HHS Public Access

Author manuscript

Dev Cogn Neurosci. Author manuscript; available in PMC 2015 May 06.

Published in final edited form as:

Dev Cogn Neurosci. 2014 April ; 8: 40–54. doi:10.1016/j.dcn.2014.01.003.

But do *you* think I'm cool? Developmental differences in striatal recruitment during direct and reflected social self-evaluations

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Abstract

The current fMRI study investigated the neural foundations of evaluating oneself and others during early adolescence and young adulthood. Eighteen early adolescents (ages 11–14, $M = 12.6$) and 19 young adults (ages 22–31, $M = 25.6$) evaluated if academic, physical, and social traits described themselves directly (direct self-evaluations), described their best friend directly (direct other-evaluations), described themselves from their best friend's perspective (reflected self-evaluations), or in general could change over time (control malleability-evaluations). Compared to control evaluations, both adolescents and adults recruited cortical midline structures during direct and reflected self-evaluations, as well as during direct other-evaluations, converging with previous research. However, unique to this study was a significant three-way interaction between age group, evaluative perspective, and domain within bilateral ventral striatum. Region of interest analyses demonstrated a significant evaluative perspective by domain interaction within the adolescent sample only. Adolescents recruited greatest bilateral ventral striatum during reflected social self-evaluations, which was positively correlated with age and pubertal development. These findings suggest that reflected social self-evaluations, made from the inferred perspective of a close peer, may be especially self-relevant, salient, or rewarding to adolescent self-processing – particularly during the progression through adolescence – and this feature persists into adulthood.

Keywords

self; social cognition; adolescence; puberty; medial prefrontal cortex; ventral striatum

> "We are more or less unconsciously seeing ourselves as we think others who are important to us and whose opinions we trust see us."
>
> –Rosenberg (1979, p. 97)

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Introduction

1.1 Adolescent Self-Concept Development and Peer Influence

Adolescence is a key point in a young child's life, marking the physical, psychological, and social transition from childhood to adulthood and characterized by significant changes in self-understanding, person-perception, and social influences. This stage is an important time for self-exploration and identity development (Erikson, 1963), as youths are introduced to new environments, new roles, and new role models – suggesting that one apt way of describing adolescence is a period of self-concept instability (Rosenberg, 1979; Shirk & Renouf, 1992). Two major changes in adolescent self-processing include the *content of* and *contextual influences on* self-descriptions. Changes in content are largely driven by the acquisition of advanced cognitive abilities, resulting in the greater use of psychological and abstract terminology in adolescent self-descriptions (Broughton, 1978; Harter, 1990; Rosenberg, 1979; Secord & Peevers, 1974; Selman, 1980; Steinberg & Morris, 2001). Adolescents also develop increasingly differentiated and individuated self-representations, which vary across domains and relational contexts (Harter, 1990; 1999; Harter, Waters, & Whitesell, 1998; Marsh, 1989; Masten et al., 1995; Ray et al., 2009), resulting in the development of "multiple selves" (Harter, 1998). Adolescents may view themselves differently at school as students, at home as children, and with peers as friends, revealing distinct contextual influences on self-perceptions.

At the intersection between content and contextual influences, social competence, in particular, becomes highly salient (Damon & Hart, 1982; 1988; Harter 1999; Montemayor & Einsen, 1977; Rosenberg, 1979). In a trend that Steinberg and Silverberg (1986) referred to as a dependency tradeoff, adolescents spend significantly less time with parents and more time with peers (Collins & Rusell, 1991; Csikszentmihalyi & Larson, 1984; Larson & Richards, 1991), which coincides with a similar shift in influence. As the capacity and tendency for self-reflection and social perspective-taking increases (Choudhury, Blakemore, & Charman, 2006; Damon & Hart, 1982; Dumontheil, Apperly, & Blakemore, 2009; Montemayor & Eisen, 1977; Selman, 1980), adolescents become more self-conscious (Elkind & Bowen, 1979; Rosenberg, 1979; Selman, 1980), show a greater interest in the perceived opinions of others (Elkind, 1967), and put greater weight on peer evaluations (Buhrmester, 1996; Sussman et al., 1994). Thus, for better or for worse, peers serve as strong role models and important sources of social feedback for adolescent self-evaluations (Harter, 1999; Nurmi, 2004).

1.2 A Developmental Social Neuroscience Approach

While behavioral trajectories of self-development have been studied for decades, as summarized above, a novel line of research is exploring adolescent self-processing at the neural level. Adopting a developmental social neuroscience approach offers an alternative to the common reliance on self-report methodologies, which may suffer from explicit and implicit participant biases. This approach may also help connect the underlying social, cognitive, and biological processes involved in self-development (Pfeifer et al., 2013; Pfeifer & Peake, 2011).

The current study was designed to reveal distinct neural patterns associated with personal and perceived peer evaluations across multiple domains, which would imply distinct influences on self-concept development. Specifically, we examined the patterns of activity supporting early adolescent and young adult direct self-evaluations (first-person evaluations about the participant), direct close other-evaluations (first-person evaluations about the participant's best friend), and reflected self-evaluations (third-person evaluations about the participant, from the best friend's perspective). Furthermore, we examined the distinct influences of personal and perceived peer evaluations across academic, physical, and social domains. Finally, we explored how pubertal development relates to adolescents' neural activity. The brief neuroimaging review that follows provides a foundation for the current study.

1.3 Adult Neuroimaging Research on Self-Processing

Researchers have extensively investigated the neural correlates of self-evaluation and self-reflection within adult samples using functional magnetic resonance imaging (fMRI). Typically, participants have evaluated the descriptiveness of personality traits or made mental state attributions for oneself and an "other" target. Reviews and meta-analyses (Northoff, Heinzel, de Greck, Bermpohl, Dobrowolny, & Panksepp, 2006; Pfeifer & Peake, 2011; Qin & Northoff, 2011) have highlighted the integral role of cortical midline structures (CMS), consisting of medial prefrontal cortex (mPFC; including dorsal, anterior rostral, and ventral aspects, as well as adjacent regions of anterior cingulate cortex [ACC]) and medial posterior parietal cortex (mPPC; including precuneus [Prec], posterior cingulate cortex [PCC], and retrosplenial cortex), in self-processing. These CMS support both self-reference (Zhu et al., 2012) and self-relevance (Moore et al., 2013; Moran, Lee, & Gabrielli, 2011). Additional regions engaged in these processes include striatal regions representing salience, valuation, and reward; temporal and parietal regions supporting social cognition and mental state attribution (such as temporoparietal junction [TPJ], posterior superior temporal sulcus [pSTS], and temporal poles); as well as hippocampus and insula.

