valid, this study is unable to distinguish which types of cues each group used, and if groups differentially prioritized some cues over others. Future research should manipulate the types of cues provided (e.g., cues from the eyes, mouth, or body posture) or the modality of cues provided (i.e., visual, auditory, or verbal cues), either by varying which types of cues are presented or by instructing participants to pay attention to only certain types of cues during specific blocks. Combining neuroimaging and eye-tracking methodologies may also prove useful.

A second limitation is that this study is unable to distinguish which cognitive/affective processes each group engaged in during SCE processing (i.e., emotion recognition, empathy, etc.). Future research could manipulate this, such as by explicitly instructing participants to focus on the targets' emotions (emotional inference), their own emotions for the targets (empathic processing), or the targets' singing quality (contextual knowledge processing). Research suggests that changes in task demands modulate group differences in neural recruitment during social cognitive processing (Alaerts, Swinnen, & Wenderoth, 2017).

Finally, future research should recruit both male and female participants and investigate the modulatory role of gender in SCE processing. Autism research has primarily featured all-male or predominantly male samples. However, neurotypical males and females recruit

differential neural patterns during emotion attribution and empathy processing (Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008). Thus, distinct gender profiles may exist in ASD as well. Research exploring gender differences may have theoretical and clinical implications, since autistic individuals demonstrate gender-specific symptom profiles (Lai, Lombardo, Auyeung, Chakrabarti, & Baron-Cohen, 2015).

CONCLUDING REMARKS

The aims of these studies were to explore the subjective experience and neural correlates of SCE processing in autistic adolescent males with average/above average IQ, relative to age- and IQ-matched neurotypical adolescents. ASD is commonly characterized as an “empathy disorder” (Gillberg, 1992) associated with “mindblindness” (Baron-Cohen et al., 1985; Frith, 2001); however, findings from Study I challenge these depictions by demonstrating that autistic adolescents can recognize SCEs and feel empathic SCEs for others. What is more, autistic adolescents demonstrate unimpaired detection sensitivity; they infer SCEs and feel empathic SCEs with similar intensity as neurotypical adolescents. While autistic individuals are broadly characterized by impaired or atypical PT abilities, our findings suggest that their ability to recognize SCEs and feel empathic SCEs is not inhibited by heightened PT demands. Thus, real-world interpersonal challenges may likely reflect difficulties translating affective information into socially-appropriate responses, but not impaired inferential or empathic abilities.

Interestingly, investigating incongruent SCE attributions offered a more nuanced understanding of SCE processing in ASD. While autistic adolescents can appropriately identify and rate the intensity of conveyed SCEs, during heightened PT demands, they *additionally* infer more intense SCEs that reflect the situational context (even when targets do not explicitly convey these emotions). This suggests that the emotional inferences of autistic individuals may be more

strongly impacted by personal expectations of situationally-appropriate reactions, which may reflect a strict adherence to rule-following. This response pattern is associated with attenuated real-world cognitive empathy. Thus, an overreliance on learned social rules may serve as a compensatory strategy for less reflexive mentalizing in autistic youths.

Results from Study II lend support for this interpretation. While ASD is commonly characterized by broad neural dysfunction within social cognition, emotion, and empathy networks, our findings reveal that autistic and neurotypical adolescents recruit strikingly similar neural patterns during SCE processing. When group differences were observed, they were often modulated by PT demands or the situational context, suggesting that autistic adolescents do not demonstrate global neural dysfunction. Specifically, autistic adolescents demonstrated differential recruitment of brain regions implicated in social cognition, visual perception, salience processing, and sensorimotor processing, which were modulated by changes in PT demands and the situational context. One interpretation, which converges with results from Study I, is that autistic adolescents may engage in greater social norm referencing/social conceptual knowledge processing when they observe targets conveying contextually-inappropriate emotions. An over-reliance on abstract rule-following may serve as a compensatory strategy for less reflexive mentalizing or for difficulties integrating discrepant mental state and contextual information. In addition, autistic adolescents may be particularly sensitive to social rule violations or embarrassing situations, which they may perceive as more emotionally salient.

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Foot notes:

¹ The authors use the term "autistic" to reflect identity-first language, which is, at present, the preferred terminology of many self-advocates.

² Here, the term "atypical" represents "neurodivergent". It is a comparative term, relative to "neurotypical". The term "atypical" does not represent "incorrect", just like the term "neurotypical" does not represent "correct".

³ Here, the term "appropriately" reflects expected behaviors, based on neurotypical definitions of social standards.

