Social Cognitive and Affective Neuroscience Advance Access published October 9, 2015

Social Cognitive and Affective Neuroscience, 2015, 1–10

doi: 10.1093/scan/nsv095
Original article

Neural mechanisms of social influence in adolescence

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Abstract

During the transformative period of adolescence, social influence plays a prominent role in shaping young people's emerging social identities, and can impact their propensity to engage in prosocial or risky behaviors. In this study, we examine the neural correlates of social influence from both parents and peers, two important sources of influence. Nineteen adolescents (age 16–18 years) completed a social influence task during a functional magnetic resonance imaging (fMRI) scan. Social influence from both sources evoked activity in brain regions implicated in mentalizing (medial prefrontal cortex, left temporoparietal junction, right temporoparietal junction), reward (ventromedial prefrontal cortex), and self-control (right ventrolateral prefrontal cortex). These results suggest that mental state reasoning, social reward and self-control processes may help adolescents to evaluate others' perspectives and overcome the prepotent force of their own antecedent attitudes to shift their attitudes toward those of others. Findings suggest common neural networks involved in social influence from both parents and peers.

Key words: social influence; adolescence; functional MRI; mentalizing; self-control; reward

Introduction

Adolescence is a period of social reorientation during which young people begin to develop the identities that will define their adult relationships, interests and social roles (Adams and Marshall, 1996). As a part of the process of social identity formation, adolescents must integrate the perspectives of others with their own to create a unique, coherent sense of self. Parents remain a crucial source of feedback and authority, but sensitivity to peer attitudes also becomes essential as adolescents begin to navigate more complex social environments (Wentzel and Caldwell, 1997; Tarrant *et al.*, 2001; McLean, 2005). Adolescents must therefore cope with potential discrepancies between parent and peer attitudes, and the relative influence of parents and peers differs across domains (Smetana *et al.*, 2006). Moreover, alongside the psychological developments that characterize adolescence, recent research has shown that neural structures continue to mature, with significant changes in brain regions that support cognitive, motivational and affective processes (Nelson *et al.*, 2005). The adolescent brain is thought to be highly flexible and plastic (Crone and Dahl, 2012) and therefore may be particularly sensitive to social input (Blakemore and Mills, 2014). The potential of social influence to shape the developmental trajectories of adolescents, for good and for ill, makes the study of influence in relation to its neural correlates in the changing adolescent brain an important research objective.

Interestingly, the substantial neurobiological developments that occur throughout this period occur predominantly in regions that exert considerable impact on social processes (for review, see Blakemore, 2008; Casey *et al.*, 2008). Structurally, primary motor and sensory regions mature early, but regions implicated in complex social cognition and self-control continue to develop throughout adolescence (Gogtay *et al.*, 2004; Sowell *et al.*, 2004; Mills *et al.*, 2014). At a functional level, considerable changes are observed in the recruitment of mentalizing regions, with correlated improvements in empathic behavior and interpersonal skills (Blakemore *et al.*, 2007). Activity in self-control regions also becomes increasingly refined over time (Casey *et al.*, 2000; Bunge *et al.*, 2002; Durston *et al.*, 2006). Importantly, neural regions associated with such functions as mental state reasoning and self-control are still developing during the adolescent period, with implications for social identity formation and the potential to be influenced by one's social context. Taken together, the extant literature paints a picture of

Received: 12 February 2015; **Revised:** 30 May 2015; **Accepted:** 13 July 2015

the adolescent brain as a continuously evolving structure, in which neural activity becomes more precisely adapted to affective, cognitive and social demands.

In spite of recent advances in our understanding of the changing adolescent brain, we know very little about the neural mechanisms involved specifically in social influence processes. A few studies have considered the neural pathways that mediate the effects of social influence on risky decision making in adolescents (Chein *et al.*, 2011; Telzer *et al.*, 2015), but research on the basic mechanisms supporting social influence itself is still relatively incomplete. Previous research does, however, suggest several candidate neural processes that may serve as the foundation for an effective analysis of social influence in adolescence. First, functional and structural variation in right ventrolateral prefrontal cortex (RVLPFC) have been associated with individual differences in susceptibility to social influence (Campbell-Meiklejohn *et al.*, 2010, 2012). In particular, greater activity in the RVLPFC correlates with participants' willingness to alter their opinions about works of music when faced with strangers' discrepant attitudes (Campbell-Meiklejohn *et al.*, 2010). Second, social influence may rely on mentalizing - the process of considering and thinking about others' mental states. Thus, mentalizing regions including dorsomedial prefrontal cortex (DMPFC), temporoparietal junction (TPJ) and the precuneus/PCC may contribute to social influence because of the importance of these regions during adolescence for understanding the significance of others' beliefs and attitudes for the self (Pfeifer *et al.*, 2007; Pfeifer *et al.*, 2009). Indeed, Falk *et al.* (2014) found that mentalizing network [DMPFC, right TPJ (RTPJ) and PCC] activity during social exclusion in adolescents predicted later responsiveness to peer influence regarding risky (simulated) driving behavior. Lastly, social influence may be associated with reward processing, as the need to belong and fit in increases during adolescence (Brown and Lorh, 1987; Doremus-Fitzwater *et al.*, 2010; Somerville *et al.*, 2010). For this reason, aligning one's attitudes with those of important others may be experienced as rewarding (Blakemore and Mills, 2014) and be associated with activity in reward regions. Indeed, several studies have suggested that reward learning may exert a substantial impact on social influence processes through activity in the nucleus accumbens (NAcc) and ventromedial prefrontal cortex (VMPFC; Klucharev *et al.*, 2009; Zaki *et al.*, 2011; Cascio *et al.*, 2015).

