

Social Comparison in the Brain: A Coordinate-Based meta-Analysis of Functional Brain Imaging Studies on the Downward and Upward Comparisons

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Abstract: Social comparison is ubiquitous across human societies with dramatic influence on people's well-being and decision making. Downward comparison (comparing to worse-off others) and upward comparison (comparing to better-off others) constitute two types of social comparisons that produce different neuropsychological consequences. Based on studies exploring neural signatures associated with downward and upward comparisons, the current study utilized a coordinate-based meta-analysis to provide a refinement of understanding about the underlying neural architecture of social comparison. We identified consistent involvement of the ventral striatum and ventromedial prefrontal cortex in downward comparison and consistent involvement of the anterior insula and dorsal anterior cingulate cortex in upward comparison. These findings fit well with the "common-currency" hypothesis that neural representations of social gain or loss resemble those for non-social reward or loss processing. Accordingly, we discussed our findings in the framework of general reinforcement learning (RL) hypothesis, arguing how social gain/loss induced by social comparisons could be encoded by the brain as a domain-general signal (i.e., prediction errors) serving to adjust people's decisions in social settings. Although the RL account may serve as a heuristic framework for the future research, other plausible accounts on the neuropsychological mechanism of social comparison were also acknowledged. *Hum Brain Mapp* 00:000–000, 2017. © 2017 Wiley Periodicals, Inc.

Key words: activation likelihood estimation (ALE); common-currency hypothesis; meta-analysis; reinforcement learning; social comparison

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INTRODUCTION

Social comparison—“Is this person better looking? More successful?”—is a key and inevitable aspect of human social life. Social comparison has an early evolutionary origin and emerges early in human life. Nonhuman primates evaluate their outcomes in relative terms, comparing their own pay-offs with those of available others [Brosnan et al., 2005] and humans exhibit distinct reactions to different relative outcomes (e.g., equal vs. unequal) as early as 15 months of age [Geraci and Surian, 2011; Sommerville et al., 2013]. Furthermore, social comparison often occurs fast, requires few cognitive resources, and can happen automatically [Galinsky and Schweitzer, 2015]. For instance, subliminal exposure to the picture of Albert Einstein resulted in lower self-evaluations about one’s intelligence, whereas subliminal exposure to the picture of a clown led to higher self-evaluations about one’s intelligence [Stapel and Blanton, 2004].

Similar to absolute outcomes, relative outcomes derived from social comparison processes can have dramatic impacts on personal well-being and interpersonal interactions [Bault et al., 2008; Gibbons and Buunk, 1999; Hughes and Beer, 2013; Muscatell et al., 2012; Olson et al., 2014; Rutledge et al., 2016; Zhen et al., 2016]. Evidence from a worldwide survey revealed that the impact of relative income was even larger than that of absolute income on self-reported happiness [Ball and Chernova, 2008]. Likewise, social comparison processes play a critical role in the etiology and maintenance of mood disorders (e.g., depression) [Feinstein et al., 2013; Swallow and Kuiper, 1988; Tabachnik et al., 1983]. Furthermore, social comparison can also influence interpersonal relationships—it can sometimes help build healthy group affiliation [Baumeister and Leary, 1995; Brosnan et al., 2005; Mitchell and Heatherton, 2009], but it can also cause envy and scorn experiences that increase psychological distance between people [Fiske, 2010].

The fundamental mechanisms underlying social comparison have always drawn psychologists’ interest [Anderson et al., 2006; Dvash et al., 2010; Lindner et al., 2014; Moore et al., 2014; Mussweiler et al., 2004; Swencionis and Fiske, 2014; Taylor and Lobel, 1989]. The social comparison theory posits that people are driven to compare themselves to others for accurate self-evaluations [Festinger, 1954]. Specifically, people compare themselves to others in two opposite directions—downward and upward comparisons—that differ in motivations, comparison targets and consequences [Latané, 1966; Wills, 1981]. On the one hand, downward comparison refers to comparing to those who are considered to be doing worse. Downward comparison is most likely done to fulfill the motivation of self-enhancement. This type of comparison elevates positive emotion such as relief or *schadenfreude* and reduces anxiety [Amoroso and Walters, 1969; Crocker and Gallo, 1985; Gibbons, 1986; Jankowski and Takahashi, 2014]. Accordingly, downward comparison often enhances or protects subjective well-being [Suls et al., 2002; Wills, 1981]. On the other hand, upward comparison

refers to comparing to those who are thought to be doing better. Upward comparison is most likely done to fulfill the motivation of self-improvement. This type of social comparison invokes threat to the self [Brickman and Bulman, 1977] and provokes negative emotions such as envy [Chester et al., 2013; Jankowski and Takahashi, 2014; Tesser et al., 1988]. In short, downward comparison—being better than others—is often associated with positive feelings, whereas upward comparison—being worse than others—usually triggers negative feelings [Dvash et al., 2010; Swencionis and Fiske, 2014].

Building on extensive behavioral studies in the domain of social psychology, the past decade has witnessed an increased interest in unveiling the neural signatures of social comparison [Bault et al., 2011; Beer and Hughes, 2010; Fliessbach et al., 2007; Hughes and Beer, 2013; Luo et al., 2015; Wu et al., 2012]. To have participants compare themselves to others, these studies usually employed experimental paradigms in which participants are exposed to both their own and another person’s/group’s performance or outcomes [Boksem et al., 2011; Fliessbach et al., 2007; Qiu et al., 2010; Zhen et al., 2016; Zink et al., 2008]. These studies suggest that downward comparison often evokes activation of the ventral striatum (VS) and ventromedial prefrontal cortex (vmPFC) known to be implicated in primary or monetary reward processing [Bartra et al., 2013; Du et al., 2013; Fliessbach et al., 2012; Kang et al., 2013; Zink et al., 2008]. For instance, Dvash and colleagues [2010] showed that a relative gain—an absolute loss in the context of another person’s greater loss—induced activation in the VS similar to the one measured when experiencing an absolute gain. In contrast, a relative loss—an absolute gain in the context of another person’s greater gain—was associated with deactivation in the VS similar to the one measured when experiencing an absolute loss. Furthermore, vmPFC and VS have often been shown to be involved when one wins in interpersonal competitive games [Beyer et al., 2014; Delgado et al., 2008; Fareri and Delgado, 2014; Kätsyri et al., 2012; Mobbs et al., 2013; Votinov et al., 2015]. Therefore, recent neuroimaging findings are in line with the idea that downward comparison is represented in an analogous manner to the striato-cortical encoding of material reward [Lindner et al., 2014].

On the contrary, upward comparison has been shown to recruit the dorsal anterior cingulate cortex [dACC; Takahashi et al., 2009] and anterior insula [AI; Steinbeis and Singer, 2014]. For instance, a recent meta-analysis has revealed consistent activations of the AI and dACC by disadvantageous outcomes pertaining to resource allocation (e.g., unequal and disadvantageous offers in the ultimatum game) [Feng et al., 2015]. Likewise, being inferior to others in performance or competence can induce an envy feeling that was associated to the activity of the dACC or AI [Steinbeis and Singer, 2014; Takahashi et al., 2009]. For instance, in Takahashi et al.’s [2009] study, subjects were presented with target persons who possessed superior or average ability and quality. The

authors found that superior others, compared to average others, triggered higher self-reported envy and stronger dACC activation. In addition, neural responses of dACC to superior others were correlated with envy feelings, such that people who exhibited stronger dACC responses reported higher envy scores. Finally, losing to others in interpersonal competitive games also involves the AI and dACC [Beyer et al., 2014a,b]. Considering the reliable involvement of the dACC and AI in processing negative events in the non-social domain, including but not limited to physical pain and monetary loss [Craig, 2009; Lamm et al., 2011; Lieberman and Eisenberger, 2008; Shackman et al., 2011; Wu et al., 2014a], previous findings on upward comparison suggest common neural signatures of social and non-social loss.

Taken together, previous neuroimaging studies on human social comparison have revealed a neural network consisting of VS, vmPFC, AI and dACC that is also engaged in non-social reward/loss processing. These findings suggest that the influence of social comparison on human behaviors is implemented through a similar neuropsychological mechanism with non-social reward/loss. In this regard, we propose a plausible domain-general neuropsychological mechanism associated with reinforcement learning (RL). The RL framework argues that humans improve choices by adjusting behaviors according to prediction errors, i.e., the differences between the predicted and actual reward of an action [Schultz et al., 1997; Schultz, 2006]. Importantly, these error signals are often encoded in the neural activity of VS, vmPFC, dACC and AI [Haber and Behrens, 2014; Palminteri et al., 2012; Rushworth et al., 2011; Santesso et al., 2008], brain regions that have been shown to be involved in social comparisons. Accordingly, downward comparison activating the VS and vmPFC might signal positive prediction errors (i.e., better than one's expectations) whereas upward comparison activating the dACC and AI might signal negative prediction errors (i.e., worse than one's expectations). These error signals might facilitate behavioral adjustments and thus improve performance in the context of social comparison or competition. The RL model extends previous psychological hypotheses on social comparison by providing a more general framework.

