The Value and Utilization of Social Evaluative Feedback: A Neurodevelopmental Perspective

The value and utilization of social evaluative feedback: a neurodevelopmental perspective

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Abstract

Adolescence is characterized by increased frequency of peer feedback, greater preoccupation with peer approval, and more intensified emotional responses to rejection than other phases of the lifespan. Of particular interest, prolonged or severe rejection has been linked to depression and suicide, and adolescents' social sensitivity comes at a time when we see a sharp rise in the onset of psychiatric disorders. This dissertation aims to identify why adolescents are uniquely impacted by social evaluation by examining a) age-related differences in how peer feedback is used to update views of the self and of peers b) whether differential weighting of neural feedback signals to acceptance and rejection is associated with these shifts and c) whether adolescents are more motivated to seek out peer feedback than adults.

Results indicate that adolescents and adults perceive social evaluation in very different ways. After receiving equivalent rates of peer acceptance and rejection, adolescents demonstrated a feedback-induced decrease in self-views, whereas adults showed an increase in self-views. Meanwhile, adolescents maintained impressions of peers even after being rejected, while adults downgraded impressions of peers who rejected them (Paper 1). Using fMRI, we found that adolescents' tendency to experience a drop in self-views and adults' tendency to experience a boost was associated with asymmetrical neural feedback signaling in the ventral medial prefrontal cortex (vmPFC), a region broadly involved in self-referential processing.

Specifically, adolescents exhibited increased vmPFC signaling for rejection, whereas adults showed increased vmPFC activation for acceptance. In addition, adults' tendency to subsequently update impressions of peers based on feedback was associated with greater activation for rejection compared to acceptance in the caudate, a region of the striatum broadly involved in feedback-based learning (Paper 2). In order to determine whether adolescents were more motivated to obtain peer feedback, the value of peer feedback was inferred via physical effort exertion using a hand dynamometer to measure grip strength. Findings revealed that adolescents exerted more effort than adults for peer feedback, regardless of whether they believed they would be accepted or rejected. Meanwhile, adults exerted less effort for peer feedback they believed would be rejection, suggesting that adults may selectively pursue feedback that reinforces positive self-views (Paper 3).

Together, these studies provide evidence that social evaluation is valued and utilized differently across age. Adults showed self-protective biases in how they sought, processed, and integrated peer feedback that preserved and enhanced positive self-views. Adolescents, on the other hand, pursued and internalized peer feedback in ways that may generally promote social learning, thereby maximizing social competence and group affiliation during this time of social reorientation. This work informs how normative development gives rise to adaptive social processes and may help explain why biased processing of social evaluation could render adolescents especially vulnerable to the harmful effects of rejection.

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Background and Introduction

Adolescence is a period of development that constitutes the transition from childhood to adulthood. Beginning at the onset of pubertal maturation (Shirtcliff, Dahl, & Pollak, 2009), adolescence is characterized by dramatic changes in physical, neurobiological, and psychological maturation (Spear, 2000). Though marked by achievements in cognitive abilities, adolescents face a number of new challenges, including newfound independence, a developing sense of self, and the need to navigate an increasingly complex social environment (Brown, 1990; Somerville, 2013). As individuals enter adolescence and begin to spend more time with peers (Larson, 2001), dependence on parental support gives way to increased reliance on peer relationships (Brown, 1990). As such, peer approval and acceptance take on newfound importance in guiding adolescents' decision-making to maximize social bonds (Rubin, Bukowski, & Parker, 2007).

Accordingly, adolescents become prone to intensified emotional reactions to peer acceptance and rejection (Sebastian, Viding, Williams, & Blakemore, 2010; Somerville, 2013). This sensitivity not only comes at a time when peer rejection is particularly common (Wang, Iannotti, & Nansel, 2009), but also at a time when peer rejection may be particularly damaging. For example, peer rejection has been shown to increase risk for several negative outcomes in adolescents, including social avoidance, anxiety, depression, suicidal ideation, excessive risk-taking and substance use (Prinstein & Aikins, 2004; Rubin et al., 2007). These negative consequences have been shown to have long-term effects on mental health (Rigby, 2000), which may result from complex interactions between neurobiological and social factors (see Crone & Dahl, 2012). Given that adolescence is a period marked by increased risk for the onset of mood and anxiety disorders (Kessler, Avenevoli, & Merikangas, 2001; Paus, Keshavan, & Giedd, 2008), it is important to understand why peer rejection may contribute more dramatically to alterations in mood and self-esteem during adolescence compared to other phases of the lifespan.

Social evaluation and self-views

Humans are an inherently social species that have evolved a fundamental drive to belong, elevating social acceptance as a core need (Baumeister & Leary, 1995). Without stable social support, individuals are at increased risk for many negative outcomes, including low levels of life satisfaction and higher rates of morbidity and mortality (Cacioppo & Hawkley, 2003). As such, humans are attuned to monitor their social inclusion status guided by cues of acceptance and rejection. This social information is highly valuable as it guides whether certain behaviors will facilitate or impede social affiliation.

The drive for social support and belonging may be especially strong during adolescence, marked by increased complexity of the social environment and relationships (Brown, 1990). In addition to preoccupation with peer approval (Brown, 1990; Somerville, 2013b), peer groups are dynamically changing during this developmental period (Cairns, Leung, Buchanan, & Cairns, 1995). Adolescents are also continuing to refine social competency (Harter, 1988) and develop a sense of self or self-concept (Harter, Waters, & Whitesell, 1998; Pfeifer et al., 2009; Sebastian, Burnett, & Blakemore, 2008). Self-views can be understood as the combination of self-esteem (i.e., confidence in one's worth or abilities) and perceived belonging to certain social categorizations (Leary & Tangney, 2012; Pfeifer & Peake, 2012). Peer evaluation may an especially potent modulator of self-views during adolescence, given the role of social evaluation in guiding adolescents' ability to strengthen social bonds. Indeed, peer rejection and ostracism are more likely to lead to feelings of unworthiness and distress during adolescence compared to other ages (O'Brien & Bierman, 1988; Sebastian, Viding, et al., 2010). Furthermore, peer rejection and associated low self-esteem could contribute to serious difficulties in adulthood. In a seminal prospective study, adolescents with low self-esteem were more likely to have poorer mental and physical health, worse economic prospects, and higher levels of criminal behavior during adulthood when compared to adolescents with high self-esteem (Trzesniewski et al., 2006).

Adults, on the other hand, have been shown to maintain positive self-views (Chavez, Heatherton, & Wagner, 2016), often to the extent of demonstrating biased or inflated self-assessment (Baumeister, 1982; John & Robins, 1994). Adults also tend to rate themselves as having more positive and less negative attributes than others, known as the "above average effect" (Beer, Chester, & Hughes, 2013; Beer & Hughes, 2010; Brown, 1986; Chambers & Windschitl, 2004), and are more likely to implicitly associate themselves with positive attributes (Greenwald & Farnham, 2000). When confronted with negative or rejecting feedback, adults have been found to exhibit self-protective processes that preserve or enhance positive self-views (Baumeister, 1982; Beauregard & Dunning, 1998; Beer et al., 2013; Campbell & Sedikides, 1999; Dunning & Cohen, 1992; Rudman, Dohn, & Fairchild, 2007). Researchers have also found that adults make less favorable appraisals of others, more extreme downwards comparisons, and even show antagonistic or retaliatory behavior towards others following negative feedback (Achterberg, Duijvenvoorde, K, Bakermans-Kranenburg, & Crone, 2016; Beauregard & Dunning, 1998; Chambers & Windschitl, 2004; DeWall, Twenge, Gitter, & Baumeister, 2009; Hughes & Beer, 2012b; Vohs & Heatherton, 2004), perhaps in an effort to devalue the source of negative feedback. Adults' tendency to enact these self-protective biases in the service of maintaining favorable self-views has been linked with positive outcomes related to health and wellbeing (Alloy & Abramson, 1979; Peterson & Seligman, 1987; Rizley, 1978). While adults demonstrate behaviors that protect self-views, it is unclear whether adolescents exhibit similar responses when confronted with rejection. When attempting to understand the role of peer evaluation in the development of self-views, it is important to examine how such information is incorporated into representations of the self.

Importantly, the adolescent self-concept is in its developing stages and is largely informed by evaluative feedback from peers and family members, otherwise known as contingent self-esteem (Bos, Huijding, Muris, Vogel, & Biesheuvel, 2010). Previous work has demonstrated that appraisals made by peers' parents and teachers are associated with self-appraisal and impact real developmental outcomes (Harter et al., 1998). For example, adolescents who reported believing others saw them as rule breakers were more likely to engage in delinquent behavior (Bartusch & Matsueda, 1996). Likewise, adolescents who thought their parents saw them as academically competent demonstrated better future performance in math and science (Bouchey & Harter, 2005). As such, feedback appears to be an important component of the normative development of one's identity.

Development of feedback-based learning

To be successful in navigating a new social environment, adolescents must readily incorporate social feedback and flexibly adjust behavior, reflecting updated representations of social goals and expectations (Nelson & Guyer, 2011). For example, if a teen receives feedback that a certain behavior is not approved by a set of peers, this experience should motivate him or her to curtail that behavior in order to increase likelihood of future belonging with this group. This type of adjustment is supported by feedback-based learning, which can be defined as the process of updating an internal representation following an outcome. According to computational theories of reinforcement learning (Sutton & Barto, 1981), one robust type of updating signal results from violations in expectation, when an expected outcome does not align with the actual outcome (otherwise known as prediction errors). A positive prediction error occurs when an outcome is better than expected, whereas a negative prediction error occurs when an outcome is worse than expected. In this way, prediction error functions as a weighted parameter that is incorporated into the expected value of a given choice going forward (Sutton & Barto, 1981).

Neuroscientific studies have established that feedback-based learning is subserved by the corticostriatal circuit, a distributed network of brain regions (e.g., midbrain, striatum, cingulate cortex, medial prefrontal cortex). The corticostriatal circuit is critical for coding and updating reward representations, including prediction errors (Haber & Knutson, 2010; Schultz, Dayan, & Montague, 1997; Shohamy et al., 2004), whereby positive prediction error leads to an increase in phasic dopaminergic firing and negative prediction error leads to an attenuation (Schultz et al., 1997; Ungless, Magill, & Bolam, 2004). Previous neuroimaging studies have found that activation in the ventral striatum, a target area of dopaminergic midbrain neurons, tracks prediction errors (O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003; Pagnoni, Zink, Montague, & Berns, 2002; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Rodriguez P. F., Aron A.R., & Poldrack R.A., 2006).

Another important region responsible for determining how evaluation shapes self-views is the medial prefrontal cortex (mPFC). Prior research has shown that the mPFC, which comprises a set of interconnected subregions, is critical to social feedback processing as it integrates a broad set of information, including social (Amodio & Frith, 2006) and emotional cues (Etkin, Egner, & Kalisch, 2011), reward and value (Rangel & Hare, 2010), and representations of the self (Northoff & Bermpohl, 2004). While this region is involved in many complex cognitive processes, it is central to the prioritization of a broad set of inputs to inform goals, expectations, and future behavior. In addition to feedback-based learning (Haber & Knutson, 2010), the mPFC has also been shown to represent perceived social status (Powers, Wagner, Norris, & Heatherton, 2013), self-referential processing (Mitchell, Macrae, & Banaji, 2006; Wagner, Haxby, & Heatherton, 2012) and self-concept (Beer & Hughes, 2010; Chavez & Heatherton, 2015; Korn, Prehn, Park, Walter, & Heekeren, 2012; Somerville, Kelley, & Heatherton, 2010). As such, the mPFC is understood as a region that computes affective meaning, involved in both value-based signal updating and self-relevant information processing (Roy, Shohamy, & Wager, 2012).

Importantly, the very systems that support feedback-based learning undergo vast developmental changes during adolescence. This may, in part, explain recent research suggesting age-related differences in feedback-based learning and responses to rewards. Previous research examining adolescent responses to feedback-based learning has found that adolescents draw upon the corticostriatal circuit to enact successful learning to positive and negative feedback (Christakou et al., 2013; Cohen et al., 2010; Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008; Jones et al., 2011; van den Bos, Cohen, Kahnt, & Crone, 2012; van der Schaaf, Warmerdam, Crone, & Cools, 2011). Additional findings suggest that adolescents exhibit exaggerated behavioral and striatal response to both positive (Ernst et al., 2005; Galvan et al., 2006) and negative outcomes (Galvan & McGlennen, 2012), such as winning or losing money or tasting appetitive or aversive liquids. Studies specifically designed to measure prediction error across development have yielded inconsistent results. While some studies have found that adolescents demonstrate exaggerated behavioral and neural response to positive (Cohen et al.,

2010) and negative prediction error (Hauser, Iannaccone, Walitza, Brandeis, & Brem, 2015; Javadi, Schmidt, & Smolka, 2014), others have not detected age differences in prediction error signaling (Christakou et al., 2013; Duijvenvoorde et al., 2008; van den Bos et al., 2012). Learning in the social environment, on the other hand, might operate differently than in non-social reward learning paradigms, due to the enhanced salience of peer evaluation during adolescence. Currently, it is not yet clear whether adolescents show such age-related perturbations in social feedback-based learning.

To date, only a few studies have examined this question. Jones and colleagues (Jones et al., 2014) examined developmental differences in response to a probabilistic social learning task, wherein a peers' propensity to like the participant was a set contingency within the reinforcement-learning model. Adolescents showed a slower learning rate for positive prediction error, which is to say that adolescents did not weigh recent outcomes of unexpected acceptance as heavily as other ages in subsequent decision-making choices (Jones et al., 2014). Others have found that compared to adults, adolescents demonstrate heightened striatal activation in response to unexpected positive feedback, which corresponded to decreased memory accuracy of social acceptance (Jarcho et al., 2015). While these findings are preliminary, they suggest that adolescents respond to and learn from peer feedback differently than adults, as supported by differences in learning rates, neural activation, and memory performance.

Neural feedback-based learning mechanisms may play an important role in adolescent-specific responses to peer evaluation. Peer feedback during adolescence could produce differential learning signals along the corticostriatal circuit that, ultimately, lead to biased shaping of self-views. These responses could in turn impact psychological well-being. While there are many social explanations as to why adolescents respond differently to positive and negative feedback compared to adults, researchers have become increasingly focused on neurodevelopmental factors that may be responsible for age-related changes in social cognition (Blakemore, Winston, & Frith, 2004). This not only includes hormonal changes associated with the onset of puberty, but also the continued development of the brain (Nelson, Leibenluft, McClure, & Pine, 2005). Recently, a number of functional magnetic resonance imaging (fMRI) studies have revealed that adolescence is a dynamic phase of neurodevelopment, associated with reward-related hyper-responsiveness of corticostriatal circuit (Ernst et al., 2005; Galvan et al., 2006; Somerville, Hare, & Casey, 2011). Given that processing of social feedback draws upon this circuit (Jones et al., 2011), it stands to reason that peer acceptance or rejection, especially when the outcome is unexpected, may be represented differently (and may modulate self-views differently) across age. Therefore, it is important to consider the ontogenetic trajectory of social-affective learning, as normative changes related to brain development may render adolescents uniquely positioned to biased processing of peer evaluation.

Neurodevelopmental shifts during adolescence

Over the past decade, there has been growing interest in understanding the neuromaturational processes that underlie complex social changes during adolescence. Research using MRI has advanced the study of the brain and related adolescent-specific behavior (e.g., preoccupation with and hyper-responsiveness to social evaluation). Adolescence is characterized by heightened responsivity to socioemotional cues (social cues that elicit an affective response; Somerville, 2013b), with a seemingly limited capacity to regulate and override responses to such cues (Silvers et al., 2012; Spear, 2000; Tottenham, Hare, & Casey, 2011). These behavioral attributes are paralleled by dramatic shifts in hormonal and neurobiological systems that target key brain regions involved in social and affective processing (Nelson et al., 2005). Neuroimaging studies examining the neural mechanisms that support social and emotional processes point to a staggered model of neurodevelopment, wherein subcortical structures, like the striatum, develop relatively earlier than cortical regions, like the prefrontal cortex (Somerville & Casey, 2010). This suggests that subcortical structures contributing to affective drive may develop earlier than cortical structures that help regulate affective drive.

In order to understand how neuromaturational processes contribute to adolescents' hyper-responsiveness to socioemotional cues, several researchers have examined developmental differences in neural activation in response to social acceptance and rejection (Guyer, Choate, Pine, & Nelson, 2012; Sebastian, Roiser, et al., 2010) and its association with well-being. Researchers have developed experimental tasks that deliver self-relevant social feedback to participants in a laboratory setting (Jarcho et al., 2015; Sebastian, Viding, et al., 2010; Silk et al., 2012; Somerville, Heatherton, & Kelley, 2006). These tasks involved playing a ball-tossing game on the computer, deciding whom to chat with on the internet, and making a first impression of likability. By and large, adolescents have shown exaggerated emotional responses, on both behavioral and neural levels, in these tasks. Adolescents have reported more dramatic changes in mood following both peer acceptance (Guyer et al., 2012) and rejection (Sebastian, Viding, et al., 2010). Studies have also found age-related differences in neural activation when anticipating and receiving peer feedback. When anticipating positive feedback, neural activation in the striatum and subgenual cingulate cortex increased linearly with age (Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010). When receiving feedback, adolescents have shown increased activation in regions that support socioemotional processing (e.g., medial prefrontal cortex) and less activation in regulatory regions (e.g., lateral prefrontal cortex), when compared to other ages (Sebastian, Viding, et al., 2010). In addition, adolescents that reported lower levels of social connectedness exhibited heightened pupillary responses—an index of salience detection—following peer rejection (Silk et al., 2012). Taken together, these findings suggest that social evaluation evokes different behavioral and neural responses across development.

Peer rejection and clinical risk during adolescence

When attempting to understand the role of peer evaluation in the development of self-views, it is important to examine the correlates and consequences of peer rejection. Peer rejection in the form of teasing and ridicule is a common form of negative treatment and even punishment among adolescents (Wang et al., 2009). Prolonged peer rejection has been associated with the development of externalizing behaviors (e.g., truancy, school dropout, delinquency; Coie, Lochman, Terry, & Hyman, 1992) and internalizing emotional disorders, such as depression and anxiety (French, Conrad, & Turner, 1995). Students who are bullied and have low social support are at highest risk for poor mental health outcomes (Rigby, 2000), with strongest links to depression (Hawker & Boulton, 2000). Indeed, peer rejection and ostracism during adolescence have been prospectively linked to depression over a year later (Prinstein & Aikins, 2004).

Others posit that this phase of social and neurobiological change has serious implications for the development of psychiatric disorders (Lee et al., 2014; Nelson et al., 2005; Powers & Casey, 2015). Adolescence is a period marked by heightened personal relevance of peer rejection, and this period is also associated with a sharp rise in onset of mental illness (Kessler et al., 2001; Paus et al., 2008). From an epidemiological perspective, peak age of onset for any psychiatric disorder, including depression, is 14 years old (Kessler et al., 2005). Prevalence rates increase dramatically from 1% to 17-25% by the end of adolescence (Kessler et al., 2001), with the greatest number of new cases emerging between the ages of 15 and 18 (Hankin et al., 1998). Additionally, adolescent onset of these disorders is associated with a more severe and disabling prognosis of illness (Zisook et al., 2007). Thus, it is important to understand how neurodevelopmental changes shape social learning in the context of peer evaluation, as well as the associated impact on self-views.

The Current Research

In my dissertation research, I build on this line of work by examining how social evaluation is valued and processed across age and the underlying neural mechanisms that subserve the accompanying impact on self- and other-views. Understanding how adolescents process and learn from social evaluation could provide insight into the apparent increase in concern over peer approval and accompanying impact on adolescents' well-being.

The overarching goal of this dissertation is to examine how normative brain development leads to age-specific differences in how individuals approach and learn from peer acceptance and rejection. Further, I examine whether these differences relate to changes in self-views and views of others. The specific hypotheses of the current proposal are: 1) compared to children and adults, adolescents will utilize rejection over acceptance to inform self-views; 2) during peer evaluation, neural activation in the corticostriatal circuit will explain biased feedback processing in adolescents; 3) despite their increased sensitivity to peer rejection, adolescents will nonetheless demonstrate greater valuation of social evaluation, whereas adults will more strategically seek out social evaluation to protect their self-views from rejection.

Paper 1: Development of self-protective biases in response to social evaluative feedback

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Abstract

Adolescence is a developmental period marked by heightened attunement to social evaluation. While adults have been shown to enact self-protective processes to buffer their self-views from evaluative threats like peer rejection, it is unclear whether adolescents avail themselves of the same defenses. The current study examines how social evaluation shapes views of the self and others differently across development. N=107 participants ages 10-23 completed a reciprocal social evaluation task that involved predicting and receiving peer acceptance and rejection feedback, along with assessments of self-views and likability ratings of peers. Here we show that, despite equivalent experiences of social evaluation, adolescents internalized peer rejection, experiencing a feedback-induced drop in self-views, whereas adults externalized peer rejection, reporting a task-induced boost in self-views and deprecating the peers who rejected them. The results identify co-developing processes underlying why peer rejection may lead to more dramatic alterations in self-views during adolescence than other phases of the lifespan.

Significance Statement

The growing popularity of social media, especially among youth, has resulted in peer feedback (including rejection) pervading everyday life. Given that peer ostracism has been linked to depression and suicide, it is critical to understand the psychological impact of peer feedback from a developmental perspective. We demonstrate that adolescents and adults use peer feedback to inform views of themselves and of others in very different ways. Of particular interest, early adolescents internalized rejection from peers and felt worse about themselves, whereas adults exhibited evidence of self-protective biases that preserved positive self-views. This work advances theoretical insights into how development shapes social-evaluative experiences, and informs sources of vulnerability that could put adolescents at unique risk for negative mental health outcomes.

Introduction

Interactions with peers naturally engender social evaluation, a normative social experience that helps people learn to become competent group members. While peer rejection that is prolonged or extreme can give rise to negative self-views that persist over time (Williams, 2007), adults generally protect themselves from these pernicious effects by engaging cognitive processes that facilitate the maintenance of positive self-views (i.e., self-protective biases; Campbell & Sedikides, 1999). However, it is currently unclear how self-protective biases develop and whether adolescents, who exhibit heightened sensitivity to peer evaluation (Somerville, 2013), are able to draw upon these same defenses.

When faced with threats to the self, such as feedback of failure or social rejection, adults exhibit compensatory behaviors that help them buffer and enhance their self-views (Baumeister, 1982; Beauregard & Dunning, 1998; Hughes & Beer, 2012b). Adults have been shown to blame negative feedback on external (e.g., bad luck) rather than internal sources (e.g., ability; Bernstein, Stephan, & Davis, 1979) and to devalue the source of feedback to challenge its importance (Dunning & Cohen, 1992). Researchers have also found that adults make less favorable appraisals of others (Beauregard & Dunning, 1998; DeWall, Twenge, et al., 2009; Vohs & Heatherton, 2004) and show antagonistic or retaliatory behavior towards others following negative feedback (Achterberg et al., 2016). This collection of self-protective processes is theorized to maintain favorable self-views and is broadly linked with improved well-being (Alloy & Abramson, 1979). While adults benefit from this self-protective bias in the face of negative evaluation, it is unclear how this process develops across the lifespan.

Adolescence is a period of development characterized by an increase in social attunement and concern with being accepted by peers (Brown, 1990; Somerville, 2013b). Previous research has revealed that adolescents, compared to children and adults, are especially oriented to recognize negative socio-emotional cues (Thomas, De Bellis, Graham, & LaBar, 2007) and are prone to intensified emotional and stress responses to peer evaluation (Sebastian, Viding, et al., 2010; Silk et al., 2012; Somerville et al., 2013; Stroud et al., 2009). Thus, adolescence may be a time in which individuals are especially vulnerable to the impact of peer rejection on self-views. Given adolescents' heightened sensitivity to rejection and the sharp rise in onset of mental illness during adolescence (Kessler et al., 2001), it is important to understand how adolescents process and integrate social evaluation into their views of self and others.

The current study investigates whether adolescents employ self-protective processes using a well-validated paradigm that has been shown to elicit genuine experiences of social evaluation (Gunther Moor et al., 2010; Powers, Somerville, Kelley, & Heatherton, 2013;

Somerville et al., 2006, 2010). Participants spanning pre-adolescence through young adulthood (N = 107; ages 10 – 23) were told they were taking part in a multi-site study investigating how individuals formulate first impressions of peers. This cover story set up a reciprocal social evaluation task (Figure 1) in which participants predicted whether each peer would like them, and subsequently received feedback indicating whether the peer liked or disliked the participant. Before and after the task, participants evaluated the likability of each peer and completed a self-esteem questionnaire (Harter, 1983, 1988; Neemann & Harter, 1986).

This diverse dataset enabled analyses targeting age-related differences in how individuals process these evaluative feedback experiences on several levels. In the domain of self-views, we evaluated expectations of being liked or disliked across development using both explicit (i.e., participants' predictions) and implicit (i.e., associated response time) measures. We also examined age-related differences in the extent to which participants' self-views were enhanced or diminished following the social evaluation task.

Additionally, we aimed to identify developmental differences in the degree to which participants updated impressions of peers following social evaluation by having participants rate the likability of each peer before and after the task. Analyses examined whether participants' ratings of peers changed in accordance with being accepted or rejected (i.e., liking an individual more after they had provided positive feedback; liking them less after they had provided negative feedback).

Lastly, we examined participants' performance on a surprise memory test following the social evaluation task to a) ensure that participants remembered the feedback they received, which would allow us to interpret subsequent findings as task-induced, and b) determine memory equivalency across age, which would provide evidence that subsequent findings were not driven by developmental differences in learning.