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SUPPLEMENTAL METHODS

Exclusionary Criteria

Diagnostic Exclusionary Criteria. Participants were excluded if they had a neurological disorder, including: seizure disorder, central nervous system infection (e.g., meningitis), brain tumor, muscular or myotonic dystrophy, significant visual impairment (e.g., strabismus, visual handicap), or color blindness. Participants were also excluded if they had MRI contraindications, including: metallic braces or ferromagnetic orthodontia; metallic implants/metal fragments in their body; required a pacemaker or electronic medical implants; tattoos on their face, head or neck; habitual involuntary movement or twitching of their face, arms, or legs; hyperactivity; or claustrophobia. NT participants were also excluded if they had a psychiatric diagnosis, including schizophrenia, bipolar disorder, recurrent major depression, Tourette's syndrome, attention deficit disorder, attention deficit hyperactivity disorder, conduct disorder, serious emotional disturbance, obsessive compulsive disorder, dyslexia, delay in learning to speak, learning disorder, anxiety disorder, mood disorder, drug dependency, or mental retardation/intellectual disability. NT participants were also excluded if they or a first-degree relative had a diagnosis of ASD (or concern thereof). ASD participants were excluded if they had a diagnosis of schizophrenia, Tourette's syndrome, dyslexia, or mental retardation/intellectual disability. ASD participants were not excluded if they had a diagnosis of depressive disorder, anxiety disorder, attention deficit disorder, or attention deficit hyperactivity disorder, given their high comorbidity and overlapping symptomatology. All participants had a FSIQ $\geq$ 75 (according to the two-subscale FSIQ score on the WASI-II) (Wechsler, 2011).

ASD diagnosis was confirmed based on combined Autism Diagnostic Observation Schedule (ADOS; Lord et al., 2000) social + communication scores (raw scores $\geq$ 7+), Social

Responsiveness Scale (SRS; Constantino, 2002) total scores (T scores=55+), and Autism Spectrum Rating Scales (ASRS; Goldstein & Naglieri, 2013) total scores and DSM-V scores (T scores=60+). NT participants were excluded if they fell within the autism range on either the SRS or ASRS. (NT participants did not complete the ADOS).

82 participants enrolled in this research project. 16 ASD participants and 10 NT participants were excluded (ASD: n=6 diagnostic criteria; n=2 IQ criteria; n=3 MRI contraindications; n=2 noncompliance; n=1 deceased; NT: n=4 diagnostic criteria; n=3 MRI contraindications; n=1 withdrawal; n=2 old version of the task). Two ASD participants were not invited to the MRI appointment because their IQ data were initially scored incorrectly. After data were correctly rescored, they were deemed eligible to participate but data collection was complete. One ASD participant was not invited to the MRI appointment due to oversampling (participants who clearly met diagnostic criteria were prioritized for ADOS appointments). Thus, 56 participants (30 ASD, 26 NT) were included in the final analyses for Study I, and 52 participants (27 ASD, 25 NT) were included in the final analyses for Study II.

MRI Data Exclusionary Criteria. Participants were excluded from the final MRI analyses if >30% of the volumes of each run (or >30% of the total volumes) had motion artifact. In cases where >30% of the volumes of only one run had motion artefact, these individual runs were excluded from the analyses, but participants were not excluded. Motion artefact was characterized using both automated and manual artefact detection methods. First, using scripts developed in the University of Oregon's DSN Lab (<http://github.com/dsnlab/auto-motion>), motion parameters were transformed into Euclidian distance for translations (x, y, z) and rotations (pitch, roll, yaw). These distances, along with the mean and standard deviation of voxel intensity for each volume, were used to detect volumes affected by motion. Volumes that

exceeded 0.3 mm movement in Euclidian distance; volumes that were greater than 3 standard deviations above or 1.5 standard deviations below the mean voxel intensity across subjects; and volumes that were greater than 3 standard deviations above or below the mean standard deviation of voxel intensity across subjects were marked. Volumes that were immediately preceded by and followed by volumes marked as described above were also marked (i.e., “sandwich volumes”). Finally, motion artefact was assessed by visually inspecting 4d movies of each volume per participant (created and viewed in FSL).

Demographics

Study I Demographics. Participants in the ASD group ranged from 137.90 to 203.80 months (11 years 6 months to 16 years 11 months), with a mean age of 173.97 months (14 years 5 months). Participants in the NT group ranged from 132.00 to 211.10 months (11 years 0 months to 17 years 7 months), with a mean age of 179.94 months (14 years 8 months). PDS scores for the ASD group ranged from 1.0-4.0 (pubertal stage: n=2 pre-puberty; n=1 early puberty; n=13 mid puberty; n=13 late puberty; n=1 post-puberty). PDS scores for the NT group ranged from 1.2-3.6 (pubertal stage: n=1 pre-puberty; n=3 early puberty; n=12 middle puberty; n=10 late puberty; n=0 post-puberty). Groups did not differ on age, $t(54)=0.51$, *ns*; pubertal development, $t(54)=-0.17$, *ns*; nor pubertal category, $X^2(4)=2.49$, *ns*. All participants had a FSIQ of at least 75 (ASD: 77-141, $M=109.43$; NT: 93-140, $M=116.15$), and groups did not differ on FSIQ, $t(54)=1.68$, *ns*. Both groups were predominantly Caucasian, reflecting local demographics (ASD: n=27 Caucasian; n=1 Hispanic; n=2 multi-ethnic; NT: n=18 Caucasian; n=4 Hispanic; n=2 multi-ethnic; n=2 missing data), and groups did not differ on ethnic representation, $X^2(2)=2.97$, *ns*. Groups did not differ on maternal education (ASD: n=0 public school; n=3 high school; n=2 trade school; n=7 associate degree; n=11 undergraduate degree; n=6 post-graduate