Another crucial factor that may modulate the psychological and neural mechanisms of influence in adolescence is the source of social influence. Although a few studies have begun to emerge which examine how peers or strangers influence decision making in adults (e.g. Zaki *et al.*, 2011) and adolescents (e.g. Falk *et al.*, 2014; Cascio *et al.*, 2015), we do not as yet have much information about how different sources may impact social influence processes. The two most important sources of social influence for adolescents are family members [especially parents (Brown *et al.*, 1993)] and peers (Gardner and Steinberg, 2005). However, the relative importance of parental and peer sources seems to shift over the course of adolescence, at least in some domains (Smetana *et al.*, 2006). Peer influence seems to increase in early adolescence (cf. Scalici and Schulz, 2014 sample of 11- to 14-year-olds) but the predominance of parental influence seems to reassert itself in late adolescence. For example, in a recent study of risk perception in a large sample of adolescents, Knoll *et al.* (2015) found that influence from peers diminished with age, and that peer influence was only more impactful than adult influence for younger adolescents. Parental influence is therefore not likely to be replaced by peer influence during adolescence (Brown *et al.*, 1993). Rather, new types of relationships and new forms of influence are formed and added to the adolescent's social network without replacing previous ones (Krosnick and Judd, 1982; Chassin *et al.*, 1986; Bauman *et al.*, 2001; Walls *et al.*, 2009). Parents may also exert indirect influence through their impact on peer selection (Van Ryzin *et al.*, 2012). In light of the complex and changing effects of parental and peer influence during adolescence, it is important to clarify whether these sources of influence recruit common or distinct psychological and neural mechanisms.

To date, previous fMRI work on social influence has largely focused only on two kinds of sources: strangers (e.g. Campbell-Meiklejohn *et al.*, 2010; Falk *et al.*, 2014) and group ratings (e.g. Klucharev *et al.*, 2009; Zaki *et al.*, 2011). In this study, we used fMRI to investigate the neural basis of peer and parental influence on adolescents' subjective evaluations of artwork. We felt that works of art would provide a neutral domain, with potentially flexible attitudes that are not already saturated with influence from either group. While undergoing scanning, participants received information regarding their own peers' or parents' actual attitudes (i.e. there was no deception) and immediately provided their own evaluation of the artwork stimulus. Shifts in participants' attitudes toward those of their peer (i.e. peer influence) or those of their parent (i.e. parental influence) were assessed based upon participant ratings of each stimulus acquired prior to the scanning session. Thus, we were able to examine neural activity associated with the actual unfolding of social influence processes as they occur for adolescents when evaluating the attitudes of real sources of social influence in their lives. Integrating the results of prior literature on social influence, we anticipated that peer and parental influence would depend upon the interplay between neural systems involved in (i) self-control (RVLPFC), (ii) theory of mind/mentalizing [DMPFC, RTPJ, left TPJ (LTPJ), and precuneus] and (iii) reward processing (NAcc and VMPFC). Importantly, we also examined potential differences and overlap in the neural processes involved in social influence based on the influence source (parent *vs* peer).

Methods

Participants

Twenty adolescent participants were recruited for this neuroimaging study along with their primary caregiver. One participant's data were excluded from analysis (see below) due to excessive motion artifacts, and therefore the final sample included 19 adolescents, all of whom were in the 10th or 11th grade (Mean age = 17.56 years, range = 16.44–18.43; 12 males). All participants were Mexican-American students at a local high school in which 70% of enrolled students received free or subsidized lunches. Most parents had not completed a high-school education. Participants were ineligible if they were left-handed, using psychoactive medications or drugs, had been diagnosed with a neurological or psychiatric disorder, were pregnant, had a history of claustrophobia or presented any other condition that would render participation in fMRI research hazardous. Other exclusion criteria were employed (see details in Stimulus Selection below) so as to ensure that the prerequisite number of stimulus items were available for each planned experimental condition, as well as to control for confounds. Participants provided written informed consent approved by the University of California, Los Angeles (UCLA) Institutional Review Board.

Stimulus selection

Stimulus images were selected from a set of 259 works of classical and contemporary art, encompassing a wide range in terms of both style and subject matter. Adolescents and their primary caregiver each independently provided ratings of each stimulus item several weeks prior to the scan by completing an online survey, in which they indicated their liking of the image on a scale from 0 to 100 (anchored respectively at 'Dislike' and 'Like'). Stimulus ratings were also available from 40 of the participants' actual peers at school. These 40 peers were other participants in the study (20 of whom completed the current fMRI study). Participants were not informed who the 40 peers were but were told they were students in their school.

In order to manipulate social influence for the scanner task, stimulus items were selected on which participants' ratings differed substantially from those of their parents or peers. On the basis of available participant, peer and parental stimulus ratings, stimuli were individually selected for each participant so as to comprise five mutually exclusive groups (such that no stimulus image was present in more than one group), as follows: (i) 20 items for which the parent's ratings were at least 20 points lower (more negative) than those of the participant, (ii) 20 items for which the parent's ratings were at least 20 points higher (more positive) than those of the participant, (iii) 20 items for which at least one peer's rating was at least 20 points lower (more negative than those of the participant, (iv) 20 items for which at least one peer's rating was at least 20 points higher (more positive) than those of the participant and finally (v) 20 additional items randomly selected as controls. Participants for whom such groups of items could not be generated were excluded from participation. This generally occurred when participants had predominantly negative or predominantly positive attitudes toward the set of stimulus items as a whole. Of the 23 participants recruited for the neuroimaging study, 3 were excluded in this manner, yielding a final sample size of 20. It is important to note that social influence trials were controlled for relative positivity/negativity of evaluation, relative to the participant's previous attitude.

fMRI paradigm

While undergoing fMRI, participants completed an artwork rating task in which they indicated the extent to which they liked or disliked each of the ideographically selected stimulus items (see Stimulus Selection above). Artwork stimuli were presented either without feedback (for Control Trials) or in the presence of on-screen parent/peer ratings (Parent Influence and Peer Influence Trials, see Figure 1). On each trial, participants rated the presented work of art using an on-screen scale ranging from 0 to 100 (anchored at Dislike and Like, respectively). Participants were instructed that the value '50' should be treated as neutrality, reflecting neither liking nor disliking of the selected item. Trials were presented in blocks, each consisting of one of the three conditions: Parental Influence (40 items), Peer Influence (40 items) and No Influence (20 items). Participants were instructed that, on some trials, they would see the rating that either their parent or one of their peers had provided.