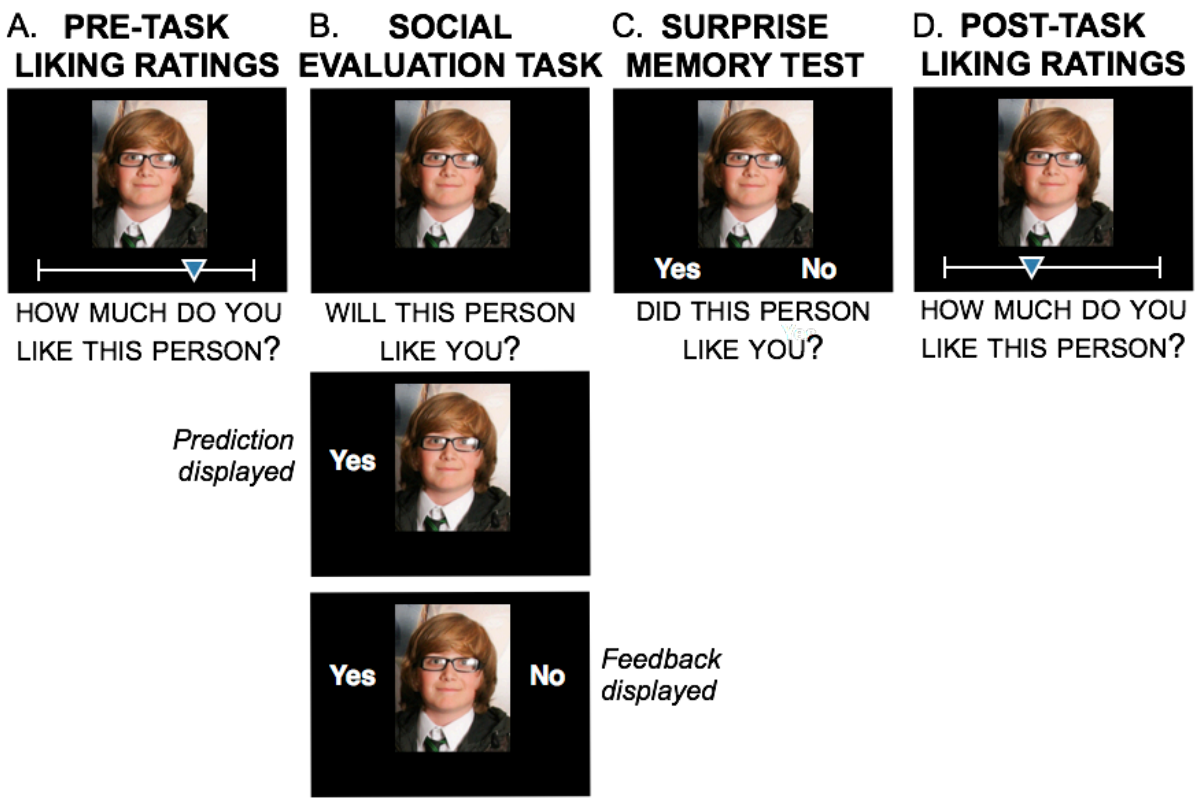

Figure 1. Schematic representation of experimental task. Prior to the study visit, participants submitted a photograph that was ostensibly sent out to unknown, age-matched peers to be rated on likability. A) Participants rated the likability of the peers before the task. B) During the task, participants predicted whether they thought the peer liked them or not, and then were shown the (supposed) peer rating. C) Following the task, participants completed a surprise memory test, querying memory for whether each peer liked or disliked them. D) Participants re-rated the likability of each peer.

Methods

Participants.

One hundred and nineteen healthy individuals were recruited from the local Boston and Cambridge communities and a final sample of 107 were included in the current study. Participants were aged 9.98-23.29 (M=16.45 years, SD=3.71) and 49.5% female, with gender distributed equivalently across age (Logistic regression: B=-.019, p=.719). The Committee for the Protection of Human Subjects at Harvard University approved all research procedures. See *Supplemental Materials* for details.

Pre-visit procedure.

Approximately one week prior to the study appointment, participants submitted a digital headshot photograph. Participants believed that their photographs would be traded with other study locations and rated by the unknown peer-aged participants in other cities based on how likable they looked. Participants also made pre-task likability ratings of the same peers online before their study visit. For these pre-task ratings, participants viewed each peer along with the question *"How much do you think you would like this person?"*. Participants responded by using their mouse to click along a continuous scale from "not at all" to "very much" (Figure 1A). The output of this scale ranged from 1-100 and this numerical value was used in subsequent analyses. Participants were told that the other participants had used the same survey to rate their photograph.

Study visit.

Participants completed the SPP (Harter, 1983, 1988; Neemann & Harter, 1986) before the task to quantify baseline (pre-task) self-views. We administered the Child (ages 9-14; Harter, 1983), Adolescent (ages 15-17; Harter, 1988), and College-Aged (ages 18-23; Neemann & Harter, 1986) versions of the questionnaire as validated. During the task, participants viewed the photographs of the peers, predicted whether that peer liked or disliked them, and received feedback indicating whether the peer liked or disliked them (Figure 1B; Gunther Moor et al., 2010; Powers, Somerville, et al., 2013; Somerville et al., 2006; Somerville, Kelley, et al., 2010). Following the social evaluation task, participants completed a surprise memory test where they viewed photographs of all 160 peers again in random order and indicated whether each peer had liked them or not during the task by selecting "Yes" or "No" with a self-paced button press (Figure 1C). After the memory test, participants completed the SPP (Harter, 1983, 1988; Neemann & Harter, 1986) again, which allowed us to quantify task-induced shifts in self-views. Participants also re-rated the likability of each peer using the same scale used for the pre-task likability ratings (Figure 1D). All participants were questioned using a funnel debriefing procedure to confirm their belief in the cover story. Details on participants, task design and stimulus development are provided in the *Supplemental Materials*.

Summary of age analysis approach.

Analyses querying for age effects were performed in two steps, see *Supplemental Materials* for details. First, we conducted linear or linear mixed-effects (LME; for dependent variables with repeated measures) regression analyses using the *nlme* package in R (Pinheiro, Bates, DebRoy, & Sarker, 2014) to evaluate the statistical significance of standard linear and nonlinear (quadratic, cubic) age-related patterns of change. The optimal age model was chosen based on model fit statistics (Akaike Information Criterion; AIC; Akaike, 1974). Parameter estimates (B) are reported in unstandardized units.

For the present dataset, these analyses frequently favored models that included multiple higher order age predictors, suggesting complex age-related patterns. Therefore, we undertook a second analysis step more sensitive to complex age patterns to query whether nonlinear curves, derived through data-driven methods, would improve fit over and above the traditional regression models. Generalized additive models (GAM) or generalized additive mixed models (GAMM; for dependent variables with repeated measures) were built using the *mgcv* package in R (Wood, 2017), which generated a data-driven function summarizing age-dependent change through thin plate regression smoothing splines. This analysis yields solutions that are stabilized using leave-one-out cross-validation, and permitted formal model comparison to determine whether the spline-based model fit was superior to the fit of the traditional linear regression analyses, based on AIC. The model yielding the lowest AIC value was selected for statistical inference. In addition, we conducted traditional age group binning analyses to illustrate convergence (see *Supplemental Materials*). For each model we report the R-squared as an effect size estimate, which summarizes the variance explained.

Results

Views of self.

Explicit: prediction of peer feedback.

We computed the proportion of trials where participants predicted they would be liked to determine whether individuals exhibited explicit biases in their expectations of peer acceptance. In general, participants predicted they would be liked 53.22% of the time (SE=1.32%; min=19.60%, max=85.00%), which is an overestimation compared to the base rate of 50% (participants received 50% acceptance and 50% rejection feedback across the task; one-sample $t(106)=2.439$, $p=.016$).

Primary analyses tested whether individuals of different ages expected to be liked at different frequencies. The cubic regression model with all three age predictors was identified as the optimal model (AIC: -124.6) as compared to a quadratic model (AIC: -122.2), linear model (AIC: -122.4), and null model with no age predictors (AIC: -119.5). When examining each age term within the cubic model, predictions of being liked increased linearly with age (B=0.299, p=.025) and also followed a cubic function (B=-0.274, p=.039). The quadratic age predictor was not significant (B=0.176, p=.184).

For comparison, we built a GAM to generate a data-driven nonlinear age fit using a thin plate regression smoothing spline. Model comparison revealed that the spline-based model (AIC: -124.4; 9.39% variance explained) and the cubic regression model (AIC: -124.6; 9.91% variance explained) were nearly equivalent in fit quality, although the cubic model slightly outperformed the spline model. Because the spline-based model was internally cross-validated and, thus, more robust and replicable, we present this model in Figure 2. The observed pattern indicated that young adolescents predicted they would be liked less frequently than young adults, who overestimated the extent to which they would be accepted by peers. The highly similar cubic fit is displayed in the *Supplemental Materials* (Figure S6) to demonstrate convergence.

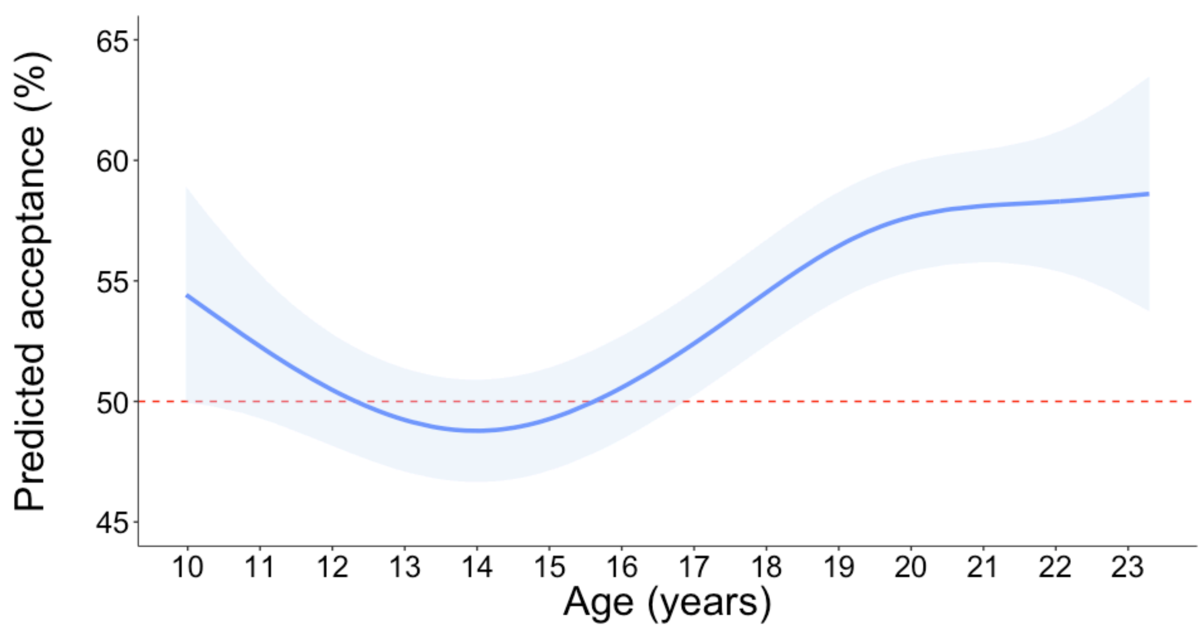

Figure 2. Relative to adolescents, young adults overestimated how much they would be liked by peers. Graph shows a blue fit line of predicted values of acceptance expectancy (percent of trials predicted acceptance) based on the thin plate regression smoothing spline model. Blue shading indicates the standard error of the mean (SEM). Red dotted line denotes actual rate of acceptance (50%).

Implicit: prediction response times.

Participants took an average of 1345ms (SE=33.52ms) to predict whether they would be liked or disliked by peers, with very few non-responses (1.7% of all trials). Overall, response times were equivalent across age ($r(105)=0.024$, $p=.802$). Across all participants, response times for predicting acceptance (M=1363ms, SE=33.83ms) and rejection (M=1350ms, SE=34.43ms) did not differ (paired t-test: $t(106)=1.023$, $p=.308$).

Prior work has demonstrated that response time biases can reflect implicit conceptual conflict (Greenwald, McGhee, & K, 1998; Stroop, 1935), such that slowing reflects cognitive interference induced when pairing incongruent constructs and speeding reflects facilitative association when pairing congruent constructs. We evaluated participants' response times when predicting they would be liked or disliked as an index of congruence with self-views. Based on these frameworks, comparison of response times when making a prediction allowed us to obtain a proxy measure of cognitive interference, wherein slower responses to one prediction (e.g., rejection) over the other (e.g., acceptance) suggests a need to override a stronger association with the competing prediction (e.g., acceptance).

To examine age effects, we fit linear regression models evaluating age-related change with prediction response time difference score (rejection – acceptance) as the dependent variable. The cubic model with all three age predictors (AIC: -122.9) was equivalent to the linear model (AIC: -122.9), and superior to the quadratic and null models (AIC: -121.7, -121.2, respectively). The cubic model was chosen for thoroughness and revealed a marginally significant linear increase with age (B=0.260, p=.052). The quadratic and cubic age terms were not significant (quadratic: B= 0.117, p=.378; cubic: B=-0.233, p=.082).

Model comparison revealed that the spline-based model was a better fit of the data (AIC: -124.4; 8.52% variance explained) than the cubic regression model (AIC: -122.9; 6.97% variance explained); see Figure 3. Specifically, early adolescents exhibited slower reaction times for predicting acceptance than rejection, suggestive of an internal heuristic more consistent with expecting rejection from others. Conversely, older participants exhibited slower reaction times for predicting rejection relative to acceptance, suggestive of an internal heuristic more consistent with expecting others to accept them.

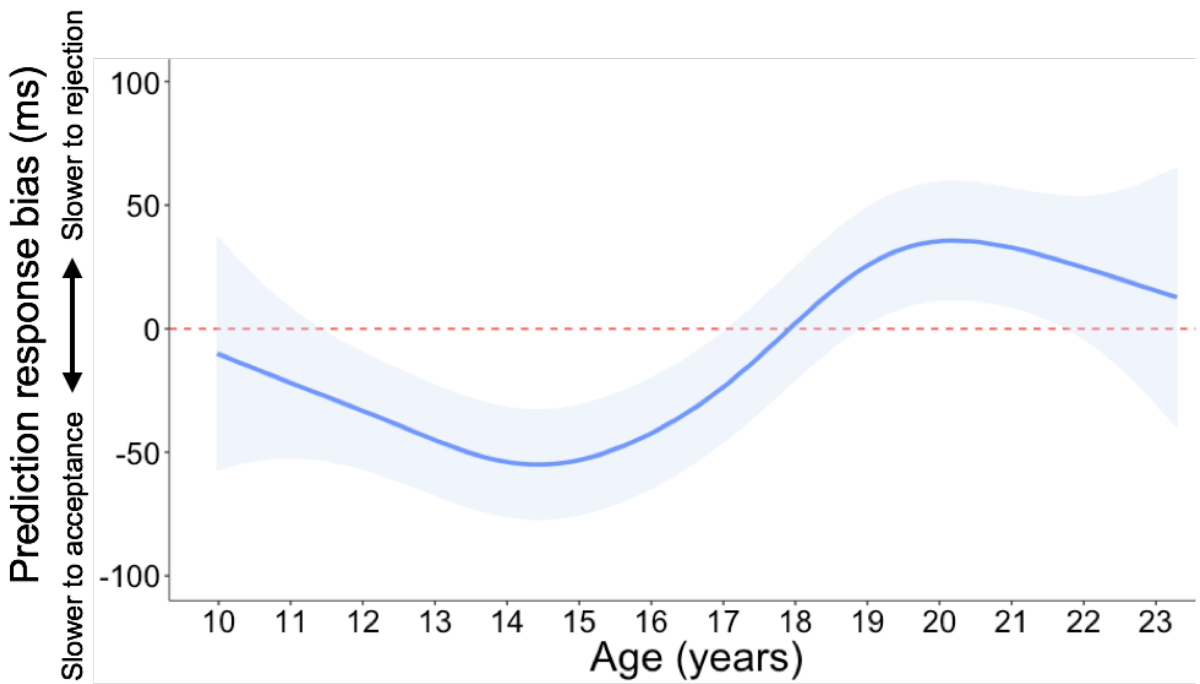

Figure 3. Response time bias for predicting rejection vs. acceptance differs with age. Blue fit line of predicted values depicts age-related changes in the prediction response bias score based on the thin plate regression smoothing spline model. Blue shading indicates the SEM. Red dotted line denotes no prediction response bias.

Changes in views of self.

Self-views were assessed before and after the social evaluation task using the Self Perception Profile (SPP; Harter, 1983, 1988; Neemann & Harter, 1986), which measures global self-esteem. Pre-task data indicated that at baseline, participants' reported self-views were consistent with published norms of each age-specific scale (see *Supplementary Table* S1), with an average of 3.12 (SE=0.06; scale: 1-4; min=1.2, max=4.0). Participants endorsed comparable levels of self-views at baseline across age (r(104)=0.061, p=.537). These findings built confidence in our ability to isolate task-induced changes in self-views that was not biased by baseline differences.

To examine the extent to which the social evaluation task impacted views of self differently across development, we computed the percent change score comparing pre- to post-task scores on the SPP. Positive change scores indicated enhanced self-views and negative change scores indicated reduced self-views as induced by the task. Across the entire sample, participants did not demonstrate a significant task-induced change in self-views (t(103)=1.463, p=.146).

When testing for developmental differences, linear regressions with percent change score as the dependent variable revealed significant age-related change. The linear model (AIC: -175.6) was superior to the cubic (AIC: -174.4), quadratic (AIC: -173.9), and null (AIC: -173.1) models, demonstrating a significant linear effect of age (B=0.219, p=.037).

Model comparison showed that the spline-based model (AIC: -176.2; 8.85% variance explained) outperformed the linear regression model (AIC: -175.5; 4.21% variance explained); see Figure 4. This pattern indicated that early adolescents experienced a unique drop in self-views, whereas self-enhancement emerged during the transition to adulthood.

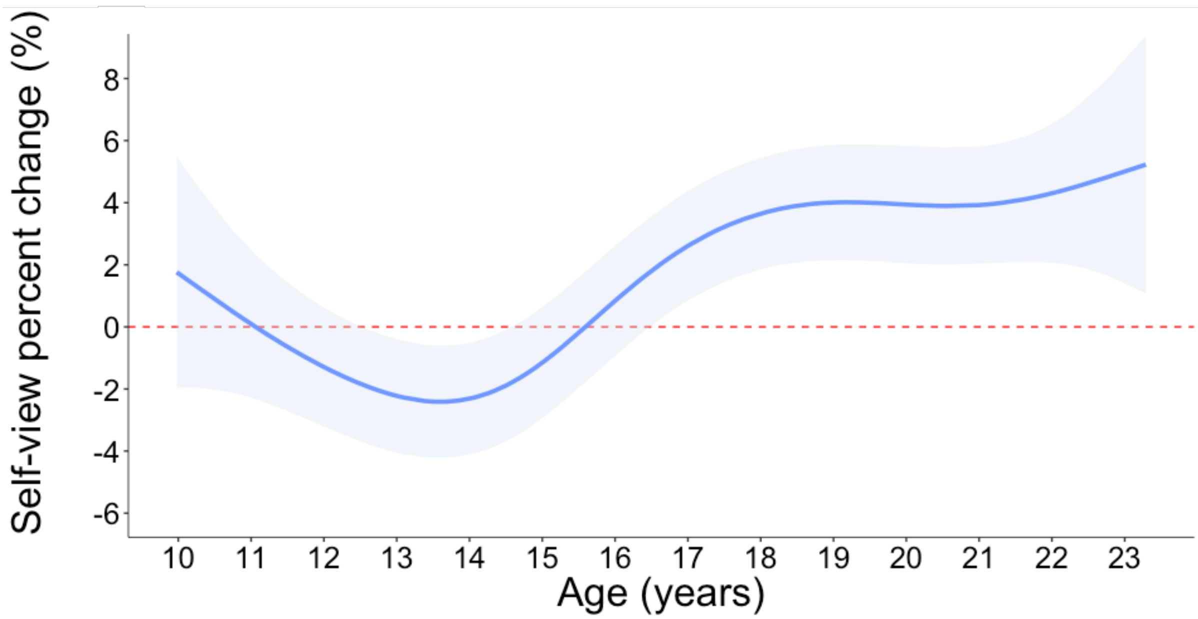

Figure 4. Task-induced changes in self-views differed across development. Graph shows blue fit line of predicted values of the percent change in self-esteem score pre-task vs. post-task based on the thin plate regression smoothing spline model. Blue shading indicates the SEM. Red dotted line denotes no change in self-views.

Views of others.

Changes in likability ratings of peers.

Before and after the social evaluation task, participants rated the likability of each peer on a sliding scale, which output a value from 1-100. On average, participants rated peers as relatively neutral prior to the task (M= 45.59, SE=1.44). A test for age differences in pre-task likability ratings indicated that baseline ratings were equivalent across age (r(105)=0.071, p=.464), suggesting the age-customized stimulus sets were well balanced.

A difference score subtracting the post-task from pre-task ratings quantified whether participants enhanced impressions of a peer following acceptance (positive difference score) and reduced impressions of the peer following rejection (negative difference score). Across the sample as a whole, ratings became more positive following acceptance (M=0.37 SE=0.94) and more negative following rejection (M=-3.16, SE=1.09; B=0.035, p<.001), suggesting that participants “upgraded” peers who provided positive feedback and “downgraded” their impressions of peers who provided negative feedback.

Key analyses tested whether the tendency to increase ratings of peers after acceptance and decrease ratings of peers after rejection varied with age. LME regressions with the likability difference score as the dependent variable, subject as a random effect, feedback type (acceptance, rejection), age (linear, quadratic, cubic), and age interactions as predictors revealed that the linear model (AIC: -431.9) was superior to the cubic (AIC: -426.4), quadratic (AIC: -428.5), and null models (AIC: -424.9). The optimal linear model revealed a significant interaction between feedback type and linear age (B=0.340, p=.001).

Model comparison showed that the spline-based model (AIC: -429.9; 2.30% variance explained (adj.[1])) was a poorer fit of the data relative to the LME model (AIC: -431.9; 2.73% variance explained (adj.)). Therefore, the LME-based model is carried forward for inference and depicted in Figure 5. Results suggest that being accepted or rejected by peers exerted a greater influence how individuals viewed their peers with increasing age. While children and early adolescents maintained impressions of peers regardless of peer feedback, young adults updated impressions of peers based on whether that peer accepted or rejected them.

[1] R^2 was adjusted for this analysis due to the repeated measures nature of the data. The adjustment penalized R^2 based on the number of parameters in the model.

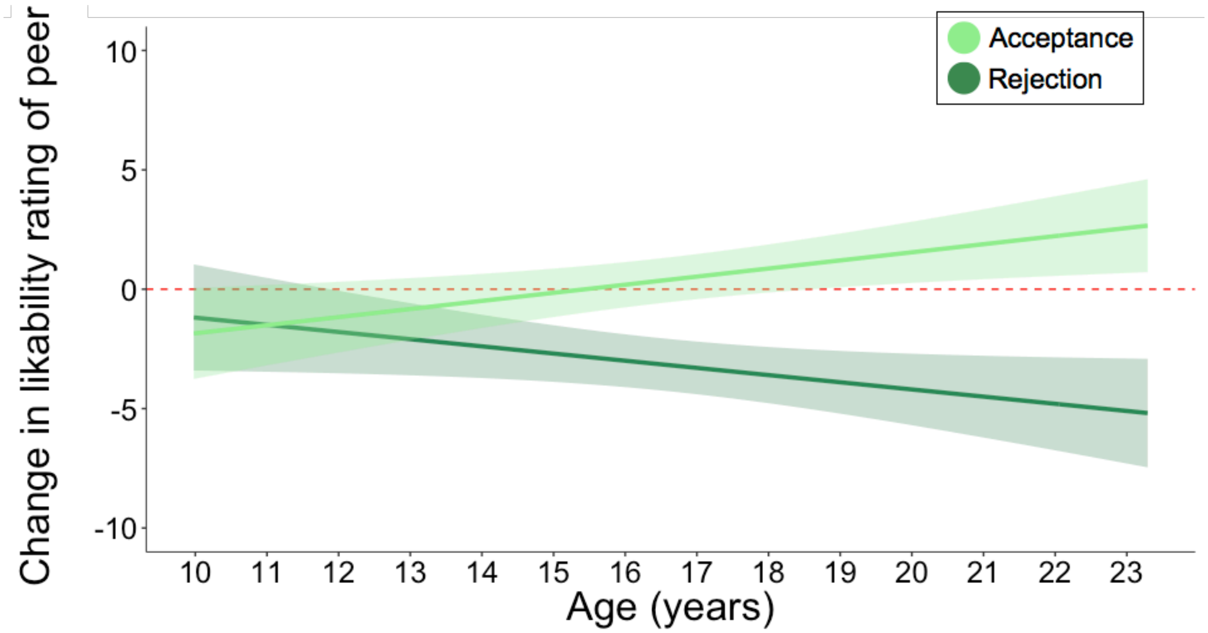

Figure 5. Feedback-specific changes in likability ratings of peers emerged with age. Graph shows fit line of predicted values of the difference score in peer likability rating pre-task vs. post-task as a function of feedback type based on the linear regression. Light green line indicates change in likability rating following acceptance and dark green line indicates change in likability rating following rejection. Shading indicates the SEM. Red dotted line denotes no change in likability ratings of peers.

Memory control analysis.

Following the social evaluation task, participants completed a surprise memory test of the feedback they received. Overall, participants accurately remembered 62.74% (SE=.73%) of the feedback they received, which was significantly above chance (50%; $t(106)=17.474$, $p<.001$). Age analyses showed that participants remembered when they were liked or disliked equivalently across age (main effect and interaction with age: ps>.132; see *Supplemental Materials* for details). Importantly, these results rule out the possibility that the differences in processing of peer feedback described herein are a byproduct of superior source memory for the feedback received at any particular age. Instead, the baseline information available to update impressions was equivalent across age, but processed and integrated differently to update representations of the self or others.

Discussion

Understanding how individuals process and learn from social evaluation across development could provide key insights into adolescents' preoccupation with peer approval and the accompanying impact of social feedback on adolescents' well-being. Here we used a well-validated social evaluation task to probe how peer feedback influenced participants' self-views and the views of their peers. Across explicit and implicit measures of behavior we found evidence that adolescents expected and internalized rejection, which negatively impacted their self-views, while adults expected acceptance and processed peer evaluation in a way that enhanced self-views. Furthermore, adolescents' impressions of their peers were unaffected by the feedback they received, whereas adults deprecated the peers who rejected them. Together, these findings implicate co-developing processes of reactivity to rejection and self-protective defenses that result in adolescents internalizing and adult externalizing negative social feedback.