1.4 Pediatric Neuroimaging Research on Direct Self- and Other-Processing

There are relatively few neuroimaging studies examining self-processing within developmental samples. Thus, it is difficult to ascertain the full extent to which the neural correlates of adolescent and adult self-evaluations are similar, and if neural patterns generalize across multiple domains. Previous research has highlighted the role of CMS and striatal regions in youth self-processing, converging with the adult literature (Ersner-Hershfield, Wimmer, & Knutson, 2009; Northoff et al., 2006). Ray and colleagues (2009) found that self-referential memory in male youths (7–13yo) was positively correlated with activity in rostral ACC (as well as subgenual ACC, medial orbital frontal cortex, caudate, and bilateral inferior frontal regions), and suggested that rostral ACC, in particular, is a neural substrate of psychological self-representations. Research by Pfeifer and colleagues (2007; 2013) similarly underscored the role of CMS and ventral striatum (VS) in self-other differentiation. In a cross-sectional study examining self-evaluations, preadolescents (9–10yo) and young adults (23–31yo) recruited greater mPFC during direct self-evaluations and greater mPPC during direct other-evaluations about a fictional character, Harry Potter (Pfeifer, Lieberman & Dapretto, 2007). However, preadolescents recruited greater mPFC than adults during direct self-evaluations. Complementary results were found longitudinally (Pfeifer et al., 2013). During late childhood (*M* = 10yo) and early adolescence (*M* = 13.1yo), youths recruited greater mPFC and VS during direct self-evaluations and greater mPPC (as well as lateral PFC and TPJ) during direct other-evaluations. There were also age-related increases in ventral mPFC (vmPFC) activity during direct self-evaluations. These increases were more robust in the social domain, compared to the academic domain, and positively correlated with pubertal development in the social domain. These findings suggest that the development of social self-evaluations is related to biological changes and not just interpersonal ones, and further highlight the potential influence of pubertal development on neural patterns of social self-processing.

1.5 Pediatric Neuroimaging Research on Reflected Self-Processing

A related line of research has examined the influence of perceived peer evaluations on youth self-processing. Pfeifer and colleagues (2009) investigated the role of evaluative perspective on neural patterns supporting self-evaluations. Early adolescents (11–13yo) recruited greater mPPC and TPJ than adults (22–30yo) during direct self-evaluations; however, this activity did not differ from adolescent or adult reflected self-evaluations, suggesting that adolescent self-processing may be more strongly influenced by the perceived evaluations of others. In addition, adolescents recruited greater mPFC and mPPC during reflected *academic* self-evaluations from their *mother's* perspective and reflected *social* self-evaluations from their *best friend's* perspective. This suggests that neural responses during adolescent self-processing may be sensitive to both the perspective adopted and its relevancy to a given evaluative domain.

Research has also highlighted the role of CMS and striatal regions in anticipated (inferred) evaluations of unknown peers, which could be viewed as a form of reflected self-evaluations. Guyer and colleagues (2009) found that youths (8–17yo) recruited VS, insula, hypothalamus, and hippocampus during inferred peer social evaluations, and females showed age-related increases during inferred evaluations of high interest, relative to low interest, peers. Furthermore, youths recruited greater cortical (ACC) and striatal (caudate and putamen) activity during peer acceptance (receipt of positive social feedback) than peer rejection (Guyer et al., 2012). Research examining a wider age range (8–25yo) reported similar CMS and striatal recruitment during inferred and received positive peer social evaluations, greater activity during received positive evaluations from highly-rated peers, and age-related increases during inferred positive peer evaluations (Davey, Allen, Harrison, Dwyer, Yucel, 2010; Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010). Together, these studies underscore the saliency of peer social evaluations, particularly of highly regarded peers, in youth self-processing and suggest that this effect can be observed at the neural level.

1.6 Current Study

The current study integrated Pfeifer and colleagues' (2007; 2009; 2013) research on self-processing and extended it across additional evaluative perspectives and domains. Distinguishing between evaluative perspectives is important, given the heightened saliency of peers during adolescence (Collins & Rusell, 1991; Csikszentmihalyi & Larson, 1984;

Larson & Richards, 1991; Steinberg & Silverberg, 1986) and the potentially greater influence of *perceived*, relative to *actual*, peer evaluations, on self-perceptions (Shruger & Schoeneman, 1979; Tice & Wallace, 2003). While past research has typically used familiar, yet personally-unknown “other” targets, such as Harry Potter (Pfeifer et al., 2007, 2009, 2013) or President George Bush (Kelley et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Powell, Macrae, Cloutier, Metcalfe, & Mitchell, 2009), the current study used a close peer, given the growing saliency of close friendships during adolescence. This target more aptly controlled for familiarity, intimacy, age, and salience. The current study also used a novel, high-level control task, malleability-evaluations, where participants evaluated if traits could change (in general, not just with respect to themselves). Unlike previously used low-level controls (such as counting vowels, capital letters, or syllables), this task incorporated the semantic and evaluative demands inherent in self- and other-evaluations.

The current study also examined several domains of self-evaluations. Parcelling academic, physical, and social domains is important, given the bourgeoning of multiple, context-dependent “selves” during adolescence (Harter, 1998) via a myriad of changes, such as those experienced in academic demands and expectations during the transition into middle school, in physical appearance and abilities during the transition into puberty, and in social roles and peer influence during the transition into new social circles. Furthermore, this is the first study to investigate the neural correlates of psychological and physical self-evaluations within a developmental sample. Finally, given research highlighting the role of biological, in addition to interpersonal, changes on adolescent self-evaluations (Gunther Moor et al., 2010; Guyer et al., 2009; Pfeifer et al., 2013), the current study examined the relationship between pubertal development and neural responses in adolescence. Past research supports our hypotheses:

1. Across domains, adolescents and adults will recruit CMS during direct self-, direct other-, and reflected self-evaluations. Direct self-evaluations will recruit CMS (particularly mPFC) and striatal regions (e.g., VS); direct other-evaluations will recruit CMS (particularly mPPC); and reflected self-evaluations will recruit CMS, striatal regions, and social cognition regions (e.g., pSTS, TPJ, and temporal poles).

2. Across domains, adolescents will recruit greater CMS and social cognition regions during direct self-evaluations than adults, but similar CMS during direct other-evaluations.

3. Adolescents will recruit greater striatal regions during reflected self-evaluations than adults, and this activity will be greatest within the social domain.

4. Pubertal status will be positively correlated with CMS and striatal activity during adolescent direct and reflected self-evaluations, particularly within the social domain.

Method

2.1 Participants

Typically-developing young adults (N = 20) and early adolescents (N = 22) were recruited for the study. One adult and four adolescents were excluded due to scanner failure or significant artefacts, resulting in 19 adults (9 males) and 18 adolescents (9 males) in the final analyses. Adults (22–31yo, *M* = 25.6) were primarily graduate students (2 advanced undergraduate students) currently attending the University of Oregon. These students represented a range of academic disciplines, including psychology, English, business, architecture, and international studies. Adolescents (11–14yo, *M* = 12.6) were middle school students, not attending home school. Adolescents were recruited via flyers from the surrounding Eugene area, as well as from a departmental database of interested families. Participants were primarily Caucasian (adults: 74% Caucasian, 10% Latino, 5% Asian, 10.5% decline to respond; adolescents: 72% Caucasian, 17% multiracial, 11% decline to respond), and age groups did not differ by ethnicity. Data on household income and maternal education were only collected from the adolescent group. Mean annual household income was between $55,000 and $65,000, although annual income ranged from below $25,000 to $125,000. Maternal education was at the high school level or higher; approximately 39% of mothers had a bachelor's degree and 17% had a professional degree. Participants were screened for major neurological, psychological, and medical disorders, and all participants were right-handed. Adolescents provided written informed parental consent and assent, and adults provided written informed consent, according to the guidelines outlined by the University of Oregon Institutional Review Board. Participants were compensated $25 per hour for their time.