During No Influence trials, no information was provided to participants regarding the ratings of either the parent or their peers. Each No Influence trial began with a 2 s display of the words 'No Feedback', after which the artwork stimulus item and the rating scale were displayed on the screen, with the response cursor initially placed at the middle value, '50'. Participants had a maximum duration of 10 s to rate the stimulus using the on-screen scale. The task was self-paced such that the trial ended upon participant response.

During Parental and Peer Influence trials, either the parent's rating or a peer's rating of the stimulus item was presented on-screen, in order to potentially influence participants' own ratings (see Figure 1 for example trials). Each Parental or Peer Influence trial began with a 2 s display of the words 'Your Parent's rating was X' or 'Your Peer's rating was X', as appropriate, where X was replaced with the actual value of the parent or of one of the participant's peers. The artwork stimulus item and the rating scale then appeared on-screen as in the No Influence trials (with the response cursor initially placed at the middle value of 50), with the important difference that the parent or peer rating also remained on screen. The precise location of the parent or peer rating was indicated by a colored line intersecting the scale at the appropriate location, with the numerical value of the parent or peer rating presented just below. As in the No Influence trials, participants had a maximum duration of 10 s to indicate their liking or disliking. Importantly, the parent or peer influence rating is presented prior to the actual appearance of the artwork on-screen. Thus, it is not likely that participants responded on any given trial before having noted the rating of the other individual (peer or parent).

Trials were presented over the course of two functional runs, with 2 blocks of 10 Parental Influence trials, 2 blocks of 10 Peer Influence trials and 1 block of 10 No Influence trials in each run. Both Parental Influence and Peer Influence conditions were balanced across runs, such that each contained an equal number of trials on which social influence ratings were relatively higher and relatively lower than the participant's own. Stimuli were presented in a pseudorandom order so as to maximize design efficiency, with jittered intertrial intervals drawn from an exponential distribution with a mean of 5 s. No more than 2 occurrences of Parent Influence, Peer Influence or No Influence blocks could occur sequentially. Scale movement and stimulus duration were determined on the basis of pilot testing, such that participants could comfortably make their judgments, move the on-screen scale and confirm their responses in the allotted time.

fMRI data acquisition

All imaging data was acquired using a 3.0-T Siemens Trio scanner at the Center for Cognitive Neuroscience at UCLA. Across two functional runs, T2*-weighted echo-planar images were acquired during completion of experimental tasks described above (slice thickness = 3 mm, gap = 1 mm, 36 slices, repetition time (TR) = 2000 ms, echo time (TE) = 25 ms, flip angle = 90°, matrix = 64 × 64, field of view = 200 mm). An oblique slice angle was used to minimize signal dropout in ventral medial portions of the brain. In addition, a T2-weighted, matched-bandwith anatomical scan was acquired for each participant (TR = 5000 ms, TE = 34 ms, flip angle = 90°, matrix = 128 × 128; otherwise identical to EPIs). Lastly, we acquired a T1-weighted magnetically prepared rapid acquisition gradient echo anatomical image (slice thickness = 1 mm, 176 slices, TR = 2530 ms, TE = 3.31 ms, flip angle = 7°, matrix = 256 × 256, field of view = 256 mm).

fMRI data preprocessing and analysis

Functional data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). Within each

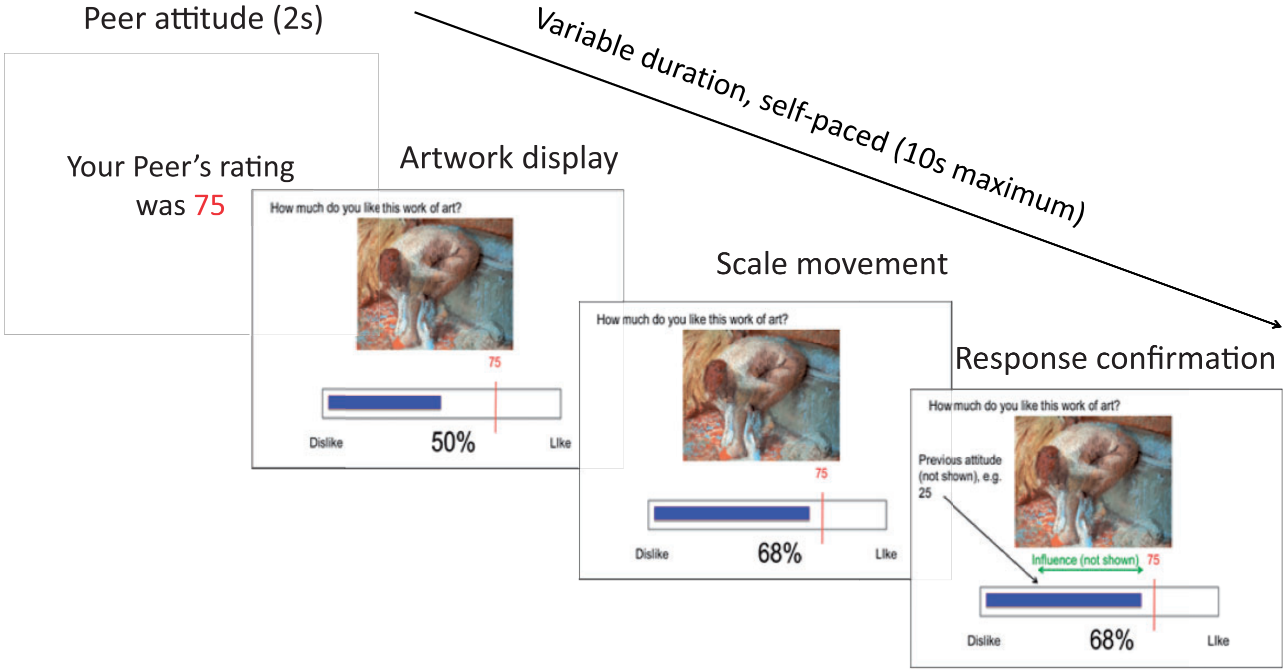

Fig. 1. Participants indicated their liking of various artwork stimuli with and without social influence information. In the Peer Influence condition, an initial presentation (2 s) informed participants of the attitude of one of their peers. Next, the given artwork stimulus was presented, along with the response scale and the peer's rating (in red). Participants then manipulated the scale, moving it to the desired value, and finally confirmed their response. The final panel above shows the operationalization of social influence in this study (shift in rating in the direction of the peer's or parent's attitude – here an influence score of 43 (68 [response] 25 [previous attitude]) is indicated). Participants had 10 s maximum duration to respond, followed by a jittered inter-trial interval (ITI). The entire period from the presentation of social influence information (first panel) through to the participant's response selection (final panel) was modeled as a variable epoch.