Participants' explicit expectations of peer acceptance indicated that young adults overestimated how often peers would like them. These findings align with previous work positing that healthy adults maintain inherently positive or inflated self-views (Baumeister, 1982; Chavez et al., 2016) and report having more positive and less negative attributes than others, known as the "above average effect" (Chambers & Windschitl, 2004; Hughes & Beer, 2012b). By contrast, adolescents exhibited lower, yet more accurate, rates of predicted acceptance. Though few studies have directly compared expectations of social acceptance across age, these findings are consistent with one prior study showing that early adolescents expected to be liked less frequently than adults (Gunther Moor et al., 2010). The current study identifies a developmental shift in explicit expectation of acceptance that troughs during adolescence and rises during the transition from adolescence to young adulthood.

In addition, we compared participants' response times when predicting acceptance and rejection as an implicit index of cognitive interference (Greenwald et al., 1998; Stroop, 1935). Young adults showed relatively faster responses when predicting acceptance compared to rejection, which could reflect an internal schema more consistent with expecting acceptance. Similar tendencies have been demonstrated previously, wherein adults displayed faster response times when associating the self with positive attributes (Greenwald & Farnham, 2000). Adolescents exhibited the reverse trend of longer response times to predict acceptance, which could reflect the fundamentality of biased expectancies of rejection in adolescence. In all, these findings demonstrate robust differences in social expectancies across development, with the transition from adolescence to adulthood characterized by a shift from rejection-congruent to acceptance-congruent expectations.

This study also revealed age-related differences in how peer feedback impacts self-views. Though the social evaluation task delivered an equivalent rate of 50% acceptance and 50% rejection feedback, this mixed evaluative experience was incorporated into self-views in strikingly different ways across development. Late adolescents and young adults reported a boost in self-views, which is consistent with a long history of research demonstrating that adults activate compensatory self-enhancement mechanisms following negative feedback, including increases in explicit and implicit self-views (Baumeister, 1982; Rudman et al., 2007). By contrast, early adolescents experienced a drop in self-views following exposure to the same social feedback, suggesting that adolescents may not exhibit the self-protective biases that buffer adults against negative self-views following rejection. These findings extend previous work underscoring the strong negative affective reaction adolescents show in response to peer rejection (Sebastian, Viding, et al., 2010; Stroud et al., 2009). Although the present study did not explicitly measure emotional reactions to the social feedback, the adolescent-specific reduction in self-views suggests a prioritization of rejection cues during adolescence. Taken together, our findings indicate that adolescents exhibit a particular sensitivity to rejection whereas self-protective biases, which emerge later in development, buffer adults from the harmful effects of rejection experiences.

When comparing likability ratings of peers before and after the task, adults made feedback-specific adjustments in their views of others by "downgrading" those that had rejected them and "upgrading" peers that had accepted them. The tendency for adults to rate accepting peers more favorably (Jones et al., 2011), respond to negative feedback by denigrating others (Beauregard & Dunning, 1998; DeWall, Twenge, et al., 2009; Vohs & Heatherton, 2004), and engage in retaliatory impression updating (Achterberg et al., 2016) aligns with previous work. These strategies may help to preserve self-views by promoting future affiliation with accepting rather than rejecting peers, undercutting the validity of negative feedback sources, and discouraging peers from future exclusionary behavior. Meanwhile, adolescents showed consistency in their impressions of peers, even after being rejected. These results document the developmental timescale along which feedback-dependent impression formation emerges, which is important for understanding how adolescents and adults integrate social evaluation to shape future affiliative or antagonistic social behaviors.

Developmental framework for socioevaluative sensitivity.

Our findings reveal a framework of socioevaluative processing from pre-adolescence through young adulthood. We have shown that reactivity to rejection is heightened during early adolescence, whereas self-protective processes (including retaliatory impression updating) have a more protracted emergence. The interactions between these co-developing processes may result in early adolescents exhibiting a maximal differential between heightened reactivity to rejection and the absence of self-protective biases that preserve self-views (Figure 6).

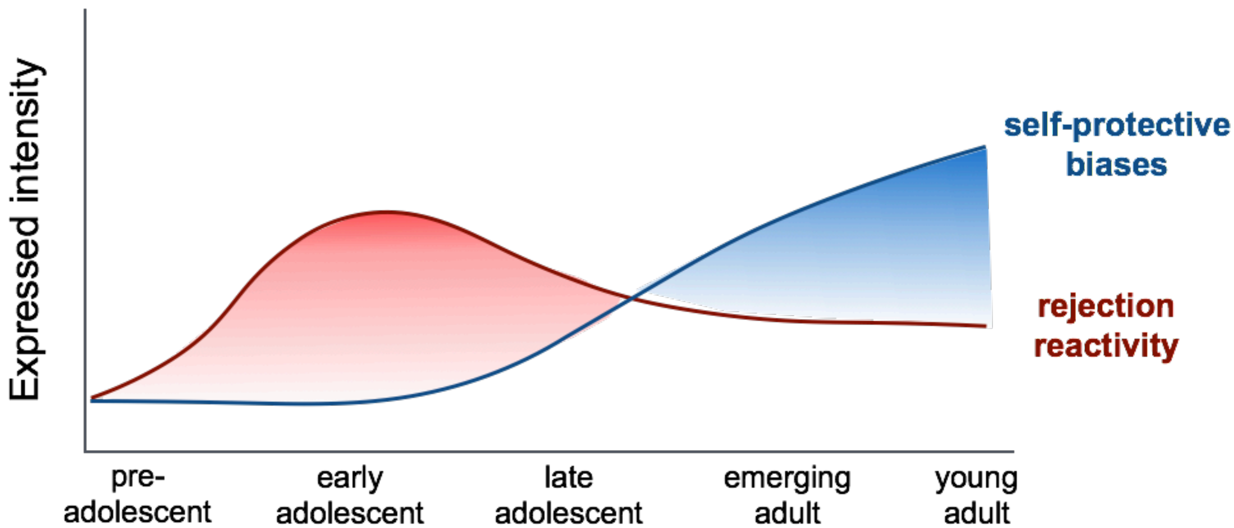

Figure 6. A hypothesized developmental framework based on the present study findings, delineating changes in combined mechanisms resulting in robust shifts in reactions to evaluative feedback experiences from adolescence to young adulthood. Based on the current data and extent literature, the red line represents reactivity to peer rejection and the blue line represents the tendency to self-protect in response to peer rejection.

Here we propose three possible mechanisms that help explain the existence and utility of the adolescent biases documented in the present study:

Regulatory capacity. In contrast to adults, we found that adolescents did not enhance self-views or denigrate impressions of rejecting peers, suggesting that adolescents do not avail themselves of the self-protective biases that adults do. One possibility is that adolescents are continuing to fine-tune the cognitive regulatory strategies that give rise to self-protective biases. Indeed, theoretical accounts describe adult self-enhancing processes as complex regulation strategies deployed to mitigate the negative affect experienced following a threat to self-positivity (Rudman et al., 2007). It is possible that the mechanisms needed to regulate affective responses to rejection and downstream effects on self-views are not fully developed during adolescence, resulting in a tendency toward internalization of negative feedback. Consistent with this perspective, prior work has demonstrated that adolescents' ability to regulate emotional and behavioral responses toward social and emotional cues continues to improve through adolescence (Silvers et al., 2012; Somerville et al., 2011; Tottenham et al., 2011). Thus, the protracted development of regulatory efficacy may account for early adolescents' lessened tendency to enact self-enhancing defenses in response to peer rejection.

The developing self-concept. Another possibility is that adolescents internalize peer rejection because their 'self-concept' is still in its developing stages. The self-concept encompasses evaluative self-knowledge and self-worth, which are informed by status or competency across multiple domains (e.g., social, athletic, appearance; Harter et al., 1998). Research has shown that adults have a complex, multi-faceted self-concept and can draw upon alternative domains of self-views to buffer against threat in a specific domain (Tesser, 2000). This may, in part, explain how adults are able to buttress self-views in response to negative feedback, as seen in the current study. Adolescents, by contrast, are in the process of building up self-referential knowledge, identity, and social group affiliations (Harter et al., 1998). As such, the relatively unfractionated adolescent self-concept may be less able to draw upon alternate sources of self-worth in the face of negative appraisals, which could lead to the stronger impact of negative peer evaluation.

Social reorientation. The transition to adolescence is accompanied by a marked change in the complexity of the social environment (Brown, 1990). Adolescents spend more time with peers (Larson, 2001), experience more fluidity in social groups (Cairns et al., 1995), and encounter more frequent feedback from peers (Wang et al., 2009). A key challenge of adolescence is to readily incorporate social feedback and flexibly adjust behavior to successfully navigate their dynamic social environments (Nelson et al., 2005). One intriguing possibility suggested by our findings is that adolescents' tendency to experience a drop in self-views yet maintain impressions of peers, even in the face of rejection, supports efforts aimed at maximizing prosocial behaviors and group affiliation. According to the sociometer theory (Leary, Tambor, Terdal, & Downs, 1995), shifts in self-views serve to reflect inclusionary status, with a drop in self-views signaling risk of exclusion. Given the critical importance of peer relationships during adolescence, it may be adaptive for teens to be especially attuned to any risk of rejection and use the internalized cues to learn from peer feedback and adjust behavior in response to new social demands, thereby ensuring future acceptance.

Adolescents' tendency to maintain impressions of peers after experiencing rejection is broadly consistent with their goal of social belongingness. While adults may be more firmly rooted in their social network and can afford to behave in antagonistic ways following the receipt of negative feedback in service of self-protection (Rudman et al., 2007; Vohs & Heatherton, 2004), this tactic may not be optimal for adolescents who place higher value on social belonging and are still experimenting and affiliating with various social groups. Thus, it may be more beneficial for adolescents to refrain from so readily derogating others following negative feedback.

Limitations and future directions.

The present study was designed to investigate how social evaluation was incorporated into self- and other-views at different developmental stages. Our findings demonstrated clear convergence in rejection-related biases in early adolescence and self-protective biases in early adulthood, while individuals between adolescence and adulthood showed "partial profiles" of reactivity to rejection and self-protective biases. Pre-adolescents showed little change in self- and other-views, despite understanding the task and showing robust memory for social feedback, constituting a potentially meaningful null result that warrants further investigation. Having established these age-dependent changes, a key next step will be to test for causal links between these factors, and to explicitly test the proposed developmental mechanisms detailed above. In addition, future work incorporating real social feedback from known peers, such as classmates, would allow for more ecologically valid inferences. Such a design would also be more amenable to longitudinal approaches, which were not possible in the present study due to the use of deception.

Conclusions.

The current study reveals a developmental framework of socioevaluative processing, which delineates age-specific changes in co-developing processes that shape the integration of peer feedback across age. The resulting adolescent-specific internalization of social feedback may reflect a key challenge of this phase of development: growth in social competence and group affiliation along with progressive tuning of cognitive strategies that help individuals thrive in complex social worlds as adults.

Paper 2: Neural feedback signals differentially guide impression updating of self and others across development

Alexandra M. Rodman, Katherine E. Powers, Erik K. Kastman, and Leah H. Somerville

Abstract

During a time when peer approval is especially important, adolescents have been found to internalize peer rejection in ways that produce decreased self-esteem. By contrast, adults have been found to externalize peer rejection by engaging self-protective processes that preserve positive self-esteem and denigrate rejecting peers. Currently, it is not understood how neural responses to acceptance and rejection contribute to these age-related differences in processing peer feedback. Neuroimaging techniques can assist in the parsing of distinct internalizing and externalizing processes that contribute to these age-related differences in the integration of peer feedback into representations of the self and others. In the present study, 84 participants (aged 10-23) completed a reciprocal social evaluation task during fMRI to assess how peer acceptance and rejection modulate underlying neurocognitive processes that support the integration of peer feedback. Findings revealed that functional recruitment of the ventral medial prefrontal cortex, a region involved in valuation and self-referential processing, was greater for rejection feedback than acceptance feedback during adolescence, whereas adults showed the reverse pattern. Meanwhile, feedback-specific striatal activation was stronger in response to rejection than acceptance as age increased, and this increased activity tracked the tendency to denigrate rejecting peers. In sum, functional recruitment of corticostriatal regions differentially guide impression updating of self and others across development.

Introduction

The transition to adolescence is accompanied by a marked change in the complexity of the social environment (Nelson et al., 2005). Adolescents experience newfound independence accompanied by new social roles and expectations (Larson, 2001), have more dynamic fluctuations in social relationships (Cairns et al., 1995), and encounter more frequent evaluation indicating social status (Wang et al., 2009). A key challenge of adolescence is to readily incorporate social feedback and flexibly adjust behavior, reflecting updated representations of social expectations (Nelson et al., 2005). Adjustment driven by feedback-based learning can be understood as the process of updating social representations and expectations to inform future behavior. According to computational theories of reinforcement learning (Sutton & Barto, 1981), one robust type of updating signal results unexpected outcomes, otherwise known as prediction errors.

Neuroscientific research has established that feedback-based learning is subserved by neural function of the corticostriatal circuit, a distributed network of brain regions (e.g., striatum, medial prefrontal cortex). Coordination within this circuit is critical for updating reward representations by integrating new information across prior experiences (Haber & Knutson, 2010; Schultz et al., 1997; Shohamy et al., 2004). Previous neuroimaging studies have found that the striatum in particular is a key region that tracks the magnitude of prediction errors: Positive prediction errors arise from outcomes that are better than expected and produce increased activity in the striatum, whereas negative prediction errors, which represent outcomes that are worse than expected, result in decreased striatal signaling (O'Doherty et al., 2003; Pagnoni et al., 2002). Prior work has shown that these same principles can be applied to the social domain of acceptance and rejection. Studies have found that participants' ability to learn rates of acceptance and rejection from peers was also supported by regions within the corticostriatal circuit, including the striatum (Jones et al., 2011). Therefore, the striatum is a target region to investigate how we process and learn from social evaluation. Here, we aim to test whether the striatum plays a key function in learning from peer acceptance and rejection to inform and update representations of the self or others.

In order to effectively navigate social interactions, people must also be able integrate social evaluation and reflect on their social standing in adaptive ways. Prior research has shown that the medial prefrontal cortex (mPFC), a hub of integration for socioaffective processing, plays a critical role in social feedback processing. The mPFC comprises a set of interconnected subregions and orchestrates the integration of a broad set of information, including social (Amodio & Frith, 2006) and emotional cues (Etkin et al., 2011), reward and value (Rangel & Hare, 2010), and representations of the self (Northoff & Bermpohl, 2004). While this region is involved in many complex cognitive processes, it is critical for the prioritization of a broad set of inputs to inform goals, expectations, and future behavior. The mPFC can be subdivided in to several subregions that are interconnected with subcortical regions in a distributed set of interlocking functional networks that serve different classes of cognitive functions (Haber & Knutson, 2010). The rostral and ventral mPFC (vmPFC), in particular, have been associated with functional connections to subcortical regions within the corticostriatal circuit (e.g., striatum), and are broadly involved in feedback-based learning (Haber & Knutson, 2010). Signals in these subregions of the mPFC have also been shown to represent perceived social status (Powers, Wagner, Norris, & Heatherton, 2013), self-referential processing (Mitchell et al., 2006; Wagner et al., 2012) and self-concept (Beer & Hughes, 2010; Chavez & Heatherton, 2015; Korn et al., 2012; Somerville et al., 2010). As such, the vmPFC, involved in many overlapping processes, is understood as a region that computes affective meaning, involved in both value-based signal updating and self-relevant information processing (Roy et al., 2012). Thus, we identify the vmPFC as a second target region we expect will be integral in shaping how evaluative feedback is integrated into views of the self. Together, the striatum and mPFC are highlighted as regions of interest that may subserve developmental trajectories of learning from peer feedback and the subsequent integration into self-views and views of others.

By applying these principles to questions about social learning and formation of self-views, we can utilize the framework of feedback-based learning to understand how neural response to social feedback informs updating of self-views and views of others as a learning process. Importantly, the very neural systems that support feedback-based learning undergo key developmental changes during adolescence (Spear, 2000). Though studies examining adolescent responses to positive and negative outcomes have shown exaggerated responses to both positive and negative cues in the ventral striatum (Braams, Duijvenvoorde, Peper, & Crone, 2015; Ernst et al., 2005; Galvan et al., 2006; Somerville et al., 2011), studies specifically designed to measure prediction error across development have yielded inconsistent results (Cohen et al., 2010; Duijvenvoorde et al., 2008; Hauser et al., 2015; Javadi et al., 2014; van den Bos et al., 2012). Of the few studies that have examined social prediction error across development, Jones and colleagues (2014) found that adolescents showed increased positive prediction error signaling in the insula compared to children and adults (Jones et al., 2014).

Clarifying age-related differences in feedback processing from a neurodevelopmental perspective may help explain adolescent sensitivity to social evaluation (Sebastian, Viding, et al., 2010; Silk et al., 2012; Somerville et al., 2013; Stroud et al., 2009). Thus, it is important to consider how neurodevelopmental differences within the corticostriatal circuit contribute to adolescent-specific internalization of rejection, which may render adolescents particularly vulnerable to the negative impact of peer rejection.

Our aims are to identify age-related differences in neural activity following social evaluation and to examine whether age-related differences in activity within the striatum and vmPFC are related to task-related behaviors (e.g., shifts in views of self and others). This study was designed to induce the experience of receiving believable peer acceptance and rejection from unknown, age-matched peers, using the same reciprocal social evaluation task used in Paper 1 (Rodman, Powers, & Somerville, 2017). Participants were told they were taking part in a multi-site study investigating how individuals formulate first impressions of peers. This cover story set up a reciprocal social evaluation task in which participants predicted whether each peer would like them. Participants subsequently received acceptance or rejection feedback, all while undergoing an fMRI scan (Figure 7). Before and after the task, participants evaluated the likability of each peer and completed a self-esteem questionnaire (Harter, 1983, 1988; Neemann & Harter, 1986). This set of outcomes enabled analyses targeting neurodevelopmental shifts that account for age-related differences in the impact of social evaluation on self-views and views of others.

Methods

Participants.

Ninety-four healthy individuals were recruited from the local Boston and Cambridge communities and a final sample of 86 were included in the current study. Participants were aged 9.98-23.29 (M=16.45 years, SD=3.87) and 47.7% female, with sex distributed equivalently across age (Logistic regression: $B=-.027$, $p=.636$). Participants' racial diversity was representative of the local community (66.3% Caucasian, 15.2% African-American, 14.0% Asian, and 4.7% Other). To ensure similarities in the demographic and socioeconomic characteristics across age, no more than 30% of adult participants were former or current students at Harvard University. Participants were recruited through online forums such as Craigslist, local newspaper advertisements, and flyers. All participants provided written informed consent and all minor participants received written permission for their participation from a parent or legal guardian. The Committee for the Use of Human Subjects at Harvard University approved all research procedures.

Exclusion criteria included history of a neurological disorder, current psychiatric disorder, current use of psychotropic medication, and any contraindications for MRI scanning (e.g., safety risks such as metal implants). A diagnostic clinical interview (Sheehan et al., 1998) was conducted during the study visit to confirm that participants did not meet criteria for current depression or anxiety disorder. Eight participants were excluded from final analyses: two due to their reported suspicion of the cover story; two due to insufficient variability in behavioral responses; two due to noncompliance resulting in incomplete data; one because experimenter-administered diagnostic interview indicated they met criteria for current neuropsychiatric disorder; and one for being under the influence of a mind-altering substance on the day of the study visit. The remaining 86 participants were included in final analyses. Sample size was determined prior to data collection based on sample sizes from an fMRI study using a similar task in a developmental population (Gunther Moor et al., 2010).

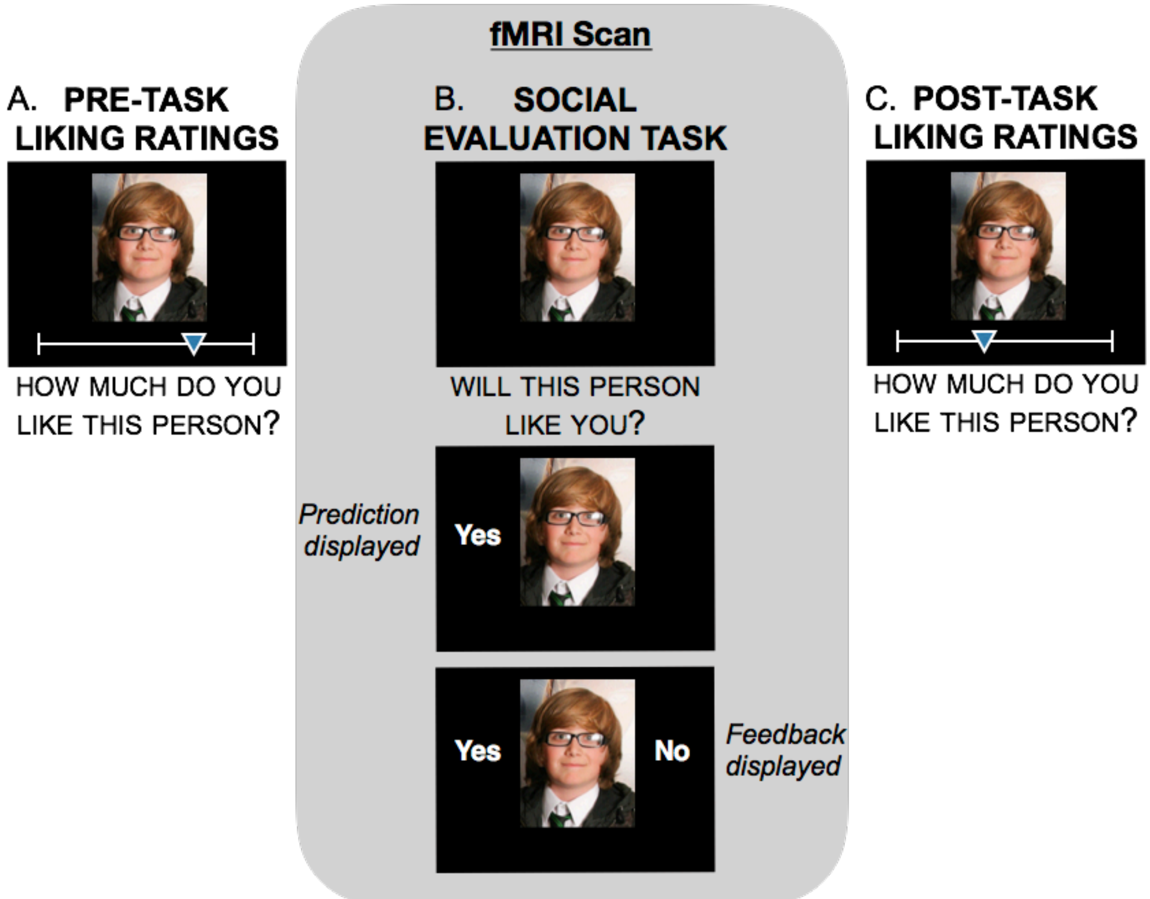

Figure 7. Schematic representation of experimental task. Prior to the study visit, participants submitted a photograph that was ostensibly sent out to unknown, age-matched peers to be rated on likability. A) Participants rated the likability of the peers before the task. B) While undergoing fMRI, participants predicted whether they thought the peer liked them or not, and then were shown the (supposed) peer rating. C) Following the scan, participants re-rated the likability of each peer.

Pre-visit procedure.

Approximately one week prior to the study appointment, participants submitted a digital headshot photograph. Participants believed that their photographs would be traded with other study locations and rated by the unknown peer-aged participants in other cities based on how likable they looked. Participants also made pre-task likability ratings of the same peers online (www.Qualtrics.com) before their study visit. For these pre-task ratings, participants viewed each peer along with the question *"How much do you think you would like this person?"*.

Participants responded by using their mouse to click along a continuous scale from “not at all” to “very much” (Figure 7A). The output of this scale ranged from 1-100 and this numerical value was used in subsequent analyses. Participants were told that the other participants had used the same survey to rate their photograph.

Study visit.

Pre-task assessments.

Participants completed the Self-Perception Profile (SPP; Harter, 1983, 1988; Neemann & Harter, 1986) before the task to quantify baseline self-views. We administered the Child (ages 9-14; Harter, 1983), Adolescent (ages 15-17; Harter, 1988), and College-Aged (ages 18-23; Neemann & Harter, 1986) versions of the questionnaire.

Task design.

Prior to scanning, participants completed 15 practice trials. Participants were given the option to become acclimated to the scanner environment by using a mock scanner. During the social evaluation fMRI task, participants viewed the photographs of the peers, predicted whether that peer liked or disliked them, and received feedback indicating whether the peer liked or disliked them (Figure 7B; Gunther Moor et al., 2010; Powers, Somerville, et al., 2013; Somerville et al., 2006; Somerville, Kelley, et al., 2010).

Each trial contained a cue, inter-stimulus interval (ISI), and feedback phase that lasted a total of 6 seconds. The cue phase (0-3000ms) presented a photograph of a peer, which remained visible for the duration of the trial (Figure 7B, top). Upon seeing the peer, participants predicted whether the peer had liked them with a button press of “Yes” or “No”. Participants were instructed to select “Yes” if they believed they were rated using the top half of the scale (higher liking score) or “No” if they believed they were rated using the bottom half of the scale (lower liking score). If participants did not make a response in the allotted time during the cue phase, responses were coded as a “miss” and participants were not shown the peer feedback for that trial (1.7% of all trials). Following the participant’s response, there was a brief delay (Figure 7B, middle; 1000-4000ms) while the participant’s prediction displayed on the left side of the screen, followed by delivery of feedback displayed on the right of the screen (Figure 7B, bottom; 2000ms) indicating whether the peer supposedly liked or disliked the participant (set at 50% acceptance, 50% rejection in pseudorandom order). Feedback was displayed in binary form as “Yes” or “No”, which participants were instructed mapped on to ratings in the top and bottom halves of the rating scale, respectively. All trials were followed by a jittered fixation cross (1500-9000ms), which was optimized in duration and sequence using the program *optseq* (Dale, Greve, & Burock, 1999) to ensures orthogonally of trial phase and conditions of interest. The task was divided into four runs of 40 trials each (approximately 28 minutes total). For information on stimuli development, see *Paper 1 Supplemental Materials*.