Of note, however, there are other explanations on the specific functions of brain areas involved in social comparison. For example, the involvement of vmPFC during downward comparison has also been thought to contribute to self-referential processing [Northoff et al., 2006; Zaki et al., 2013]. Moreover, other researchers have proposed the role of vmPFC in social perceptiveness [Morawetz et al., 2014] due to its involvement in mentalizing [Amodio and Frith, 2006; Saxe and Powell, 2006] and empathy [Bernhardt and Singer, 2012]. Both self-referential and other-regarding processes are likely to be engaged in the social comparison. Additionally, the dACC may reflect the cognitive conflict between the positive self-concept and the mismatching external feedback [Takahashi et al., 2009],

considering the important role of the dACC in monitoring and evaluating cognitive conflict [Botvinick et al., 2004; Shenhav et al., 2013, 2016]. There is also the possibility that the dACC acts as a cognitive control region to regulate the conflict [Egner, 2009]. Finally, the AI may be responsible for representing deviations from expected outcome rather than negative feelings in the context of upward comparison [Civai et al., 2012; Gu et al., 2015; Wu et al., 2016; Xiang et al., 2013]. These interpretations are not necessarily exclusive with the RL framework, in terms of understanding the process of social comparison in a more general view. Although a meta-analysis does not allow us to specifically test these hypotheses, we will discuss our findings in light of the aforementioned accounts.

Recent neuroscience studies have been examining the neural signatures of the social comparison and a couple of narrative reviews have summarized the biological basis of social comparison processes [Kedia et al., 2014b; Swencionis and Fiske, 2014]. Importantly, however, a precise characterization of the neural systems underpinning social comparison is still elusive. In this study, we utilized a coordinate-based meta-analysis to quantitatively synthesize previous neuroimaging findings on social comparison with the goal of providing a comprehensive overview of the underlying neural architecture of this phenomenon.

MATERIAL AND METHODS

Our analyses consisted of primary meta-analyses and additional validation analyses. Specifically, we first provided primary/traditional meta-analytic analyses based on all selected publications, which is a typical approach employed in coordinate-based meta-analysis studies. Second, we provided validation analyses to confirm that our primary meta-analytic results were not driven by the coordinates from a single publication using a leave-one-experiment-out (LOEO) approach.

Literature Search and Selection

A systematic online database search was performed in July of 2017 on PubMed, ISI Web of Science and Google Scholar by entering various combinations of relevant search items (e.g., ["social comparison" OR "upward comparison" OR "downward comparison" OR "competition" OR "social influence" OR "envy" OR "gloating" OR "Schadenfreude" OR "equality" OR "fair" OR "ultimatum game" OR "UG" OR "inequality aversion" OR "social preference" OR "social decision making" OR "social learning" OR "social reward" OR "social feedback" OR "peer feedback" OR "social norm" OR "social information" OR "social status" OR "social hierarchy" OR "social interaction" OR "interpersonal interaction"] AND ["fMRI" OR "magnetic resonance imaging" OR "neuroimaging"]). In addition, we explored several other sources, including (1) direct searches on the names of frequently occurring authors, (2) the bibliography and citation indices of the pre-selected articles, and (3) the reference

list of related reviews [Aoki et al., 2015; Du and Chang, 2015; Falk et al., 2012; Fehr and Camerer, 2007; Insel and Fernald, 2004; Izuma, 2013; Jankowski and Takahashi, 2014; Kedia et al., 2014b; Rilling and Sanfey, 2011; Ruff and Fehr, 2014; Swencionis and Fiske, 2014; Tricomi and Sullivan-Toole, 2015]. The search resulted into 119 potential studies, which were further assessed according to the following criteria: (i) subjects were free from psychiatric or neurological diagnoses and neuropharmacological influence; (ii) subjects performed tasks in the context of social comparison; (iii) fMRI was used as the imaging modality; (iv) whole-brain general-linear-model-based analyses (rather than region of interest [ROI] analyses) were applied; (v) statistical models for contrasts of downward/upward social comparison or relevant parametric analyses were reported; and (vi) activations were presented in a standardized stereotaxic space (Talairach or MNI). Note that for studies reporting Talairach coordinates, a conversion to the MNI coordinates was implemented with the Yale BioImage Suite Package (<http://sprout022.sprout.yale.edu/mni2tal/mni2tal.html>). Filtering search results according to the inclusion/exclusion criteria yielded a total of 59 published fMRI articles with 28 downward contrasts (266 foci, 836 subjects) and 44 upward contrasts (383 foci, 1432 subjects) reported in a standardized stereotaxic space (Table I). We restricted the meta-analysis to experiments on comparison between the self and others, not including those comparing others to each other [e.g., Cloutier et al., 2012; Farrow et al., 2011; Hughes and Beer, 2011; Kedia et al., 2014a; Lindner et al., 2008]. A complete list of excluded publications and relevant reasons are provided in Supporting Information Table S1. A flow chart illustrating the literature search and selection process is presented in Figure 1.

Primary ALE Meta-analyses

A coordinate-based meta-analysis of reported fMRI experiments was conducted by employing the revised ALE algorithm implemented with in-house MATLAB scripts [Eickhoff et al., 2009]. Applying the ALE algorithm, the reported coordinates of brain areas associated with downward comparison and upward comparison were separately converged across different experiments. The ALE determines the convergence of foci reported from different functional (e.g., blood-oxygen-level dependent [BOLD] contrast imaging) or structural (e.g., voxel-based morphometry) neuroimaging studies with published foci in Talairach or MNI space [Laird et al., 2005; Turkeltaub et al., 2002]. ALE interpreted reported foci as three-dimensional Gaussian spatial probability distributions, whose widths were based on empirical estimates of the spatial uncertainty due to the between-subject and between-template variability of the neuroimaging data [Eickhoff et al., 2009]. Within each included study, a modulated activation (MA) map was firstly created by taking the maximum probability associated with any one focus (always the closest one) for each voxel [Turkeltaub et al.,

2012]. An advantage of the modified ALE algorithm is that multiple foci from a single study will not jointly influence the individual MA value of a single voxel. The union of these individual MA maps was then calculated to obtain an ALE map across studies. This ALE map was assessed against a null-distribution of random spatial association between studies using a non-linear histogram integration algorithm [Eickhoff et al., 2012]. In addition, the average non-linear contribution of each experiment for each cluster was calculated from the fraction of the ALE values at the cluster with and without the experiment in question [Eickhoff et al., 2016]. Based on the calculated contribution, we employed two additional criteria to select significant clusters: (1) the contributions for one cluster should be from at least two experiments so that the finding would not only be driven by one single experiment; and (2) the average contribution of the most dominant experiment (MDE) should not exceed 50% and the average contribution of the two most dominant experiments (2MDEs) should not exceed 80% [Eickhoff et al., 2016].

Validation Analyses

We implemented additional analyses to validate findings derived from our primary ALE meta-analyses. Specifically, we implemented a LOEO analysis for our ALE meta-analyses on downward and upward comparisons. The LOEO approach was conducted to examine whether results from our primary meta-analyses on downward and upward social comparisons were mainly driven by a single contrast. On each fold, one contrast (i.e., experiment) was excluded and the ALE meta-analysis was conducted on the remaining $N - 1$ contrasts for downward ($N - 1 = 27$) or upward ($N - 1 = 43$) comparison, respectively. Validation findings consisted of brain regions that were identified in *every* fold of the LOEO. Importantly, results from this procedure are not mainly driven by a single contrast. For the reason of completeness, we also reported results derived from the average of all folds of LOEO (Supporting Information Fig. S1 and Table S2).

All maps were thresholded using a cluster-level family-wise error (cFWE) correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations for correcting multiple comparisons [Eklunda et al., 2016; Woo et al., 2014a].

RESULTS

Primary ALE meta-Analysis Results

Consistent maxima were found in bilateral VS and vmPFC for downward comparison (Table II; Fig. 2A). Twenty out of 28 contrasts contributed to the cluster in right VS (MDE = 13.69%; 2MDE = 24.37%). Twenty out of 28 contrasts contributed to the cluster in left VS (MDE = 8.12%; 2MDE = 15.87%). Eight out of 28 contrasts contributed to the cluster in vmPFC (MDE = 21.26%; 2MDE = 35.87%) (Table III).