functional run, image volumes were corrected for slice acquisition timing, realigned to correct for head motion, segmented by tissue type and normalized into standard Montreal Neurological Institute (MNI) stereotactic space (resampled at 3 × 3 × 3 mm). Finally, images were smoothed with an 8-mm Gaussian kernel, full width at half maximum (FWHM).

A general linear model was defined for each participant, in which trials were modeled as variable epochs spanning the duration of the entire trial, from initial presentation of social influence information (i.e. parent rating, peer rating or no feedback) to the participant's response, convolved with the canonical (double-gamma) hemodynamic response function. Three regressors of interest were modeled, including Parental Influence, Peer Influence and No Influence (Control) conditions. The model also controlled for 18 motion parameters (3 translations and rotations, their squares and first-order derivatives), and a junk regressor for acquisitions on which either translation exceeded 2 mm or rotation exceeded 2° in any direction. The time series was high-pass filtered using a cutoff period of 128 s and serial autocorrelations were modeled as an AR(1) process. Contrast images were averaged across runs for each participant and entered into a mixed effects analysis at the group level.

Analysis of functional imaging data proceeded in four steps. First, whole-brain analyses were conducted to determine regions active during the Peer Influence relative to No Influence condition as well as during the Parent Influence relative to No Influence condition. Second, a conjunction analysis revealed overlapping regions that were more responsive to both Peer Influence and Parent Influence trials relative to the No Influence condition. Third, Peer Influence and Parent Influence trials were directly compared to reveal any regions that might respond differently to parental *vs* peer feedback. Lastly, a functional region-of-interest (ROI) approach was used to examine the relationship between observed peer/parent influence and activity in task-responsive regions. Clusters exhibiting greater activity to the Peer Rating or Parent Rating trials than to the No Influence trials (in initial whole-brain analyses) were defined as functional ROIs, and parameter estimates for the respective contrasts were extracted from each ROI. Correlations between these parameter estimates and between-subject differences in mean observed Peer and Parent influence were then assessed in a condition-specific manner (i.e. Peer Influence > No Influence parameter estimates were used to predict mean Peer Influence).

Monte Carlo simulations implemented in 3dClustSim (from AFNI; Cox, 1996) were used to determine an appropriate cluster-size threshold ($k = 43$) for whole-brain analyses given the empirical smoothness of the images to ensure overall false discovery rate (FDR) of <0.05, when combined with a voxelwise significance threshold of $P < 0.005$. The task-sensitive regions identified by whole-brain analyses were used as functional ROIs for assessing between-subject activity differences associated with variation in observed social influence through linear regression (see details above). Parameter estimates were extracted from the ROIs using MarsBaR (Brett *et al.*, 2002).

Influence was computed on a trial-by-trial basis as the shift in a participant's rating of a given stimulus relative to his or her rating of the same stimulus prior to scanning. If a participant shifted their attitude away from that of the peer [parent] rating, the resulting social influence score was negative, whereas if a participant shifted their attitude towards that of the peer [parent], the resulting social influence score was positive. Positive influence was capped at a maximum determined by the difference between the influencer's rating and the participant's initial evaluation (i.e. an influence score could not be greater than the total initial difference between participant and influencer on a given stimulus item). The social influence metric used thus reflects the direct impact of the parent or peer rating on changes in participants' ratings of the stimuli. Social influence scores cannot be calculated for the No Influence (Control) condition as no parental or peer feedback was provided; for this condition, we merely computed the change in a participant's attitude (liking) toward a given artwork stimulus relative to ratings made prior to the scanning session.

As an example of social influence computation, consider a participant who has shifted her attitude toward a given work of art by 20 points, from an initial rating of 60 (slightly positive) to a final rating of 80 (extremely positive) when presented with a parental attitude of 90. Her influence score for this trial would be 20. If the participant had decreased her liking of the artwork to 40 following parental feedback of 90, her influence score would be −20. The difference between the participants' initial attitude and the peer or parent attitude was imposed as an upper limit on influence scores (i.e. the influence score could not be greater than the disparity between participant and peer/parent initial ratings). That is, if in the above scenario the participant had shifted from an initial rating of 60 to a final rating of 100 in the presence of a parental attitude of 90, the influence score would only be 30 (the portion of the shift attributable to influence) rather than the full 40 points of scale movement.

Results

Behavioral results of social influence manipulation

In the No Influence condition, participant ratings–of artwork stimuli did not change significantly ($M_{NoInfo} = -8.69$, $t(18) = -1.93$, $P = ns$). As predicted, participants showed significant social influence (relative to a null hypothesis of zero change) during the Peer Influence condition ($M_{peer} = 12.79$, $t(18) = 5.90$, $P < 0.001$). Thus, participants shifted their ratings of the artwork stimuli on average by about 13 points (out of a 100-point scale) in the direction of their peer. Chi-square and binomial sign tests can be used to test the proportion of participants exhibiting mean positive social influence (overall shift toward the attitudes of the peers) relative to a null hypothesis that an equal number of participants would show positive and negative influence. Out of 19 participants, 17 shifted their attitudes in the direction of their peers, a significant proportion (binomial sign-test $P < 0.0001$; $\chi^2(1,N = 19) = 11.84$, $P < 0.001$). Within-subjects *t*-tests indicated that mean peer influence across trials was significantly greater than zero for 13 out of 19 participants.