Post-task assessment.

Post-scanning, participants completed the SPP again, which allowed us to quantify task-induced shifts in self-views. Participants also re-rated the likability of each peer using the same scale used for the pre-task likability ratings (Figure 7C).

Debrief.

To ensure believability in the cover story, participants were questioned using a funnel debriefing procedure. All participants and parents were debriefed of the cover story and informed of the purpose of the study.

fMRI data acquisition and preprocessing.

Participants were scanned using a 3.0 Tesla Siemens Prisma MRI scanner equipped with a 32-channel head coil (Siemens Medical Systems, Erlangen, Germany) at the Harvard University Center for Brain Science. Participants first completed an anatomical scan. A T1-weighted high-resolution anatomical scan was acquired using a multiecho multiplanar rapidly acquired gradient-echo sequence with the following parameters: 176 sagittal slices, TR 2200ms, TE 1.67ms, flip angle 7°, slice thickness 1mm, voxel dimensions=1x1x1mm. During the experimental task, participants viewed the task (programmed in PsychoPy v. 1.84; Peirce, 2007) via a back-projection system and made responses on an MRI compatible button box. The presentation of the stimulus and performance during the experimental task was synchronized to fMRI volume acquisition. Functional (T2* weighted) images were collected using an interleaved echo planar sequence using the following parameters per whole-brain volume: TR 2000ms, TE 35ms, flip angle 80º, 69 axial slices, voxel resolution 2.2x2.2x2.2mm, with a multi-band acceleration factor of 3. Functional slices were oriented to a slightly greater tilt than the anterior-posterior commissure plane to minimize signal dropout due to sinus cavities.

Preprocessing of functional imaging data was carried out using the Functional MRI of the Brain Software Library (FSL v. 5.0.4; Smith et al., 2004) tools implemented in Nipype (v.0.11.0;

Gorgolewski et al., 2011) using the Lyman interface (v. 0.0.7). Each functional scan was first realigned to its middle volume, spatially smoothed with a 6mm full-width at half maximum Gaussian kernel, and high-pass filtered at 128 seconds. Functional scans were co-registered to participants' anatomical images using bbregister (v. 5.3.1; Greve & Fischl, 2009). Second-level (merging across runs) and group-level statistical maps (comparing across participants) were normalized to a Montreal Neurological Institute brain template using linear and nonlinear warping methods through the Advanced Normalization Tools software (v. 1.9.x; Avants, Tustison, & Song, 2009).

fMRI GLM.

Preprocessed images were entered into a standard general linear model (GLM) in FSL, which estimated neural responses to the cue phase and feedback phase. The following regressors were included to estimate task effects: Cue phase activity on trials where the participant predicted acceptance, Cue phase activity on trials where the participant predicted rejection, Feedback phase activity when receiving expected acceptance, Feedback phase activity when receiving unexpected acceptance, Feedback phase activity when receiving expected rejection, and Feedback phase activity when receiving unexpected rejection. The trial onsets of the cue phase and feedback phase for each condition were modeled as zero-duration events convolved with the canonical double-gamma hemodynamic response function. The model also included nuisance regressors for motion parameters, temporal derivatives for each regressor of interest, and missed trials.

Functional MRI data were evaluated for motion and signal outliers to mitigate the negative impact on signal to noise ratio and accuracy of GLM estimation. Functional volumes with motion greater than 1mm or whole-brain intensity values greater than 4.5 standard deviations away from the mean were censored from the model. Runs with more than 10% of TRs censored for motion (relative motion > 1mm) or a single-relative movement exceeding 5mm were also to be excluded. Participants with more than two unusable runs were excluded.

While trial counts of condition are in part determined by participant performance, participants with less than 8 trials per condition were excluded to ensure adequate representation of each condition. Within our sample, six participants had at least one run excluded (one with two excluded runs due to motion, three with one excluded run due to motion, and two with one excluded run due to technical malfunction). No scans had greater than 10% censored volumes and all participants had at least 2 out of 4 scans of usable data. Two participants were excluded due to insufficient variability of responses (less than 8 trials in a given condition).

Age effects.

The goal of the present study was to determine whether developmental differences exist in functional recruitment of key corticostriatal circuitry (e.g., vmPFC and striatum) during social evaluation. We have previously reported that the social evaluation task evokes differential behavioral responses to peer acceptance and rejection across age. These developmental patterns were utilized as a guide for the current study. Age was previously found to be associated with task-induced changes in views of self (nonlinear) and changes in views of others (linear). Therefore, the current study examined age effects using age as a continuous predictor (as recommended by Hartley & Somerville, 2015) with linear and nonlinear trajectories. The linear function is defined as progressively increasing or decreasing with age. The nonlinear age function was derived from a thin-plate smoothing spline regression regressing task-induced changes in self-esteem on age. This identified a non-traditional shape to the age function that dips during early adolescence and rises through late adolescence stabilizing into adulthood (see Paper 1, Figure 4). Thus, more conventional nonlinear functions (e.g., quadratic or cubic) were not appropriate. Instead, the fitted values of this spline-fit model were utilized as the nonlinear age function (Figure S7). These linear and nonlinear age functions were carried forward for analyses of age effects in the current study. No binning of age was completed during analysis and the use of labels such as adolescents and adults are utilized for descriptive purposes only.

Behavioral indices.

To determine whether age-related differences in brain function were associated with updating representations of the self and others, analyses included task-related indices of changes in self-esteem and peer ratings, which have been previously reported (Rodman et al., 2017). Beta values from whole brain analyses with nonlinear and linear age covariates were extracted from significant clusters in target regions and regressed on the associated task-related behavior, guided by our previous findings. Given that the nonlinear age function is derived from the fitted values of the spline regression, it incorporates both age and behavioral changes in self-esteem. Therefore, results from the whole-brain analysis of nonlinear age would inherently identify a region of the brain that also changes with self-esteem, wherein additional testing of brain-behavior relationship with change in self-esteem would be circular (Vul, Harris, Winkielman, & Pashler, 2009). As such, we interpret nonlinear age-related findings as simultaneously reflective of age-related differences in updating self-views. A descriptive plot of this relationship has been included for illustrative purposes (Figure 10).

As a follow up analysis, we also examined the relationship between the nonlinear age-related beta values described above and an independent measure of implicit self-view. Participants' implicit self-view was computed as the difference in reaction time when predicting acceptance vs. rejection, representative of an implicit index of cognitive interference (Greenwald et al., 1998; Stroop, 1935). Slowing to acceptance compared to rejection would indicate an implicit self-view more congruent with rejection, while slowing to rejection compared to acceptance suggest an implicit self-view more congruent with acceptance (see Paper 1, Figure 3 for more detailed description; Rodman et al., 2017). Importantly, this measure was not correlated with task-induced change in self-esteem ($r=.012$, $p=.916$), which allows us to anchor brain activation to behavior in a way that is not circular. Results from this analysis would indicate that functional recruitment of this brain region is not only involved in updating self-views, but it is also associated with implicit self-views measured during the task.

Next, we examined whether linear age-related brain function was associated with the tendency to update views of others, scaling peer ratings upwards or downwards in accordance with acceptance or rejection. This measure was computed by subtracting the pre-task from post-task likability rating of each accepting and rejection peer, then calculating the average feedback-specific difference score. A greater spread between upgrading accepting peers and downgrading rejecting peers reflects a greater tendency to utilize peer feedback to update ratings of peers. This feedback-specific rating change was used as a behavioral covariate of interest for each participant.

For all task-related covariates of interest, data were inspected for normality and outliers. Outliers were identified using the Outlier Labeling Method (Hoaglin, Iglewicz, & Tukey, 1986) with a *g* multiplier of 2.2 (Hoaglin & Iglewicz, 1987) and were then Winsorized (Dixon, 1960).

The Winsor approach involves replacing outliers with the maximum (or minimum) value within the bounds of the outlier threshold. Inspection of implicit self-views revealed no outliers. When examining the task-induced change in self-esteem, one participants did not complete the post-task SPP, resulting in 85 participants included in this analysis. Self-esteem change score from one participant was identified as an outlier and Winsorized. When examining the task-induced change in likability ratings of peers, two did not complete the post-task ratings of peers, resulting in 84 participants included in this analysis. Peer rating change score from one participant was identified as an outlier and Winsorized.

fMRI group analysis.

In order to identify age-related differences in neural functioning following social evaluation, random effects group analyses addressed the following: a) identify differences in brain function when receiving acceptance vs. rejection feedback, b) determine age-related differences in brain function when receiving acceptance vs. rejection feedback c) examine whether age-related brain function is related to task-related behaviors (e.g., views of self and views of others).

The main effect of rejection vs. acceptance feedback was examined by conducting whole brain, voxelwise t-tests for the contrasts Rejection Feedback > Acceptance Feedback, for general effects and Unexpected Rejection Feedback > Unexpected Acceptance Feedback, for effects associated with updating. Next, these contrasts were modelled with an age covariate (linear and nonlinear) to identify age-related differences in neural processing of social feedback. Whole brain maps were thresholded using whole-brain correction of $z>2.3$ using FLAME 1+2, as implemented in FSL, resulting in whole-brain threshold of $p<0.05$ family-wise error (FWE) corrected. Significant age effects identified in the activation maps were supplemented with descriptive plotting of neural response by age to visualize the directionality of effects. All clusters above this threshold and associated region labels (Harvard-Oxford Cortical and Subcortical Atlas) are reported in *Paper 2 Supplemental Materials* Table S2.

To determine whether age-related brain function was associated with task-related behavior, we examined the relationship between brain function and views of self and others as described above. To do this, betas of neural functioning during unexpected acceptance > unexpected rejection were extracted using a 6mm sphere around the local maxima of the primary clusters of interest, the striatum and vmPFC. Parameter estimates were submitted to a linear regression using the *nlme* package in R (Pinheiro et al., 2014) and each outcome of interest, implicit self-views and changes in views of others, was included in the regression as a covariate.

Results

Effect of peer feedback on neural activation.

Findings showed that receipt of acceptance and rejection feedback resulted in differential recruitment of brain function. Rejection compared to acceptance feedback was associated with significantly greater recruitment of the inferior frontal gyrus, thalamus, dorsal medial prefrontal cortex, the superior temporal sulcus and inferior parietal lobule, caudate, putamen, and thalamus. Acceptance feedback compared to rejection feedback was associated with greater functional recruitment in several regions, including the superior frontal gyrus, sensorimotor cortices, inferior parietal lobule, precuneus, midcingulate, and bilateral putamen (FWE $p<.05$, Table S2, Figure 8A).

We also sought to examine differences between acceptance and rejection when feedback was unexpected in order to investigate brain function associated with the need to update a previously held social expectation with new information. When constraining analyses to unexpected trials, examining acceptance vs. rejection also revealed a widely distributed network of brain regions. During unexpected rejection vs. unexpected acceptance, functional activation was greater in the caudate, paracentral cortex, posterior cingulate cortex, precuneus, and thalamus. During unexpected acceptance vs. unexpected rejection, there was increased functional activation in the bilateral inferior parietal lobule, mPFC, ventral lateral prefrontal cortex and frontal pole (FWE p<.05; Table 1; Figure 8B).

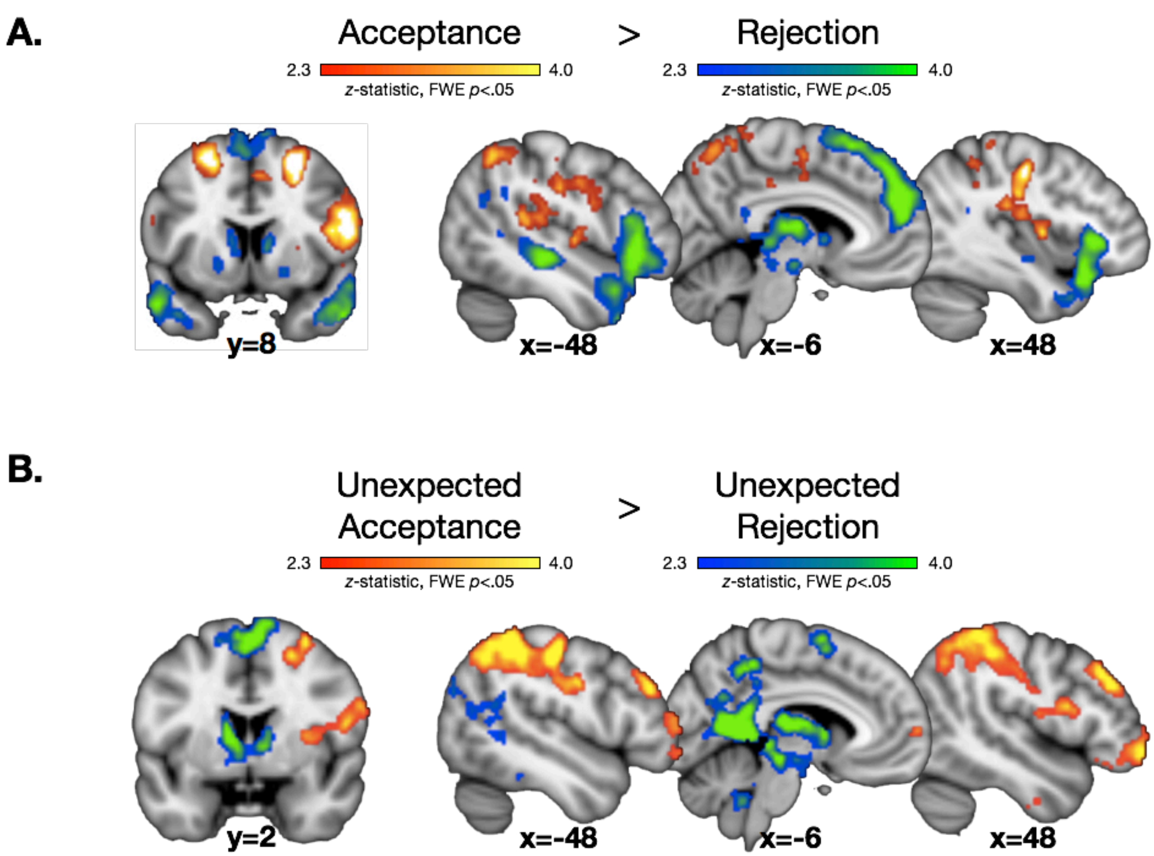

Figure 8. Brain function when receiving acceptance and rejection feedback. A. Regions that show increased functional recruitment for acceptance compared to rejection. B. Regions showing

increased functional recruitment for unexpected acceptance compared to unexpected rejection. Contrast represents whole-brain corrected t-test (FWE $p < 0.05$).

Age-related differences in social feedback processing.

A primary aim of this study was to assess the neural correlates of age-related differences in updating views of the self and others in response to social evaluation. As such, we restricted age analyses to unexpected trials.

Views of the self and nonlinear age effects.

Age-related effects were first examined for the nonlinear age function (derived from the spline fit of age and change in self-esteem), which was included as a covariate in a whole brain voxel-wise analysis for the contrast unexpected acceptance > unexpected rejection. Findings revealed that nonlinear age was associated with activation in the vmPFC, a primary target of analyses (Figure 9A; see Table S2).

In order to determine whether the nonlinear age-related effects in vmPFC functional activity were most driven by unexpected acceptance or unexpected rejection, parameter estimates during unexpected acceptance > unexpected rejection, unexpected acceptance > baseline, and unexpected rejection > baseline were extracted from a 6mm sphere around the local maxima of the vmPFC cluster (MNI coordinates: x=14, y=56, z=-12). Descriptive plots demonstrated that these age-related findings were primarily driven by differences in activation in response to unexpected acceptance, wherein response to acceptance is lowest during early adolescence and rises throughout late adolescence stabilizing in young adulthood (Figure 9B). This pattern revealed meaningful age-related differences in the relative weighting of acceptance and rejection, indicating that younger adolescents and older adolescents exhibited asymmetric feedback-related recruitment of vmPFC. During adolescence, participants showed more vmPFC-related activation to rejection relative to acceptance. This effect becomes inverted during late adolescence into adulthood, wherein vmPFC-related activation is greater for acceptance relative to rejection.

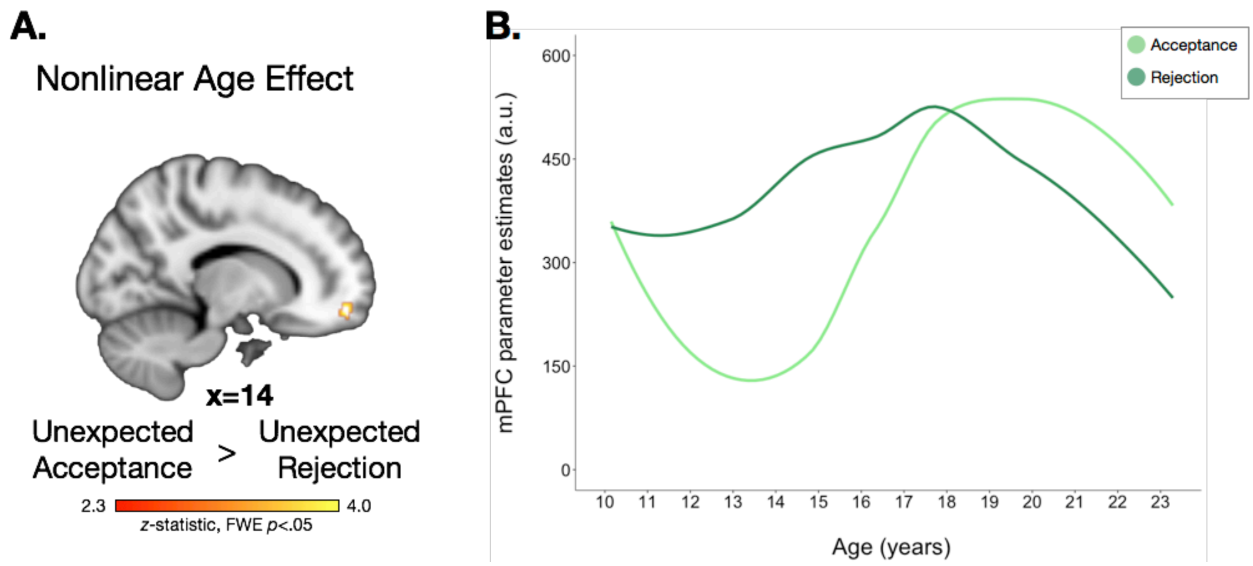

Figure 9. vmPFC (BA 11) function recapitulates the nonlinear age function, dipping in early adolescents and rising in late adolescents through adulthood, resulting in meaningful age-related differences in the relative weighting of acceptance and rejection. **A.** Whole-brain corrected (FWE $p<0.05$) statistical map illustrating functional recruitment of vmPFC during unexpected acceptance relative to unexpected rejection by nonlinear age. **B.** Parameter estimates during unexpected acceptance vs. baseline (light green) and unexpected rejection vs. baseline (dark green) were extracted from a 6mm spherical ROI created around local maxima plotted for descriptive purposes. A loess curve plotted vmPFC function against age and shows early adolescents' vmPFC response is relatively greater for rejection compared to acceptance, which reverses during late adolescence into young adulthood.

As described above, nonlinear age-effects of vmPFC activation were by definition linked with changes in self-esteem. Descriptive plots show that functional recruitment of mPFC tracks with task-induced changes in self-esteem, wherein greater vmPFC activation for acceptance relative to rejection is associated with a boost in self-esteem. In contrast, greater vmPFC activation for rejection relative to acceptance is associated with a decrease in self-esteem (Figure 10B). Statistical regression was not computed for this relationship due to the possible circularity of these analyses, given that this region was identified by using the nonlinear age covariate, derived from the fit with the behavioral data (Vul et al., 2009).

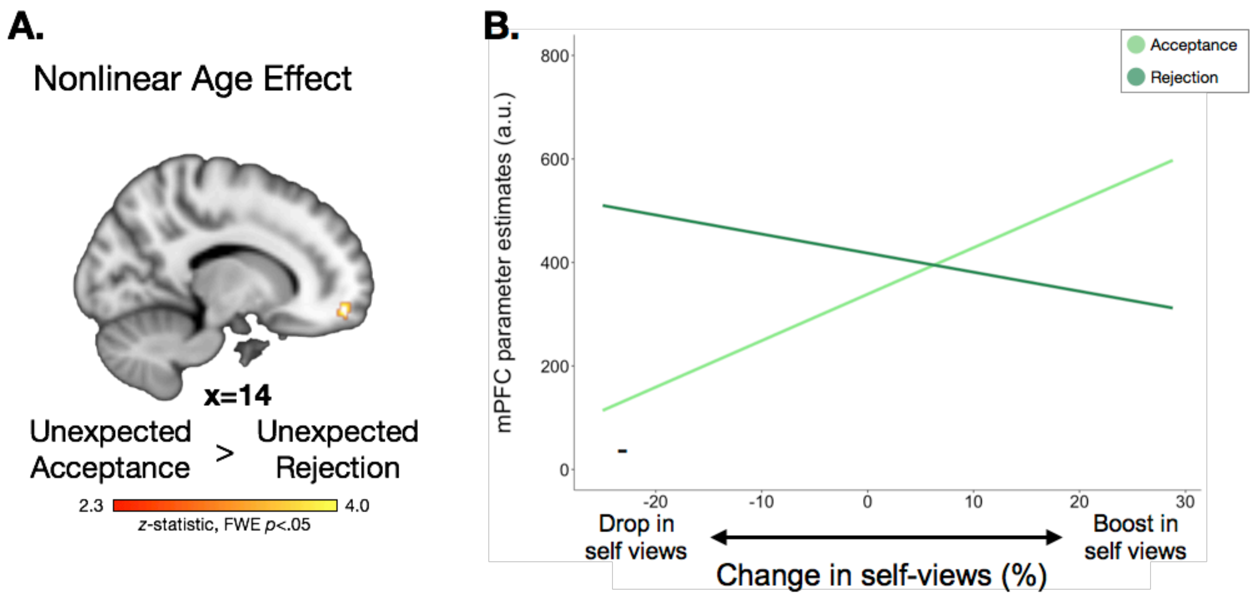

Figure 10. vmPFC function is plotted against change in self-views for descriptive purposes **A.** Whole-brain corrected statistical map illustrating functional recruitment of the vmPFC during unexpected acceptance relative to unexpected rejection by nonlinear age. **B.** Parameter estimates during acceptance vs. baseline (light green) and rejection vs. baseline (dark green) were extracted from a 6mm spherical ROI created around local maxima plotted for descriptive purposes. Fitted values for linear relationship between vmPFC function and change in self-esteem shows increased activation tracks linearly with a boost in self-views.

As a follow up analysis to test for the relationship between this vmPFC neural response and independent task-behavior, a regression examined the effect of vmPFC activation on implicit self-views. Again, implicit self-views were defined as the difference in reaction time when predicting rejection versus predicting acceptance. Slowing to rejection (a positive score) indicates an implicit self-view more congruent with acceptance, whereas slowing to acceptance (a negative score) indicates an implicit self-view more congruent with rejection. Findings revealed that brain activation during unexpected acceptance > unexpected rejection in the vmPFC increased linearly with participants' tendency to demonstrate an implicit self-view more congruent with acceptance (B=0.245, p=.023). Descriptive plots of the individual effects of acceptance and rejection suggested that this effect was driven by the vmPFC response to rejection, wherein greater vmPFC response to rejection is associated with a tendency to have an implicit self-view more congruent with rejection (Figure 11B). Importantly, vmPFC activation was not related to change in views of others (B=-0.016, p=.887), suggesting specificity to self-views.

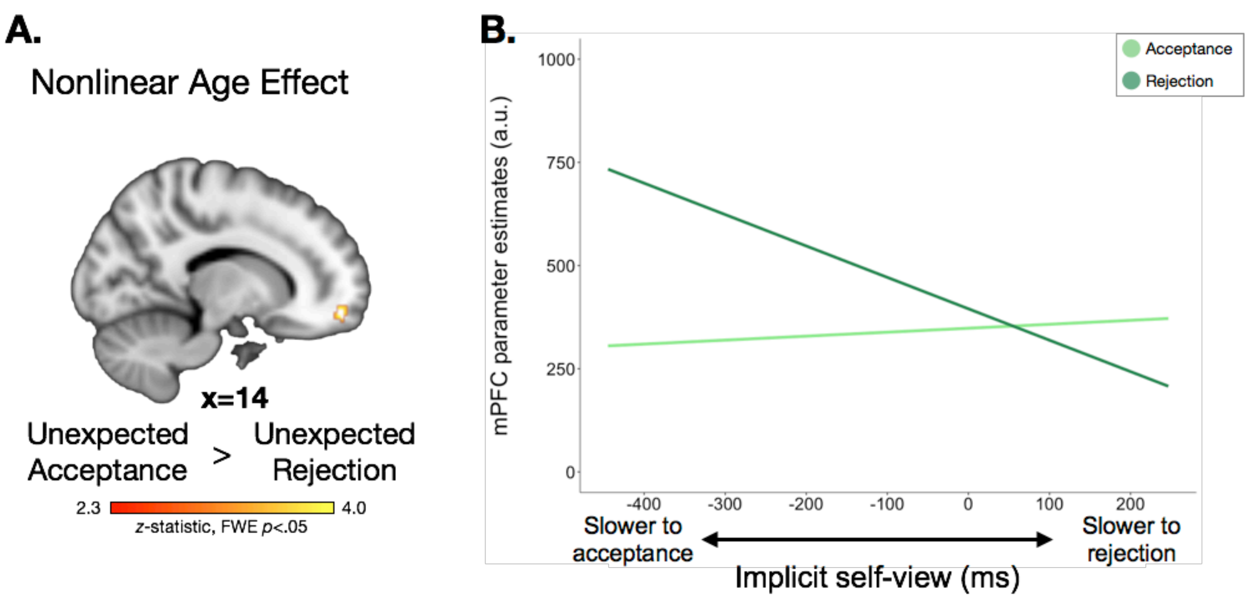

Figure 11. vmPFC function is associated with implicit self-views **A.** Whole-brain corrected statistical map illustrating functional recruitment of the vmPFC during unexpected acceptance relative to unexpected rejection by nonlinear age. **B.** Parameter estimates during, acceptance vs. baseline (light green), and rejection vs. baseline (dark green) were extracted from a 6mm spherical ROI created around local maxima plotted for descriptive purposes. A linear fitline was plotted for vmPFC function against implicit self-views (predicted rejection RT – predicted acceptance RT). A positive score indicates an acceptance-congruent implicit self-view, whereas a negative score indicates a rejection-congruent implicit self-view. Fitted values for linear relationship shows greater vmPFC response to rejection is associated more rejection-congruent implicit self-views.