TABLE I. Summary of studies included for the meta-analysis focusing on downward and upward social comparisons

Study	N	Contrast	No. of foci
<i>Downward Social Comparison</i>			
Assaf et al. [2009]	19	Self-gain/other-lost > Self-lost/other-gain	12
Beyer et al. [2014a]	40	Self-won/other-lost > Self-lost/other-won	12
Beyer et al. [2014b]	41	Self-won/other-lost > Self-lost/other-won	3
Brunnlieb et al. [2013]	15	Self-won/other-lost > Self-lost/other-won	25
Cikara et al. [2011]	18	Favored team's success/rival team's failure > control	9
Delgado et al. [2008]	17	Self-gain/other-lost > Self-lost/other-gain	5
Du et al. [2013]	19	Self-won/others-lost > self-lost/others-won	12
Dvash et al. [2010]	16	Relative gain > relative loss	6
Emmerling et al. [2016]	15	Self-won/other-lost > Self-lost/other-won	9
Fareri and Delgado [2014]	18	Self-won/others-lost > self-lost/others-won: social > non-social	8
Fliessbach et al. [2007]	33	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	8
Fliessbach et al. [2012]	64	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	2
Haruno & Frith [2010]	52	Parametric analysis, positive correlation with absolute differences between two people (self > other)	4
Hertz et al. [2017]	19	better performance (positive merit) > worse performance (negative merit)	3
Kang et al. [2013]	22	Parametric analysis, positive correlation with relative income	7
Kätsyri et al. [2012]	17	Self-won/other-lost > self-lost/other-won: human > computer	2
Krämer et al. [2007]	15	Self-won/other-lost > Self-lost/other-won	15
Kishida et al. [2012]	27	parametric analysis, positive correlated with change of self's rank	2
Le Bouc and Pessiglione [2013]	32	Parametric analysis, positive correlation with relative income	2
Lindner et al. [2014]	30	Performed better > performed worse; parametric analysis, positive correlation with performance deviations in downward comparisons	12
Ligneul et al. [2016]	28	win > loss compared to another- win > loss in control condition	9
Mobbs et al. [2013]	15	Self-won/other-lost > Self-lost/other-won	1
Morawetz et al. [2014]	28	Self-won/other-lost > Self-lost/other-won	5
Op de Macks et al. [2016]	58	higher social hierarchy > monetary gain	2
Steinbeis and Singer [2014]	45	Parametric analysis, positive correlation with experienced Schadenfreude (Self-won/other-lost > Self-won/other-won)	7
van den Bos et al. [2013]	40	Self-won/others-lost > Self-not-won/other-won	2
Votinov et al. [2015]	69	Self-gain/other-no gain > self loss/other-no loss; self-no loss/other-loss > self-no gain/other-gain	65
Zink et al. [2008]	24	Self-won/other-lost > Self-lost/other-lost	17
<i>Upward Social Comparison</i>			
Baumgartner et al. [2011]	32	disadvantageous outcomes > equal outcomes	17
Beyer et al. [2014a]	40	Self-lost/other-won > Self-won/other-lost	7
Beyer et al. [2014b]	41	Self-lost/other-won > Self-won/other-lost	5
Cikara et al. [2011]	18	Favored team's failure/rival team's success > control	3
Civai et al. [2012]	19	disadvantageous outcomes > equal outcomes	12
Corradi-Dell'Acqua et al. [2016]	19	disadvantageous outcomes > equal outcomes	21
Emmerling et al. [2016]	15	Self-lost/other-won > Self-won/other-lost	4
Fatfouta et al. [2016]	23	disadvantageous outcomes > equal outcomes	18
Farmer et al. [2016]	18	disadvantageous outcomes > equal outcomes	6
Feng et al. [2016]	40	disadvantageous outcomes > equal outcomes	10
Fliessbach et al. [2012]	64	disadvantageous outcomes > equal outcomes	1
Gospic et al. [1983]	17	disadvantageous outcomes > equal outcomes	4
Gradin et al. [2015]	25	disadvantageous outcomes > equal outcomes	10
Guo et al. [2013a]	18	disadvantageous outcomes > equal outcomes	10
Guo et al. [2013b]	21	disadvantageous outcomes > equal outcomes	13
Güroğlu et al. [2011]	68	disadvantageous outcomes > equal outcomes	9
Halko et al. [2009]	23	disadvantageous outcomes > equal outcomes	22
Harlé and Sanfey [2012]	38	disadvantageous outcomes > equal outcomes	12
Haruno & Frith [2010]	52	Parametric analysis, positive correlation with absolute differences between two people (other > self)	9

TABLE I. (continued).

Study	N	Contrast	No. of foci
Haruno et al. [2014]	62	parametric analysis, positive correlation with disadvantageous outcomes	4
Hu et al. [2016]	23	disadvantageous outcomes > equal outcomes	4
Kirk et al. [2011]	40	disadvantageous outcomes > equal outcomes	11
Kirk et al. [2016]	50	parametric analysis, positive correlation with disadvantageous level	11
Kishida et al. [2012]	27	parametric analysis, negative correlated with change of self's rank	2
Krämer et al. [2007]	15	Self-lost/other-won > Self-won/other-lost	2
Lamichhane et al. [2014]	18	disadvantageous outcomes > equal outcomes	3
Lindner et al. [2014]	30	Performed worse > performed better	16
Lingeul et al. [2017]	28	superior other > inferior other	2
Op de Macks et al. [2016]	58	lower social hierarchy > monetary loss	1
Roalf [2010]	27	disadvantageous outcomes > equal outcomes	8
Sanfey et al. [2003]	19	disadvantageous outcomes > equal outcomes	17
Servaas et al. [2015]	114	disadvantageous outcomes > equal outcomes	32
Steinbeis and Singer [2014]	45	Parametric analysis, positive correlation with experienced Envy (Self-lost/other-won > Self-lost/other-lost)	2
Takahashi et al. [2009]	19	Superior others (high related) > average others; Superior others (low related) > average others	2
van den Bos et al. [2013]	40	Self-not-won/other-won > Self-won/others-lost	4
Verdejo-García et al. [2015a]	19	disadvantageous outcomes > equal outcomes	4
Verdejo-García et al. [2015b]	44	disadvantageous outcomes > equal outcomes	13
White et al. [2013]	20	parametric analysis, positive correlation with disadvantageous level	8
White et al. [2014]	21	parametric analysis, positive correlation with disadvantageous level	7
Wu et al. [2014a,b]	18	parametric analysis, negative correlation with subjective utility	7
Wu et al. [2015]	27	disadvantageous outcomes > equal outcomes	1
Zheng et al. [2015]	25	disadvantageous outcomes > equal outcomes Self-unequal/other-equal > Self-unequal/other-unequal	15 15
Zhou et al. [2014]	28	disadvantageous outcomes > equal outcomes	4
Zink et al. [2008]	24	Self-lost/other-won > Self-lost/other-lost	10

N, number of subjects.

For upward comparison, consistent maxima were found in dACC and bilateral AI (Table II; Fig. 2B). Twenty-seven out of 44 contrasts contributed to the cluster in dACC (MDE = 9.14%; 2MDE = 17.86%). Twenty-eight out of 44 contrasts contributed to the cluster in right AI (MDE = 9.86%; 2MDE = 19.06%). Twenty-six out of 44 contrasts contributed to the cluster in left AI (MDE = 8.94%; 2MDE = 15.95%) (Table III).

Validation Results (LOEO Analyses)

For downward comparison, consistent maxima in bilateral VS (Table IV; Fig. 3A) were identified in all folds of the ALE-LOEO.

For upward comparison, consistent maxima in dACC and bilateral AI were identified in all folds of the ALE-LOEO (Table IV; Fig. 3B). Therefore, the results of the LOEO approach corroborated the findings of our primary ALE meta-analysis.

DISCUSSION

Social comparison impacts people's well-being and decision making in various ways. Downward comparison—being better than others—often reduces anxiety, induces joyful feelings (e.g., *schadenfreude*) and satisfies the need for self-enhancement [Amoroso and Walters, 1969; Dohmen et al., 2011]. In contrast, upward comparison—being worse than others—often induces unpleasant feelings (e.g., envy), triggers threat to the self [Aoki et al., 2014; Bault et al., 2008; Dvash et al., 2010; Fiske, 2010; Takahashi et al., 2009], but also provides information for self-improvement [Tesser et al., 1988; Wood, 1989]. With a coordinate-based approach, this meta-analysis quantitatively examined brain areas consistently recruited by downward and upward comparisons based on previous functional brain imaging studies. Our results demonstrated consistent involvement of bilateral VS and vmPFC for downward comparison, as well as consistent involvement of bilateral AI and dACC

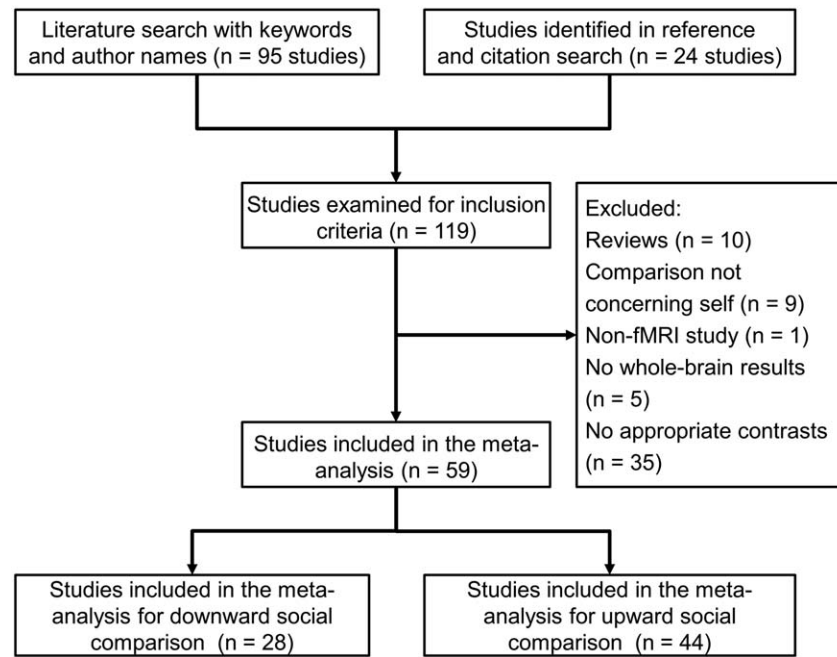


Figure 1.
Flowchart of literature search and selection process.

for upward comparison. Critically, our main findings remained robust after excluding the effect of a single contrast using a LOEO approach.