Participants also showed significant social influence (relative to a null hypothesis of zero change) during the Parental Influence condition ($M_{parental} = 22.46$, $t(18) = 12.16$, $P < 0.001$). Within-subjects *t*-tests indicated that all participants showed significant parental influence, which is extremely unlikely to occur by chance (binomial sign-test $P < 0.00001$; $\chi^2(1,N = 19) = 19$, $P < 0.001$). Within-subjects *t*-tests indicated that mean parental influence across trials was significantly greater than zero for all participants. Participants showed significantly more influence to parents than to peers ($M_{diff} = 9.68$, $t(18) = 6.34$, $P < 0.001$).

Neural correlates of social influence

Peer and parental influence trials relative to control. In order to assess neural responses to peer and parental influence during the art judgment task, we first conducted a whole-brain analysis in which Peer and Parent trials were each compared separately to the Control condition (in which no social feedback was provided). These contrasts reveal the recruitment of broadly similar neural regions in the presence of both peer and parental influences (Table 1 and Figure 2a). Specifically, during Peer > Control, adolescents demonstrated activity in brain regions associated with mentalizing, such as the DMPFC, RTPJ and LTPJ, the precuneus and the left temporal pole. Greater activity to Peer relative to Control trials was also observed in areas associated with self-control, including the RVLPFC the left ventrolateral prefrontal cortex (LVLPFC), the right middle frontal gyrus (RMFG) and the left middle frontal gyrus (LMFG). Among regions implicated in social reward, the VMPFC was found to be more active to Peer than Control trials. Similarly, during Parent > Control, adolescents demonstrated greater activity in mentalizing regions such as the RTPJ, LTPJ and precuneus as well as self-control regions such as the RVLPFC and the LMFG. Greater activity was also observed to Parental Influence trials in the VMPFC (Table 1 and Figure 2b).

Table 1. Summary of whole-brain analysis: Contrasts between conditions

Test Effect/Anatomical Region	*t*	*x*	*y*	*z*	*k*
Peer ≥ Control (No Feedback)					
Right temporoparietal junction	9.25	54	−60	36	768
Left temporoparietal junction	5.01	−49	−68	40	254
RVLPFC	8.89	47	50	−3	146
LVLPFC	5.11	−40	42	−7	72
Left temporal pole	3.49	−57	−4	−26	51
Right inferior temporal gyrus	6.55	62	−50	−12	95
Left inferior temporal gyrus	5.58	−57	−63	−10	43
VMPFC	5.62	4	55	−18	76
DMPFC	5.36	−7	47	42	257
Right middle frontal gyrus	5.50	40	22	36	177
Left middle frontal gyrus	5.20	−43	11	45	116
Left middle temporal gyrus	4.93	−65	−18	−19	44
Right supplemental motor area	4.93	21	38	51	70
Precuneus	4.90	6	−63	42	119
Control ≥ Peer (No Feedback)					
Left superior temporal gyrus	3.58	−52	−24	7	54
Parent ≥ Control (No Feedback)					
VMPFC	4.12	22	52	−17	136
Right temporoparietal junction	5.93	59	−63	31	693
Left temporoparietal junction	4.41	−45	−61	36	428
Precuneus	3.69	28	−72	55	336
Left middle frontal gyrus	5.61	−34	16	52	58
RVLPFC	5.07	44	51	−5	67
Control (No Feedback) ≥ Parent					
None					
Parent ∩ Peer ≥ Control (No Feedback)					
Right temporoparietal junction	5.65	57	−64	37	376
Left temporoparietal junction	4.41	−42	−52	46	190
Precuneus	5.92	−6	−64	40	109
RVLPFC	5.07	48	44	−5	60

A direct comparison of the parent and peer trials revealed greater activity to the Parental Influence condition only in visual cortex. No regions were selectively active to Peer relative to Parent trials in whole-brain analysis.

Common activations to both peer and parental influence trials. The apparent overlap in the neural responses to peer and parental influence relative to control was formally tested using a conjunction analysis (Parent ∩ Peer > Control), with the minimum statistic approach (Nichols *et al.*, 2005) which identified voxels that were statistically significant in both the Parent > Control

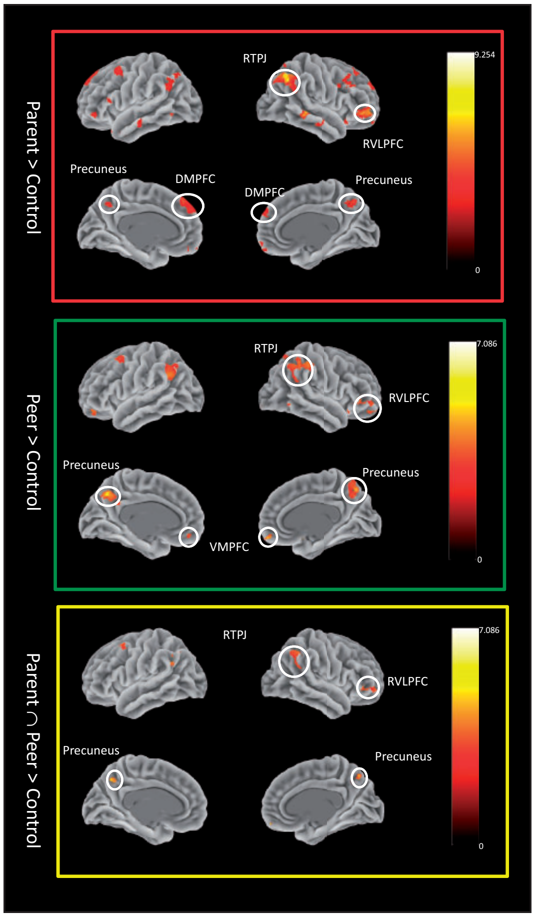

Fig. 2. Regions exhibiting significantly greater activity during Peer and Parent Influence trials relative to Control (No Influence), cluster-corrected FDR $P < 0.05$. (A) Parent > Control contrast (B) Peer > Control contrast (C) Conjunction contrast (Parent ∩ Peer > Control). Clusters identified in the Parent > Control and Peer > Control contrasts were employed as functional ROIs for further analyses of individual differences (see text).

and Peer > Control contrasts. This conjunction analysis revealed significant activity to both Parent and Peer trials in the RTPJ, LTJP, precuneus and RVLPFC. These results suggest that regions associated with mentalizing and self-control are responsive to social feedback from both peers and parents (Table 1 and Figure 2c).