Views of others and linear age effects.

Another aim of this study was to assess for the relationship between age-related differences in brain activation to social evaluation and the associated changes in views of peers. Age-related effects were examined with a linear age function, which was included as a covariate in a whole brain voxelwise analysis for the contrast unexpected rejection > unexpected acceptance. Findings revealed that linear age was positively associated with activation in the left caudate, a second target region (FWE p<.05; Figure 12A). No other significant clusters were identified in this contrast or in the reverse contrast. Descriptive plots demonstrate that caudate response to feedback does not discriminate between acceptance or rejection until mid-adolescence through adulthood, when participants demonstrate increasingly greater response to rejection relative to acceptance (Figure 12B).

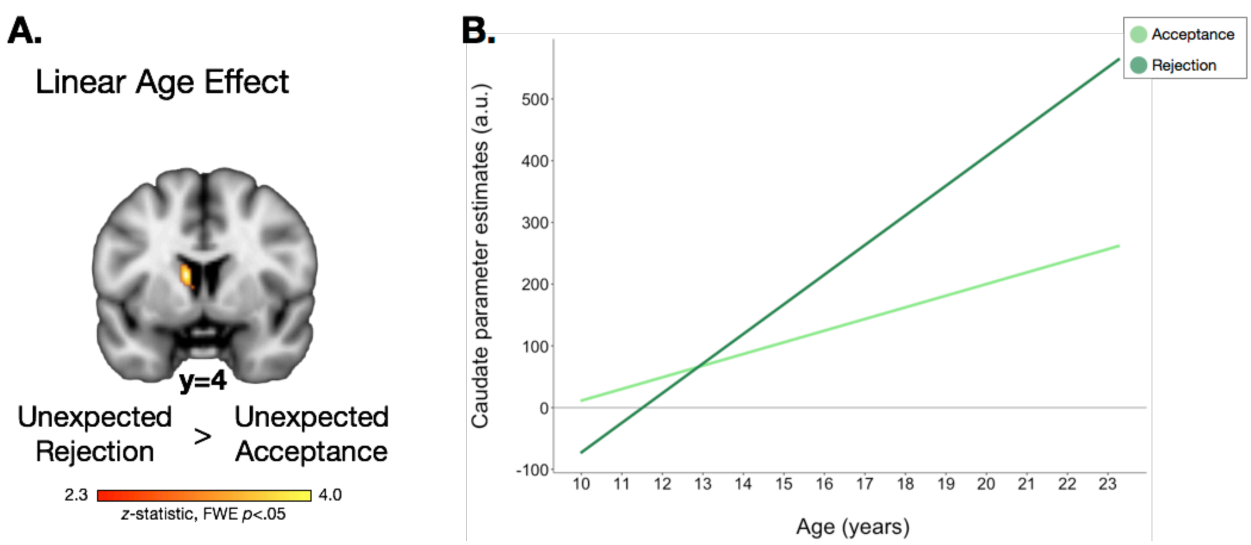

Figure 12. The differential in caudate response to rejection over acceptance increases with age. **A.** Whole-brain corrected statistical map illustrating functional recruitment of the caudate during unexpected rejection relative to unexpected acceptance by linear age. **B.** Parameter estimates during acceptance vs. baseline (light green), and rejection vs. baseline (dark green) were extracted from a 6mm spherical ROI created around local maxima plotted for descriptive

purposes. Fitted values for linear relationship was plotted for caudate activation against age which showed that the relative differential in caudate response to rejection over acceptance increases with age.

Previously, we identified a linear relationship between age and the tendency to update (e.g., upgrade or downgrade) likability ratings of peers in accordance with acceptance or rejection, respectively (Rodman et al., 2017). Therefore, we sought to examine whether brain activation in the caudate was associated with these changes in ratings of peers. Parameter estimates during unexpected rejection > unexpected acceptance were extracted from a 6mm sphere around the strongest local maxima of the caudate cluster (MNI coordinates: x=-10, y=2, z=12). A regression examined the effect of caudate function on participants' tendency to update ratings of peers in accordance with acceptance or rejection. Findings revealed that functional recruitment of the caudate was significantly associated with participants' tendency to upgrade accepting peers and downgrade rejecting peers ($B=0.248$, $p=.023$). In order to determine whether the age-related and task-related effects in caudate function were most driven by rejection or acceptance, parameter estimates during these basic conditions were also extracted and plotted to assist in the interpretation of these findings (Figure 13B). Descriptive plots revealed that as the divergence in caudate response to rejection over acceptance increases, so does the divergence in upgrading accepting peers and downgrading rejecting peers. In addition, the association between caudate response updating peer ratings was strongest following rejection feedback. Importantly, activation in the caudate was not associated with change in self views ($B=0.048$, $p=.660$) or implicit self-views ($B=0.117$, $p=.282$), demonstrating a specificity for updating impressions of others.

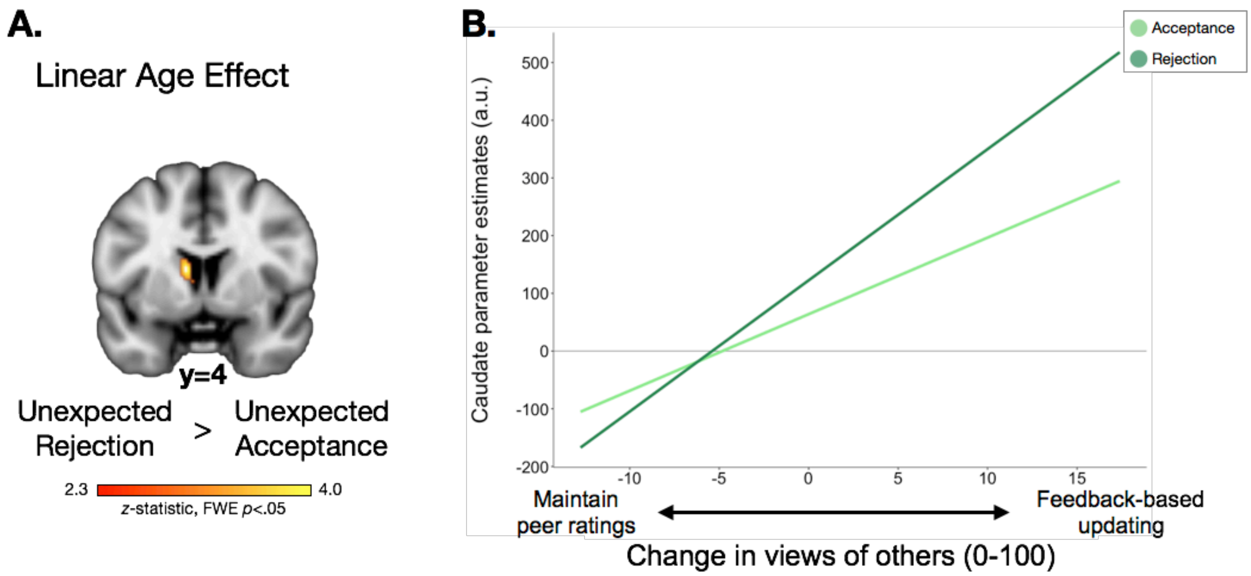

Figure 13. Caudate function tracks feedback-specific change in views of others **A.** Whole-brain corrected statistical map illustrating functional recruitment of the caudate during unexpected rejection relative to unexpected acceptance by linear age. **B.** Parameter estimates during acceptance vs. baseline (light green) and rejection vs. baseline (dark green) were extracted from a 6mm spherical ROI created around local maxima plotted for descriptive purposes. Fitted values for linear relationship between caudate function against feedback-specific changes in peer rating shows increase in caudate activation for rejection over acceptance tracks with tendency to downgrade rejecting peers.

Discussion

Examining how individuals process and learn from social evaluation from a neurodevelopmental perspective provides key insights into the mechanism underlying rejection sensitivity during adolescence and the self-protective process that buffers adults from rejection. Here, we used a well-validated social evaluation task during fMRI to probe how neural processing of peer feedback impacted participants' task-induced changes in self-views and views of others. When receiving social evaluation, findings revealed age-related differences in functional recruitment of the vmPFC, a region that integrates feedback signals and self-referential processing (Roy et al., 2012), and this activation was associated with task-induced changes in self views. Additionally, age-related differences in neural activation were also evident within the caudate, a region of the striatum associated with feedback-based learning (Jones et al., 2011), which was associated with feedback-dependent changes in views of others. Together, these findings suggest that feedback-based signaling within the corticostriatal circuit subserve impression updating for self and others following social evaluation. Importantly, signaling within these regions weigh acceptance and rejection asymmetrically across age, revealing meaningful relative differences in how acceptance and rejection inform views of self and others.

In general, fMRI findings indicated that neural recruitment differed when receiving rejection vs. acceptance feedback. Rejection was associated with activation in several regions generally involved in social cognition, salience detection, and reward learning, including the superior temporal sulcus, inferior frontal gyrus, dorsomedial prefrontal cortex, and striatum. Acceptance was found to be associated with regions generally involved in selective attention, including the inferior and superior parietal lobule, frontal eye fields, and mid cingulate cortex. These findings are broadly consistent with the extant literature, wherein previous research has identified similar regions, including the dorsomedial prefrontal cortex, inferior frontal gyrus/anterior insula, in response to negative feedback and regions including the posterior cingulate, parietal lobule in response to positive feedback (Achterberg et al., 2016; Davey, Allen, Harrison, Dwyer, & Yücel, 2010; Gunther Moor et al., 2012, 2010; Hughes & Beer, 2012b; Sebastian et al., 2011; Sebastian, Viding, et al., 2010; Somerville et al., 2010). This lends confidence that the social evaluation task in the current study elicited similar differential neural recruitment in response to acceptance and rejection.

Age-related differences in social feedback processing.

Views of the self and nonlinear age effects.

The current study showed evidence of age related differences in neural response to acceptance and rejection. Findings revealed that feedback-specific differences in vmPFC activation tracked with nonlinear age effects, dropping in early adolescence and rising through late adolescence into adulthood. Further examination of this effect demonstrated asymmetrical weighting of acceptance and rejection across age. Early adolescents showed greater activation in the vmPFC following rejection compared to acceptance, whereas late adolescents and adults demonstrated the reverse pattern. These age-related differences in neural response to feedback also tracked with implicit self-views and task-induced updating of self-views. The tendency for adults to show greater vmPFC response to acceptance and its association with more positive self-views (e.g., implicit self-view and task-induced boost in self-esteem) is consistent with prior work demonstrating that adults show greater vmPFC activation when expecting or receiving acceptance (Powers, Somerville, et al., 2013; Somerville et al., 2006), when making positive compared to negative self-attributes (Beer & Hughes, 2010; Korn et al., 2012), and even when associating positive traits with a close friend relative to a stranger (Hughes & Beer, 2012a). Previous research examining attention allocation via eye-tracking has also found that following exclusion, adults allocated less attention to negative social cues and selectively attended more to signs of social acceptance (DeWall, Maner, & Rouby, 2009), which supports the notion that adults' vmPFC signaling reflects a self-protective process that preserves positive self-views in the face of rejection.

Adolescents' tendency to show greater vmPFC response to rejection relative to acceptance, on the other hand, is also in line with previous work. Prior studies examining learning rates from positive and negative feedback have found age-related differences, wherein younger participants showed faster learning rates to negative feedback compared to positive feedback (Hauser et al., 2015; van den Bos et al., 2012), whereas older participants learned better than from positive feedback (van den Bos et al., 2012). This pattern has also been associated with corticostriatal function, wherein stronger mPFC-striatal coupling decreased with age and increased with negative learning rate (van den Bos et al., 2012). In the domain of social feedback learning, similar age-related differences were found, such that adolescents were less likely to update in response to positive feedback, which was reflected in reduced neural response to acceptance compared to rejection (Jarcho et al., 2015; Jones et al., 2014). Adolescents' sensitivity to rejection as reflected in the vmPFC extends previous work underscoring the strong negative affective reaction adolescents show in response to peer rejection (Sebastian, Viding, et al., 2010; Stroud et al., 2009), suggesting that adolescents may not exhibit the self-protective biases that buffer adults against negative self-views following rejection. Importantly, our findings indicated specificity in updating related to self-views as opposed to views of others, which is consistent with previous research indicating a ventral to dorsal gradient in cognition about self and other, respectively (Denny, Kober, Wager, & Ochsner, 2012).

Overall, we found that functional recruitment of vmPFC in response to social feedback codes for a learning signal that updates self-views, weighting acceptance and rejection differentially across age. Converging evidence across a large body of literature has suggested that ventral regions of the mPFC are more attuned to self-referential processing, and further that activity in the vmPFC tracks subjective value of cues and outcomes in the environment. A recent meta-analysis examining the varied overlapping functions of the vmPFC, which includes learning, value, and integration of self, surmised the role of the vmPFC as a generator of affective meaning (Roy et al., 2012). These findings in the vmPFC build upon our current understanding of social feedback processing and suggest that the rejection sensitivity displayed by adolescents and self-protective biases enacted by adults is, in part, supported by asymmetrical functional recruitment of the vmPFC.

Views of others and linear age effects.

This study also revealed linear age-related differences in functional recruitment of the caudate, wherein greater activation for rejection relative to acceptance increased with age and this pattern was related to updating representations of peers in accordance with whether they were accepting or rejecting. While past studies have shown that positive and negative feedback differentially modulate increases and decreases striatal activation, respectively, other work has shown that both positive and negative prediction error can result in increased activation in the caudate (Asaad & Eskandar, 2011; Rodriguez et al., 2006). Furthermore, a recent study examining the directionality of caudate function as it relates to the encoding of valence and surprise revealed that the caudate responds to surprise in addition to the valence of prediction error (Fouragnan, Queirazza, Retzler, Mullinger, & Philiastides, 2017). Given that we have previously shown adults' tendency to predict acceptance more often than adolescents and demonstrate an implicit self-view congruent with acceptance, it stands to reason that with increasing age comes increasing surprise at being rejected and is, therefore, associated with greater caudate signaling. This was supported by a regression testing the effect of participants' tendency to predict acceptance (proportion) on in response to unexpected response (unexpected rejection > rest; $B=-0.283$, $p=.008$). When considering the role of the caudate as a region that signals updating views of others, our findings are in line with previous work in adults showing that activation in the striatum is associated with making judgments about others (Korn et al., 2012). Thus, recruitment of the caudate in adults may signal surprise at receiving rejection that is then coded and integrated into representations of others, especially when attributing negative information to others.

In the present study, adolescents did not show a distinction in caudate activity when receiving rejection compared to acceptance, and this mirrored adolescents' tendency to maintain likability ratings of peers, regardless of whether they were accepted or rejected. While the finding that adolescents do not differentiate between positive and negative feedback is inconsistent with prior work in social prediction error processing (Jones et al., 2014), it is consistent with some previous work on non-social feedback-based learning (Duijvenvoorde et al., 2008; van den Bos et al., 2012). A previous study examining reinforcement learning across development found that striatal activation for positive and negative prediction errors was comparable during adolescence (van den Bos et al., 2012). Similarly, another study found that neural activation for positive and negative feedback was comparable during early adolescence compared to children and adults, suggesting this is an age of transition, during which a shift towards increased influence of negative feedback occurs (Duijvenvoorde et al., 2008). Additionally, given that we have previously shown that adolescents expect to receive acceptance approximately 50% of the time (Rodman et al., 2017), and a possible function of the caudate is to track surprising events (Fouragnan et al., 2017), then one interpretation of this finding is that adolescents lack surprise for either acceptance or rejection.

These fMRI findings suggest that asymmetrical caudate activation to social evaluation may help adults preserve self-views by up-weighting signals of rejection, associated with the subsequent deprecation of peers, undercutting the validity of negative feedback sources.

Meanwhile, adolescents showed less differentiation in caudate activation when receiving rejection vs. acceptance which tracked with their consistency in peers' impressions, even after being rejected. These results document the neurodevelopmental timescale along which feedback-dependent impression formation emerges.

Conclusion.

Taken together, these findings suggest that adolescents' neural response to social evaluation shows a vmPFC-related prioritization of peer rejection to inform views of the self that tracks with a decrease in self-esteem, whereas functional recruitment of the caudate does not differentiate between acceptance and rejection during adolescence, and may contribute to the tendency for adolescents to maintain views of peers, even after having been rejected. By contrast, vmPFC response in adults suggests prioritization of acceptance feedback to inform views of self, which corresponds to self-protective process that boosts self-esteem. In addition, adults show functional recruitment of the caudate that prioritized rejection to inform views of others, resulting in the downgrading of rejecting peers. These findings build upon the findings reported in Paper 1: the current study illuminates the contribution of acceptance and rejection to the processes of adolescent-specific rejection sensitivity and adult-specific self-protective biases and reveals the underlying neural mechanisms that drive them.

Paper 3: How adolescents and adults translate social value to action: Age-related shifts in strategic physical effort exertion for peer evaluation

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Abstract

Adolescents are more preoccupied by peer approval compared to other age groups. While prior work suggests that adolescents are especially vigilant of and emotionally responsive to peer evaluation, it is unclear how valuable this feedback is to adolescents compared to adults. The present study aimed to evaluate developmental changes in motivation to receive social feedback from peers by using a traditional framework of a cost-benefit trade off. According to this framework, individuals demonstrate greater effort exertion when they are more motivated to obtain an object or outcome of value. Thus, the use of the current physical effort paradigm allows us to infer value from the amount of effort exerted. Using money as a benchmark, this study informs how social evaluation is valued differently across age. One hundred and two participants aged 12-23 completed a social evaluation task in which they were asked to predict whether they would be accepted by peers and squeeze a hand dynamometer past a specified threshold to find out whether the peer judged them positively or negatively. Grip force analyses identified how much effort participants were willing to exert in order to obtain peer feedback, and how expectancy of acceptance or rejection differentially shaped effort exertion across development. This was measured in two ways: by examining maximum force reached on a trial (peak grip force) and whether participants chose to exert effort at all (choice selection). Findings

revealed that adolescents exerted more effort to obtain peer feedback, even when they believed they would be rejected, and showed comparable motivation to obtain social evaluation as money. Adults, on the other hand, showed greater discernment in effort exertion, wherein they exerted less effort when they expected rejection and showed greater motivation to obtain money than social evaluative information. In all, the current study provides evidence that social evaluation is valued differently across age and is shaped by the expectation of being accepted or rejected.

Introduction

The need for social belonging is a pervasive and powerful human drive described as a core need (Baumeister & Leary, 1995). Lack of stable social support puts individuals at greater risk for many negative outcomes, higher rates of morbidity and mortality (Cacioppo & Hawkley, 2003; Uchino, 2006). As such, we are attuned to monitor our social inclusionary status as informed by cues of acceptance and rejection. This social information is highly valuable as it guides how and whether to engage in affiliative behavior.

The drive for social support and belonging may be especially strong during adolescence, a period characterized by a marked change in the complexity of the social environment and relationships (Brown, 1990). In addition to preoccupation with peer approval (Brown, 1990; Somerville, 2013b), peer groups are dynamically changing during this developmental period (Cairns et al., 1995). Adolescents are continuing to refine social competency (Harter, 1988) and the self-concept is in its developmental stages, largely shaped by feedback (Harter et al., 1998; Pfeifer et al., 2009; Sebastian et al., 2008). As such, social evaluative information may be especially valuable to adolescents as a way to maintain a gauge of social status during a relatively unstable social time.

While value cannot be measured directly, it can be inferred from motivation exerted to obtain a desired object or outcome and allows for direct comparison across individuals, circumventing the need to rely on subjective report of value. From this perspective, the more motivated an individual is to expend effort and obtain an outcome, the more valued the outcome. This notion called incentive-motivation refers to the invigorating effect a valued outcome has on behavior, including physical work output or effort (Niv, Daw, Joel, & Dayan, 2007). Seminal work has demonstrated that in adults, incentive motivation to engage in effortful behavior scales with the value of a prospective reward (Klein-Flügge, Kennerley, Friston, & Bestmann, 2016; Kool, McGuire, Rosen, & Botvinick, 2010; Pessiglione et al., 2007; Schmidt, Lebreton, Cléry-Melin, Daunizeau, & Pessiglione, 2012). In addition to modulating behavior to obtain valued outcomes, incentive motivation can also shape action selection (e.g., choosing whether to pursue an outcome; Hauber & Sommer, 2009; Kurniawan et al., 2010; Tversky & Kahneman, 1981), such that outcomes deemed low in value can guide strategic cancellation, or opting-out, of an action entirely (Botvinick, Huffstetler, & McGuire, 2009; Hartmann, Hager, Tobler, & Kaiser, 2013; Westbrook, Kester, & Braver, 2013). Examination of adolescents' motivation to obtain social information should parallel prior work utilizing monetary incentive, such that increase in physical effort is indicative of greater valuation of social evaluative information.

Some previous work has suggested that social information might hold inherent value. For example, research has demonstrated monkeys' willingness to sacrifice a reward (juice) to see photos of high status conspecifics (Deaner, Khera, & Platt, 2005). Others have found that anticipating social feedback, especially acceptance, recruits the same neural circuitry as anticipating money (Powers, Somerville, et al., 2013; Spreckelmeyer et al., 2009). Likewise, receipt of positive feedback compared to neutral feedback leads to increases in positive affect and reward-related neural response (Izuma, Saito, & Sadato, 2008; Rademacher et al., 2010). Research examining attentional bias has found adults to be attuned to cues of potential acceptance or affiliation, especially following rejection (DeWall, Maner, et al., 2009; Powers, Worsham, Freeman, Wheatley, & Heatherton, 2014). While studies have shown that simply sharing social information about oneself is inherently rewarding (Tamir & Mitchell, 2012), it is unclear whether the reverse, obtaining information about oneself, is similarly as valued as these other examples of social information.

Based on the research reviewed, there is reason to believe that social evaluative information is valuable, as it informs social belonging and approval, which are key to survival. Nonetheless, direct examination of the value of social information, and evaluative feedback in particular, has not been tested. In the present study, we used objective tools measuring physical exertion to quantify how motivated individuals were to obtain social evaluative information, a measure of its value. In particular, we sought to a) determine whether participants exert effort for social evaluation b) examine whether this social evaluative information is valued differently depending on expectations of acceptance or rejection and whether this differs across age, and c) compare these indices of value to a benchmark of monetary reward. To address these questions, we adapted a well-validated physical effort paradigm (Kurniawan et al., 2010; Pessiglione et al., 2007; Schmidt et al., 2012) using a novel social cue of evaluation. Participants spanning early adolescence through young adulthood (N=102; ages 12–23) were instructed to exert force on (i.e., squeeze) a hand dynamometer to learn what peers thought of them.

Methods

Participants.

A separate sample of 109 healthy individuals were recruited from the local Boston and Cambridge communities. Exclusion criteria included history of a neurological disorder and current psychiatric disorder. Seven participants were excluded from final analyses for failure to comply with the requirements of participation or experimental procedures. The remaining 102 participants were included in data analyses. All participants provided informed written consent and all minor participants received written permission for their participation from a parent or legal guardian. The Committee for the Protection of Human Subjects at Harvard University approved all research procedures. Sample size was determined prior to data collection based upon the sample size (N=20) and effect size of high compared to low monetary reward on grip force (partial eta=.869) from a recent physical effort paradigm in adults (aged 19-27; Schmidt et al., 2012). We quintupled the size of their sample of adults to account for our interest in the developmental trajectory of motivational processes and novel extension of this task into the social domain.

Participants were aged 12.03-23.77 years (M=18.19, SD=3.52) and 47.62% female. Distribution of males and females did not vary significantly across age (logistic regression: B=.011, p=.849). The ethnic and racial diversity of participants in our sample was broadly representative of the local community of Cambridge and Boston, MA (study sample included 58.5% Caucasian, 17.0% Asian, 9.4% African-American, and 8.5% Multi-racial; 1.9% elected not to disclose this information). To ensure similarities in the demographic and socioeconomic characteristics across age, no more than 25% of the older participants in our sample were current or former students at Harvard University. Participants were recruited through online forums such as Craigslist, advertising in local newspapers, and flyers.

Study Visit.

Pre-task procedure.

This reciprocal social evaluation paradigm is a well-established task that elicits genuine responses to social evaluation (Gunther Moor et al., 2010; Rodman et al., 2017; Somerville et al., 2006, 2010). Approximately one week prior to the study appointment, participants submitted a digital headshot photograph. Participants believed that their photographs would be sent to other study locations in different cities and rated by unknown, age-matched peers. Each peer ostensibly rated the participant's photograph based on the prompt, "*Imagine you are starting at a new school. How much do you think you would want to be friends with this person*?". Just before beginning the task, participants guessed how each peer rated them based on their photograph. For this prediction rating, participants saw a photograph of each peer and responded to the prompt, "*How much did this person want to be friends with you?"* by using their mouse to click along a continuous scale from "not at all" to "very much" (output ranged from 1-100). Responses were recorded via Qualtrics, a secure online survey platform. Values were z-scored to adjust for individual differences in scale usage. Out of all prediction ratings for all subjects, two ratings were identified as outliers using the Outlier Labeling Method and Winsorized (Hoaglin et al., 1986).

Social evaluation task.