Our meta-analysis first identified a consistent involvement of the VS and vmPFC in downward comparison. Based on the role of these regions in reward processing [Carlson et al., 2011; Cromwell et al., 2005; McClure et al., 2004; Rushworth et al., 2011; Sescousse et al., 2015], our findings dovetail with the notion that downward comparison is experienced as rewarding [Bault et al., 2011; Dvash et al., 2010; Fließbach et al., 2007]. Prior studies have shown the involvement of the VS in the processing of other types of social rewards, including good reputation [Izuma et al., 2008; Meshi et al., 2013] and social approval [Izuma et al., 2010]. These findings have led researchers to propose that the VS and vmPFC, in addition to being key brain areas for material reward (e.g., food and money) processing, also play a crucial role in registering a broad spectrum of social rewards [Delgado, 2007].

Our meta-analysis next revealed consistent engagement of the bilateral AI and dACC in response to upward comparison. These findings echo the assertion that relative losses or being inferior to others might be experienced as negative feelings in the social contexts [Dvash et al., 2010; Steinbeis and Singer, 2014; Takahashi et al., 2009]. In accord with the current findings, prior studies have implicated these regions in many other social loss or social pain contexts, including the observation of other's physical pain [Cui et al., 2015; Gu et al., 2012; Singer, 2006], the

experience of social exclusion [Eisenberger et al., 2003; Eisenberger, 2012; Rotge et al., 2015] and the exposure to deceased loved one's pictures [Gündel et al., 2003]. Furthermore, similar regions have been reliably engaged by a broad range of negative event processing in the non-social domain [Apkarian et al., 2005; Craig et al., 1996; Peyron et al., 2000].

Taken together, our findings indicate that reward- and loss-related processing induced by downward and upward comparisons respectively—which are social in nature—induce reward/loss-relevant brain responses very similar to those observed for non-social reward/loss processing. Our results thus suggest that neuropsychological signatures of social comparison could be understood in a more general framework.

Indeed, the VS, vmPFC, AI, and dACC identified in the current meta-analysis play a key role in encoding prediction errors during general RL involving non-social reward/loss processing [Dideren et al., 2016; Garrison et al., 2013; Hare et al., 2008; Hayden et al., 2011; Limongi et al., 2013; Liu et al., 2011; Modirrousta and Fellows, 2008; Nieuwenhuis et al., 2005; Rushworth and Behrens, 2008]. Therefore, the consistent involvement of the VS, vmPFC, AI and ACC during social comparison might reflect prediction errors that signal the need for behavioral changes. In line with this idea, Bault et al. [2011] highlighted the impact of social comparison on behavior adjustment by showing that social gains (i.e., winning a higher score than the other player) induced a more

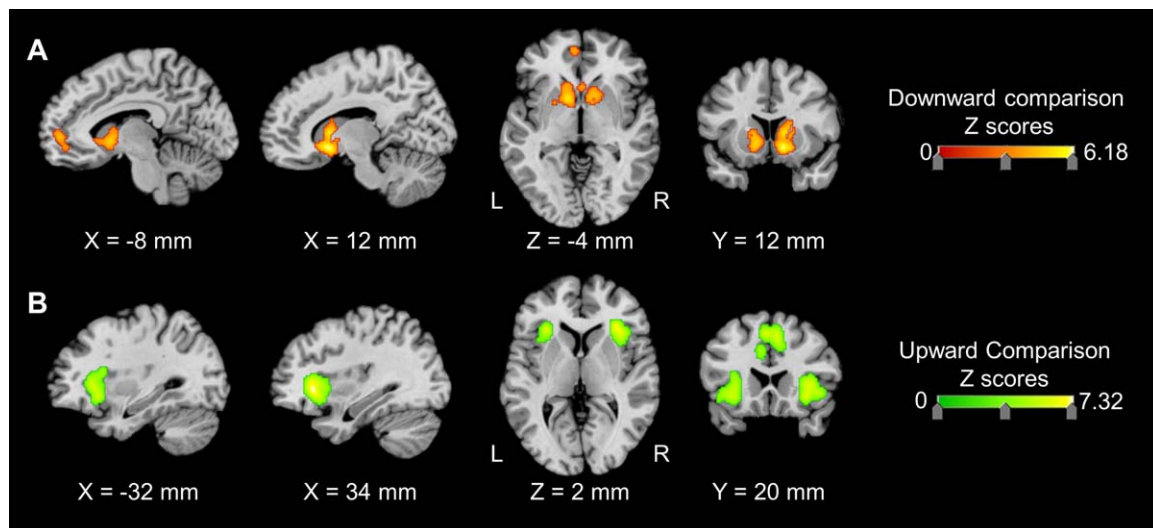
TABLE II. ALE meta-analysis results for downward social comparison and upward social comparison

Brain Regions	BA	MNI Coordinates (mm)			Peak Z score	Cluster Size (voxels)
		x	y	z		
<i>Downward Social Comparison</i>						
R VS	-	12	10	−10	6.18	578
L VS	-	−12	8	−8	5.62	448
vmPFC	10	−8	52	0	4.29	140
<i>Upward Social Comparison</i>						
dACC	32	−4	16	46	7.31	952
R AI	13	34	24	−4	7.32	846
L AI	13	−30	24	0	6.17	679

BA, Brodmann area; L, left; R, right; VS, ventral striatum; AI, anterior insula; vmPFC, ventromedial prefrontal cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

competitive behavioral pattern—seeking more rewarding and risky options—in subsequent trials. At the neural level, activity of the VS to social gains predicted the activation of medial prefrontal cortex in subsequent choices in the social context, which might serve as the neural substrates of behavior adjustments induced by social comparisons. These findings are in line with the RL account positing that social reward/loss induced by social comparison may be encoded by the brain as a domain-general signal (i.e., prediction errors) serving to adjust people's decisions in the social settings [Bhanji and Delgado, 2014; Montague and Lohrenz, 2007; Rilling and Sanfey, 2011].

In the context of social comparison, a dominant prediction may be being equal with others, as people have a tendency to believe that others are like oneself [Gilovich et al., 1983]. Accordingly, the equality in performance or outcomes between oneself and others may serve as a social expectation (or “social norm”) when no further information is provided [Blake et al., 2014; Civai et al., 2012; Fehr and Schmidt, 1999]. When people received feedbacks indicating differences between self and others, norm prediction errors might be detected [Montague and Lohrenz, 2007]. On the one hand, downward comparison indicating superiority to others might induce positive norm prediction errors (better

**Figure 2.**

Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for downward social comparison and upward social comparison. A) Consistent maxima for

downward social comparison were found in the bilateral ventral striatum (VS), and ventromedial prefrontal cortex. B) Consistent maxima for upward social comparison were found in bilateral anterior insula (AI) and dorsal anterior cingulate cortex (dACC). L, left; R, right. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE III. Average contribution of each experimental contrast for significant clusters identified for the meta-analysis of downward and upward social comparisons