degree; n=1 declined to answer; NT: n=1 public school; n=2 high school; n=2 trade school; n=2 associate degree; n=6 undergraduate degree; n=11 post-graduate degree; n=2 missing data), $X^2(5)=6.52$, *ns*. In addition, groups did not differ on paternal/spousal education (ASD: n=0 public school; n=8 high school; n=0 trade school; n=3 associate degree; n=6 undergraduate degree; n=10 post-graduate degree; n=1 declined to answer; n=2 missing data; NT: n=2 public school; n=3 high school; n=0 trade school; n=3 associate degree; n=5 undergraduate degree; n=7 post-graduate degree; n=1 declined to answer; n=3 missing data; n=2 data not available), $X^2(4)=3.94$, *ns*. Groups also did not differ on annual household income (ASD: n=4 \$0-\$25,000; n=1 \$25,000-\$40,000; n=8 \$40,000-\$75,000; n=6 \$75,000-\$100,000; n=8 \$100,000+; n=3 declined to answer; NT: n=0 \$0-\$25,000; n=7 \$25,000-\$40,000; n=5 \$40,000-\$75,000; n=6 \$75,000-\$100,000; n=6 \$100,000+; n=2 missing data), $X^2(4)=9.33$, *ns*.

Study II Demographics. Participants in the ASD group ranged from 137.90 to 203.80 months (11 years 5 months to 16 years 11 months), with a mean age of 176.42 months (14 years 8 months). Participants in the NT group ranged from 133.30 to 211.10 months (11 years 1 month to 17 years 7 months), with a mean age of 178.74 months (14 years 10 months). PDS scores for the ASD group ranged from 1.0-4.0, with a mean of 2.67 (pubertal stage: n=1 pre-puberty; n=1 early puberty; n=11 mid puberty; n=13 late puberty; n=1 post-puberty). PDS scores for the NT group ranged from 1.20-3.60, with a mean of 2.62 (pubertal stage: n=1 pre-puberty; n=3 early puberty; n=12 middle puberty; n=10 late puberty; n=0 post-puberty). Groups did not differ on age, $t(50)=0.40$, *ns*; pubertal development, $t(50)=-0.28$, *ns*; nor pubertal category, $X^2(4)=3.36$, *ns*. All participants had a FSIQ of at least 75 (ASD: 77-141, $M=109.33$; NT: 93-140, $M=116.56$), and groups did not differ on FSIQ, $t(50)=1.69$, *ns*. Both groups were predominantly Caucasian, reflecting local demographics (ASD: n=24 Caucasian; n=1 Hispanic; n=2 multi-ethnic; NT: n=18

Caucasian; n=4 Hispanic; n=2 multi-ethnic; n=1 missing data), and groups did not differ in ethnic representation, $X^2(2)=2.49$, *ns*. Groups did not differ on maternal education (ASD: n=0 public school; n=3 high school; n=1 trade school; n=7 associate degree; n=10 undergraduate degree; n=5 post-graduate degree; n=1 declined to answer; NT: n=1 public school; n=2 high school; n=2 trade school; n=2 associate degree; n=6 undergraduate degree; n=11 post-graduate degree; n=1 missing data), $X^2(5)=7.49$, *ns*. In addition, groups did not differ on paternal/spousal education (ASD: n=0 public school; n=8 high school; n=3 associate degree; n=5 undergraduate degree; n=8 post-graduate degree; n=1 declined to answer; n=2 missing data; NT: n=2 public school; n=3 high school; n=3 associate degree; n=5 undergraduate degree; n=7 post-graduate degree; n=1 declined to answer; n=2 missing data), $X^2(6)=4.05$, *ns*. Groups also did not differ on annual household income (ASD: n=4 \$0-\$25,000; n=1 \$25,000-\$40,000; n=7 \$40,000-\$75,000; n=6 \$75,000-\$100,000; n=6 \$100,000+; NT: n=0 \$0-\$25,000; n=7 \$25,000-\$40,000; n=5 \$40,000-\$75,000; n=6 \$75,000-\$100,000; n=6 \$100,000+; n=1 missing data), $X^2(4)=8.83$, *ns*.

Behavioral Measures

Revised Self-Consciousness Scale-Child. Participants completed the Revised Self-Consciousness Scale for Children (RSCS-C; Scheier & Carver, 1985), a 29-item questionnaire used to assess the tendency to feel self-conscious and socially anxious. The RSCS-C has three subscales: Public Self-Consciousness (11 items), Private Self-Consciousness (11 items), and Social Anxiety (7 items). Example items include: “I often check the way I look”, “I’m always trying to understand myself”, and “I feel scared when I meet someone new”. Participants rated the descriptiveness of these statements using a 5-point Likert scale, ranging from “Strongly disagree” to “Strongly agree”. Public Self-Consciousness and Private Self-Consciousness

subscale scores were calculated. Subscales missing more than 1 item, and measures missing more than 3 items were not scored.