Each trial began with a display showing the vertical grip progress bar on the left side of the screen with a yellow line indicating the threshold required for that trial (40% max or 80% max). A photograph of each of the peers was presented in the center of the screen and these cues remained visible for the duration of the trial (Figure 14A, left). As in prior work, participants were instructed to press the space bar when they were ready to begin squeezing to isolate the execution phase of the timeseries (Kurniawan et al., 2010). Participants were instructed to squeeze the dynamometer to find out what the peer had said about them. During the grip phase (3000ms), participants squeezed the hand dynamometer until the progress bar exceeded the yellow threshold line, at which point the line turned green to indicate the participant had successfully reached the threshold (Figure 14A, middle). The feedback phase (2000ms) indicated whether the threshold was reached, at which point participants were shown either a “Yes” or “No”. Yes and No corresponded to the top and bottom half of the rating scale, representing whether the peer wanted to be friends with the participant. The social task contained 60 trials in total, each with a different peer, equally split between easy and hard difficulty. Peer photographs were equal in sex distribution and racial diversity was reflective of the local community (see *Paper 1 Supplemental Materials* for more information on stimulus development).

Money task.

The task structure for the money task was identical to the social evaluation task. On each trial, participants were shown a cue was presented representing the monetary value at stake ($0.05 or $0.75). If successful, participants were shown “Win!” on the right side of the screen and unsuccessful trials showed nothing. The money task contained 32 trials in total, equally split across the four conditions (easy $0.05, easy $0.75, hard $0.05, hard $0.75). At the end of the study visit, participants received performance-contingent payouts in cash.

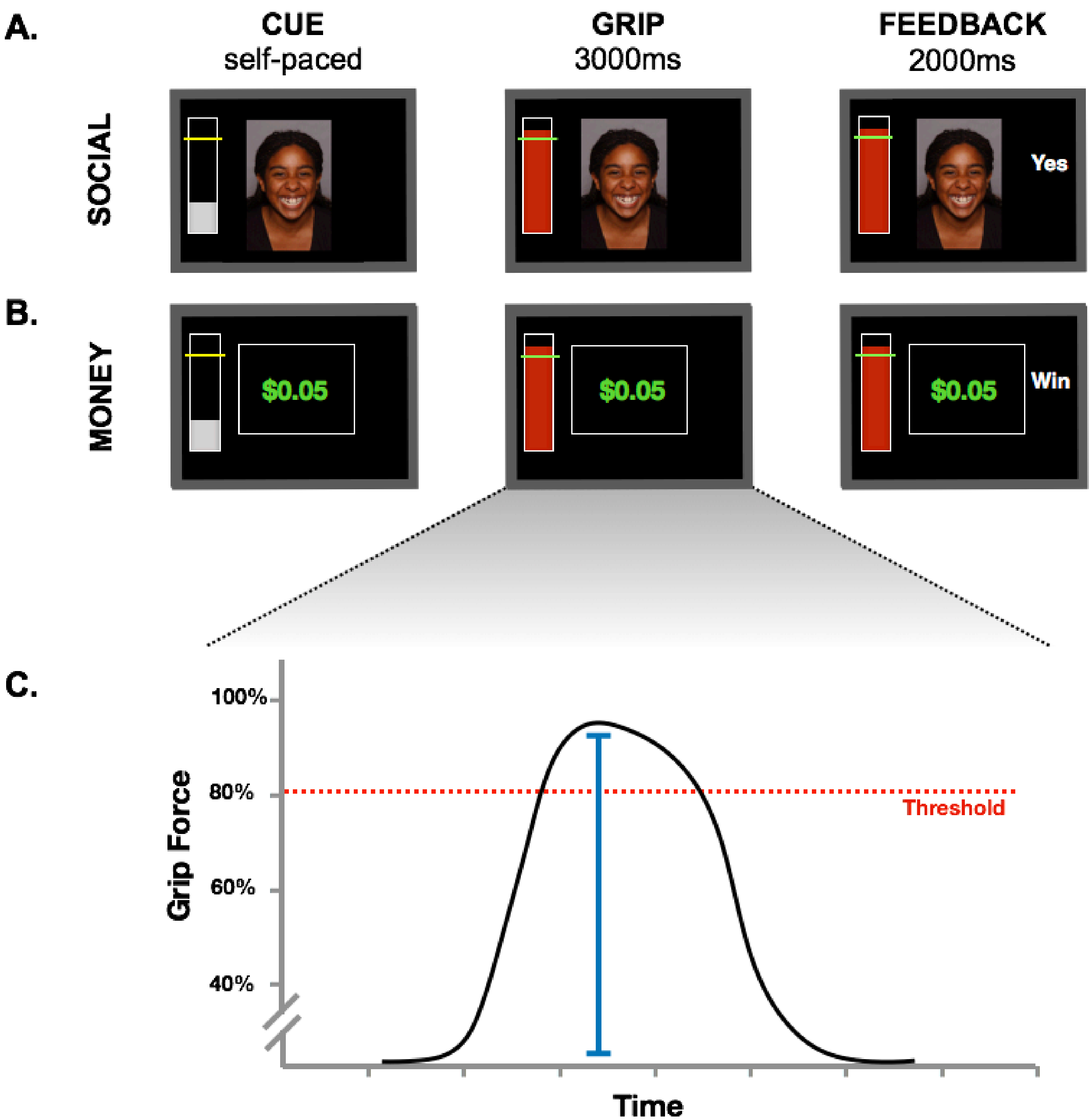

Figure 14. Schematic representation of the experimental task. Participants completed a version of the task to obtain money and a version of the task to obtain social feedback information. First, participants were presented with a cue indicating the difficulty of the trial (yellow line). For the social task (A), a photograph of each peer was presented. For the money task (B), the cue

indicated how much money to be won. During the grip phase of the trial, participants had to reach the yellow threshold line (40% for easy, 80% for hard as shown above) in order to win the money or receive the peer feedback. The red progress bar indicated the grip force in real time and the yellow threshold line turned green once reached. Following the grip phase, feedback was presented indicating whether the participants successfully squeezed the dynamometer. On the right side of the screen, participants were either presented with the peer feedback ('Yes', 'No') or told that they won the money ('Win'). (C) This study quantifies outcome variables from the experimental task including peak grip force (blue) and opt-out trials.

Grip force procedure.

The experimental task was presented using PsychoPy2 v. 1.84, which interfaced with Biopac, Inc. (Goleta, CA) hand dynamometer hardware. Grip force was recorded using a hand dynamometer (Biopac TSD121B-MRI), made of two molded plastic cylinders that, when squeezed, compress an air tube. Air pressure was converted into voltage by a transducer, wherein isometric compression resulted in changes in voltage proportional to the exerted force. This input was sent to a Biopac DA100C module and converted from analog to digital signal using a custom-built 3.5mm breakout board connected to a National Instruments USB-6009 multifunction IO box. This digital signal was sampled at 60Hz and used a real-time input to PsychoPy to provide real-time visual feedback during the task, wherein participants saw a vertical bar on the screen rise and fall proportionally to their grip force (Figure 14).

Before beginning the experimental task, participants completed a step-wise calibration procedure to account for individual grip strength levels. Participants were instructed to use their dominant hand, which was positioned and secured by the experimenter to maintain consistency within session and across participants. These individualized strength thresholds were used to customize the relative difficulty of trials in the task, effectively adjusting for cross-participant variability in hand strength. During the calibration, participants repeatedly attempted to reach the top of a vertical bar representing sequentially higher grip levels on each successive attempt until they were no longer able to reach the threshold. At this time, the calibration portion concluded, and the maximum grip force was recorded. This maximum grip calibration value was used to proportionally define the thresholds used in the subsequent tasks on an individual basis (easy threshold: 40% of maximum; hard threshold: 80% of maximum), as in prior work (Kurniawan et al., 2010; Schmidt et al., 2008). This calibration procedure was repeated immediately following the social task and the money task to quantify possible fatigue effects (see Control Analyses).

Post-task procedure.

The debriefing procedure was the same as that used in Paper 1 and all participants included believed the cover story.

Analytical approach.

Peak force was computed for each trial as the maximum grip force applied within a trial, expressed in units of percent of MGS, as in prior work (Pessiglione et al., 2007). Opt out trials were defined as trials in which participants did not make a good-faith effort. For easy trials, grip force that did not exceed half the distance to the threshold, or 20%, were considered opt-outs trials. For hard trials, a trial was considered an opt-out if the grip force did not exceed the average peak grip force for easy trials (money task: 56.74%; social task: 54.79%). Overall, 96 trials during the money task (2.86% of trials) and 299 trials during the social evaluation task (4.89% of trials) were considered opt-out trials. Opt-out trials were tallied for frequency in each condition for each participant.

Group analyses used mixed-effects (LME) regression approaches for outcome variables of peak grip force (linear regression) and opt-out trials (logistic regression). LME models included predictors representing trial reward (low or high monetary amount; predicted rejection or acceptance), difficulty (easy, hard), participant age (linear, quadratic), and their interactions as predictors of interest. In addition, participant was included as a random effect, and MGS and trial number were included as nuisance covariates to account for baseline differences in strength and trial order. We evaluated two patterns of age-related change, linear and quadratic (adolescent-peaking) effects by inputting polynominal age terms as orthogonalized covariates of interest using the *poly* function in R. All age analyses were completed using age as a continuous. As such, linear models included a linear age predictor and quadratic models included both linear and quadratic age predictors. Akaike Information Criterion (AIC; Akaike, 1974) model fit statistics were used for the LME models to determine the optimal age model and all reported findings are based on the optimal model for each outcome variable (see Table S3). Thin-plate smoothing spline regressors, the nonlinear approach used in Paper 1, were never a better fit of the data than the linear and quadratic age regressors according to AIC model fit statistics and are, therefore, not reported. All parameter estimates (B) are reported in unstandardized units.

Results

Prediction ratings.

Participants responded to the question "*how much would this person want to be friends with you?*" using a continuous scale from "not at all" to "very much", the output of which was 0-100. On average, participants predicted an output of 46.26 (SD=23.43). As participants got older, they were more likely to expect that peers would want to be friends with them (r(101)=.307, p=.002). In the current sample, we did not find that the spline-age effect (AIC: -2814.56) was a better fit of the data than that linear model (AIC=-2814.56). This prediction output was z-scored within each participant for all future analyses.

Incentive-driven effort exertion.

Social evaluation task.

We found that the task manipulation functioned as expected, wherein participants exerted higher peak grip force during hard (M=87.17% of distance to MGS, SD=8.12%) compared to easy trials (M=54.79% of distance to MGS, SD=9.77%; B=0.316, p<.001).

We then compared peak grip force according to participants' predictions of being accepted or rejected by each participant. Overall, grip force was greater when participants believed they would be accepted by peers (M=74.48%, SD=18.57%) than when they believed they would be rejected (M=69.68%, SD=18.45%; B=0.002, p=.027). The interaction between prediction score and difficulty was not significant (B=-0.0004, p=.825; Figure S8). These results demonstrate that social feedback elicits an incentive-induced increase of physical effort when participants expect the outcome to be positive.

When testing whether predictions of being accepted differentially impacted motivation across age, findings revealed a significant interaction between quadratic age and prediction score (B=0.174, p=.018), suggesting that adolescents, especially late adolescents, showed equivalently high peak force across both accept and reject trials, whereas younger and older participants exerted less effort when they expected to be rejected. Young adults, in particular demonstrated the greatest differences between peak force by prediction type, exerting more effort when they predicted they would be accepted. The main effect of age and other age interactions were not significant (ps>.083; Figure 15).

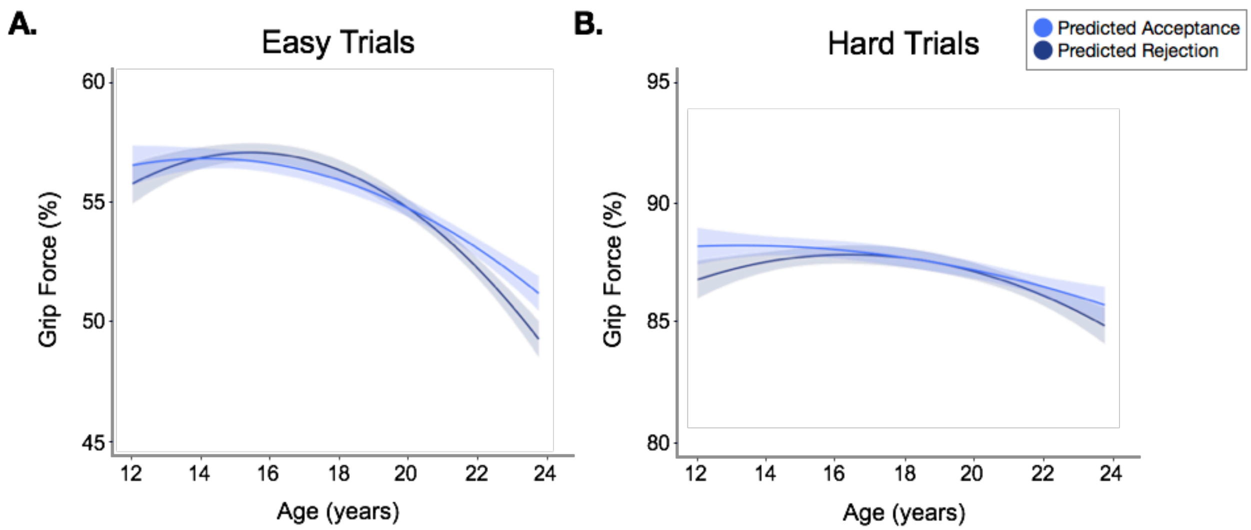

Figure 15. Adolescents, especially late adolescents, exerted effort for social evaluation regardless of expectation, whereas younger and older participants exerted less effort when they believed they would be rejected. Graph shows fitted values of quadratic relationships between peak force and age by difficulty and prediction (median split for illustrative purposes). Shading indicates the SEM.

For comparison, we examined peak force effort exertion for trials with high and low monetary reward. Participants also exerted significantly more force for high value trials (M=72.79%, SD=18.11%) compared to low value trials (M=70.46%, SD=17.89%; B=0.024, p<.001; Figure S8). However, results differed from the social evaluation task with respect to whether incentive value had a differential effect on peak grip force across age. The optimal LME model for the money task revealed no main effect of age (linear: B=-0.294, p=.366; quadratic: B=-0.430, p=.154) or interaction effect of age and value (linear: B=0.042, p=.778; quadratic: B=-0.145, p=.330). The interaction between age, value, and difficulty was also not significant (ps>.196). Thus, results indicate that participants exerted greater force for high-value monetary outcomes, and did so equivalently across age. These age-related differences in motivation to obtain money compared to social feedback motivate the direct comparison of the social task and money task trials.

Money and social evaluation task combined.

We examined participants' motivation to obtain money compared to social evaluation across tasks. Overall, all participants regardless of age were more motivated to work for money (M=71.59%, SD=18.01%) than for social evaluation (M=70.08%, SD=18.51%; B=0.016, $p<.001$). This was especially true during easy trials (B=0.012, $p<.001$) and when the outcome was higher in value: relatively higher money vs. predicted acceptance (B=-0.015, $p<.001$).

We next examined whether motivation for monetary reward vs. social evaluation differed with age. Findings revealed that the greater effort expended for monetary reward over social evaluation was especially true for young adults when value was high (Quadratic age by value by task: B=0.789, $p=.013$) or during easy trials (Quadratic age by difficulty by task: B=1.330, $p<.001$). The quadratic shape of this relationship is reflective of the overall shape of the social evaluation task and the age-related differences. Upon examination of descriptive plots (Figure 16), this difference between tasks is driven by young adults. The main effect of age and all other task-dependent terms were not significant (ps>.099). Findings suggest that when pitting monetary reward against social evaluation, late adolescents valued them relatively equally regardless of predicted evaluation, which is in contrast to young adults, who show a preference for monetary reward over social evaluation, especially when the money at stake is relatively high (Figure 16).

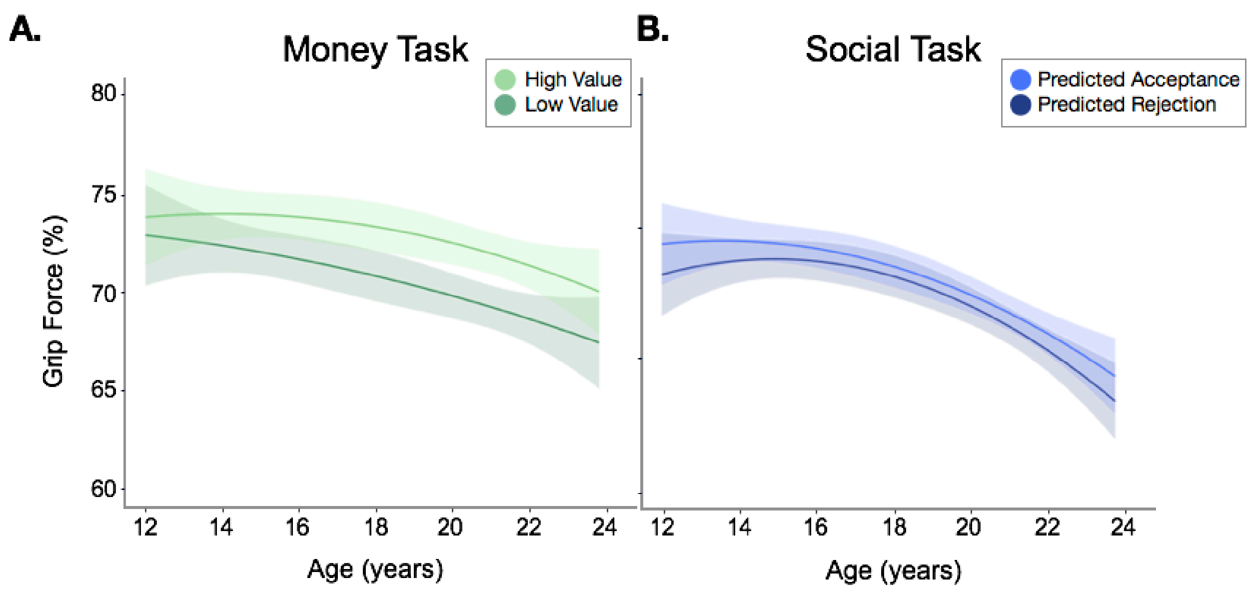

Figure 16. When pitting monetary reward against social evaluation, older participants valued monetary reward more than social evaluative information, especially when monetary reward is high. Graph shows fitted values of quadratic relationship between peak force grip and age by value (prediction displayed as median split for illustrative purposes). Shading indicates the SEM.

Strategic conservation of effort.

Opt-out trials were examined to determine whether participants differentially chose to forgo the opportunity to know whether they had been accepted or rejection by a peer. Descriptive data showed an extremely low instance of opting out of easy trials (N=19 trials; 0.3% of trials), therefore difficulty level was not included as a predictor and analyses were conducted collapsed across easy and hard trials. Overall, participants opted-out significantly more on trials when they expected to be rejected (N=160 trials) than trials they expected to be accepted (N=139 trials; logistic B=-.255, p=.014), demonstrating less willingness to work when rejection seemed imminent.

Analyses also queried whether opt-out trials varied by age. The optimal LME model revealed a main effect of linear age, wherein adults (N=255 trials) tended to opt out of more trials than adolescents (N=44 trials; B=0.335, p=.016). The interaction between linear age and prediction was not significant (B=0.027, p=.361). Results suggest that participants opted out (mostly of hard trials) when predicting rejection. In addition, older participants engaged in opt-out behavior more often than younger participants (Figure 17).

These findings parallel opt-out behavior when exerting effort for monetary reward. Once again, there was a low incidence of opt-out trials in the easy condition (N=2), therefore difficulty level was not included as a predictor and analyses were conducted collapsed across easy and hard trials. When reward value was low, \$0.05, participants opted-out significantly more (N=79 trials) than high value trials (N=15 trials; logistic B=-6.804, p<.001), demonstrating less willingness to work for low value trials (Figure S1B). Lastly, analyses queried whether opt-out trials varied by age. The optimal LME model revealed no main effect or interaction effect of linear age (ps>.270).

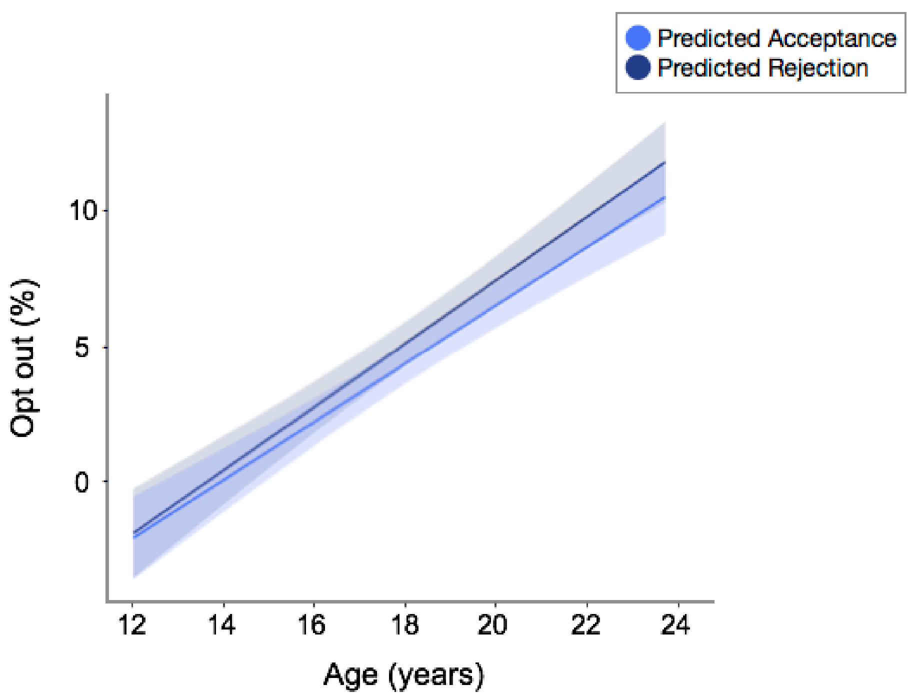

Figure 17. Participants opted out of trials more often when they believed they would be rejected. Older participants strategically conserved energy by opting out of high effort trials more often

than low effort trials. Graph shows linear relationship between opt-out trials and age by predicted evaluation (median split for illustrative purposes). Shading indicates the SEM.

Control analyses.

Additional analyses were conducted to evaluate whether the age-related differences described above for high vs low value trials were associated with age-related differences in fatigue effects. To explore the possibility of fatigue effects, MGS was collected before (M=4.139, SD=1.492), between (M=4.034, SD=1.522), and after (M=4.023, SD=1.520) the tasks. A difference score was computed for each pair and regressed on age, controlling for MGS. Findings showed that fatigue did not differ by age across the completion of these tasks (Max 1 vs. Max 2: B=-0.034, p=.095; Max 2 vs. Max 3: B=.006, p=.780; Max 1 vs. Max 3: B=-0.029, p=.208). As such, these age-related findings cannot be explained by differences in overall fatigue. While MGS increases significantly with age (B=0.157, p<.001), MGS was included as a nuisance covariate in all models to control for baseline differences.

Discussion

Understanding the value of social evaluative information across development is important in contributing to our understanding of why social evaluation is processed differently across development. We have previously shown that adolescents internalize rejection, while adults enact self-protective processes that internalize acceptance and externalize rejection (Rodman et al., 2017). In the current study, we found that adolescents are eager to obtain social evaluative information, even when they believe they will be rejected, whereas adults exerted effort more strategically, exerting less when they believed they would be rejected.

Our findings suggest that participants are motivated to expend physical effort to obtain social evaluative information, rendering it inherently valuable. Adults demonstrated that they valued social information, but more so when they believed they would be accepted compared to rejected and no more than a low value monetary reward. This is in line with previous work that suggests social information is rewarding (Deaner et al., 2005), especially when adults believe the feedback will be positive (Powers, Somerville, et al., 2013; Spreckelmeyer et al., 2009). Previous studies have also shown that adults avoid cues of rejection feedback as demonstrated by an attentional bias task (DeWall, Maner, et al., 2009). The current findings are consistent with our previous work in Paper 1 and Paper 2, wherein adults show signs of self-protective behaviors and show less motivation to obtain social evaluation when rejection is imminent. A positive self-view has been shown to be associated with greater wellbeing, thereby rendering this behavior adaptive (Alloy & Abramson, 1979; Peterson & Seligman, 1987). It is also possible that adults may have a more fully developed self-concept (Sebastian et al., 2008), social network (Cairns et al., 1995), and perceive themselves as socially competent (Neemann & Harter, 1986), and therefore have less of a need to continually consume feedback and adjust behavior. It may be more important for adults to preserve their positive self-views. Thus, adults are more motivated to obtain positive compared to negative social evaluation, in particular. We contend that while the motivation to obtain information about social standing is adaptive, adults prioritize preservation of their positive self-views. Furthermore, this data suggests the possibility that adults shy away from expected rejection in everyday social interactions for this reason, thereby protecting and reinforcing self-views, even if incomplete.

Importantly, our findings indicated this pattern does not hold true for adolescents. Adolescents demonstrated a greater willingness to exert effort, regardless of whether they expected to be accepted or rejected. Adolescents also chose to exert effort for almost every trial, opting out of fewer trials than adults. Lastly, adolescents valued social evaluation just as much as they valued monetary reward, regardless of whether they expected to be accepted or rejected. That is to say that adolescents valued obtaining peer feedback when they expected to be rejected just as much as they valued winning the high value money. This suggests that adolescents are highly motivated to obtain social evaluative information about themselves and that they stand to gain from both acceptance and rejection, likely for the developmental reasons stated above. It is possible that the tendency for adolescents to show more motivation to obtain social evaluation, even in the face of rejection, ultimately enhances social competency and group affiliation. Given the critical importance of peer relationships during adolescence, it may be adaptive for adolescents to be high consumers of social feedback information as a means to learn from peer feedback (mistakes) and adjust behavior in response to new social information, thereby enhancing competence and chance of belonging.

In addition, the adolescent self-concept is in its developing stages (Sebastian et al., 2008) and is largely informed by evaluation from peers and family members (Pfeifer et al., 2009), otherwise known as contingent self-esteem (Bos et al., 2010). Previous work has demonstrated that actual appraisals made by peers' parents and teachers are associated with self-appraisal and impact real developmental outcomes (Harter et al., 1998), which has been shown to be associated with positive (e.g., academic achievement) and negative outcomes (e.g., delinquency; Bartusch & Matsueda, 1996; Bouchey & Harter, 2005). Ultimately, the value of social evaluative information as a means of learning social competence and informing self-concept is both normative and renders adolescents vulnerable to the deleterious and depressogenic effects of peer rejection (Bos et al., 2010; Prinstein & Aikins, 2004). To this end, future studies should examine the role of psychopathological processes in the valuation of social feedback.