Cluster name	Study	N	Contrast	Average contribution (%)
<i>Downward Social Comparison</i>				
R VS	Assaf et al. [2009]	19	Self-gain/other-lost > Self-lost/other-gain	5.02
	Beyer et al. [2014a]	40	Self-won/other-lost > Self-lost/other-won	5.19
	Beyer et al. [2014b]	41	Self-won/other-lost > Self-lost/other-won	6.00
	Brunnlieb et al. [2013]	15	Self-won/other-lost > Self-lost/other-won	1.86
	Cikara et al. [2011]	18	Favored team's success/rival team's failure > control	2.08
	Delgado et al. [2008]	17	Self-gain/other-lost > Self-lost/other-gain	2.10
	Du et al. [2013]	19	Self-won/others-lost > self-lost/others-won	1.95
	Dvash et al. [2010]	16	Relative gain > relative loss	6.90
	Emmerling et al. [2016]	15	Self-won/other-lost > Self-lost/other-won	4.65
	Fareri and Delgado [2014]	18	Self-won/others-lost > self-lost/others-won: social > non-social	4.27
	Fliessbach et al. [2007]	33	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	6.43
	Fliessbach et al. [2012]	64	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	6.05
	Krämer et al. [2007]	15	Self-won/other-lost > Self-lost/other-won	2.95
	Kishida et al. [2012]	27	parametric analysis, positive correlated with change of self's rank	4.01
	Le Bouc and Pessiglione [2013]	32	Parametric analysis, positive correlation with relative income	4.71
	Lindner et al. [2014]	30	Performed better > performed worse; parametric analysis, positive correlation with performance deviations in downward comparisons	10.70
	Mobbs et al. [2013]	15	Self-won/other-lost > Self-lost/other-won	3.29
	Morawetz et al. [2014]	28	Self-won/other-lost > Self-lost/other-won	5.26
	Steinbeis and Singer [2014]	45	Parametric analysis, positive correlation with experienced Schadenfreude (Self-won/other-lost > Self-won/other-won)	2.90
	Votinov et al. [2015]	69	Self-gain/other-no gain > self loss/other-no loss; self-no loss/other-loss > self-no gain/other-gain	13.67
L VS	Assaf et al. [2009]	19	Self-gain/other-lost > Self-lost/other-gain	7.19
	Beyer et al. [2014a]	40	Self-won/other-lost > Self-lost/other-won	6.22
	Cikara et al. [2011]	18	Favored team's success/rival team's failure > control	2.75
	Delgado et al. [2008]	17	Self-gain/other-lost > Self-lost/other-gain	5.95
	Du et al. [2013]	19	Self-won/others-lost > self-lost/others-won	1.45
	Dvash et al. [2010]	16	Relative gain > relative loss	6.63
	Emmerling et al. [2016]	15	Self-won/other-lost > Self-lost/other-won	4.90
	Fareri and Delgado [2014]	18	Self-won/others-lost > self-lost/others-won: social > non-social	6.92
	Fliessbach et al. [2007]	33	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	7.37
	Fliessbach et al. [2012]	64	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	7.75
	Hertz et al. [2017]	19	better performance (positive merit) > worse performance (negative merit)	3.95
	Krämer et al. [2007]	15	Self-won/other-lost > Self-lost/other-won	2.89
	Kishida et al. [2012]	27	parametric analysis, positive correlated with change of self's rank	3.80
	Le Bouc and Pessiglione [2013]	32	Parametric analysis, positive correlation with relative income	8.12
	Ligneul et al. [2016]	28	win > loss compared to another- win > loss in control condition	4.82
	Lindner et al. [2014]	30	Performed better > performed worse; parametric analysis, positive correlation with performance deviations in downward comparisons	2.11
	Morawetz et al. [2014]	28	Self-won/other-lost > Self-lost/other-won	6.40
	Steinbeis and Singer [2014]	45	Parametric analysis, positive correlation with experienced Schadenfreude (Self-won/other-lost > Self-won/other-won)	3.31
	Votinov et al. [2015]	69	Self-gain/other-no gain > self loss/other-no loss; self-no loss/other-loss > self-no gain/other-gain	5.65
vmPFC	Zink et al. [2008]	24	Self-won/other-lost > Self-lost/other-lost	1.80
	Brunnlieb et al. [2013]	15	Self-won/other-lost > Self-lost/other-won	13.71
	Du et al. [2013]	19	Self-won/others-lost > self-lost/others-won	14.19
	Fliessbach et al. [2007]	33	Self-won/other-lost > self-lost/other-won + self-lost/other-lost	14.34

TABLE III. (continued).

Cluster name	Study	N	Contrast	Average contribution (%)
	Hertz et al. [2017]	19	better performance (positive merit) > worse performance (negative merit)	10.04
	Kätsyri et al. [2012]	17	Self-won/other-lost > self-lost/other-won: human > computer	0.79
	Krämer et al. [2007]	15	Self-won/other-lost > Self-lost/other-won	11.03
	Ligneul et al. [2016]	28	win > loss compared to another- win > loss in control condition	14.61
	Votinov et al. [2015]	69	Self-gain/other-no gain > self loss/other-no loss; self-no loss/other-loss > self-no gain/other-gain	21.26
<i>Upward Social Comparison</i>				
dACC	Baumgartner et al. [2012]	32	disadvantageous outcomes > equal outcomes	0.39
	Cikara et al. [2011]	18	Favored team's failure/rival team's success > control	0.42
	Civai et al. [2012]	19	disadvantageous outcomes > equal outcomes	9.14
	Corradi-Dell'Acqua et al. [2016]	19	disadvantageous outcomes > equal outcomes	0.79
	Fatfouta et al. [2016]	23	disadvantageous outcomes > equal outcomes	4.12
	Feng et al. [2016]	40	disadvantageous outcomes > equal outcomes	3.35
	Guo et al. [2013a]	18	disadvantageous outcomes > equal outcomes	4.32
	Guo et al. [2013b]	21	disadvantageous outcomes > equal outcomes	2.73
	Güroğlu et al. [2011]	68	disadvantageous outcomes > equal outcomes	5.32
	Halko et al. [2009]	23	disadvantageous outcomes > equal outcomes	2.83
	Harlé and Sanfey [2012]	38	disadvantageous outcomes > equal outcomes	3.40
	Haruno & Frith [2010]	52	Parametric analysis, positive correlation with absolute differences between two people (other > self)	5.20
	Haruno et al. [2014]	62	parametric analysis, positive correlation with disadvantageous level	3.04
	Hu et al. [2016]	23	disadvantageous outcomes > equal outcomes	3.04
	Kirk et al. [2011]	40	disadvantageous outcomes > equal outcomes	2.39
	Kirk et al. [2016]	50	parametric analysis, positive correlation with disadvantageous level	7.86
	Kishida et al. [2012]	27	parametric analysis, negative correlated with change of self's rank	4.01
	Lindner et al. [2014]	30	Performed worse > performed better	1.90
	Sanfey et al. [2003]	19	disadvantageous outcomes > equal outcomes	5.18
	Servaas et al. [2015]	114	disadvantageous outcomes > equal outcomes	8.72
	Takahashi et al. [2009]	19	Superior others (high related) > average others; Superior others (low related) > average others	4.83
	van den Bos et al. [2013]	40	Self-not-won/other-won > Self-won/others-lost	3.32
	Verdejo-García et al. [2015b]	44	disadvantageous outcomes > equal outcomes	2.83
	White et al. [2013]	20	parametric analysis, positive correlation with disadvantageous level	2.16
	White et al. [2014]	21	parametric analysis, positive correlation with disadvantageous level	2.75
	Zheng et al. [2015]	25	disadvantageous outcomes > equal outcomes Self-unequal/other-equal > Self-unequal/other-unequal	2.97
R AI	Zhou et al. [2014]	28	disadvantageous outcomes > equal outcomes	2.95
	Baumgartner et al. [2012]	32	disadvantageous outcomes > equal outcomes	9.86
	Beyer et al. [2014a]	40	Self-lost/other-won > Self-won/other-lost	2.07
	Beyer et al. [2014b]	41	Self-lost/other-won > Self-won/other-lost	3.08
	Cikara et al. [2011]	18	Favored team's failure/rival team's success > control	1.78
	Civai et al. [2012]	19	disadvantageous outcomes > equal outcomes	6.42
	Corradi-Dell'Acqua et al. [2016]	19	disadvantageous outcomes > equal outcomes	1.33
	Fatfouta et al. [2016]	23	disadvantageous outcomes > equal outcomes	5.13
	Feng et al. [2016]	40	disadvantageous outcomes > equal outcomes	2.95
	Guo et al. [2013a]	18	disadvantageous outcomes > equal outcomes	2.53
	Guo et al. [2013b]	21	disadvantageous outcomes > equal outcomes	2.93

TABLE III. (continued).

Cluster name	Study	N	Contrast	Average contribution (%)
L AI	Halko et al. [2009]	23	disadvantageous outcomes > equal outcomes	6.15
	Harlé and Sanfey [2012]	38	disadvantageous outcomes > equal outcomes	3.00
	Haruno & Frith [2010]	52	Parametric analysis, positive correlation with absolute differences between two people (other > self)	2.22
	Haruno et al. [2014]	62	parametric analysis, positive correlation with disadvantageous level	3.05
	Kirk et al. [2011]	40	disadvantageous outcomes > equal outcomes	3.53
	Kirk et al. [2016]	50	parametric analysis, positive correlation with disadvantageous level	0.68
	Lindner et al. [2014]	30	Performed worse > performed better	5.71
	Roalf [2010]	27	disadvantageous outcomes > equal outcomes	3.69
	Sanfey et al. [2003]	19	disadvantageous outcomes > equal outcomes	3.20
	Servaas et al. [2015]	114	disadvantageous outcomes > equal outcomes	9.20
	van den Bos et al. [2013]	40	Self-not-won/other-won > Self-won/others-lost	3.28
	White et al. [2013]	20	parametric analysis, positive correlation with disadvantageous level	0.09
	White et al. [2014]	21	parametric analysis, positive correlation with disadvantageous level	1.85
	Wu et al. [2014a,b]	18	parametric analysis, negative correlation with subjective utility	2.85
	Wu et al. [2015]	27	disadvantageous outcomes > equal outcomes	2.97
	Zheng et al. [2015]	25	disadvantageous outcomes > equal outcomes Self-unequal/other-equal > Self-unequal/other-unequal	3.64
	Zhou et al. [2014]	28	disadvantageous outcomes > equal outcomes	3.55
	Zink et al. [2008]	24	Self-lost/other-won > Self-lost/other-lost	3.25
	Baumgartner et al. [2012]	32	disadvantageous outcomes > equal outcomes	3.89
	Beyer et al. [2014a]	40	Self-lost/other-won > Self-won/other-lost	2.37
	Civai et al. [2012]	19	disadvantageous outcomes > equal outcomes	8.94
	Corradi-Dell'Acqua et al. [2016]	19	disadvantageous outcomes > equal outcomes	2.49
	Fatfouta et al. [2016]	23	disadvantageous outcomes > equal outcomes	3.74
	Feng et al. [2016]	40	disadvantageous outcomes > equal outcomes	4.71
	Gospic et al. [1983]	17	disadvantageous outcomes > equal outcomes	4.25
	Gradin et al. [2015]	25	disadvantageous outcomes > equal outcomes	0.98
	Guo et al. [2013a]	18	disadvantageous outcomes > equal outcomes	3.80
	Guo et al. [2013b]	21	disadvantageous outcomes > equal outcomes	4.04
	Halko et al. [2009]	23	disadvantageous outcomes > equal outcomes	4.68
	Harlé and Sanfey [2012]	38	disadvantageous outcomes > equal outcomes	4.98
	Haruno & Frith [2010]	52	Parametric analysis, positive correlation with absolute differences between two people (other > self)	3.66
	Haruno et al. [2014]	62	parametric analysis, positive correlation with disadvantageous level	4.05
	Hu et al. [2016]	23	disadvantageous outcomes > equal outcomes	3.23
	Kirk et al. [2011]	40	disadvantageous outcomes > equal outcomes	2.22
	Kirk et al. [2016]	50	parametric analysis, positive correlation with disadvantageous level	2.49
	Op de Macks et al. [2016]	58	lower social hierarchy > monetary loss	4.84
	Roalf [2010]	27	disadvantageous outcomes > equal outcomes	2.07
	Sanfey et al. [2003]	19	disadvantageous outcomes > equal outcomes	3.50
	Servaas et al. [2015]	114	disadvantageous outcomes > equal outcomes	7.01
	Steinbeis and Singer [2014]	45	Parametric analysis, positive correlation with experienced Envy (Self-lost/other-won > Self-lost/other-lost)	4.20
	van den Bos et al. [2013]	40	Self-not-won/other-won > Self-won/others-lost	3.37