Toronto Alexithymia Scale-20 Item. Participants completed the Toronto Alexithymia Scale-20 Item (TAS-20; Bagby, Parker, & Taylor, 1994) a 20-item questionnaire used to assess alexithymic tendencies. Alexithymia reflects meta-cognitive abilities (particularly for internalized emotions) and has been associated with empathic abilities. The TAS-20 has three subscales: Difficulty Identifying Feelings (7 items), Difficulty Describing Feelings (5 items), and Externally-Oriented Thinking (8 items). Example items include: “I am often confused about what emotion I am feeling”, “It is difficult for me to find the right words for my feelings”, and “I prefer to analyze problems rather than just describe them”. Participants rated the descriptiveness of these statements using a 5-point Likert scale, ranging from “Strongly disagree” to “Strongly agree”, and all three subscale scores were calculated. According to TAS-20 scoring instructions, subscales missing more than 1 item and measures missing more 2-3 items were not scored.

Reading the Mind in the Eyes Task-Child. Participants completed the Reading the Mind in the Eyes Task-Child (RMET-C; Baron-Cohen, Wheelwright, Scahill, Lawson, & Spong, 2001), a 28-item task used to assess cognitive empathy. Participants viewed photographs of eyes and inferred emotional or mental states by selecting one of four labels. Example labels include: “angry”, “friendly”, “unkind”, and “a bit worried”. A total score was calculated.

Strange Stories Task-Revised. Participants completed the Strange Stories Task-Revised (White, Hill, Happé, & Frith, 2009), a 16-vignette task used to assess cognitive empathy. 8 vignettes featured scenarios representing double-bluffs, white lies, and advanced PT demands to assess mental state attribution (ToM items), and 8 vignettes assessed physical state attribution (Physical items). Answers received a score of “0” to “2”, and total ToM scores were calculated.

Interpersonal Reactivity Index. Participants completed the Interpersonal Reactivity Index (IRI; Davis, 1983), a 28-item questionnaire used to assess empathic tendencies. The IRI has four subscales, consisting of 7 items: Perspective-Taking (the tendency to spontaneously adopt others' psychological point of view), Fantasy (the tendency to imaginatively adopt the feelings and actions of fictitious characters in movies, books, or plays), Empathic Concern (the "other-oriented" tendency to feel sympathy and concern for unfortunate others), and Personal Distress (the "self-oriented" tendency to feel personal anxiety and unease in stressful interpersonal settings). Example items include: "I try to look at everybody's side of an argument before I make a decision", "I really get involved with the feelings of the characters in a story", "I often have tender, concerned feelings for people less fortunate than me", and "In emergency situations, I feel worried and anxious". Participants rated the descriptiveness of these statements using a 5-point Likert scale, ranging from "Does not describe me well" to "Describes me very well". Total scores for the Perspective-Taking, Empathic Concern, and Personal Distress subscales were calculated. Subscales missing more than 1 item and measures missing a total of 3 or more items were not scored.

Basic Empathy Scale. Participants completed the Basic Empathy Scale (BES; Jolliffe & Farrington, 2006), a 20-item questionnaire used to assess empathic tendencies. The BES has two subscales, Cognitive Empathy and Affective Empathy, consisting of 9 and 11 items, respectively. Jolliffe and Farrington (2006) argued that the BES and IRI may assess distinct constructs. Affective Empathy scores on the IRI may best reflect the tendency to feel sympathy for others, while Affective Empathy scores on the BES may best reflect the tendency to emotionally resonate with others. Cognitive Empathy scores on the IRI may best reflect the ability and tendency to adopt others' perspectives, while Cognitive Empathy scores on the BES may best

reflect the ability and tendency to understand others' mental states. Example items from the BES include: "I have trouble figuring out when my friends are happy" and "After being with a friend who is sad about something, I usually feel sad". Participants rated the descriptiveness of these statements using a 5-point Likert scale, ranging from "Strongly disagree" to "Strongly agree", and both subscale scores were calculated. Subscales missing more than 1 item and measures missing a total of 2 or more items were not scored.

Social Responsiveness Scale. Parents/guardians completed the Social Responsiveness Scale (SRS; Constantino, 2002), a 65-item questionnaire that assesses autism-related social impairments, which distinguishes ASD from other psychological disorders. The SRS consists of a total score and five subscales: Social Awareness (8 items), Social Cognition (12 items), Social Communication (22 items), Social Motivation (11 items), and Autistic Mannerisms (12 items). Example items include: "Expressions on his or her face don't match what he or she is saying", "Has difficulty than other children with changes in his or her routine", and "Is socially awkward, even when he or she is trying to be polite". Parents/guardians rated the descriptiveness of these statements using a 4-point Likert scale, ranging from "Not true" to "Almost always true", and a total T score was calculated. Missing items were replaced with median scores provided by the SRS manual. Participants in the ASD group were included if they received a T score of 55 or above. Participants in the NT group were included if they received a T score of 59 or less.