Neural correlates of between-subjects variance in peer and parent influence. Next, in order to test whether task-responsive regions exhibited neural activity that covaried with between-subject differences in observed social influence, we utilized a functional ROI approach. Parameter estimates were extracted from each of the clusters identified by the Parent > Control and Peer > Control contrasts (see Table 1 and Figure 2a and b) that fell within our *a priori* regions [e.g. DMPFC, RTPJ, LTJP, precuneus (mentalizing); RVLPFC (self-control) or VMPFC (reward)]. An NAcc cluster was not identified in either the Parent > Control or Peer > Control contrasts and was therefore not included in this analysis. Parameter estimates were then correlated with between-subject differences in peer and parental influence to reveal regions whose activity covaried with actual influence scores. The parameter estimates thus employed were condition-specific: that is, clusters identified from the Parent > Control contrast were correlated with parental influence, while clusters identified from the Peer > Control contrast were correlated with peer influence.

Mean peer influence scores were significantly associated with parameter estimates from mentalizing regions: DMPFC ($r = 0.59$, $P = 0.009$), RTPJ ($r = 0.53$, $P = 0.02$) and left temporal pole ($r(17) = 0.54$, $P = 0.016$); as well as regions implicated in both self-control: RVLPFC ($r(17) = 0.53$, $P = 0.019$), LVLPFC ($r(17) = 0.47$, $P = 0.041$), right middle frontal gyrus ($r(17) = 0.47$, $P = 0.041$) and left middle frontal gyrus ($r(17) = 0.59$, $P = 0.008$), and reward: VMPFC ($r(17) = 0.50$, $P = 0.028$). Thus, the more active these regions were when viewing peer ratings, the more likely participants were to revise their own attitudes to bring them in line with those of their peers. For scatter plots of parameter estimates as a function of mean peer influence for a selected subset of these regions (see Figure 3). Similar effects were found for parental influence. Across participants, variation in parental influence was significantly associated with parameter estimates from three of the functional ROIs defined by the Parent > Control contrast: LMFG ($r(17) = 0.56$, $P = 0.013$), precuneus ($r(17) = 0.52$, $P = 0.023$) and LTPJ ($r(17) = 0.47$, $P = 0.04$). For scatter plots of parameter estimates from these regions as a function of mean parental influence (see Figure 4). Additionally, none of the clusters implicated in the Parent > Control or Peer > Control contrasts that fell outside the mentalizing, self-control and reward regions (e.g. regions) were significantly associated with social influence.

Discussion

Understanding the neural mechanisms of social influence is important, given the social significance of influence processes throughout the life course, and especially during adolescence. A clearer picture of the brain basis of social influence will enhance our appreciation of the contexts in which peers, parents and other influences may have significant impact on adolescents' decision-making processes. The present research sought to characterize the neural correlates of social influence in adolescence by analyzing the focal period during which peer and parent attitudes were integrated with those of the participants. The results provide evidence for the recruitment of a diverse set of brain regions implicated in mentalizing, self-control and reward.

First, processing both peer and parental attitudes involved activity in the MPFC, RTPJ, LTPJ, precuneus, RVLPFC and VMPFC. Second, activity in these regions correlated with between-subject differences in observed social influence. These findings suggest that social influence in adolescence is a complex and nuanced process which may involve both mental state reasoning as well as inhibition of one's own antecedent attitudes, with such changes in one's attitudes eliciting a reward response. Insofar as adolescence involves a constant negotiation of identity, in which young people's attitudes are aligned with and differentiated from those of parents and peers, adolescents may be sensitive to the social significance of their attitudinal positions *vis-à-vis* those of others (Ryan *et al.*, 1997; Vernberg *et al.*, 1999; Bryant *et al.*, 2003; Blakemore and Mills, 2014). Mentalizing may be essential for adolescents to adequately process the implications of their attitudes in an evolving social context, taking into account the reasons that parents and peers might have for holding discrepant views. Self-control resources may help adolescents to suppress the potency of their own antecedent attitudes, and when necessary, harmonize their own positions with those of others. Finally, reward processing may reflect the