2.2 Procedure

2.2.1 Measures—To assess IQ, adolescents completed the Kauffman Brief Intelligence Test-II (KBIT-II; Kaufman & Kaufman, 2004) within one month of their scan. Full scale IQs, as well as verbal and quantitative subscale IQs, were in the average to above average range (*M*s = 114, 116, and 108, respectively). IQ was only available for adolescent participants; however all participants were advanced undergraduate or graduate students, suggesting similar average to above average IQs.

To assess pubertal development, adolescents completed gender-specific versions of the Pubertal Developmental Scale (PDS; Peterson, Crockett, Richards, & Boxer, 1988) Average PDS scores were calculated by averaging all scores except the comparative question, where participants evaluated their perceived rate of development relative to their peers. The average PDS score was similar for males and females, 2.3. Using the pubertal category scoring guidelines provided by Crockett and colleagues (see Petersen et al., 1988), the mean (and mode) pubertal stage for both male and female participants was "midpuberty" (*M* = 2.9 and 3, Mode = 3 and 3, for males and females, respectively). Furthermore, there were no significant age group differences between male and female adolescents [$t(16) = 0.65$, *ns*). These findings supported combining average male and female PDS scores into an aggregate variable representing total average PDS scores and conducting puberty- and age-related analyses collapsed across genders. Although not discussed here, participants also completed several questionnaires assessing various traits and abilities, such as perceived self-competence, social comparison, and mentalizing.

2.2.2 Neuroimaging Task—Participants were presented with positively- and negatively-valenced trait phrases and instructed to adopt different perspectives to evaluate if the phrases were descriptive of a specified target. Trait valence was balanced across perspective and domain conditions and across participants. Trait phrases broadly represented general academic, physical, and social domains (as in Moran et al., 2011; Pfeifer et al., 2007; 2009; 2013), such as "studies hard", "very good-looking", and "very popular" (see Table S1 in Supplementary Materials for complete list and piloting information). Evaluative perspectives included direct self-evaluations, direct other-evaluations, reflected self-evaluations, and malleability-evaluations. Participants were instructed to make malleability-evaluations with respect to "people in general" (not just themselves). Participants provided the name of a same-sex, same-age (± two years) best friend, which was used in the neuroimaging task.

The MRI paradigm was a mixed block/event-related design, consisting of four block types representing evaluative perspective and three event types representing trait domain. This resulted in a total of 12 conditions, with 12 events per condition. The task included two runs presented in a counterbalanced order across participants. Each run included eight blocks (2 blocks of each evaluative perspective). Each block was approximately 40 seconds long and included nine events (see Figure 1). Blocks began with an initial instruction screen presented for 3.5 seconds, each event was presented for 3.5 seconds, and each interstimulus interval (ISI) was 0.5 seconds. Using a button box, participants had approximately 4 seconds to process and respond (yes/no) to each event. Events were pseudorandomly intermixed by domain within evaluative perspective blocks in an optimized fashion, using computerized genetic algorithms. Rest intervals between blocks were approximately 12 seconds, but jittered (according to a gamma distribution) to create variable intervals between event types. Participants were trained extensively on the paradigm and reminded of the instructions at the start of the scan.

2.2.3 Data Acquisition and Analysis—Self-report and behavioral data (KBIT-II and PDS scores, button responses, and reaction times [RTs] from the neuroimaging task) were analyzed using SPSS 16.0. When sphericity assumptions were violated, Greenhouse-Geisser adjustments were utilized. Mean RTs were calculated across each of the twelve conditions.

Imaging data were acquired using a Siemens Allegra 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 prescription of the slices in the following scans. Blood oxygen-level dependent, echo-planar images (BOLD-EPI; 207 volumes per run) were acquired across the whole brain with a T2*-weighted gradient echo sequence (TR = 2000 ms, TE = 30 ms, flip angle = 80°, matrix size = 64 × 64, in-plane resolution = 3.12 × 3.12 mm, 32 slices, slice thickness = 4 mm, interleaved acquisition) along the anterior commissure-posterior commissure (AC-PC) transverse oblique plane, as determined by the midsagittal section, and a high-resolution T2-weighted structural scan was acquired coplanar to the functional sequence (TR = 5000 ms, TE = 34 ms, flip angle = 90°, matrix size = 128 ×

128, in-plane resolution = 1.56 × 1.56 mm, 1 slice, slice thickness = 4 mm). The functional sequence included prospective acquisition correction (PACE; Thesen, Heid, Muller, & Schad, 2000) and motion correction to adjust for head motion. Mean levels of motion were greatest within the x-plane in both adults and adolescents, which corresponded to averages of 0.12 and 0.13 mm, respectively, [$t(34) = -0.60$, *ns*]. Maximum levels of motion were greatest within the z-plane in both adults and adolescents, which corresponded to 0.96 and 1.51 mm, respectively, [$t(34) = -2.00$, *ns*]. There were no significant group differences. MATLAB (R2011b) and eM's Stimulus Software (MSS) were used to present stimuli (via back-projection) and collect participant responses and RTs. Foam padding was used to prevent head movement, and earplugs and headphones were worn to protect hearing.

Imaging data were preprocessed and analyzed using NeuroElf (http://neuroelf.net) and Statistical Parametric Mapping 8.0 (SPM8; Wellcome Department of Imaging Neuroscience, London, UK) software implemented in MATLAB. Images were first converted from DICOM to NIfTI (Neuroimaging Informatics Technology Initiative) format using MRIconvert (http://lcni.uoregon.edu/~jolinda/MRIConvert), robustly skull-stripped using the Brain Extraction Tool implemented in FMRIB Software Library (FSL), and manually reoriented to the AC-PC line. The high-resolution structural image was normalized to the SPM canonical T1-structural template. Functional images were slice-time corrected, realigned to the mean functional image, coregistered to the structural image, segmented, normalized, and smoothed using a 6mm full-width, half-maximum (FWHM) isotropic Gaussian kernel.

For each participant, condition effects were estimated according to the general linear model, using a canonical hemodynamic response function. To address age group differences in mean RT (see behavioral results in Supplementary Materials), trial durations were modeled as participant RTs (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). A 128 second high pass filter (appropriate because the design was estimated using events, not blocks) was used to remove low-frequency noise. and an autoregressive model, AR(1), was used to estimate temporal autocorrelation. Single subject models included twelve regressors of interest (each evaluative perspective and domain condition) and eight nuisance regressors (six motion parameters representing translations and rotations during motion correction, a variable representing individual trials with major visually-detected artefacts, and a variable representing instructions and skipped trials). Planned linear contrasts were created to identify regions where activity was greater for each condition compared to implicit resting baseline. These contrasts were then entered into a group model to estimate population effects. No explicit masks were used in either single subject or group level models.

To investigate developmental differences in neural recruitment during self-processing, in particular interaction effects between age group, evaluative perspective, and domain, a 2 (age group: adults/adolescents) × 4 (evaluative perspective: direct self/direct other/reflected self/malleability) × 3 (domain: academic/physical/social) whole-brain, repeated-measures ANOVA was conducted, with age group as the between-subjects factor and evaluative perspective and domain as the within-subjects factors. To correct for multiple comparisons, whole-brain, voxel-wise and cluster-extent thresholds were calculated using Monte Carlo simulations with AlphaSim implemented in AFNI. This resulted in a voxel-wise threshold of

$p < 0.005$ and a cluster-extent threshold of $k = 64$ voxels (corresponding to $p < 0.05$ *FWE*-corrected). To further investigate developmental interaction effects, region of interest (ROI) analyses were conducted using the Marsbar toolbox for SPM (http://marsbar.sourceforge.net). Parameter estimates were extracted from clusters representing significant developmental differences and entered into two 4 (evaluative perspective) × 3 (domain) repeated-measures ANOVAs, in order to compare activity between age groups. To investigate the role of pubertal development on adolescent self-processing, parameter estimates were correlated with average PDS scores, as well as with age and average PDS scores after controlling for age. (See fMRI results for separate comparisons of adolescent and adult neural recruitment in Supplementary Materials.)