The SRS manual states that T scores of 76 or greater typically represent children within the "severe range"; T scores of 60-75 typically represent children within the "mild to moderate range"; and T scores of 59 or less typically represent children in the "normal range". However, the manual also states that T scores of 55-59 may represent children with very mild, "high

functioning” ASD. Thus, participants in the ASD group who fell within this range and met criteria on the ASRS and ADOS were included.

Autism Spectrum Rating Scale. Parents/guardians completed the Autism Spectrum Rating Scales (ASRS; Goldstein & Naglieri, 2013) with the DSM-V update, a 71-item questionnaire used to assesses symptoms and behaviors associated with ASD, which also supports diagnostic decision-making and intervention design. The ASRS consists of three ASRS subscales (Social/Communication, Unusual Behaviors, and Self-Regulation), which combine to make an ASRS total score; a DSM-V total score; and eight treatment subscales (Peer Socialization, Adult Socialization, Social/Emotional Reciprocity, Atypical Language, Stereotypy, Behavioral Rigidity, Sensory Sensitivity, and Attention). Example items include: “share fun activities with others”, “insist on doing things the same way each time”, and “become bothered by some fabrics or tags on clothes”. Parents/guardians rated the descriptiveness of these statements using a 5-point Likert scale, ranging from “Never” to “Very frequently”. An ASRS total T score (reflecting the tendency to endorse behavioral traits similar to those demonstrated by autistic individuals), and an ASRS DSM-V total score (reflecting symptoms directly related to DSM-V diagnostic criteria), were calculated, along with two treatment subscales of interest, Peer Socialization (reflecting an attenuated interest and ability to successfully participate in activities that support the development and maintenance of peer relationships), and Social/Emotional Reciprocity (reflecting an attenuated ability to appropriately emotionally respond to others in social situations). Missing items were prorated, according to the ASRS manual. T scores of 70-85 classified as “very elevated”; T scores of 65-69 classified as “elevated”; T scores of 60-64 classified as “slightly elevated”; T scores of 40-59 classified as “average”; and T scores of 25-39 classified as “low”. Participants in the ASD group were included if they scored as “very

elevated”, “elevated”, or “slightly elevated” (60 or greater) on the ASRS total T score and ASRS DSM-V total score. Participants in the NT group were included if they scored as “average” or “low” on both scores.

Autism Spectrum Quotient-Adolescent. Parents/guardians completed the Autism Spectrum Quotient-Adolescent (AQ-A; Baron-Cohen, Hoekstra, Knickmeyer, & Wheelwright, 2006), a 50-item questionnaire used to assess autistic traits (not restricted to clinical symptoms). Example items include: “S/he finds social situations easy”, “S/he tends to notice details that others do not”, and “S/he prefers to do things the same way over and over again”. Parents/guardians rated the descriptiveness of these statements using a 4-point Likert scale, ranging from “Definitely disagree” to “Definitely agree”, and a total score was calculated. Missing items were addressed as described above, which was consistent with the approach recommended by Auyueng and colleagues (2008). (Measures missing a total of 5 or more items were not scored.) While the ASRS and SRS are frequently used in diagnostic decision-making, the AQ-A is not. Thus, the AQ-A was not used as an exclusionary measure.

Social Competence with Peers Questionnaire-Pupil. Participants completed the Social Competence with Peers Questionnaire- Pupil (SCPQ-Pu; Spence, 1995), a 10-item self-report questionnaire used to assess social competence. Example items include: “I get on well with my classmates”, “I find it easy to make friends”, and “I see my friend or friends on weekends”. Participants rated the descriptiveness of these statements using a 3-point Likert scale, ranging from “Not true” to “Mostly true”, and a total score was calculated. Measures missing more than 1 item were not scored.

Social Competence with Peers Questionnaire-Parent. Parents/guardians of the participant completed the Social Competence with Peers Questionnaire-Parent (SCPQ-P; Spence,

1995), a 9-item parent-report questionnaire used to assess social competence. Statements included on the SCPQ-P were mostly overlapping with the SCQ-Pu. Parents/guardians rated the descriptiveness of these statements using a 3-point Likert scale, ranging from “Not true” to “Mostly true”, and a total score was calculated. Measures missing more than 1 item were not scored.

Weschler Abbreviated Scales of Intelligence-II. To assess generalized intelligence, participants completed the Weschler Abbreviated Scales of Intelligence-2nd Edition (WASI-II; Wechsler, 2011). The WASI-II includes four subtests: Block Design, Vocabulary, Matrix Reasoning, and Similarities. Only the Vocabulary and Matrix Reasoning subtests were administered, resulting in a 2-subscale Full Scale IQ (FSIQ) score.