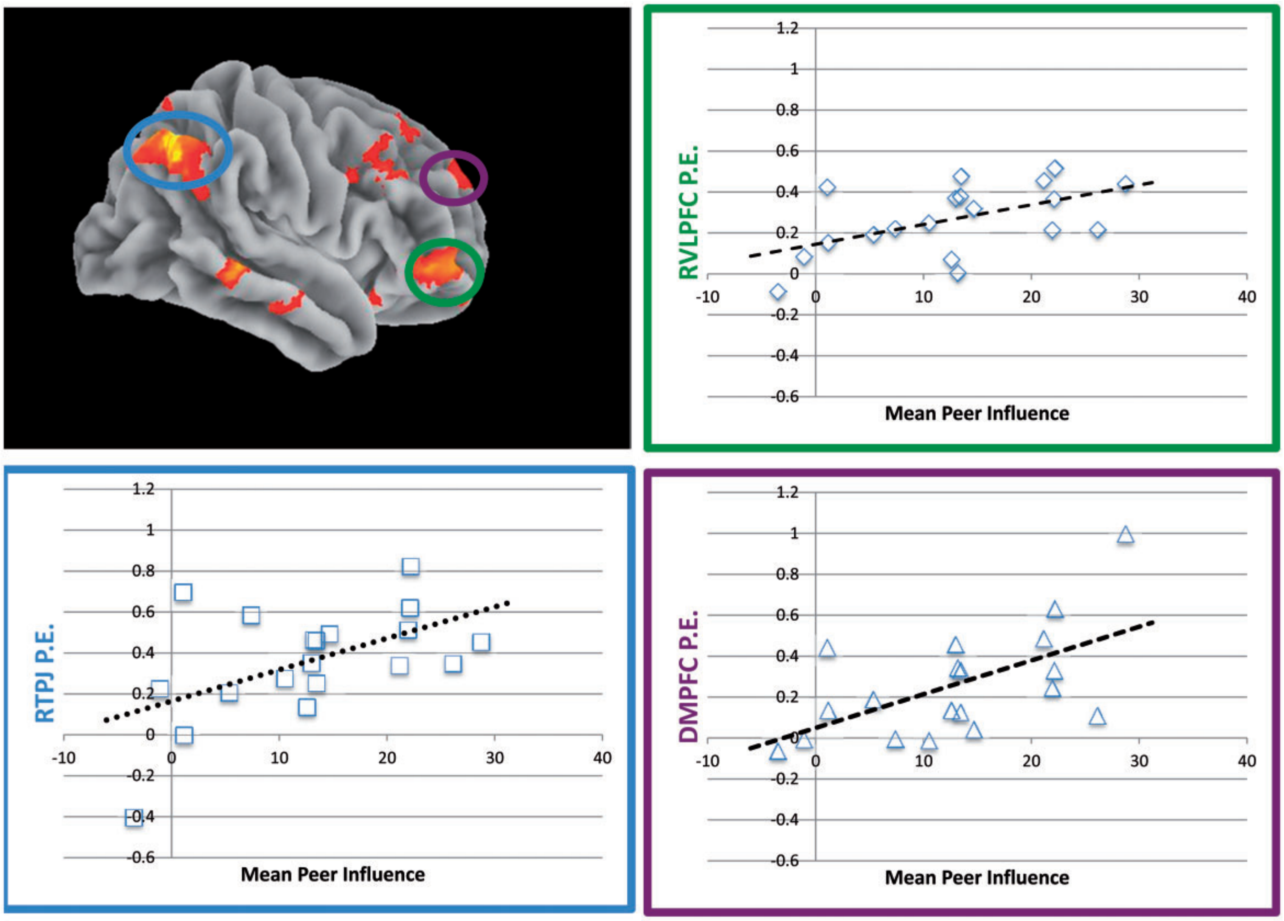

Fig. 3. Parameter estimates (from the Peer > Control contrast) from selected ROIs (DMPFC, RTPJ, and RVLPFC) are plotted against participants' mean peer influence score out of the available 100-point scale. In each case, participants' peer influence scores (attitude shift in the direction of the peers' position) were significantly correlated with parameter estimates from the displayed ROIs. Details are presented in the text, along with additional ROIs that showed a positive correlation with mean social influence.

intrinsic value adolescents associate with conforming to their peers and may enhance the efficacy of social influence pressures over time through reinforcement learning (cf. Klucharev *et al.*, 2009).

Interestingly, the neural correlates of peer and parental influence appear similar, even though these sources can provide adolescents with very different perspectives and enjoin upon them different courses of action. Peers and parents alike evoked activity in similar brain regions during social influence, and similar neural systems were associated with between-subject variation in susceptibility to peer and parental influence. Thus, while peers and parents often play distinct roles in adolescence, they may ultimately exert their influence in similar ways or through overlapping mechanisms. Additional work may profitably focus on the circumstances under which parental and peer influence may diverge, or the various factors that render adolescents more susceptible to influence from parental or peer sources. For example, parents may exert profound influence on adolescents' choices when values or moral concerns are made salient, whereas peers might be more influential in shaping adolescents' social activities and relationships at school. The artwork stimuli employed in this study likely represents a neutral domain, in which neither parents nor peers possess a decisive advantage in influence. As a result, such stimuli probably highlight regions recruited for influence from both sources, and indeed, the present research emphasizes overall similarities in the underlying neural mechanisms. Taken together, our results suggest that a common set of neural regions are involved in both peer and parental influence during adolescence.

Importantly, while this study employed real parental and peer attitudes as sources of social influence, peers and parents were not directly present to evaluate participants' responses or provide interactive feedback in real time. Future research should therefore examine how the presence or absence of real peers and close others during social influence impacts attitude change and neural processing. Notably, prior studies have found that the actual presence of peers may exert a profound impact on the social meaning that adolescents attach to their behaviors and decision-making processes, with elevated reward-related activity in the ventral striatum during decision making in the presence of peers (e.g. Chein *et al.*, 2011; Smith *et al.*, 2014; Cascio *et al.*, 2015). The attitudes of actual peers may therefore serve as a powerful force of social reinforcement through reward mechanisms that have been characterized more thoroughly in adults (e.g. Jones *et al.*, 2011).

Future research should consider the ways in which the continued development of the brain may affect adolescents' susceptibility to social influence. While our study does not have a child or adult comparison group, Pfeifer *et al.* (2007, 2009) show that adolescents tend to recruit mentalizing regions to a greater