Discussion and Conclusions

Summary of findings

This dissertation investigates value and impact of social evaluation across age, using behavioral and neuroimaging techniques. Papers 1 and 2 examined how age-related differences in peer feedback processing, both on the behavioral and neural level, shape updated representations of the self and of others. Paper 1 findings showed that after receiving mixed positive and negative social feedback, adolescents internalized peer rejection and felt worse about themselves, whereas adults engaged in self-protective process that preserved self-views. In a subset of these participants, Paper 2 examined neural function supporting processing and utilization of peer feedback. Results demonstrated that adults showed more activation in the ventral striatum and ventral medial prefrontal cortex, and that activity in these regions were associated with their tendency to boost self-views and denigrate rejecting peers, respectively. These papers reveal a neurodevelopmental framework for understanding how peer feedback is utilized across development. Paper 3 examined motivational value of social evaluation as compared to monetary reward across age. Physical effort to obtain either social evaluation or money was used as objective measures of value. Findings revealed that social evaluative information was valued differently across age. Adolescents exerted greater effort to obtain social information than adults, regardless of whether they believed they would be accepted or rejected. By contrast, adults showed more strategic discernment in effort exertion: Adults exerted less effort for social evaluative information when they believed they would be rejected.

Together, these findings are consistent with the notion that adolescence is a developmental stage in which feedback is sought out and used for the purposes of ensuring future social belonging. As such, we identify adolescence as a phase wherein normative processing of social evaluation is expected to lead to periods of low self-views. This may also render adolescents vulnerable to negative psychological outcomes that stem from prolonged or extreme social rejection. The following sections outline the proposed neurodevelopmental framework and clinical considerations.

Implications

Neurodevelopmental framework for socioevaluative sensitivity

fMRI findings in Paper 2 align with Paper 1's theoretical framework of socioevaluative processing from pre-adolescence through young adulthood. We have suggested that reactivity to rejection is heightened during early adolescence, whereas self-protective processes have a more protracted emergence. This results in early adolescents exhibiting a maximal differential between heightened reactivity to rejection and the absence of self-protective biases that preserve self-views. When examining this theoretical framework alongside the vmPFC and caudate activation from Paper 2, we observe a recapitulation of the proposed framework of socioevaluative processing, (Figure 5), wherein vmPFC- and caudate-related activation in adults is associated with enhancement of self-views and downgrading rejecting peers, respectively (self-protective processes), whereas vmPFC-related activation was related to internalization of rejection (rejection reactivity). While this framework is proposed as capturing normative developmental process, it is important to consider these tendencies in the context of clinical risk.

Clinical implications

Adolescence is marked by a dramatic increase in time spent with peers and concern with gaining approval, rendering them especially vulnerable to profound negative impacts of peer rejection. Given that adolescents are subjected to social feedback in their daily lives at an unprecedented rate due to the popularity of social media, this work illuminates a key development-by-social-context intersection that could be particularly impactful on adolescent health (Crone & Konijn, 2018).

At first glance, the adolescent profile of vulnerable self-views and a lower expectation to be liked may appear on the surface to parallel research on adults who report sensitivity to social rejection, low self-esteem, or depression. Previous research in adults with these characteristics (e.g., low self-esteem) show lower expectations of social acceptance compared to adults with higher self-esteem (Alloy & Abramson, 1979; Downey & Feldman, 1996; Nezlek, Kowalski, Leary, Blevins, & Holgate, 1997; Powers, Somerville, et al., 2013; Somerville, Kelley, et al., 2010). Furthermore, individuals with low self-esteem are less able to buffer themselves from the blow of negative feedback following negative feedback or rejection (Shrauger & Lund, 1975), as they do not enact self-serving biases to the same degree as those with high self-esteem (Greenwald & Farnham, 2000) or at all (Baumeister, 1982; Beauregard & Dunning, 2001; Campbell & Sedikides, 1999). These individuals also do not down-grade their judgments of others in the service of self-image preservation (Beauregard & Dunning, 1998; Brown & Gallagher, 1992; Vohs & Heatherton, 2004).

Although adolescents show surface similarities with populations of adults with depression, rejection sensitivity, or low self-esteem, we contend that these developmental findings should not pathologize the normative trajectories observed in the present study. We believe it is more likely that adolescents, on average, exhibit these biased feedback patterns and continue to build up mechanisms that will allow (most of) them to emerge as adults who possess the self-protective biases described above. However, there may be a subset of adolescents who have an increased clinical risk or experience prolonged and extreme peer rejection that may have a higher likelihood of experiencing psychopathology as a result of how the adolescent brain responds to social rejection.

Costs and benefits to adolescent evaluative processing

The presented findings were revealed in a sample of heathy, normally developing children, adolescents, and adults, which suggests that the age-related patterns described are normative and potentially adaptive. To this point, we have speculated on the more adaptive utility of this developmental difference in social feedback processing as a means of learning how to behave in socially competent ways that ensures future social acceptance and belonging. While the current findings involving internalization of negative feedback may be critical for normative social development, high-risk adolescents may tip the balance toward pathological levels of low self-views, often associated with depression (Davey, Yücel, & Allen, 2008). Some suggest this phase of socioaffective sensitivity has serious implications for the development of psychiatric disorders (Lee et al., 2014; Nelson et al., 2005; Powers & Casey, 2015), especially given the sharp rise in onset of mental illness during adolescence (Kessler et al., 2001; Paus et al., 2008). Prior work has shown that chronic peer rejection has been associated with the development of externalizing behaviors (e.g., truancy, school dropout, delinquency; Coie, Lochman, Terry, & Hyman, 1992) and internalizing emotional disorders, such as depression and anxiety (French et al., 1995). Those at highest risk for poor mental health outcomes, especially depression, are students who are bullied and have low social support (Hawker & Boulton, 2000; Rigby, 2000). Future research should examine how response to rejection could shed light on adolescents' risk for psychopathology. Moreover, these insights into the differential processing of peer feedback could be leveraged in future work as an intervention to challenge negative distortions of social standing, which is a core technique of cognitive behavioral therapy (Beck, 1979).

Limitations and outstanding questions

The present dissertation aimed to demonstrate how mixed experiences of social feedback were incorporated into self- and other-views at different developmental stages. The multi-measure approach, combining subjective and objective measures of response to social evaluation using behavioral and neuroimaging techniques, constitutes a key strength of this collection of studies. However, this study should be considered in light of its limitations and the unresolved questions that have emerged from this investigation.

First, although the propensity for adults to experience a boost in self-esteem following rejection has been well-established in the literature (Baumeister, 1982; Greenberg & Pyszczynski, 1985; Pyszczynski, Greenberg, Solomon, Arndt, & Schimel, 2004; Rudman et al., 2007), there are some other influential studies that have found the reverse pattern, wherein adults experience a drop in self-esteem following negative feedback (Buckley, Winkel, & Leary, 2004; Heatherton & Polivy, 1991; Vohs & Heatherton, 2001). This has been especially influential in the development of sociometer theory (Leary, Haupt, Strausser, & Chokel, 1998), which posits that self-esteem functions as a barometer of social inclusionary status. One possible explanation for such discrepancies is the varied time-points at which self-esteem is measured. Whereas our studies measured changes in self-esteem after the entire collection of feedback, others have measured changes in self-esteem or affect in a more immediate fashion (e.g., trial-by-trial basis). It is possible that these self-protective processes unfold over time in dynamic ways, such that an immediate measurement of self-esteem may capture an initial drop that is recouped over time with the implementation of complex, regulatory strategies that ultimately result in a boost in self-esteem (Jussim, Yen, & Aiello, 1995).

Second, it is also critical to discern the extent to which individual differences and experimental design factors influenced outcomes of interest. Previous research has demonstrated that many study design factors (e.g., public or private feedback) can influence the extent to which self-serving biases are enacted (Brown & Gallagher, 1992; Campbell & Sedikides, 1999). Others suggest that individual differences, such as trait narcissism (John & Robins, 1994) or childhood history of trauma (Will, Lier, Crone, & Güroğlu, 2016), can play a large role in moderating the impact of negative feedback on self-views. Future work can remedy this by explicitly testing the individual differences that make some adolescents more vulnerable to the negative impact of rejection than others.

Third*,* previous research has shown that social feedback can be weighted differently depending on prior judgments and expectations (Delgado, Frank, & Phelps, 2005; Guyer et al., 2012). In a study by Delgado and colleagues (2005), moral characteristics of trading partners in a trust game modulated feedback-based brain activation in the striatum associated with updating impressions of the trading partner. Neural activation increased and decreased as expected following outcomes that were positive or negative when playing against a partner that was perceived as ‘neutral’. However, responses flattened when playing against a perceived ‘good’ partner, suggesting that prior expectations about moral character can diminish learning signals and override momentary feedback learning. In the context of social evaluation, similar principles may dictate the extent to which participants weigh approval or rejection from a peer. For example, rejection from a peer that I perceive as generally misanthropic may be less informative, and, ultimately, less readily incorporated into self-views, than rejection from a peer that seems fairly affable. From this perspective, rejection could be easily *explained away* and forgotten, serving as an adaptive filter that is both efficient and protective against less meaningful instances of peer rejection. In Papers 1 and 2, we attempted to address this question by asking participants post-task to answer the question, "*How much do you think this peer liked the other participants*?" and instructed participants to answer on a continuous scale from "not at all" to "very much". This question proved to be difficult for the younger participants to comprehend and, therefore, was not included in the current findings. In order to address this question, future analyses could experimentally manipulate information about each peer that tags how 'nice' or 'mean' the peer is in order to determine whether weighting of feedback varies according to how anomalous the feedback seemed to the participant.

Fourth, there is also increased interest in examining complex social behavior within the framework of computational modeling (Behrens, Hunt, & Rushworth, 2009). The extent to which prediction errors alter the expected value of subsequent trials, thereby influencing behavior, is known as the learning rate. A high learning rate reflects a tendency to weigh recent outcomes more heavily, whereas a low learning rate reflects a tendency to integrate outcomes over a longer feedback history. Though not always detected, previous research has found age-related differences in the context of learning rate. In a study by van den Bos and colleagues (2012), negative learning rate was found to decrease linearly with age, while positive learning rate was found to increase linearly with age. Adolescents appear to occupy a state of transition, wherein learning rates for both positive and negative feedback are about equal (van den Bos et al., 2012). Similar findings have been reported elsewhere (Christakou et al., 2013; Hauser et al., 2015). While Jones and colleagues (2014) found that adolescents have a lower learning rate for positive social feedback compared to adults, it would be interesting to examine this effect beginning at a younger age as it may align with the linear age effect described earlier. In the context of peer evaluation, an adolescent-specific tendency to weigh previous feedback more heavily than children or adults, might indicate that adolescents' perception of self and whether they will be liked is more malleable and vulnerable to momentary (trial-by-trial) peer evaluation. Future work should apply principles of computational modeling to examine whether developmental differences in trial-by-trial patterns of learning, on both a behavioral and neural level, carry predictive value in whether peer feedback is incorporated into self-views.

Conclusions

Extensive developmental research has demonstrated that adolescence is a time characterized by increased importance of peer relationships, sensitivity to rejection and negative psychological outcomes associated with rejection. However, theoretical models do not currently explain whether feedback is valued differently across age or why peer feedback has such deleterious effects during adolescence. Here, we found that adolescents are motivated to receive social evaluation, good or bad, and do not protect themselves from negative feedback as adults do. In addition to this greater motivation to obtain feedback, adolescents show a greater tendency incorporate negative feedback into self-views. This internalization is partially explained by shifts in brain function that are characteristic of adolescence. Specifically, we found that neural activation in regions undergoing normative developmental changes were integral in coding feedback signals to update representations of the self and others. These findings build upon our understanding of the biological contributions to adolescents' sensitivity to their social environments and provide a mechanistic perspective of why the psychological well-being of some adolescents is vulnerable to the depressogenic effects of peer rejection.

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APPENDIX

Paper 1 Supplemental Methods

Age analysis approach.

Analyses were performed using a two-step process to query age effects and interrogate nonlinear patterns in the data. When computing linear or linear mixed-effects (for dependent variables with repeated measures) regression analyses, the *lm* and *lme* functions of the *nlme* package in R (Pinheiro et al., 2014) were used to evaluate the statistical significance of standard age-related patterns of change (linear, quadratic, cubic). For models with repeated-measure dependent variables, subject was included as a random effect. Quadratic and cubic models contained lower order age terms and polynominal age terms were input as orthogonalized covariates of interest using the *poly* function. As such, the linear model included a linear age predictor, the quadratic model included linear and quadratic age predictors, and the cubic model included linear, quadratic, and cubic age predictors.

When computing generalized additive models or generalized additive mixed models (for repeated measures dependent variables) the *gam* and *gamm* functions of the *mgcv* package in R (Wood, 2017) were used to solve for patterns of age-dependent change using thin plate regression smoothing splines. This spline fitting technique does not require *a priori* assumptions (e.g., knots), and yields solutions that are penalized for complexity to avoid overfitting the data. All model comparisons were performed within-class of regression.

Participants.

One hundred and nineteen healthy individuals aged 10-23 were recruited from the local community. Participants' ethnic and racial diversity was representative of the local community (70.1% Caucasian, 13.2% African-American, 10.2% Asian, and 6.5% Hispanic). To ensure similarities in the demographic and socioeconomic characteristics across age, no more than 30% of adult participants were former or current students at Harvard University. All participants included in the final analyses reported fully believing the cover story. All online questionnaires were collected using the secure online platform Qualtrics. Participants were recruited through online forums such as Craigslist, advertising in local newspapers, and flyers. All participants provided informed written consent and all minor participants received written permission for their participation from a parent or legal guardian. Sample size was determined prior to data collection based upon sample sizes from a study using a similar task in a developmental population (Gunther Moor et al., 2010). A power analysis could not be conducted because the effect of this feedback-based task on changes in self-views (the key target dependent variable) has not been used in prior developmental work to our knowledge.

Exclusion criteria included history of a neurological disorder, current psychiatric disorder, and current use of psychotropic medication. A diagnostic clinical interview(Sheehan et al., 1998) was conducted during the study visit to confirm that participants did not meet criteria for current depression or anxiety disorder. 12 participants were excluded from final analyses: five due their reported suspicion of the cover story; two due to insufficient variability in behavioral responses; two due to noncompliance resulting in incomplete data; two because experimenter-administered diagnostic interview indicated they met criteria for current neuropsychiatric disorder; and one for being under the influence of a mind-altering substance on the day of the study visit. The remaining 107 participants were included in key analyses.

For all dependent variables of interest, data were inspected for normality and outliers. Outliers were identified using the Outlier Labeling Method (Hoaglin et al., 1986) with a *g* multiplier of 2.2 (Hoaglin & Iglewicz, 1987) and were then Winsorized (Dixon, 1960). The

Winsor approach involves replacing outliers with the maximum (or minimum) value within the bounds of the outlier threshold. When completing the analysis examining the task-induced change in self-views, three additional participants were not included in this analysis because they did not complete the post-task self-esteem survey resulting in 104 participants included in this analysis. Data from one participant aged 18.27 were identified as an outlier and Winsorized. When completing the analysis examining the task-induced change in likability ratings of peers, five additional participants were not included in this analysis because they did not complete the post-task ratings of peers, resulting in 102 participants included in this analysis. Data from one participant aged 11.21 were identified as an outlier and Winsorized.

Task Design.

The cue phase (0-3000ms) presented a photograph of a peer, which remained visible for the duration of the trial (Figure 1B, top). Upon seeing the peer, participants predicted whether the peer had liked them with a button press of “Yes” or “No”. Following the participant’s response, there was a brief delay (Figure 1B, middle; 1000-4000ms) while the participant’s prediction displayed on the left side of the screen, followed by delivery of feedback displayed on the right of the screen (Figure 1B, bottom; 2000ms) indicating whether the peer supposedly liked or disliked the participant (set at 50% acceptance, 50% rejection in pseudorandom order). Feedback was displayed in binary form as “Yes” or “No”, which participants were instructed mapped on to ratings in the top and bottom halves of the rating scale, respectively. If participants did not make a response in the allotted time during the cue phase, responses were coded as a “miss” and participants were not shown the peer feedback for that trial (1.7% of all trials).

Stimuli.

We developed four sets of 160 face stimuli composed of headshot photographs of "peers" (ostensibly submitted by other participants) for four age groups (9-11, 12-14, 15-17, 18+). Prior to conducting the study, we compiled a large database of candidate face stimuli depicting close-up headshots of individuals of various ages, sexes and ethnicities from available stimulus sets (Egger et al., 2011; Jones et al., 2011; Tottenham et al., 2009) and from open access image databases (e.g., Flickr, Pixabay, Wikimedia, Stockvault, Freeimages).

These candidate images were then rated by a separate group of adult participants (N=220) recruited through Amazon Mechanical Turk. These individuals rated images on: perceived age of the person (i.e., 9-11, 12-14, 15-17, 18+), perceived ethnicity of the person (i.e., Caucasian, Asian or Pacific Islander, Hispanic, African American, Native American, or Other), perceived likability of the person (1 = (not at all) – 5 = (very much)), and whether the photograph looked like a realistic profile picture, the type of headshot peers may submit (Yes/No).

Based on these ratings, stimuli were sorted into four subsets of age-matched images to represent the other peers in the study. Each subset contained 160 images with a similar variety of ethnic backgrounds (no more than 60% Caucasian), equal portions of male and female images, images that the majority of raters considered to be realistic, and comparable ratings of likability. All faces were cropped, centered, re-sized, and presented against a black background.

The stimulus subsets were then validated to ensure comparability in likability using ratings from participants in the current study. Peer likability ratings were equal across age-specific stimulus subsets ($F(3,106)=.704$, $p=.552$). For the experimental task, face stimuli were pseudorandomized and counterbalanced so that each face delivered positive feedback and negative feedback at approximately equal rates across participants.

Paper 1 Supplemental Results

Memory control analysis.

Linear mixed effects regressions with memory accuracy as the dependent variable, subject as a random effect, feedback type (acceptance, rejection), age (linear, quadratic, cubic), and age interactions revealed that the null model without age predictors (AIC: -287.1) was superior to the cubic (AIC: -277.9), quadratic (AIC: -281.6), and linear models (AIC: -285.4). This indicates that memory for social feedback did not vary as a function of age. To confirm the lack of age effects, we examined the significance level of age effects within the linear age model. There was no significant main effect of age (B=0.262, p=.132) and no significant age by feedback type interaction (B=-0.231, p=.345; see Figure S5). Because there were no effects of age, more complex nonlinear models were not interrogated.

Age group analysis based on binned data.

Age binning procedure.

We examined age-related differences across 2.5 year bins, an interval that allowed for equal distribution of participants across the entire sample: 10-12.5 years old (pre-adolescents; N=20), 12.5-15 years old (early adolescents; N=23), 15-17.5 years old (late adolescents; N=22), 17.5-20 years old (emerging adults; N=19), 20-23 years old (young adults; N=23).

Explicit: prediction of peer feedback age group comparisons.

A one-way ANOVA with proportion of predicted acceptance as a dependent variable and age group as a between subjects factor revealed that predictions of being liked varied significantly with age ($F(4,106)=3.363$, $p=.013$; Figure S1). Post-hoc between group comparisons (corrected for multiple comparisons using Tukey's method) revealed that early adolescents (M=47.17%, SE=3.00%) predicted they would be liked significantly less often than emerging adults (M=59.15%, SE=2.91%; $t(40)=-2.833$, p(corr.)=.031) and young adults (M=58.03%, SE=2.81%; $t(44)=-2.642$, p(corr.)=.045). All other age group comparisons were not significant (ps(corr.)>.160).

Next, we examined the degree to which participants exhibited biased expectations of acceptance compared to the base rate of 50% (all participants received 50% acceptance and 50% rejection feedback across the task). Separate one-sample t-tests of each age group revealed that this effect was carried by the adults (emerging adults: $t(18)=3.146$, $p=.006$; young adults: $t(22)=2.856$, $p=.009$), whereas the other age groups' predictions did not differ from 50% (all ps>.356). In sum, while pre-, early, and late-adolescents were objectively more accurate in their expectations of peer acceptance, they predicted being liked less frequently than emerging and young adults, who overestimated the extent to which they would be accepted by peers.

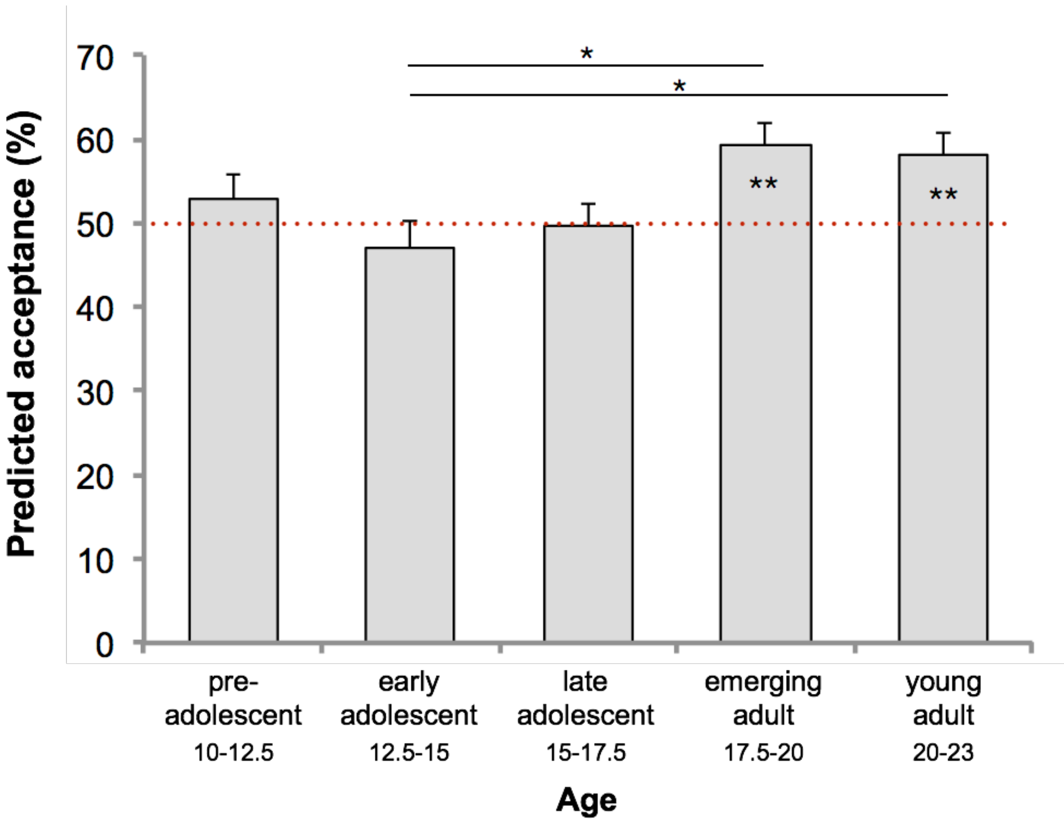

Figure S1. Relative to adolescents, young adults overestimated how much they would be liked by peers. Graph shows average percentage of acceptance predictions for each age group. Error bars indicate standard errors of the mean (SEM). Red dotted line denotes actual rate of acceptance (50%). Key: * p<.05, ** p<.01.

Implicit: prediction response times age group comparisons.

A one-way ANOVA with the prediction response time difference score (acceptance – rejection) as the dependent variable and age group as the between subjects factor revealed a significant effect of age (F(4,106)=3.446, p=.011; Figure S2). Post-hoc between group comparisons revealed that when compared to other age groups, early adolescents, the same group that anticipated being liked by peers the least often, were slowest to predict acceptance compared to rejection (M=78.6ms, SE=28.5ms). This pattern was significantly different from emerging adults who showed an opposite pattern of speeding to predict acceptance (M=-58.2ms, SE=31.5ms; t(40)=3.221, p(corr.)=.008). No other group comparisons reached significance (all ps(corr.)>.103).

Results of one-sample t-tests within age group (against the null hypothesis of zero response time bias) indicated that early adolescents were significantly slower when predicting acceptance as compared to rejection (t(23)=2.759, p=.011). By contrast, emerging adults were somewhat slower when predicting rejection relative to acceptance (t(18)=-1.846, marginal p=.081). All other participant groups did not exhibit differences in response time for acceptance compared to rejection (all ps>.218). In sum, early adolescents exhibited an internal heuristic more consistent with expecting rejection from others, whereas emerging adults demonstrated an internal heuristic more consistent with expecting others to accept them.