Pubertal Development Scale. Participants completed the male version of the Pubertal Development Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988), a 6-item questionnaire used to assess sex-specific pubertal development. Items assessed changes in height, facial hair growth, body hair growth, skin changes, and voice deepening, as well as an item assessing perceived development relative to one’s peers. Mean PDS scores were calculated by averaging across all items except the comparative item. Pubertal categories were also calculated using scoring guideline provided by Crockett and colleagues (1988). Total scores were calculated for items assessing facial hair growth, body hair growth, and voice change: pre-puberty=3; early puberty=4 or 5 (no 3-point responses); mid-puberty=6-8 (no 4-point responses); late puberty=9-11, and post puberty=12. In cases where participants made a 3-point response but scored within the early puberty range, or made a 4-point response but scored within the middle puberty range, scores were assigned to the next category (middle puberty and later puberty, respectively).

Addressing Missing Data

Missing data were addressed according to procedures provided in task-specific manuals. When no specific instructions were provided, missing data were addressed via imputation: total scores were calculated as the raw total plus the raw mean times the number of missing items. Measures with greater than 10% missing data were not scored (and subscales with greater than 10% missing data were also not scored).

Self-Conscious Emotions Task

Task Design. The block-design MRI-compatible SCET consisted of two runs, with 15 clips per run and 3 clips per condition (EmbLo, EmbHi, PrideLo, PrideHi, Neutral). (See Figure S1 for example stimuli.) Emotion and neutral clips were presented in a pseudo-random order, based on a Latin square design, and participants viewed the clips in the same order. (See Table S1 for presentation order.) After viewing each clip, participants used an MRI-compatible button box to rate how embarrassed and how proud each singer felt using a 4-point Likert scale. (The order of emotion ratings was counterbalanced, such that half of participants made embarrassment ratings first and half made pride ratings first.) “1” represented “none”, “2” represented “low”, “3” represented “medium”, and “4” represented “high”. For neutral control clips, participants pressed “0” for “blur”. (See Figure S2 for an example of the rating scale). Participants were allotted 4 seconds to make each rating. Upon pressing a button, a blue triangle appeared above the number the participants pressed, indicating their response. Participants could change their answers by pressing a different button. (If participants pressed multiple buttons in response to a clip or responded in a way that was uncharacteristic of previous responses, the lead researcher made a note of these clips. Outside the MRI, participants watched any clips in question and confirmed their responses. In most cases, participants confirmed that their last response was their desired response.) A 4 second rest period followed emotion ratings, where participants passively

viewed a white fixation cross on a black background. Jitter was interspersed between clips, rating periods, and rest periods. (See Figure S3 for task schematic.)

Figure S1.

Still images of Self-Conscious Emotions Task Stimuli

A.

B.

Panel A: Still image of embarrassment video clip. *Panel B:* Still image of pride video clip.

Table S1.
Self-Conscious Emotions Task Stimuli Presentation Order

Run	Trial	Condition
Run 1	1	PrideHi
	2	Neutral
	3	EmbLo
	4	EmbHi
	5	PrideLo
	6	PrideHi
	7	EmbLo
	8	Neutral
	9	PrideLo
	10	EmbHi
	11	EmbLo
	12	PrideHi
	13	PrideLo
	14	Neutral
	15	EmbHi
Run 2	1	EmbHi
	2	Neutral
	3	PrideLo
	4	PrideHi
	5	EmbLo
	6	PrideLo
	7	EmbHi
	8	EmbLo
	9	Neutral
	10	PrideHi
	11	EmbHi
	12	PrideLo
	13	Neutral
	14	EmbLo
	15	PrideHi

Note. Videos were presented in a fixed order for all participants. However, the order of embarrassment and pride ratings (whether participants made embarrassment ratings first or pride ratings first) was counterbalanced across participants. EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands; PT=perspective-taking.

Figure S2.*Self-Conscious Emotions Task Rating Scale* **Figure S3.***Self-Conscious Emotions Task Schematic* **Paradigm Design and Piloting Information.**

Song Selection. A list of popular songs (predominantly songs sung on televised singing competitions, such as American Idol, or found on pop song compilation disks) were compiled and piloted by an independent sample of 37 middle school students for level of familiarity, likeability, and likelihood of being sung in a singing competition. The aim of the pilot was to exclude songs that were either broadly unfamiliar or disliked by adolescents. Familiarity was assessed using a binary score of “0” or “1”. Likeability was assessed using a 3-point Likert scale,

where “1” represented “Don't like”, “2” represented “OK”, and “3” represented “Like”.

Likelihood of being sung in a singing competition was assessed using a 3-point Likert scale, where “1” represented “No”, “2” represented “Maybe”, and “3” represented “Yes”.

Songs were included in the final list if over two-thirds (66.66%) of pilot participants rated them as familiar, over half (50%) of pilot participants rated them as likeable, and over half (50%) of pilot participants rated them as likely to be sung in singing competition. Of the songs used in the final stimuli set, 71.05-100% of pilot participants rated them as familiar (rated as a “1”), 63.33-100% of pilot participants rated them as likeable (rated as a “2” or “3”, representing “OK” or “Like”), and 56.25-87.01% rated them as likely to be sung in a singing competition (rated as a “2” or “3”, representing “Maybe” or “Yes”). (See Table S2 for titles and artists of included songs.)