TABLE III. (continued).

Cluster name	Study	N	Contrast	Average contribution (%)
	White et al. [2014]	21	parametric analysis, positive correlation with disadvantageous level	2.26
	Zheng et al. [2015]	25	disadvantageous outcomes > equal outcomes Self-unequal/other-equal > Self-unequal/other-unequal	3.96
	Zink et al. [2008]	24	Self-lost/other-won > Self-lost/other-lost	4.22

N, number of subjects; L, left; R, right; VS, ventral striatum; AI, anterior insula; dACC, dorsal anterior cingulate cortex; vmPFC, ventromedial prefrontal cortex.

than expected) that are coded by the VS and vmPFC, leading to joyfull feelings in such circumstances. This kind of signal may motivate people to seek behaviors that maintain their advantages. On the other hand, upward comparison indicating inferiority to others might induce negative norm prediction errors (worse than expected) which are processed by the AI and dACC. These negative prediction errors are likely to serve as progenitors of negative feelings (e.g., envy) in response to upward comparison [Montague and Lohrenz, 2007]. This kind of signal may motivate people to seek behaviors that would change this situation. However, the influence of social comparison on human behaviors could be more complex, depending on a variety of social contexts (e.g., comparing with in-group or out-group others) [Blanton et al., 2000], gender [Jones, 2001], and cultures (e.g., collectivism or individualism) [Kang et al., 2013]. More studies are needed in this interesting line of research.

Notably, it should be noted that the RL account is mainly based on the observations that social and non-social reward/loss engages overlapping brain regions. However, such evidence has been demonstrated to be insufficient for the inference of similar functions of the overlapping regions between different tasks, due to the reason that commonly

used brain imaging techniques (e.g., fMRI) only provide pooled signal from a large volume of gray matter rather than signal of individual neurons [Logothetis, 2008]. Further studies with advanced imaging techniques (e.g., multi-voxel pattern analysis and fMRI adaptation paradigms) would provide promising approaches to compare the neural patterns of overlapping regions at the sub-voxel level [Corradi-Dell'Acqua et al., 2016; Woo et al., 2014b]. Therefore, these techniques could be used to assess the functional significance of overlaps in activity induced by social comparisons and non-social reward/loss processing. Until now, this line of research has yielded inconsistent findings; some evidence has shown that social and non-social experiences induce similar multi-voxel neural patterns [Corradi-Dell'Acqua et al., 2011; Corradi-Dell'Acqua et al., 2016], whereas other evidence has indicated that social and non-social experiences elicit distinct neural patterns [Krishnan et al., 2016; Wager et al., 2013; Woo et al., 2014b]. Moreover, pharmacological studies provide another way to examine whether social and non-social reward/loss processing shared common neuropsychological mechanisms. Consistent with the RL account, several studies have demonstrated that physical pain-killers could decrease self-

TABLE IV. Significant clusters identified in all folds (100%) of the leave-one-experiment-out (LOEO) analysis for downward social comparison and upward social comparison

Brain Regions	BA	MNI Coordinates (mm)			Probability	Cluster Size (voxels)
		x	y	Z		
<i>100% Downward Social Comparison</i>						
R VS	-	14	8	-14	1	228
L VS	-	-16	4	-12	1	149
<i>100% Upward Social Comparison</i>						
R AI	47	34	16	-16	1	554
L AI	47	-30	18	-14	1	372
dACC	32	10	24	32	1	439
dACC	32	8	26	22	1	29

BA, Brodmann area; L, left; R, right; VS, ventral striatum; AI, anterior insula; dACC, dorsal anterior cingulate cortex; clusters with size over 5 voxels are reported.

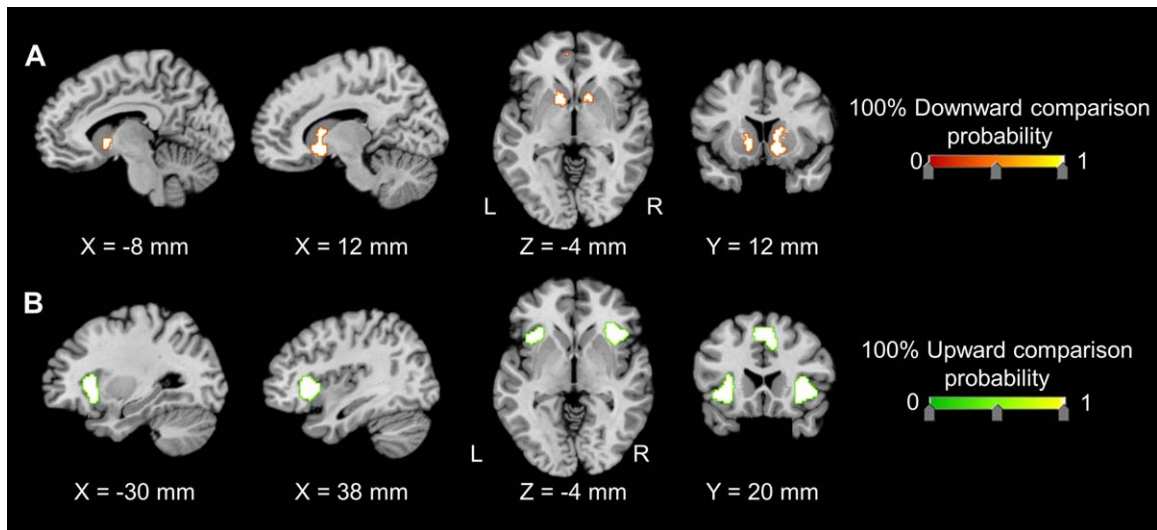


Figure 3.

Significant clusters identified in all folds of the leave-one-experiment-out (LOEO) analysis for downward social comparison and upward social comparison (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations). A) Consistent maxima for

downward social comparison were found in the ventral striatum (VS). B) Consistent maxima for upward social comparison were found in the bilateral anterior insula (AI) and dorsal anterior cingulate cortex (dACC). L, left; R, right. [Color figure can be viewed at wileyonlinelibrary.com]

reported social distress and the corresponding neural responses [DeWall et al., 2010] and even empathy for the distress of others [Mischkowski et al., 2016].

Finally, it is noteworthy that there are many other accounts on the functions of brain regions revealed in the current meta-analysis. In particular, vmPFC has been shown highly involved in self-related and social processing [Northoff et al., 2006; Zaki et al., 2013]. Our meta-analysis only included those social comparison contexts in which the self is concerned, and thus coincides with this account. In addition, the account of theory-of-mind ability and empathy for vmPFC also hints the process of mentalizing during comparing the self with others. Furthermore, the convergence for downward comparison also covers a part of dorsal striatum, which has been found to be related to motor control [Doyon et al., 2003]. Finally, the AI and dACC were found to be commonly involved in conflict process [Botvinick et al., 1999; Fan et al., 2008], cognitive control [Chein and Schneider, 2005; Egner, 2009], and salience detection [Menon and Uddin, 2010; Seeley et al., 2007]. A previous meta-analysis indicated that the ACC might be the region where pain, negative affect and cognitive control are integrated [Shackman et al., 2011]. Likewise, the AI has also been identified in a variety of tasks associated with cognition, emotion or the interaction between them [Gu et al., 2012, 2013a,b; Fan et al., 2011]. However, these potential accounts do not necessarily contradict with the RL framework, since the control/error signal used for behavior adjustment might manifest in different

forms depending on specific contexts, including emotional salience and conflict with others [Lindner et al., 2014].