Results

3.1 Interaction Between Age Group, Evaluative Perspective, and Domain

To investigate developmental differences associated with making evaluations across differing perspectives and domains, a 2 (age group) × 4 (evaluative perspective) × 3 (domain) whole-brain, repeated-measures ANOVA was conducted (see Table 1). Significant main effects were found for age group, evaluative perspective, and domain, which were qualified by significant interaction effects between age group and evaluative perspective and between age group, evaluative perspective, and domain. The main effect of age group revealed activity in inferior parietal and occipito/temporal regions, as well as some frontal areas, TPJ, mPPC, and cerebellum. The main effect of evaluative perspective revealed activity predominantly in CMS, including ventral and anterior rostral mPFC, rostral ACC, mPPC, as well as ventrolateral PFC, TPJ, and other inferior frontal and inferior parietal regions (see Figure 2, as well as Figure S1 in Supplementary Materials). Contrary to our hypothesis, but as suggested by separate analyses for each age group (see imaging results and Table S1 in Supplementary Materials), adolescents did not engage CMS and social cognition regions significantly more than adults during direct self-evaluations (as indicated by the absence of a significant interaction effect between age group and evaluative perspective in these regions). However, there was a significant three-way interaction effect between age group, evaluative perspective, and domain. This interaction revealed two clusters of activity in VS, one in each hemisphere, extending across the caudate, putamen, and into portions of inferior frontal gyrus (see Figure 3 and Table 1).

3.2 Region of Interest Analyses

To further examine the significant three-way interaction, *post-hoc* ROI analyses were conducted separately for each age group, where parameter estimates from the two significant VS clusters were extracted and entered into two 4 (evaluative perspective) × 3 (domain) repeated-measures ANOVAs. Within the left VS cluster [−12 21 −6], there was no significant interaction between evaluative perspective and domain within the adult sample [$F(1, 18) = 1.59$, *ns*]; however, there was a significant interaction within the adolescent sample [$F(1, 17) = 8.09$, $p < 0.001$; see Figures 4a and 4b]. This pattern replicated in the right VS cluster [27 30 3]. While there was no significant interaction between evaluative perspective and domain in the right VS cluster within the adult sample [$F(1, 18) = 1.36$, *ns*]; there was a significant interaction within the adolescent sample [$F(1, 17) = 7.91$, $p < 0.001$].

Follow-up, paired samples *t*-tests were conducted to decompose these interactions. Within the left VS cluster, adolescents recruited significantly less activity during direct social self-evaluations, relative to direct academic and physical self-evaluations [$t(17) = 3.37$, $p = 0.004$ and $t(17) = 4.29$ $p = 0.001$, respectively], but significantly greater activity during reflected social self-evaluations, relative to reflected academic and physical self-evaluations [$t(17) = -3.07$, $p = 0.007$ and $t(17) = -2.63$ $p = 0.018$, respectively]. Furthermore, activity was significantly greater during reflected social self-evaluations, relative to direct social self-evaluations [$t(17) = 2.51$, $p = 0.023$; see Figure 4b]. Similarly, within the right VS cluster, adolescents recruited significantly less activity during direct social self-evaluations, relative to direct academic and physical self-evaluations [$t(17) = 3.00$, $p = 0.008$ and $t(17) = 3.84$, $p = 0.001$, respectively], but significantly greater activity during reflected social self-evaluations, relative to reflected academic self-evaluations [$t(17) = -2.49$, $p = 0.023$]. However, within the right VS cluster, activity was not significantly greater during reflected social self-evaluations relative to direct social self-evaluations [$t(17) = -0.22$, *ns*].

In addition, follow-up, independent samples *t*-tests were conducted to compare adolescent and adult bilateral VS recruitment specifically during direct and reflected social self-evaluations. Recruitment of left and right VS during direct social self-evaluations significantly differed by age group [$t(35) = 33.60$, $p = 0.002$ and $t(35) = 2.61$, $p = 0.013$ for left and right VS, respectively], such that adults recruited significantly greater bilateral striatal activity, relative to adolescents. However, recruitment of left and right VS during reflected social self-evaluations did not significantly differ by age group, [$t(35) = -0.55$, *ns* and $t(35) = 0.65$, *ns* for left and right VS, respectively.]

3.3 Correlations between Neural Activity and Pubertal Development for Early Adolescents

Finally, to investigate the relationship between neural patterns of activity and pubertal development within the adolescent sample, follow-up correlation analyses were conducted between VS parameter estimates and average PDS scores (collapsed across gender). Activity in the left VS cluster [−12 21 −6] during reflected social self-evaluations was significantly positively correlated with average PDS scores [$r(17) = 0.53$, $p = 0.023$], such that as pubertal development increased, left VS activity also increased (see Figure 5). Similar to activity in the left VS cluster, activity in the right VS cluster [27 30 3] during reflected social self-evaluations was also significantly positively correlated with average PDS scores [$r(17) = 0.50$, $p = 0.034$], such that as pubertal development increased, right VS activity also increased.

Supplementary analyses demonstrated that left VS activity was also significantly positively correlated with age [$r(17) = 0.59$, $p = 0.009$], although right VS activity was not significantly correlated with age [$r(17) = 0.34$, *ns*]. However, even after controlling for age, left and right VS activity remained marginally correlated with average PDS scores [$r(15) = 0.42$, $p = 0.092$ and $r(15) = 0.43$, $p = 0.084$ for left and right VS, respectively].

Discussion

The current study was designed to extend previous neuroimaging research comparing adolescent and adult self-processing across additional evaluative perspectives and domains, as well as to further explore the potential contribution of pubertal development to patterns of neural activity. The most striking finding was a significant three-way interaction between age group, evaluative perspective, and domain within bilateral VS. Within the adolescent sample, striatal recruitment differed significantly according to the perspective adopted and domain evaluated; however, within the adult sample, striatal recruitment did not significantly differ across conditions. Consistent with our hypotheses, early adolescents recruited significantly greater striatal activity during reflected *social* self-evaluations, relative to reflected *academic* or *physical* self-evaluations. In addition, adolescents recruited significantly greater striatal activity during *reflected* social self-evaluations from their best friend's perspective, relative to *direct* social self-evaluations from their own perspective. This suggests that reflected social self-evaluations represent a unique form of self-processing during adolescence.

The results also revealed a positive correlation between pubertal development and bilateral VS activity during reflected social self-evaluations, again consistent with our hypotheses. Specifically, more advanced pubertal development was associated with greater striatal recruitment. This suggests that perceived *social* evaluations of close peers may be especially salient to adolescent self-evaluations, relative to other domains (such as academic abilities or physical appearance), and this saliency may increase with pubertal development and other age-related advances during adolescence.