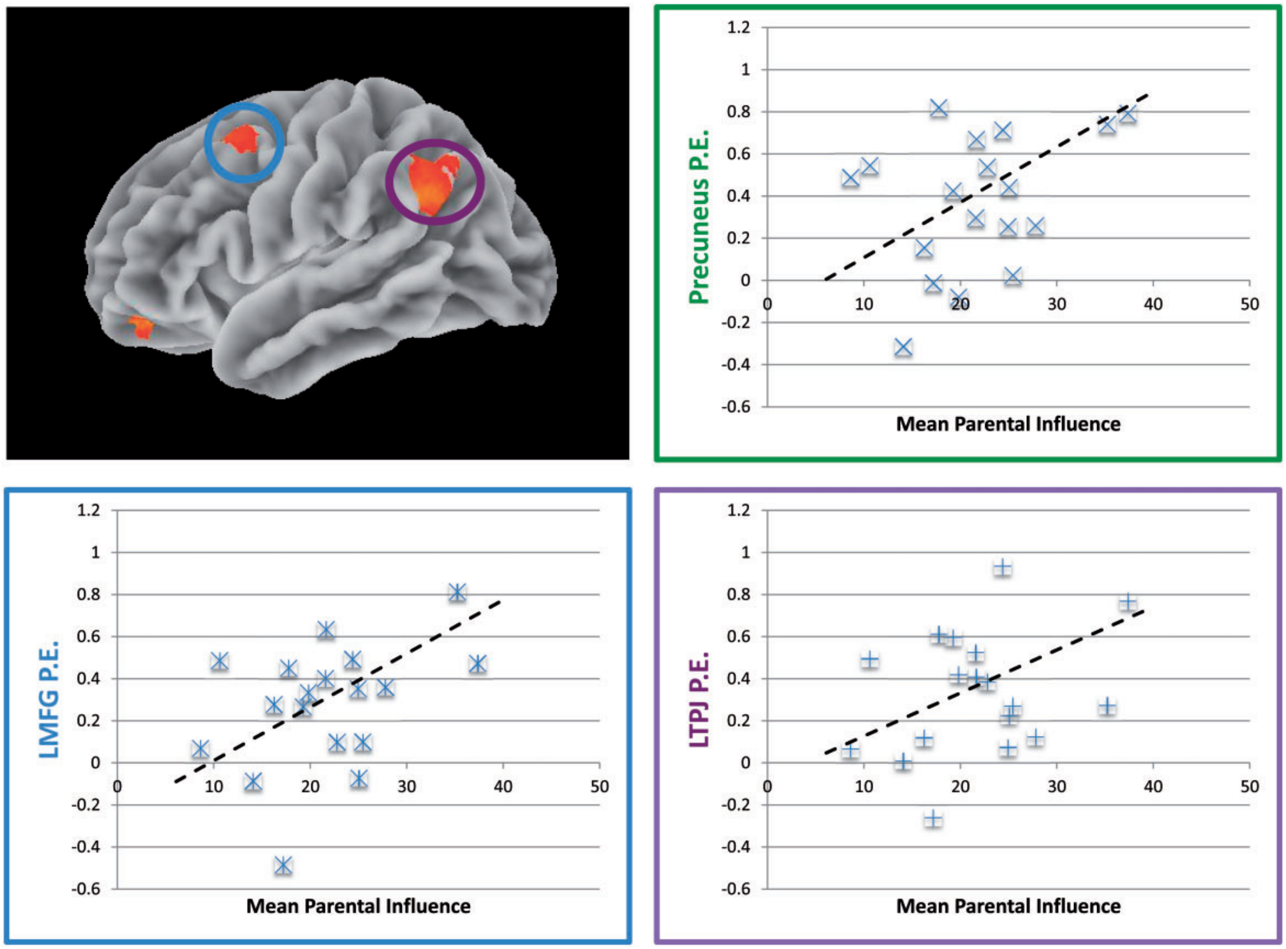

Fig. 4. Parameter estimates (from the Parent > Control contrast) from selected ROIs (LMFG, LTPJ, and Precuneus) are plotted against participants' mean parental influence score out of the available 100 point scale. In each case, participants' parental influence scores (attitude shift in the direction of the parent's position) were significantly correlated with parameter estimates from the displayed ROIs. Details are presented in the text.

extent than adults during self-knowledge retrieval and self-reflection, arguing that, for adolescents, considerations of the self are irreducibly social. Engelmann *et al.* (2012) also provide evidence that expert advice may have differential effects on adolescents and adults, with adolescents showing a greater correlation between DLPFC activity and the tendency to choose safe alternatives rather than risks. Taken together, these findings suggest that adolescents may engage mentalizing and self-control mechanisms to a greater extent than adults when assessing the overlap and divergence of their own attitudes with those of others. Thus, the results of this study are consistent with a view of social influence as an active process in which adolescents analyze and elaborate on the attitudes of others. For adults, processing and responding to the attitudes of others may (in some domains) eventually become more automatic, requiring less explicit mental-state reasoning and a lesser degree of effortful self-control. Future studies should examine developmental changes in social influence to formally test whether these neural processes are, in fact, adolescent specific.

The present research has several notable advantages over previous studies of social influence in adolescents. First, as noted earlier, it examines actual changes in attitudes in response to feedback from parents and peers, as opposed to effects on behavior of the mere presence of others. Second, we have modeled the actual period during which peer and parent attitudes are perceived, evaluated and integrated with one's own attitudes, rather than assessing social influence after-the-fact, when the relation to neural activity acquired during the scanning session becomes unclear. Third, between-subjects analyses identify regions in which activity covaried with observed social influence, which has not been true of most studies of influence. One notable exception is Campbell-Meiklejohn *et al.* (2010), which also finds both right IFG and right TPJ associated with the magnitude of social influence. Another recent study (Cascio *et al.*, 2015) reports results consistent with the present work: reward activity in the orbitofrontal cortex and ventral striatum was associated with social influence within-subjects, while responsivity of the temporoparietal junction predicted variation in influence between subjects. Taken together, the results of this study support an important role for mentalizing, self-control and reward processes in facilitating social influence from both parents and peers. Mentalizing may be necessary in order to evaluate the social significance of others' attitudes in context, while self-control mechanisms may help inhibit the force of one's antecedent attitudes. Lastly, reward processes may provide both an incentive to align one's attitudes with others, as well as a reinforcement mechanism to cement this tendency over time.

This research lays the groundwork for future studies on the neural basis of social influence in adolescence. In particular, our findings point to the potential importance of mental state reasoning, the capacity for self-control, and reward processing in enabling adolescents to align themselves with the attitudes of their parents and peers. The diversity of brain regions associated with social influence in our results suggest that the neural mechanisms mediating influence processes are complex and interactive, corresponding to the active engagement of adolescents with the shifting terrain of their evolving social worlds.

Funding

Support for this study was provided by the NICHD (R01HD057164-S, Fuligni) and NSF (NSF 1023293, Telzer & Fuligni).

Conflict of interest. None declared.

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