In summary, our meta-analysis identified (i) a convergence within the VS and vmPFC for downward comparison; and (ii) the convergence within the AI and dACC for upward comparison. Although there exists many other plausible accounts, our findings may be accounted for by the RL theory, holding that reward delivered in different modalities are evaluated by a common metric in the brain to guide decision making [Rangel et al., 2008; Sanfey, 2007]. In this regard, downward comparison might signal positive norm prediction errors coded in the VS and vmPFC and trigger pleasant feelings (e.g., *schadenfreude*). In contrast, upward comparison might signal negative norm prediction errors detected by the AI and dACC and evoke unpleasant feelings (e.g., *envy*).

Several limitations related to the current study should be noted. First, the ALE meta-analysis used in the current study considers only the reported coordinates and number of subjects in each study. In comparison, using coordinates of unthresholded statistical maps might be able to provide insights beyond existing reports that may have been biased to report matches to existing publications. Second, the RL account of functions for regions identified in the current study were based on reverse inference, and it should be noted that the RL framework utilized to interpret neural signatures of social comparison may be not mutually exclusive with other accounts. However, the RL account offers some interesting insights on the human

social comparison processes, which may provide future studies in this line a heuristic working framework.

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REFERENCES

- Amodio DM, Frith CD (2006): Meeting of minds: The medial frontal cortex and social cognition. *Nat Rev Neurosci* 7:268.
- Amoroso DM, Walters RH (1969): Effects of anxiety and socially mediated anxiety reduction on paired-associate learning. *J Pers Social Psychol* 11:388.
- Anderson C, Srivastava S, Beer JS, Spataro SE, Chatman JA (2006): Knowing your place: Self-perceptions of status in face-to-face groups. *J Pers Social Psychol* 91:1094.
- Aoki R, Matsumoto M, Yomogida Y, Izuma K, Murayama K, Sugiura A, Camerer CF, Adolphs R, Matsumoto K (2014): Social equality in the number of choice options is represented in the ventromedial prefrontal cortex. *J Neurosci* 34:6413–6421.
- Aoki R, Yomogida Y, Matsumoto K (2015): The neural bases for valuing social equality. *Neurosci Res* 90:33–40. doi:10.1016/j.neures.2014.10.020
- Apkarian AV, Bushnell MC, Treede RD, Zubieta JK (2005): Human brain mechanisms of pain perception and regulation in health and disease. *Eur J Pain* 9:463–463.
- Assaf M, Kahn I, Pearson GD, Johnson MR, Yeshurun Y, Calhoun VD, Hendler T (2009): Brain activity dissociates mentalization from motivation during an interpersonal competitive game. *Brain. Imaging Behav* 3:24.
- Ball R, Chernova K (2008): Absolute income, relative income, and happiness. *Soc Indic Res* 88:497–529.
- Bartra O, McGuire JT, Kable JW (2013): The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage* 76:412–427.
- Bault N, Coricelli G, Rustichini A (2008): Interdependent utilities: How social ranking affects choice behavior. *PloS One* 3:e3477.
- Bault N, Joffily M, Rustichini A, Coricelli G (2011): Medial prefrontal cortex and striatum mediate the influence of social comparison on the decision process. *Proc Natl Acad Sci* 108:16044–16049.
- Baumgartner T, Knoch D, Hotz P, Eisenegger C, Fehr E (2011): Dorsolateral and ventromedial prefrontal cortex orchestrate normative choice. *Nat Neurosci* 14:1468–1474.
- Baumeister RF, Leary MR (1995): The need to belong: Desire for interpersonal attachments as a fundamental human motivation. *Psychol Bull* 117:497.
- Beer JS, Hughes BL (2010): Neural systems of social comparison and the “above-average” effect. *Neuroimage* 49:2671–2679.
- Bernhardt BC, Singer T (2012): The neural basis of empathy. *Annu Rev Neurosci* 35:1.
- Beyer F, Münte TF, Erdmann C, Krämer UM (2014a): Emotional reactivity to threat modulates activity in mentalizing network during aggression. *Soc Cogn Affect Neurosci* 9:1552–1560.
- Beyer F, Münte TF, Göttlich M, Krämer UM (2014b): Orbitofrontal cortex reactivity to angry facial expression in a social interaction correlates with aggressive behavior. *Cerebr Cortex* bhu101.
- Bhanji JP, Delgado MR (2014): The social brain and reward: Social information processing in the human striatum. *Wiley Interdiscip Rev Cogn Sci* 5:61–73.
- Blake PR, McAuliffe K, Warneken F (2014): The developmental origins of fairness: The knowledge–behavior gap. *Trends Cogn Sci* 18:559–561.
- Blanton H, Crocker J, Miller DT (2000): The effects of in-group versus out-group social comparison on self-esteem in the context of a negative stereotype. *J Exp Soc Psychol* 36:519–530.
- Boksem MA, Kostermans E, De Cremer D (2011): Failing where others have succeeded: Medial frontal negativity tracks failure in a social context. *Psychophysiology* 48:973–979.
- Brickman P, Bulman RJ (1977): Pleasure and pain in social comparison. *Social comparison processes: Theoretical and empirical Perspectives* 149:186.
- Brosnan SF, Schiff HC, De Waal FB (2005): Tolerance for inequity may increase with social closeness in chimpanzees. *Proc R Soc Lond B: Biol Sci* 272:253–258.
- Brunnlieb C, Münte TF, Krämer U, Tempelmann C, Heldmann M, (2013): Vasopressin modulates neural responses during human reactive aggression. *Social neuroscience* 8:148–164.
- Botvinick MM, Cohen JD, Carter CS (2004): Conflict monitoring and anterior cingulate cortex: An update. *Trends Cogn Sci* 8: 539–546.
- Botvinick MM, Nystrom LE, Fissell K, Carter CS, Cohen JD (1999): Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402:179.
- Carlson JM, Foti D, Mujica-Parodi LR, Harmon-Jones E, Hajcak G (2011): Ventral striatal and medial prefrontal BOLD activation is correlated with reward-related electrocortical activity: A combined ERP and fMRI study. *Neuroimage* 57:1608–1616.
- Chein JM, Schneider W (2005): Neuroimaging studies of practice-related change: fMRI and meta-analytic evidence of a domain-general control network for learning. *Cogn Brain Res* 25: 607–623.
- Chester DS, Powell CA, Smith RH, Joseph JE, Kedia G, Combs DJ, DeWall CN (2013): Justice for the average Joe: The role of envy and the mentalizing network in the deservingness of others' misfortunes. *Soc Neurosci* 8:640–649.
- Cikara M, Botvinick MM, Fiske ST (2011): Us versus them social identity shapes neural responses to intergroup competition and harm. *Psychol Sci* 22.
- Civai C, Crescentini C, Rustichini A, Rumiati RI (2012): Equality versus self-interest in the brain: Differential roles of anterior insula and medial prefrontal cortex. *Neuroimage* 62:102–112.
- Cloutier J, Ambady N, Meagher T, Gabrieli J (2012): The neural substrates of person perception: Spontaneous use of financial and moral status knowledge. *Neuropsychologia* 50:2371–2376.
- Corradi-Dell'Acqua C, Hofstetter C, Vuilleumier P (2011): Felt and seen pain evoke the same local patterns of cortical activity in insular and cingulate cortex. *J Neurosci* 31:17996–18006.
- Corradi-Dell'Acqua C, Tusche A, Vuilleumier P, Singer T (2016): Cross-modal representations of first-hand and vicarious pain, disgust and fairness in insular and cingulate cortex. *Nat Commun* 7:10904.
- Craig AD (2009): How do you feel—now? the anterior insula and human awareness. *Nat Rev Neurosci* 10.
- Craig AD, Reiman EM, Evans A, Bushnell MC (1996): Functional imaging of an illusion of pain 384:258–260.
- Crocker J, Gallo L (1985): *The self-enhancing effect of downward comparison*. Paper presented at the annual meeting of the American Psychological Association, Los Angeles.