4.1 Striatal Activity and Adolescent Self-Processing: The Roles of Saliency and Peer Influence

Previous research has suggested that regions of the mesolimbic dopamine reward system, including the striatum, are commonly recruited during the processing of salience and valuation associated with reward (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; McClure, York, & Montague, 2004; Schultz, 1998). These regions are recruited during both the anticipation (Knutson, Fong, Adams, Varner, & Hommer, 2001) and receipt (Delgado, Locke, Strenger, & Fiez, 2003) of monetary (Elliot, Friston, & Dolan, 2000; Knutson, Westdorp, Kaiser, & Hommer, 2000), appetitive (Volkow et al., 2002), and social rewards (Lin, Adolphs, & Rangel, 2012). An increasingly common perspective suggests that salience or relevance may link reward-processing with self-processing (Northoff & Hayes, 2011). Research suggests that these two processes are integrated and supported by common striatal (VS and DS) and frontal (mPFC and ACC) regions (Camara, Rodriguez-Fornells, & Münte, 2009; Enzi et al., 2009; Haber & Knutson, 2010). In particular, striatal regions have been implicated in processing self-relatedness (de Greck et al., 2008) and self-relevance (Enzi et al., 2009), as well as intrinsic and personal value (Phan et al., 2004; Zink, Pagnoni, Martin, Dhamala, & Berns, 2003), self-disclosure (Tamir & Mitchell, 2012), and positive social comparison (Fliessbach et al., 2007). Such studies may suggest that either the self is reward-based and serves as a "valuation system" (de Greck et al., 2008), or that self-processing and reward-processing, while distinct, occur in parallel, such that the self is processed along a "reward continuum" (Northoff & Hayes, 2011). Regardless, this conceptual framework is relevant to the interpretation of the current findings by suggesting that adolescent reflected social self-evaluations, made from the inferred perspective of a salient social target, the participant's best friend, are highly self-relevant, salient, or rewarding.

The current findings also converge with neuroimaging research examining self-processing through the lens of peer social evaluations. Previous research has broadly implicated striatal regions in processing social influence and social relevance (Mason, Dyer, & Norton, 2009; Zaki, Schirmer, & Mitchell, 2011; for a review, see Falk, Way, & Jasinska, 2012). More specifically, CMS and striatal activity are recruited during both the anticipation and receipt of positive social evaluations (Davey et al., 2010; Gunther Moore et al., 2010; Guyer et al., 2012). Related studies have demonstrated that the salience of an adopted perspective modulates neural recruitment during adolescent self-processing. Adolescents recruit greater CMS when making inferences about the social evaluations of their peers, relative to their parents (Pfeifer et al., 2009), and greater VS when making inferences about the social evaluations of *high interest*, relative to *low interest*, peers (Guyer et al., 2009). This body of research informs the interpretation of the current findings by suggesting that inferred evaluations of a highly regarded and salient peer (such as the participant's best friend) may be particularly self-relevant, salient, or rewarding to adolescent self-processing. Furthermore, *inferred* evaluations of a close peer may be more salient to adolescent social self-evaluations, relative to not only perceived peer academic or physical self-evaluations, but also direct social self-evaluations.

While significant age group differences across conditions were primarily localized within striatal regions (VS and DS), activity also extended into IFG. Previous research has implicated inferior prefrontal regions in self-processing (Northoff, Qin, & Feinberg, 2010; Ochsner et al., 2005; Pfeifer & Peake, 2011), via support of processes such as autobiographical memory (Greenberg, Rice, Cooper, Cabeza, Rubin, & LaBar, 2005), introspective speech (Morin & Michaud, 2007), and self-relevance more broadly (Kelley et al., 2002; Tacikowski et al., 2010). Inferior prefrontal regions have also been implicated in reward processing (Rogers et al., 1999), including representing gradients of reward sensitivity (Ernst et al., 2004; Goldstein et al., 2007).

4.2 Striatal Activity and Adolescent Self-Processing: The Roles of Pubertal Development and Age

The current study also extends neuroimaging studies investigating the relationship between pubertal development and both self-processing and peer influence. Past research has reported a positive correlation between pubertal development and vmPFC recruitment during direct social, relative to direct verbal academic, self-evaluations (Pfeifer et al., 2013). Furthermore, studies have shown that striatal recruitment during inferred social evaluations of *high interest*, relative to *low interest*, peers increases with age from preadolescence to adolescence (Guyer et al., 2009).

The current study found a similar positive relationship between striatal recruitment during reflected social self-evaluations (from the inferred perspective of the participant's best friend) and pubertal development. This relationship remained marginally significant after controlling for age. However, striatal recruitment during *reflected* social self-evaluations did not significantly differ between adolescent and adult age groups, although during *direct* social self-evaluations, recruitment was significantly greater in adults than adolescents. These findings suggest that the significant three-way interaction between age group, evaluative perspective, and domain within bilateral VS was driven by both within-group differences in adolescent striatal recruitment, and between-group differences in adolescent and adult striatal recruitment. More broadly, these findings suggest that during adolescence, perceived social evaluations of highly salient peers become increasingly rewarding with pubertal development or age, and this heightened level of social saliency persists, without further increase, throughout adulthood. However, this interpretation relies on reverse inference of VS function, and should thus be considered with caution.

This proposed neurodevelopmental trajectory is consistent with the characterization of adolescence as a stage of significant social reorientation (Nelson et al., 2005), as well as reports of the heightened saliency of perceived peer evaluations during adolescence (Vartanian, 2001). This framework also complements neurobiological research demonstrating the influence of adolescent hormonal changes on the reorganization of striatal reward structures and increased dopamine release in striatal regions (Li, Lindenberger, & Bäckman, 2010), which coincides with enhanced reward sensitivity and increased reward-seeking behaviors during adolescence (Blakemore, Burnett, & Dahl, 2010; Galvan, 2010; Van Leijenhorst et al., 2010).

4.3 Main Effects of Age Group, Evaluative Perspective, and Domain: CMS and Beyond

In line with previous research, participants recruited CMS, such as ventral, anterior rostral, and dorsal mPFC; rostral, subgenual, and perigenual ACC; and Prec/PCC, during direct self-evaluations. This pattern of CMS activity was generally observed across both age groups and all three domains. Thus, the current study supports the role of CMS in self-processing, converging with past research. Likewise, CMS activity was generally observed during direct other- and reflected self-evaluations, again across age groups and domains, replicating previous findings (Heatherton et al., 2006; Mitchell, Banaji, & Macrae, 2005; Pfeifer et al., 2009; Schmitz, Kawahara-Baccus, & Johnson, 2004). It is noteworthy that while the neural correlates of direct close-other evaluations have not been previously examined in developmental samples, the patterns of CMS activity recruited during evaluations of the participant’s best friend were consistent with adult research exploring direct evaluations of similar or personally close others (Lou et al., 2004; Mitchell et al., 2005). Furthermore, the current study suggests that recruitment of CMS during self- and other-processing is domain-general, supporting both psychological and physical evaluations across development. This finding adds to the limited number of adult neuroimaging studies investigating self-processing of physical traits (Kjaer, Nowak, & Lou, 2002; Lombardo et al., 2010; Moran et al., 2011). It also supplements developmental research specifically examining self-processing within the *verbal academic* domain (Pfeifer et al., 2007; 2009; 2013), by highlighting the role of CMS across *general academic* self-processing.