Table S2.
Song Titles and Artists

Title	Artist
A Thousand Years	Christina Perry
All of Me	John Legend
Am I Wrong	Nico and Vinz
A Thousand Years	Christina Perry
Counting Stars	One Republic
Give Your Heart a Break	Demi Lovato
Grenade	Bruno Mars
Hallelujah	Rufus Wainwright
Hey Soul Sister	Train
I'm Not the Only One	Sam Smith
Lean on Me	Bill Withers
Payphone	Maroon 5
Rather Be	Clean Bandit
Rolling in the Deep	Adele
Rumor Has It	Adele
She Will Be Loved	Maroon 5
Skyfall	Adele
Somebody that I Used to Know	Gotye
Someone Like You	Adele
Stay	Rihanna
Stay with Me	Sam Smith
Style	Taylor Swift
Sugar	Maroon 5
Take Me to Church	Hozier
This is Me	Demi Lovato
Titanium	David Guetta
Treasure	Bruno Mars

Note. This list includes titles and artists of songs featured in both the practice task and MRI task. In cases where a song was featured in multiple video clips, different parts of the song were featured.

Video Clip Creation. Video clips included male and female adolescent actors pretending to compete in a singing competition. Actors were recruited from local middle and high school choir and drama groups and national singing competitions, and videos were recorded at local middle schools, high schools, and on the University of Oregon campus. Actors were instructed to

select two songs from a list of pre-piloted songs to be sung *a capella*. Each actor was assigned a short clip (~10s) from each song and were instructed to sing each clip four ways: 1) EmbLo: sing poorly, act embarrassed; 2) EmbHi: sing well, act embarrassed; 3) PrideLo: sing well, act proud; 4) PrideHi: sing poorly, act proud. Thus, each actor provided multiple clips to be piloted.

Actors were instructed to convey embarrassment and pride using facial expressions and postural gestures, based on psychological research. To convey embarrassment, actors were encouraged to tilt their head downwards and sideways, direct their eye gaze downwards and away from the audience, touch their face with their hands, hunch and slump their shoulders, and narrow their chest (Keltner, 1995, 1996; Keltner & Buswell, 1997). Judges also gave personalized feedback for conveying embarrassment, including instructing actors to shift their gaze up and down (towards and away from the audience) and act fidgety (e.g., touch their hair, rubbing their arms). Actors were instructed to convey embarrassment similarly during both embarrassment conditions (EmbLo and EmbHi) to ensure that differences in subjective ratings during conditions with different PT demands did not reflect differences in affective expression or emotional intensity.

To convey pride, actors were encouraged to tilt their head upwards and backwards, direct their eye gaze towards the audience, arch their back, expand their chest, rest their hands on their hips, and smile (Tracy, Robins, & Schriber, 2009; Tracy & Matsumoto, 2008; Tracy & Robins, 2004b, 2007c, 2008). Actors were instructed to convey pride similarly during both pride conditions (PrideLo and PrideHi), to ensure that differences in subjective ratings during conditions with different PT demands did not reflect differences in affective expression or emotional intensity. Actors were not instructed to convey a specific subtype of pride (authentic

versus hubristic); however, research suggests that individuals express authentic pride and hubristic pride using similar facial expressions and postural gestures (Tracy & Robins, 2007d).

While actors were given instructions and feedback on their performance, ultimately, they were encouraged to act natural. As such, actors were encouraged to give performances that were emotionally salient and capable of evoking feelings of empathic embarrassment or empathic pride, while also being realistic. Actors sang in front of a pair of judges (one male and one female) sitting in front of them at a table. Actors stood in front of a white screen facing the judges and a camera. Actors were videotaped from the waist up, so participants could view their emotional facial expressions and postural gestures. Only the backs of the judges' heads could be viewed, so participants could not observe the judges' facial expressions and use these expressions as cues for emotion ratings.

Actors were also recorded standing alone (with judges out of view) in front of a white screen, displaying a neutral facial expression. These clips were later used as Neutral control clips.

Video Piloting. Video clips were piloted by 21 undergraduate and graduate students. Pilot participants rated each actor's singing performance (singing ability) using a 5-point Likert scale (1=very bad, 5=very good). Pilot participants also rated each actor's perceived level of embarrassment and pride (inferred embarrassment and inferred pride) using a 4-point Likert scale (1=none, 2=low, 3=medium, 4=high). In addition, pilot participants rated their own level of embarrassment and pride for each actor (empathic embarrassment and empathic pride), using a 4-point Likert scale (1=none, 2=low, 3=medium, 4=high). Video clips were selected according to mean singing quality (mean singing quality score of 1-2.5 for EmbLo and PrideHi clips; mean singing quality score of 3.5-5 for EmbHi and PrideLo clips) and mean inferred emotion (mean

inferred embarrassment score of 2.5-4 for EmbLo and EmbHi; mean inferred pride score of 2.5-4 for PrideLo and PrideHi). No actor was featured in more than one condition (including Neutral); no singing clip was featured in more than one condition; and gender ratio was similarly distributed across conditions (EmbLo=2 males, 4 females; EmbHi=2 males, 4 females; PrideLo=1 male, 5 females; PrideHi=1 male, 5 females; Neutral=3 males, 3 females).