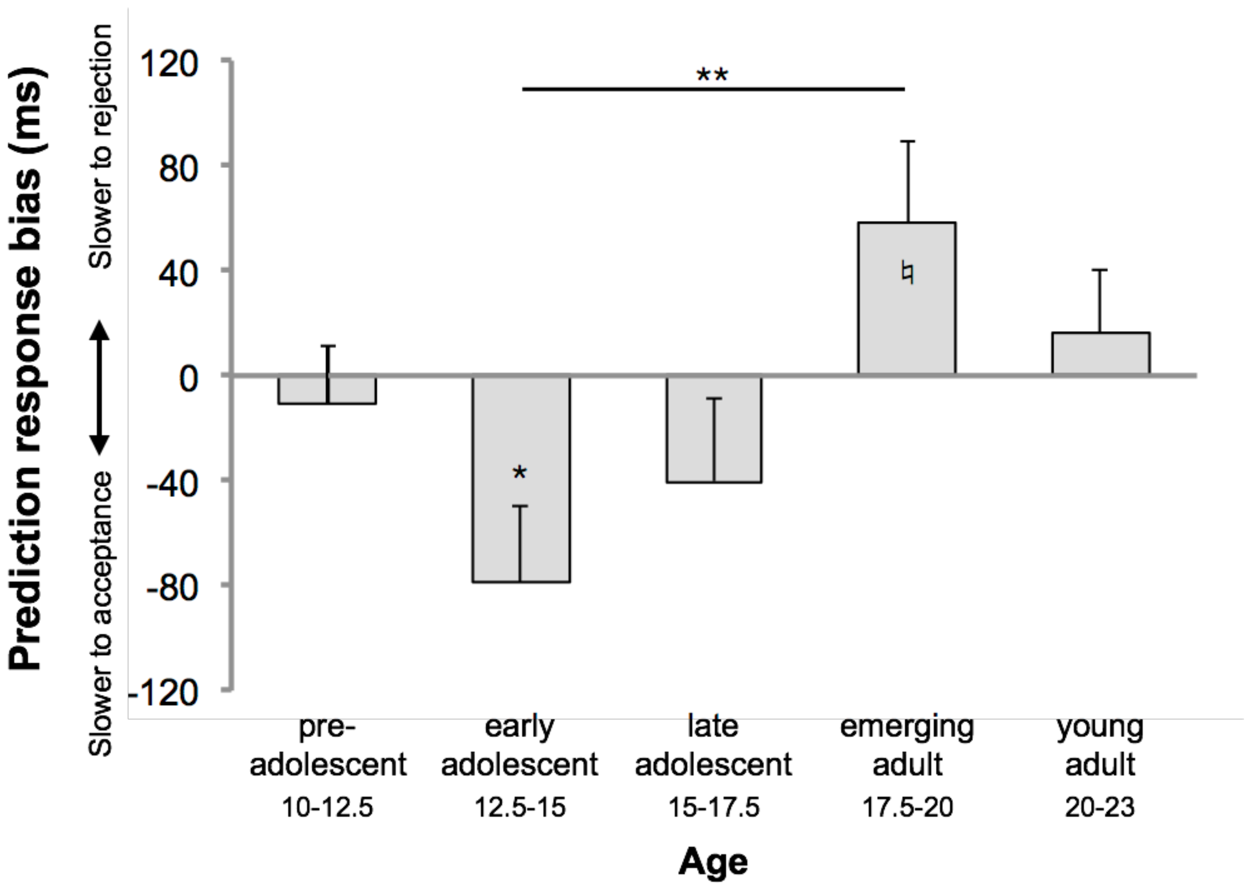

Figure S2. Response time bias for predicting rejection vs. acceptance differs with age. Graph shows difference score of prediction response RT during acceptance vs. rejection for each age group. Positive values indicate slowing when predicting rejection, whereas negative values indicate slowing when predicting acceptance. Error bars indicate SEM. Key: ♮ $p<.085$, * $p<.05$, ** $p<.01$.

Changes in views of self age group comparisons.

A one-way ANOVA with the self-esteem percent change score as the dependent variable and age group as the between subjects factor indicated there were significant age differences in task-induced changes in self-views ($F(4,103)=3.382$, $p=.012$; Figure S3). Post-hoc between group comparisons revealed that early adolescents experienced a unique drop in self-views (M=-5.08%, SE=2.48%) that differed significantly from the rise experienced by late adolescents (M=3.54%, SE=1.95%; $t(41)=-2.747$, p(corr.)=.042), emerging adults (M=4.60%, SE=2.83%; $t(37)=-2.303$, p(corr.)=.022) and young adults (M=3.86%, SE=2.03%; $t(42)=-2.808$, p(corr.)=.029). The rise in self-views experienced by all other participant groups was equivalent (all ps(corr.)>.416).

Next, a set of one-sample t-tests evaluated the magnitude of these shifts in self-views relative to a null hypothesis of zero change. Within each age group, findings revealed that the drop in self-views experienced by early adolescents was marginally significant ($t(20)=-2.049$, $p=.054$), as was the rise in self-views observed in late adolescents and young adults ($t(21)=1.816$, marginal $p=.084$; $t(22)=1.899$, marginal $p=.071$, respectively). There was not a significant task-induced change in self-views exhibited by any other age groups (all ps>.121). Taken together, these findings suggest that the experience of mixed social evaluative feedback differentially impacted self-views across age, wherein self-enhancement emerged late during adolescence.

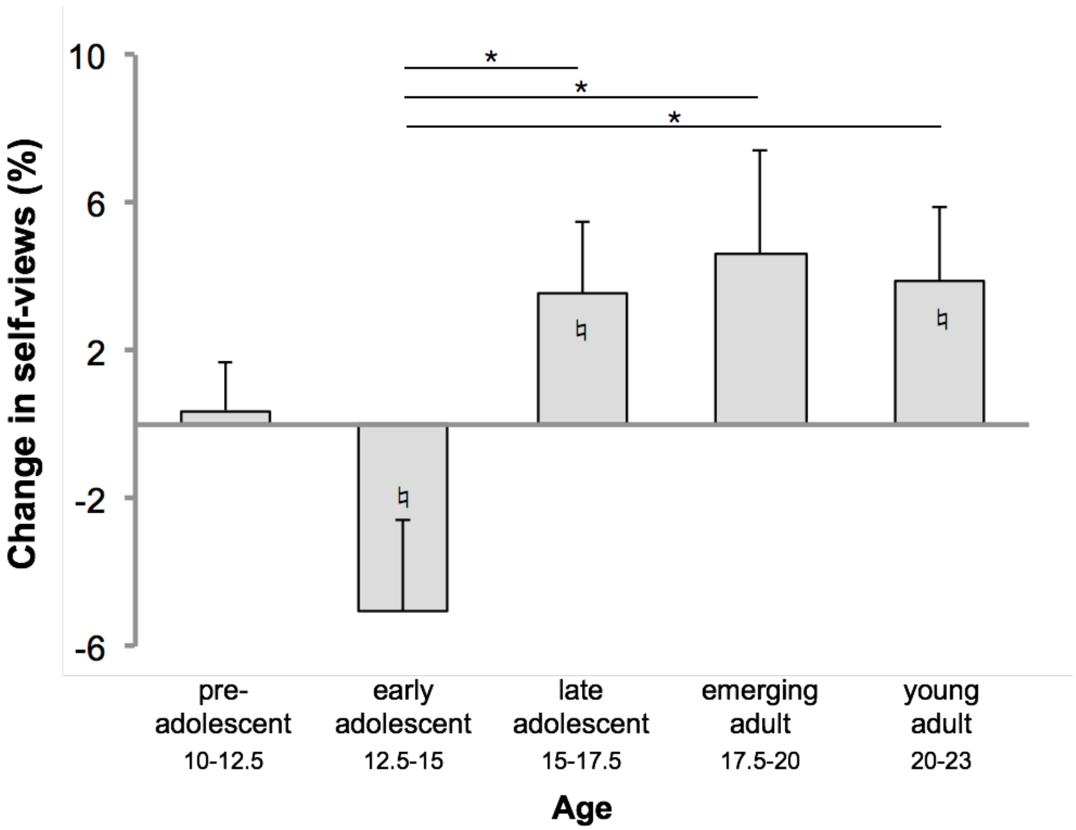

Figure S3. Task-induced changes in self-views differ across development. Graph shows the percent change in self-esteem score pre-task vs. post-task. Positive values indicate a boost in self-views, whereas negative values indicate a reduction in self-views. Error bars indicate SEM Key: ♮ p<.085, * p<.05.

Changes in likability ratings of peers age group comparisons.

Key analyses tested whether the tendency to increase liking after acceptance and decrease liking after rejection varied with age. A repeated measures ANOVA testing for age effects on change in likability ratings following acceptance and rejection revealed a significant interaction (F(4,98)=2.670, p=.037; Figure S4). Pairwise comparisons within each age group revealed that emerging adults ($M_{\Delta LIKE}$=-0.69, $SE_{\Delta LIKE}$=1.97; $M_{\Delta DISLIKE}$=-4.47, $SE_{\Delta DISLIKE}$=2.08) and young adults ($M_{\Delta LIKE}$=3.10, $SE_{\Delta LIKE}$=1.57; $M_{\Delta DISLIKE}$=-4.36, $SE_{\Delta DISLIKE}$=1.96) adjusted likability ratings of peers upwards or downwards in accordance with whether they were liked or disliked (t(17)=1.935, marginal p=.070; t(22)=6.566, p<.001, respectively). All other groups did not alter likability ratings as a function of whether they were liked or disliked (all ps>.094).

One sample t-tests were computed within each age group for acceptance and rejection feedback, separately, to compare the magnitude of these shifts in likability ratings relative to a null hypothesis of zero change. Findings revealed that emerging and young adults showed a significant decrease in likability rating of peers who rejected them (t(17)=-2.151, p=.046; t(22)=-2.220, p=.037, respectively), whereas only young adults showed an increase in likability ratings of peers that accepted them (t(22)=1.970, marginal p=.062). All other groups did not demonstrate significant changes in ratings of the peers (all ps>.127). Taken together, findings showed that being accepted or rejected by peers impacted how emerging and young adults viewed their peers, while other participant groups retained consistent evaluations of peers following social feedback.

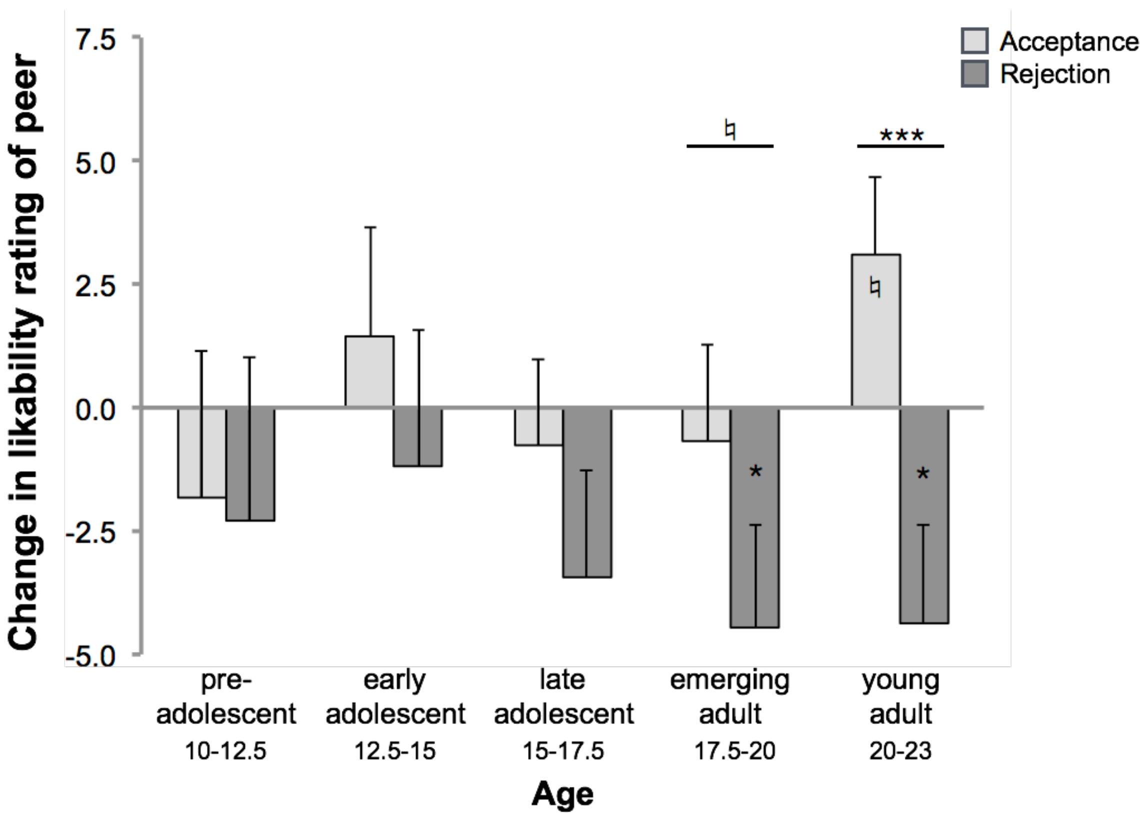

Figure S4. Feedback-specific changes in likability ratings of peers present in emerging and young adults only. Graph shows the differences score in peer likability rating pre-task vs. post-task as a function of feedback type. Light gray bars indicate change in likability rating following acceptance and dark gray bars indicate change in likability rating following rejection. Positive values indicate an upgrade in peer rating, whereas negative values indicate a downgrade in peer rating. Error bars indicate SEM Key: ♮ p<.085, * p<.05, *** p<.001.

Memory control analysis age group comparisons.

A repeated measures ANOVA with the memory accuracy as the outcome variable, feedback type (acceptance, rejection) as a within-subjects factor, and age group as the between-subjects factor revealed that the interaction between feedback type and age group was not significant (F(4,102)=.515, p=.725; Figure S5). The main effect of age was also not significant (F(4,102)=.360, p=.836).

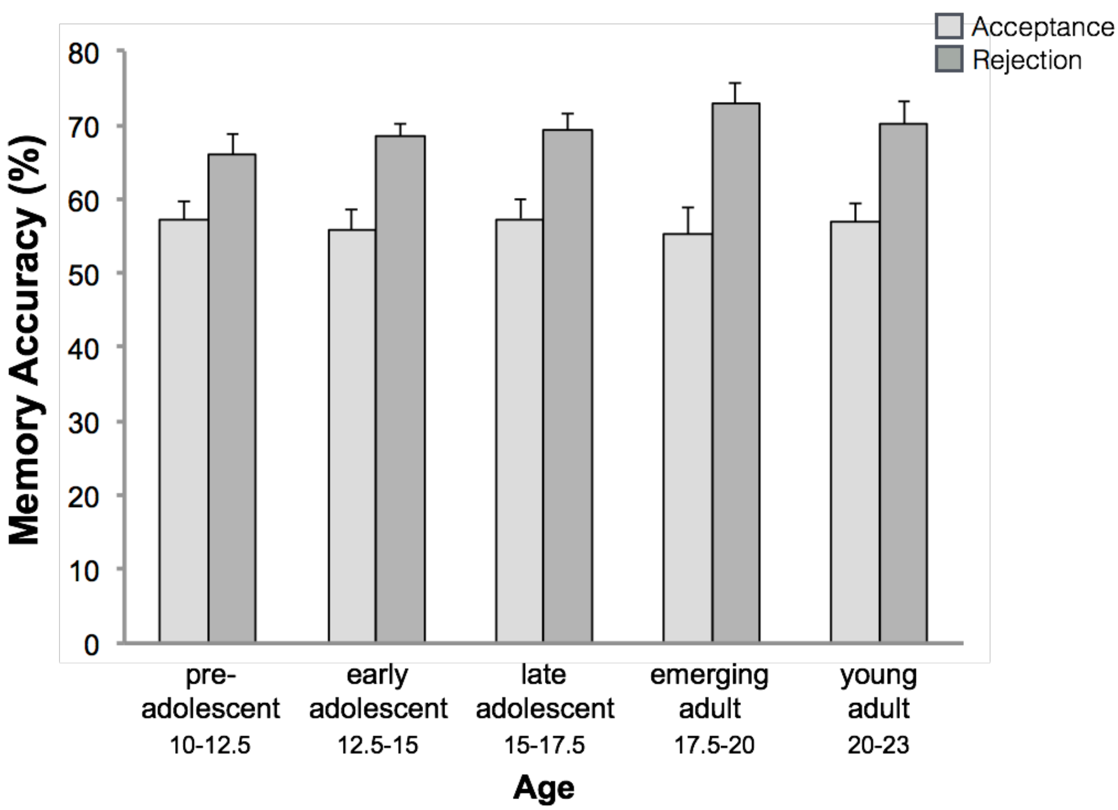

Figure S5. Memory retention control analysis. Memory accuracy for feedback is equivalent across age. Light gray bars indicate accuracy for acceptance and dark gray bars indicate accuracy for rejection. Error bars indicate SEM.

Paper 1 Supplemental Figure

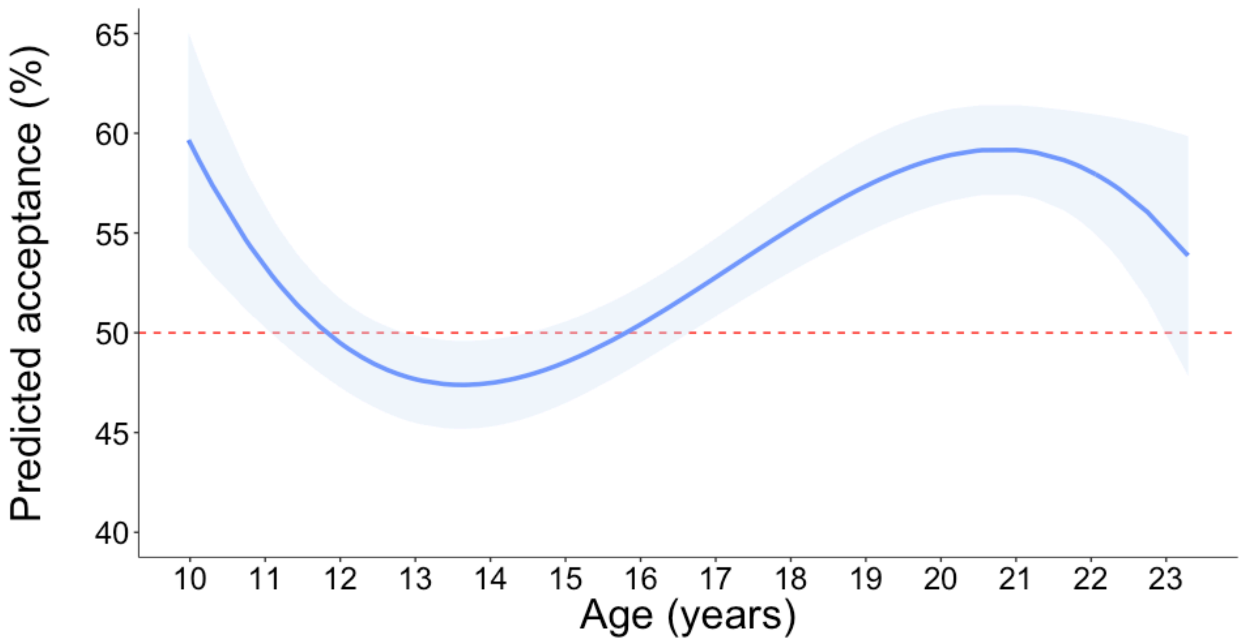

Figure S6. Relative to adolescents, young adults overestimated how much they would be liked by peers. Graph shows a blue fit line of predicted values of acceptance expectancy (percent of trials predicted acceptance) based on the traditional cubic regression model. Blue shading indicates SEM. Red dotted line denotes actual rate of acceptance (50%).

Paper 1 Supplemental Table

Age	N	$\textbf{Mean}_{\text{SAMPLE}}$	$\textbf{SE}_{\text{SAMPLE}}$	$\textbf{Mean}_{\text{NORM}}$
10-14	42	3.07	0.07	3.09
15-17	25	3.20	0.12	2.98
18-23	39	3.13	0.11	3.19

Table S1. Self-views are comparable to normed levels for each age group. Age groups binned by version of self-perception profile administered. Within each age group, participants scored a score roughly consistent with normed means (one-sample t-test against normed mean for each scale: all ps>.078).

Paper 2 Supplemental Methods

Supplemental Figure

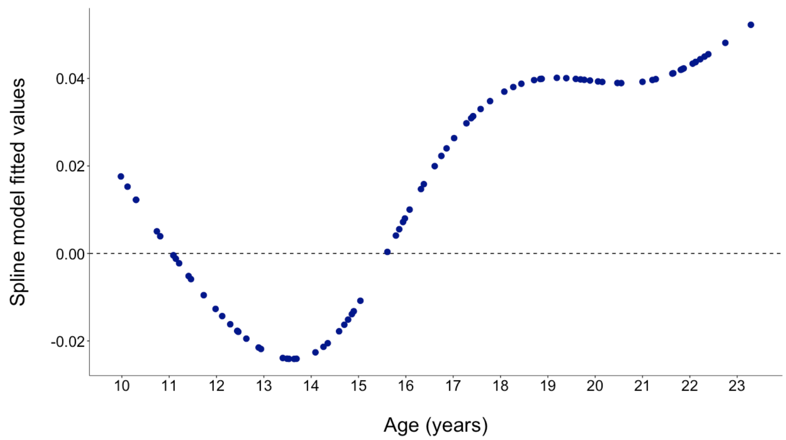

Figure S7. Nonlinear age predictor derived from spline model reported in Paper 1. Task induced changes in self-views were found to follow a nonlinear pattern that is not capture by traditional nonlinear functions (e.g. quadratic, cubic). This function describes a behavior that dips during early adolescence and rises through late adolescence remaining stable thorough adulthood.

Supplemental Table

	MNI coordinates				
Region	x	y	z	z-statistic	cluster size (k)
MAIN EFFECTS					
Acceptance vs. Rejection Feedback					
DLPFC	26	4	54	5.63	13489
precentral gyrus	-36	-16	44	4.92	7191
Rejection vs. Acceptance Feedback					
DMPFC	2	50	36	7.23	4400
Temporal pole	52	18	-26	6.36	4062
Inferior frontal gyrus	-38	20	-20	6.17	2997
Thalamus	-4	-20	10	5.82	2072
Superior temporal sulcus	-54	-26	-4	5.83	1198

Table S2. fMRI activity during acceptance vs. rejection and rejection vs. acceptance during the feedback phase. All clusters thresholded at whole-brain FWE p<.05.

Paper 3 Supplemental Materials

Supplemental Methods.

Data processing for monetary reward effort task.

Trials underwent a quality check, for which 3,186 trials passed (93.93% of all 3,392 trials). We excluded 3.24% of all trials wherein participants began gripping before the start of the grip phase, as indicated by grip force values being above 20% of the threshold at the trial onset. We also excluded trials for which participants began gripping relatively late (>1s), which occurred on trials 1.16% of all trials. A logistic regression indicated that these excluded trials did not vary significantly by value (B=0.148, p=.506). As described above, we also excluded 2.83% of trials identified as opt-out trials from measurements of peak force. The LME dependent variable peak force was inspected for outliers. One outlier was identified using the Outlier Labeling Method (Hoaglin et al., 1986) with a *g* multiplier of 2.2 (Hoaglin & Iglewicz, 1987) and were then Winsorized (Dixon, 1960). The Winsor approach involves replacing outliers with the maximum (or minimum) value within the bounds of the outlier threshold. Regression residuals were also inspected for normality and outliers.

Data processing for social evaluation effort task.

Trials underwent a quality check, for which 5,677 trials passed (92.76% of all 6,120 trials). We excluded 1.83% of all trials wherein participants began gripping before the start of the grip phase, as indicated by grip force values being above 20% of the threshold at the trial onset. We also excluded trials for which participants began gripping relatively late (>1s), which occurred on trials 2.50% of all trials. A logistic regression indicated that these excluded trials did not vary significantly by value (B=0.212, p=.467). As described above, we also excluded 4.89%

of trials identified as opt-out trials from measurements of peak force. The LME dependent variable peak force was inspected for outliers and none were found. Regression residuals were also inspected for normality and outliers.

Supplemental Table

Outcome	AIC null without age	AIC linear age	AIC quadratic age
Money: Peak Force	-6991.82	-6992.886	<u>-7001.00</u>
Money: Opt-out Trials	309.96	<u>297.86</u>	302.97
Social: Peak Force	-13058.42	-13064.57	<u>-13069.23</u>
Social: Opt-out Trials	1479.37	<u>1477.64</u>	N/A
Combined: Peak Force	-19645.04	-19515.23	<u>-1672.64</u>

Table S3. Model comparison was carried out using AIC. The optimal model (underlined) was chosen and carried forward for statistical inference. N/A indicates a model that could not converge.

Supplemental Figures

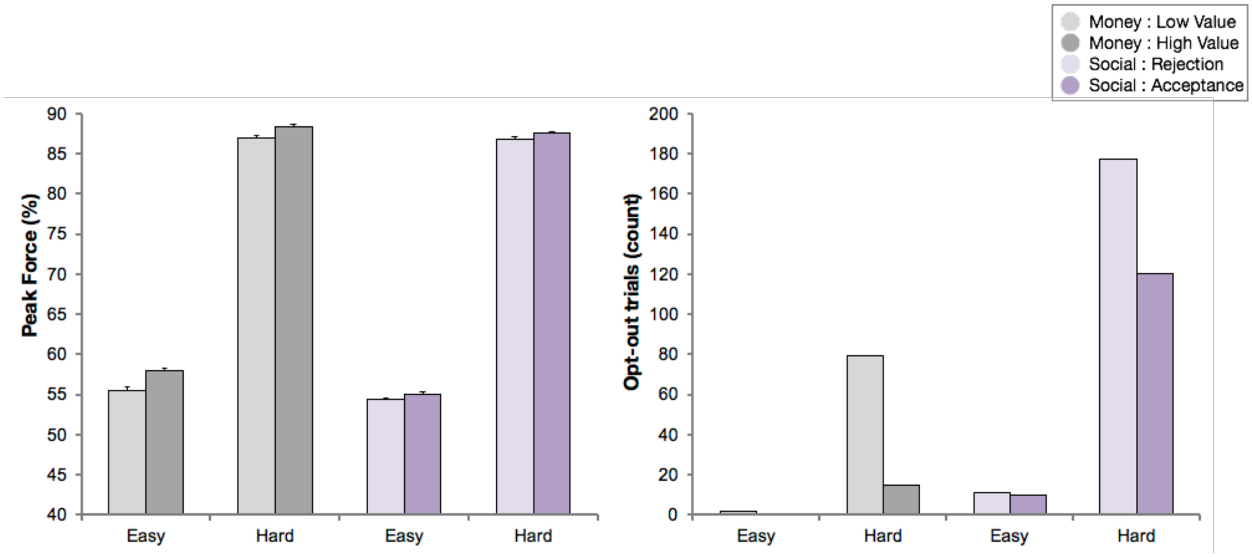

Figure S8. Main effects of Difficulty and Value on peak grip force and opt out choice behavior. A. Participants showed greater peak force when trials were hard and relatively higher in value. Bars represent standard error of the mean (SEM). B. Participants exhibited strategic choice behavior, evident in a tendency to opt out of hard, low-value trials and of hard social trials, especially those in which participants predicted to be rejected.