CMS were not the only regions centrally involved in evaluative processing. In addition to striatal regions (as discussed above), lateral frontal, temporal, and parietal regions were implicated in some evaluative processes. Young adults’ engagement of social cognition regions, such as TPJ, during reflected self-evaluations replicates past research examining mental state attribution and reflected self-evaluations of psychological traits (Ochsner et al, 2005; Pfeifer et al., 2009; Saxe, 2006). Furthermore, malleability-evaluations were supported by ventrolateral PFC and other lateral frontal and parietal regions, but not CMS, which allowed this condition to function as an effective high-level control.

In addition, across evaluative perspectives and domains, results demonstrated a main effect of age group within prefrontal regions (including precentral gyrus and superior frontal gyrus), posterior and inferior parietal regions, and middle occipital gyrus. Previous research has implicated the above frontal regions in direct psychological and physical self-processing, agentic self-processing, self-relevance, self-reference, direct psychological other-processing, memory recall, perspective taking, resting state activity, and general evaluative processing (Craik et al., 1999; Kjaer et al., 2002; Lou et al., 2002; Moran et al., 2011; Nakao et al., 2009; Ochsner et al., 2005; Pfeifer et al, 2007; Powell et al., 2009; Sebastian et al., 2012; Whitfield-Gabrielli et al, 2011; Zhu et al., 2012; for reviews see Gillihan & Farah, 2005; Legrand & Ruby, 2009; Qin & Northoff, 2011). Meanwhile, the above inferior parietal regions have been implicated in an overlapping set of processes, including direct psychological self-processing, agentic self-processing, self-relevance, and direct psychological other-processing (Kircher et al., 2002; Kjaer et al., 2002; Lou et al., 2002; Pfeifer et al., 2007; Powell et al., 2009; for reviews see Gillihan & Farah, 2005; Legrand & Ruby, 2009). Middle occipital gyrus has also been implicated in direct self- and other-processing (Leube, Knoblich, Erb, & Kircher, 2003; Ochnser et al., 2004; Tacikowski et al., 2010). In the current study, across conditions, adults generally recruited similar, but more robust, patterns of activity, relative to adolescents (see Table S2 in Supplementary Materials). In line with this trend, the main effect of age group was driven by greater recruitment in all of the aforementioned regions by the adult sample.

4.4 Developmental Trajectories in mPFC during Self-Evaluative Processing

Although results from the current study replicate *general* patterns of activity commonly observed during self- and other-processing, they do not replicate some *specific* developmental patterns previously observed within CMS. Several studies have reported an anterior-posterior developmental shift during self-processing, such that adolescents recruit greater anterior regions (like mPFC), while adults recruit greater posterior regions (Blakemore, den Ouden, Choudhury, & Frith, 2007; Burnett, Bird, Moll, Frith, & Blakemore, 2009; Gunther Moor et al., 2012; Pfeifer et al., 2007; 2009; Sebastian et al., 2012; Wang et al., 2006; for reviews, see Blakemore, 2008a; 2008b; 2012). In the current study, however, across many conditions, neural activity recruited by adolescents was clearly less robust than that of adults. Thus, while both adolescents and adults recruited similar patterns of mPFC activity during self- and other-processing, in some conditions, the magnitude of activity recruited by the adolescent group did not reach statistical significance. In particular, activity recruited during adolescent direct social self-evaluations was weaker than expected, relative to previous research (Pfeifer et al., 2013). Furthermore, contrary to our hypotheses and inconsistent with previous research (Pfeifer et al., 2009), adolescents did not recruit significant social cognition regions, such as TPJ, during direct or reflected self-evaluations, relative to malleability-evaluations, nor greater activity than adults during direct self-evaluations, relative to malleability-evaluations. These divergent findings may be driven by the implementation of a novel control condition (evaluating trait malleability), the adoption of a specific paradigm design [modeling conditions as events, not blocks, which may represent transient, not sustained, effects (e.g., Petersen & Dubis, 2011)], or the use of more conservative preprocessing/data analysis methods.

4.5 Limitations and Future Directions

The current study includes several limitations that reveal prime areas for future research. First, the current study investigated the neurodevelopmental trajectory of self-processing by adopting a cross-sectional design. This approach afforded the comparison of early adolescent and young adult self-evaluations, which can be combined with previous cross-sectional research to begin charting developmental changes in self-processing from preadolescence to early adulthood. However, cross-sectional designs assume that differences found between age groups and across studies represent changes found within participants across development. Future research would benefit from cross-sectional designs simultaneously examining multiple age groups (e.g., preadolescence, early adolescence, middle adolescence, late adolescence, and early adulthood), or additional longitudinal designs that track changes within participants across multiple time points further into adolescence. Another limitation, common to many studies, was the use of university-affiliated students to represent a young adult sample. Recruiting adults from the broader community would increase the generalizability of future findings. In addition, future research should recruit larger sample sizes to further examine the role of pubertal development, and potential associated gender differences, on neural patterns of activity. While the current study revealed a positive correlation between pubertal developmental and bilateral striatal activity during adolescent reflected self-evaluations, larger sample sizes representing a wider range of ages and pubertal stages may be able to better distinguish the unique contributions of age and pubertal development. Furthermore, while the current adolescent sample was too small to confidently conduct gender comparisons, larger sample sizes would offer significant power for these analyses. As a future direction, researchers could examine atypical self-development in various populations, including in youth with autism spectrum disorders (Pfeifer et al., 2013) or in the emergence of depression during adolescence, as this may shed additional light on normative developmental trajectories. Finally, future research could examine developmental differences in the perceived malleability of traits and coinciding neurodevelopmental patterns, as well as neurodevelopmental differences in processing trait valence.

4.6 Conclusions

The present study makes several significant contributions towards better understanding the biological and social mechanisms underlying adolescent self-concept development. Specifically, this research complements behavioral studies characterizing the influence of personal and perceived peer evaluations across psychological and physical domains. First, the current study demonstrates that bilateral VS activity significantly differentiates across conditions within the adolescent sample only, suggesting that the salience of adolescent self-evaluations differs according to the perspective adopted and the domain evaluated. Second, early adolescents recruit significantly greater bilateral VS when making reflected social self-evaluations from their best friend’s perspective. This confirms that personally close peers serve as prominent social influences during adolescence, and perceived peer evaluations are highly self-relevant, salient, or rewarding – particularly within the social domain. Third, results demonstrate that there is a positive correlation between pubertal status and bilateral VS recruitment during reflected social self-evaluations, such that more advanced pubertal development is associated with greater striatal activity. While the current study cannot distinguish the unique effects of age and pubertal status, the results offer empirical support for the increasing social saliency of peers throughout adolescence, consistent with the social reorientation theory of adolescence (Nelson et al., 2005).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

KFJ was supported by a National Science Foundation Graduate Research Fellowship (2011122786), and JHP was supported by grants from the National Institutes of Health (L40HD059442 and L40MH087356). The authors would like to thank Drs. Elliot Berkman and Sara Hodges for their comments on earlier drafts, Taylor Blackthorne for aiding in recruitment and data entry, the Lewis Center for Neuroimaging for assisting in scanning, and the Developmental Social Neuroscience Laboratory. The authors would also like to give a special thanks to the children and families who participated in this study and made this research possible.