Six video clips representing each condition were selected for the final stimuli set. (See Table S3 for more information.) Independent sample *t*-tests confirmed that there were no significant differences in mean singing quality or intensity of mean inferred emotion ratings across conditions (EmbLo vs EmbHi; ProudLo vs PrideHi; EmbLo vs ProudLo; EmbHi vs PrideHi; as well as EmbLo vs PrideHi; and PrideLo vs EmbHi; see Table S4). (In addition, there were no significant differences in the intensity of mean empathic emotion ratings between conditions of similar PT demands; e.g., EmbLo vs PrideLo; EmbHi vs PrideHi). There were differences in the intensity of mean empathic emotion ratings between conditions of different PT demands (e.g., EmbLo vs EmbHi; PrideLo vs PrideHi), but this was expected. Five additional clips (one for each condition) were selected for a practice task, to be viewed prior to the MRI scan.

Table S3.
Mean Pilot Ratings

Condition	Singing Quality	Inferred Emotion	Empathic Emotion
EmbLo	4.05	3.08	3.09
EmbHi	4.22	3.10	2.11
PrideLo	3.93	3.35	3.05
PrideHi	3.98	3.11	2.02

Note. EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands;

Table S4.
Comparison Statistics for Pilot Ratings

Factor	Comparison	<i>T</i> Statistic
Singing Quality	EmbLo vs EmbHi	$t(10) = -0.17, p = 0.872$
	PrideLo vs PrideHi	$t(10) = -1.65, p = 0.130$
	EmbLo vs PrideLo	$t(10) = 0.00, p = 1.00$
	EmbHi vs PrideHi	$t(10) = -1.28, p = 0.227$
Inferred Emotion	EmbLo vs EmbHi	$t(10) = -0.15, p = 0.881$
	PrideLo vs PrideHi	$t(10) = 1.36, p = 0.205$
	EmbLo vs PrideLo	$t(10) = -1.12, p = 0.288$
	EmbHi vs PrideHi	$t(10) = -0.17, p = 0.868$
Empathic Emotion	EmbLo vs EmbHi	$t(10) = 5.84, p < 0.001$
	PrideLo vs PrideHi	$t(10) = 7.83, p < 0.001$
	EmbLo vs PrideLo	$t(10) = 0.26, p = 0.802$
	EmbHi vs PrideHi	$t(10) = -0.81, p = 0.434$

Note. Singing quality scores for clips where singers sang poorly were reversed, such that higher scores represented greater intensity (irrespective of valence). EmbLo=embarrassment with low PT demands; EmbHi=embarrassment with high PT demands; PrideLo=pride with low PT demands; PrideHi=pride with high PT demands; PT=perspective-taking.

Video Editing. Video clips were converted from MTS files to mp4 files using Free MTS M2TS Converter. Clips were edited using Adobe Premiere Pro and modified as little as possible to maintain greatest ecological validity. Emotion clips were edited for length using the trim function (8-12 seconds; $M=9.89$ seconds), exported as mp4 files, and saved to a consistent resolution (1080 x 608) and frame rate (30 frames/second). Background noise was filtered across all clips using the de-noiser filter. A high pass filter was used to filter out low frequency background noise, and minor modifications to lighting aperture using the Lumetri Color editing panel to adjust white balance (temperature=-49.7, tint=0.6) and tone (exposure=0.5, contrast=0.6, highlights=35.5, whites=21.3, blacks=3.2) were made, as necessary (one day of recording for lighting aperture modifications). Clips were not modified to be the same volume, to preserve natural variations in auditory output associated with the expression of different emotions (i.e., proud singers often sing louder than embarrassed singers). However, volume modifications were

made, as necessary, to ensure that the volume of all clips was within a consistent range (-12 to -27 decibels).

Neutral control clips were edited for length using the trim function (8-10 seconds; M=9.50 seconds), exported as mp4 files, and saved to a consistent resolution (1080 x 608) and frame rate (30 frames/second). The video clips' original audio tracks were replaced with audio clips of instrumental version of songs, with separately recorded audio tracks of announcers (one male and one female) introducing the singers. Visual blurring was applied using a Gaussian blur set to 55 with repeated edge pixels, so that fine grain facial features and expressions could not be observed. A high pass filter was used to filter out low frequency background noise, and minor modifications to lighting aperture using the Lumetri Color editing panel to adjust white balance (temperature=-49.7, tint=0.6) and tone (exposure=0.5, contrast=0.6, highlights=35.5, whites=21.3, blacks=3.2) were made, as necessary (one day of recording for lighting aperture modifications).