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- fMRI study examined neural correlates of evaluating self and close others
- Adolescent ventral striatum (VS) response is sensitive to evaluation type and domain
- Adolescents recruit VS during social self-evaluations from best friend's perspective
- This VS response correlates with pubertal status and age throughout adolescence

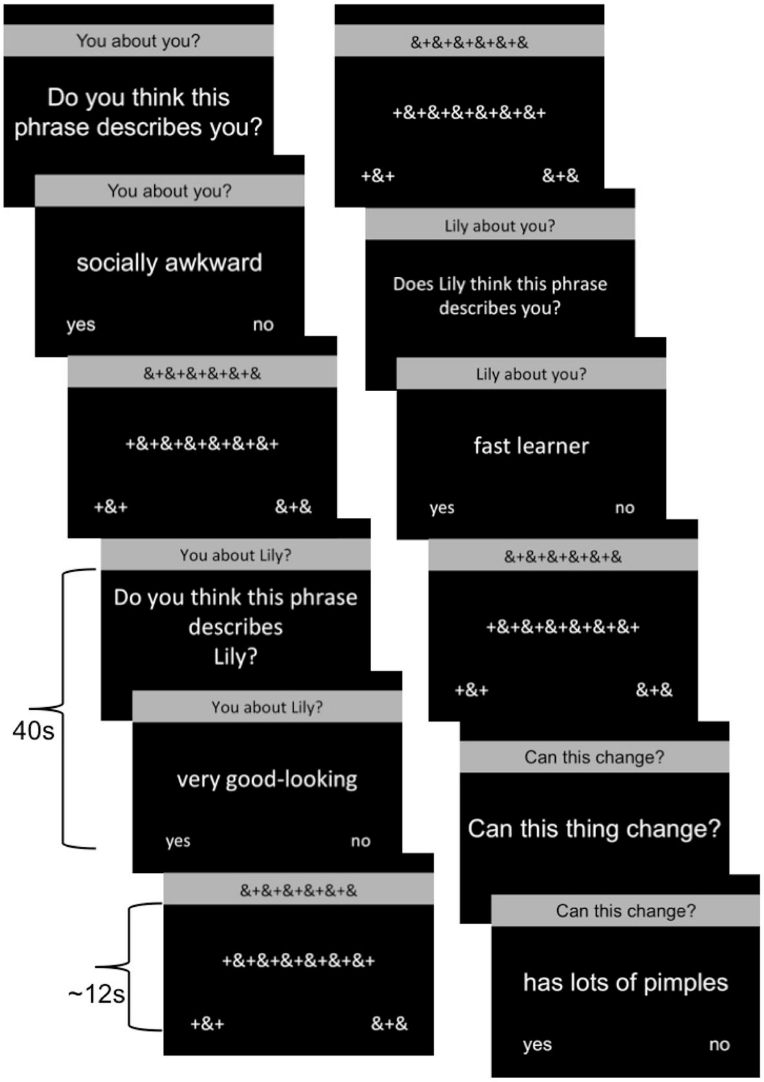

Figure 1.

Neuroimaging Task

The neuroimaging task included two runs, with eight blocks per run. At the beginning of each block, participants were instructed to evaluate trait phrases according to a given perspective, followed by a series of nine trait phrases. Phrases were positively- and negatively-valenced and represented academic, physical, and social domains (all intermixed within blocks). In between evaluation blocks were blocks of rest. *Note:* The name of each participant's best friend was always included (e.g., "Lily"); s = seconds.

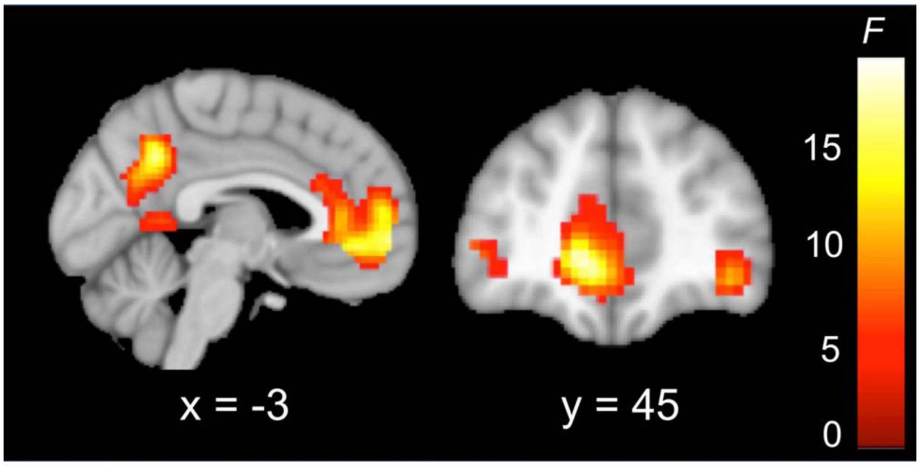

Figure 2.

Main Effect of Evaluative Perspective

Repeated measures ANOVA where evaluative perspective and domain served as the within-subjects factors and age group served as the between-subjects factor. Illustrated here is a significant main effect of evaluative perspective within cortical midline structures (engaged by direct self-, direct other-, and reflected self-evaluations) and bilateral ventrolateral prefrontal cortex (primarily engaged by malleability-evaluations). *Note:* x and y = left-right and anterior-posterior dimensions.

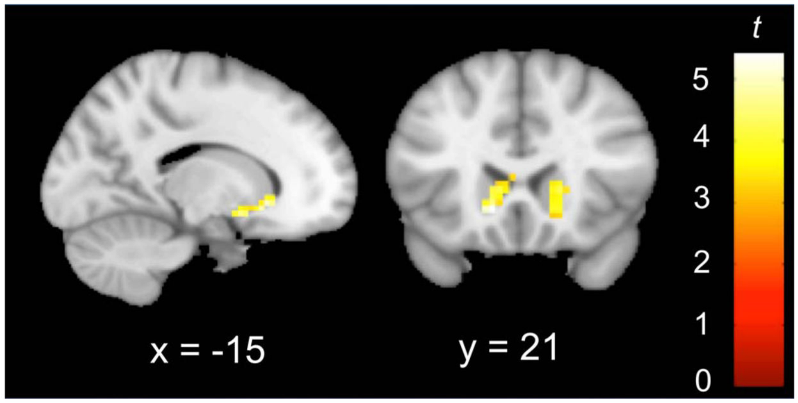

Figure 3.
Three-Way Interaction (Age Group x Evaluative Perspective x Domain)
Repeated measures ANOVA where evaluative perspective and domain served as the within-subjects factors and age group served as the between-subjects factor. Illustrated here is a significant age group x evaluative perspective x domain interaction within bilateral ventral striatum. *Note:* x and y = left-right and anterior-posterior dimensions.

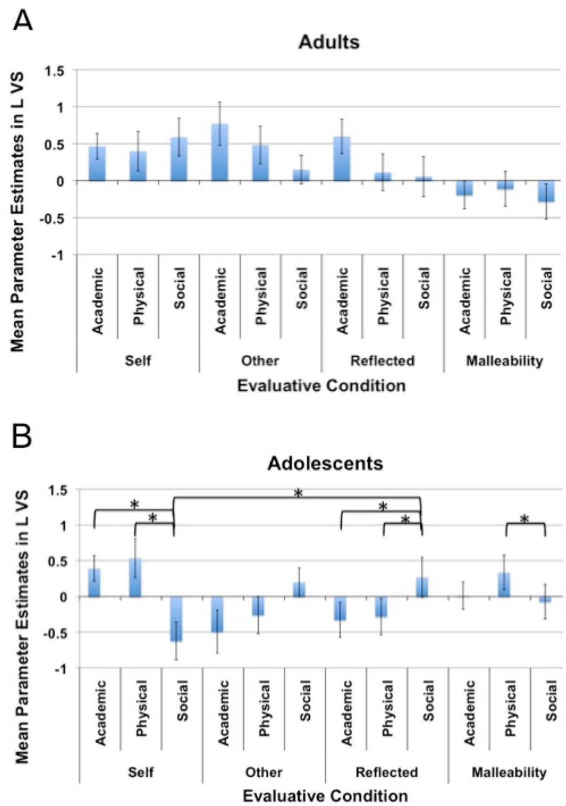

Figure 4.

Mean Parameter Estimates in Ventral Striatum Across Evaluative Conditions

Interaction between evaluative perspective and domain. Panel A illustrates mean parameter estimates representing activity in the left ventral striatum (VS) cluster during reflected social self-evaluations within the adult group. Panel B illustrates mean parameter estimates representing activity in the left VS cluster during reflected social self-evaluations within the adolescent group. *Note: L= left; VS = ventral striatum.*

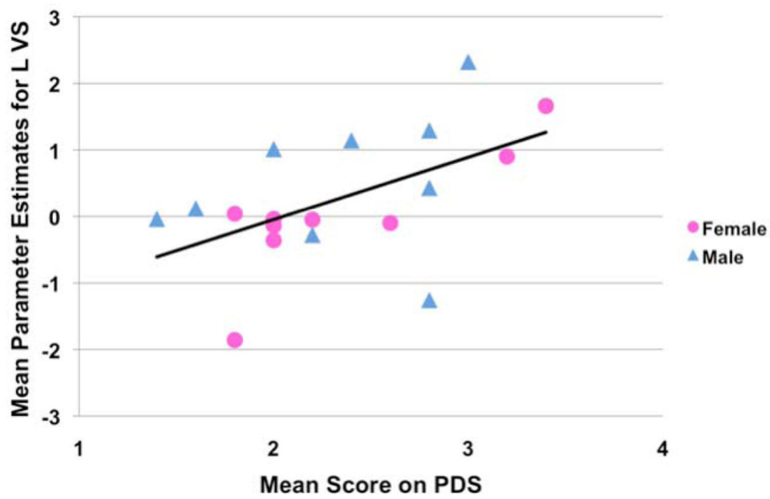

Figure 5.

Positive Relationship Between Pubertal Development and Striatal Activity During Adolescent Reflected Social Self-Evaluations

Correlation between average Pubertal Development Scale (PDS) scores and mean parameter estimates representing activity in left ventral striatum during adolescent reflected social self-evaluations. *Note: L = left; VS = ventral striatum.*

Table 1

Age Group x Evaluative Perspective x Domain Repeated Measures ANOVA

Contrast	Region	x	y	z	F	k
Main effect of age group	Precentral gyus	−42	−6	54	41.84	166
	Inferior parietal lobule	−39	−36	45	41.45	2685
	Culmen	24	−45	−15	33.19	
	Fusiform gyrus	−42	−42	−15	26.76	
	Culmen	−24	−54	−18	26.07	
	Middle temporal gyrus	39	−72	24	25.71	
	TPJ	−42	−51	21	23.83	
	Middle occipital gyrus	48	−69	−6	20.99	
	Intraparietal sulcus	−24	−69	30	20.93	
	Superior frontal gyrus	−21	9	63	22.06	139
	Precentral gyrus	45	−3	51	21.87	
	PCC	12	−60	12	20.10	67
	Middle occipital gyrus	−36	−81	9	17.07	66
Main effect of evaluative perspective	Prec	−6	−54	36	19.46	537
	PCC	−6	−54	9	7.60	
	Ventral mPFC	−9	48	3	19.40	749
	Anterior Rostral mPFC	0	54	12	14.00	
	Rostral ACC	0	36	9	12.24	
	Ventrolateral PFC	39	48	−6	11.49	83
	Middle frontal gyrus	−48	33	15	9.54	106
	IFG	−45	42	0	8.40	
	Inferior parietal lobule	−54	−42	45	9.38	137
	TPJ	−54	−54	24	6.16	
	IFG	51	15	21	8.88	498
	Middle frontal gyrus	39	33	15	7.18	
	Inferior parietal lobule	51	−45	48	7.28	65
Age group x evaluative perspective	Intraparietal sulcus	−30	−69	42	6.28	68
Main effect of domain	OFC	30	33	−15	105.48	5359

Contrast	Region	x	y	z	F	k
	IFG	−45	36	12	58.45	
	IFG	45	39	9	54.67	
	OFC	24	30	−15	49.73	
	Dorsal ACC	3	0	30	49.14	
	Amygdala/parahippocampus	−21	0	−18	32.31	
	PCC	9	−57	18	26.63	
	Pre-SMA	9	18	63	24.86	
	Amygdala/parahippocampus	18	−3	−18	23.04	
	Dorsal mPFC	−3	54	27	18.97	
	Prec	3	−57	39	16.36	
	Caudate	9	6	9	9.80	
	Middle temporal gyrus	54	−3	−18	36.12	145
	Fusiform gyrus	−51	−57	−12	35.17	256
	Middle temporal gyrus	−57	−9	−15	28.33	120
	TPJ	−42	−60	27	23.34	195
	Lingual gyrus	15	−78	−6	17.05	175
	Superior parietal lobule	−27	−66	42	15.34	319
	Inferior parietal lobule	−48	−48	51	12.15	
	TPJ	42	−54	27	15.05	154
	Ventral mPFC/Rostral ACC	9	48	−9	13.35	94
Age group x domain	-	-	-	-	-	-
Evaluative perspective x domain	RSC	−6	−54	15	5.48	126
	Superior frontal sulcus	24	30	45	4.75	80
	VS	6	0	3	4.66	297
	DS	12	0	18	4.64	
	DS	−12	9	12	4.60	
Age group x evaluative perspective x domain	VS	−12	21	−6	5.41	73
	IFG	−18	9	−15	4.75	
	DS	−6	18	3	4.17	
	IFG	27	30	3	4.84	79
	VS	15	18	−9	4.52	

Contrast	Region	x	y	z	F	k
	DS	18	21	3	4.25	

Note: Corrected for multiple comparisons (*FWE* $p < 0.05$) with magnitude and spatial extent thresholds at $p < 0.005$ and $k = 64$ voxels, respectively. Minimum cluster size thresholds were calculated using Monte Carlo simulations in AFNI. *k*-values and *F*-values are reported for peak voxels of each cluster. Additional subpeaks within larger clusters are included for descriptive purposes. TPJ = temporoparietal junction; PCC = posterior cingulate cortex; mPFC = medial prefrontal cortex; ACC = anterior cingulate cortex; PFC = prefrontal cortex; IFG = inferior frontal gyrus; OFC = orbital frontal cortex; Pre-SMA = pre-supplementary motor area; Prec = precuneus; DS = dorsal striatrum; RSC = retrosplenial cortex; VS = ventral striatum.