- Cromwell HC, Hassani OK, Schultz W (2005): Relative reward processing in primate striatum. *Exp Brain Res* 162:520–525.
- Cui F, Abdelgabar A-R, Keysers C, Gazzola V (2015): Responsibility modulates pain-matrix activation elicited by the expressions of others in pain. *Neuroimage* 114:371–378.
- Delgado MR (2007): Reward-related responses in the human striatum. *Ann N Y Acad Sci* 1104:70–88.
- Delgado MR, Schotter A, Ozbay EY, Phelps EA (2008): Understanding overbidding: Using the neural circuitry of reward to design economic auctions. *Science* 321:1849–1852.
- DeWall CN, MacDonald G, Webster GD, Masten CL, Baumeister RF, Powell C, Combs D, Schurtz DR, Stillman TF, Tice DM, Eisenberger NI (2010): Acetaminophen reduces social pain: Behavioral and neural evidence. *Psychol Sci* 21:931–937.
- Diederen KM, Spencer T, Vestergaard MD, Fletcher PC, Schultz W (2016): Adaptive prediction error coding in the human mid-brain and striatum facilitates behavioral adaptation and learning efficiency. *Neuron* 90:1127–1138.
- Dohmen T, Falk A, Fliessbach K, Sunde U, Weber B (2011): Relative versus absolute income, joy of winning, and gender: Brain imaging evidence. *J Public Econ* 95:279–285.
- Doyon J, Penhune V, Ungerleider LG (2003): Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia* 41:252–262.
- Du E, Chang SW (2015): Neural components of altruistic punishment. *Front Neurosci* 9:6.
- Du X, Zhang M, Wei DTao, Li W, Zhang Q, Qiu J, Zuo X-N (2013): The neural circuitry of reward processing in complex social comparison: Evidence from an event-related fMRI study. *PloS One* 8:e82534.
- Dvash J, Gilam G, Ben-Ze'ev A, Hendler T, Shamay-Tsoory SG (2010): The envious brain: The neural basis of social comparison. *Hum Brain Mapp* 31:1741–1750.
- Egner T (2009): Prefrontal cortex and cognitive control: Motivating functional hierarchies. *Nat Neurosci* 12:821–822.
- Eickhoff SB, Bzdok D, Laird AR, Kurth F, Fox PT (2012): Activation likelihood estimation meta-analysis revisited. *Neuroimage* 59:2349–2361.
- Eickhoff SB, Laird AR, Grefkes C, Wang LE, Zilles K, Fox PT (2009): Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Hum Brain Mapp* 30:2907–2926.
- Eickhoff SB, Nichols TE, Laird AR, Hoffstaedter F, Amunts K, Fox PT, Bzdok D, Eickhoff CR (2016): Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *Neuroimage* 137:70–85.
- Eisenberger NI (2012): The neural bases of social pain: Evidence for shared representations with physical pain. *Psychosom Med* 74:126.
- Eisenberger NI, Lieberman MD, Williams KD (2003): Does rejection hurt? An fMRI study of social exclusion. *Science* 302:290–292.
- Eklunda A, Nichols TE, Knutssona H (2016): Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proc Natl Acad Sci* 113:E4929.
- Emmerling F, Schuhmann T, Lobbstaal J, Arntz A, Brugman S, Sack AT (2016): The role of the insular cortex in retaliation. *PLoS One* 11:e0152000. doi:10.1371/journal.pone.0152000
- Falk EB, Way BM, Jasinska AJ (2012): An imaging genetics approach to understanding social influence. *Front Hum Neurosci* 6:168.
- Fan J, Hof PR, Guise KG, Fossella JA, Posner MI (2008): The functional integration of the anterior cingulate cortex during conflict processing. *Cerebr Cortex* 18:796–805.
- Fan Y, Duncan NW, de Greck M, Northoff G (2011): Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neurosci Biobehav Rev* 35:903–911.
- Fareri DS, Delgado MR (2014): Differential reward responses during competition against in-and out-of-network others. *Soc Cogn Affect Neurosci* 9:412–420.
- Farmer H, Apps M, Tsakiris M, Foxe J (2016): Reputation in an economic game modulates premotor cortex activity during action observation. *Eur J Neurosci* 44:2191–2201.
- Farrow TF, Jones SC, Kaylor-Hughes CJ, Wilkinson ID, Woodruff PW, Hunter MD, Spence SA (2011): Higher or lower? The functional anatomy of perceived allocentric social hierarchies. *Neuroimage* 57:1552–1560.
- Fatfouta R, Meshi D, Merkl A, Heekeren HR (2016): Accepting unfairness by a significant other is associated with reduced connectivity between medial prefrontal and dorsal anterior cingulate cortex. *Soc Neurosci* 1–13.
- Fehr E, Camerer CF (2007): Social neuroeconomics: The neural circuitry of social preferences. *Trends Cogn Sci* 11:419–427.
- Fehr E, Schmidt KM (1999): A theory of fairness, competition, and cooperation. *Q J Econ* 114:817–868.
- Feng C, Azarian B, Ma Y, Feng X, Wang L, Luo YJ, Krueger F (2016): Mortality salience reduces the discrimination between in-group and out-group interactions: A functional MRI investigation using multi-voxel pattern analysis. *Hum Brain Mapp*
- Feng C, Luo YJ, Krueger F (2015): Neural signatures of fairness-related normative decision making in the ultimatum game: A coordinate-based meta-analysis. *Hum Brain Mapp* 36:591–602.
- Feinstein BA, Hershenberg R, Bhatia V, Latack JA, Meuwly N, Davila J (2013): Negative social comparison on Facebook and depressive symptoms: Rumination as a mechanism. *Psychol Popular Media Culture* 2:161.
- Festinger L (1954): A theory of social comparison processes. *Hum Relations* 7:117–140.
- Fiske ST (2010): Envy up, scorn down: How comparison divides us. *Am Psychol* 65:698.
- Fliessbach K, Philippis CB, Trautner P, Schnabel M, Elger CE, Falk A, Weber B (2012): Neural responses to advantageous and disadvantageous inequity. *Front Hum Neurosci* 6:165.
- Fliessbach K, Weber B, Trautner P, Dohmen T, Sunde U, Elger CE, Falk A (2007): Social comparison affects reward-related brain activity in the human ventral striatum. *Science* 318:1305–1308.
- Galinsky A, Schweitzer M (2015): Friend & foe: When to cooperate, when to compete, and how to succeed at both. New York: Crown Business. 320 p.
- Garrison J, Erdeniz B, Done J (2013): Prediction error in reinforcement learning: A meta-analysis of neuroimaging studies. *Neurosci Biobehav Rev* 37:1297–1310.
- Geraci A, Surian L (2011): The developmental roots of fairness: Infants' reactions to equal and unequal distributions of resources. *Dev Sci* 14:1012–1020.
- Gibbons FX (1986): Social comparison and depression: Company's effect on misery. *J Pers Soc Psychol* 51:140.
- Gibbons FX, Buunk BP (1999): Individual differences in social comparison: Development of a scale of social comparison orientation. *J Pers Soc Psychol* 76:129.
- Gilovich T, Jennings DL, Jennings S, (1983): Causal Focus and Estimates of Consensus - an Examination of the False-Consensus Effect. *J. Pers. Soc. Psychol.* 45:550–559.
- Gospic K, Mohlin E, Fransson P, Petrovic P, Johannesson M, Ingvar M, Fehr E (2011): Limbic justice—amygdala

- involvement in immediate rejection in the ultimatum game. *PLoS Biol* 9:e1001054.
- Gradin VB, Pérez A, MacFarlane JA, Cavin I, Waiter G, Engelmann J, Dritschel B, Pomi A, Matthews K, Steele JD (2015): Abnormal brain responses to social fairness in depression: An fMRI study using the Ultimatum Game. *Psychol Med* 45:1241–1251.
- Gu X, Gao Z, Wang X, Liu X, Knight RT, Hof PR, Fan J (2012): Anterior insular cortex is necessary for empathetic pain perception. *Brain* 135:2726–2735.
- Gu X, Hof PR, Friston KJ, Fan J (2013): Anterior insular cortex and emotional awareness. *J Comp Neurol* 521:3371–3388.
- Gu X, Liu X, Van Dam NT, Hof PR, Fan J (2013): Cognition–emotion integration in the anterior insular cortex. *Cerebr Cortex* 23:20–27.
- Gu X, Wang X, Hula A, Wang S, Xu S, Lohrenz TM, Knight RT, Gao Z, Dayan P, Montague PR (2015): Necessary, yet dissociable contributions of the insular and ventromedial prefrontal cortices to norm adaptation: Computational and lesion evidence in humans. *J Neurosci* 35:467–473.
- Guo X, Zheng L, Cheng X, Chen M, Zhu L, Li J, Chen L, Yang Z (2013a): Neural responses to unfairness and fairness depend on self-contribution to the income. *Soc Cogn Affect Neurosci* nst131.
- Guo X, Zheng L, Zhu L, Li J, Wang Q, Dienes Z, Yang Z (2013b): Increased neural responses to unfairness in a loss context. *Neuroimage* 77:246–253.
- Gündel H, O'Connor M-F, Littrell L, Fort C, Lane RD (2003): Functional neuroanatomy of grief: An FMRI study. *Am J Psychiatry* 160:1946–1953.
- Güroğlu B, van den Bos W, van Dijk E, Rombouts SA, Crone EA (2011): Dissociable brain networks involved in development of fairness considerations: Understanding intentionality behind unfairness. *Neuroimage* 57:634–641.
- Haber SN, Behrens TE (2014): The neural network underlying incentive-based learning: Implications for interpreting circuit disruptions in psychiatric disorders. *Neuron* 83:1019–1039.
- Halko M-L, Hlushchuk Y, Hari R, Schürmann M (2009): Competing with peers: Mentalizing-related brain activity reflects what is at stake. *Neuroimage* 46:542–548.
- Hare TA, O'Doherty J, Camerer CF, Schultz W, Rangel A (2008): Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *J Neurosci* 28:5623–5630.
- Harlé KM, Sanfey AG (2012): Social economic decision-making across the lifespan: An fMRI investigation. *Neuropsychologia* 50:1416–1424.
- Haruno M, Frith CD (2010): Activity in the amygdala elicited by unfair divisions predicts social value orientation. *Nat Neurosci* 13:160–161.
- Haruno M, Kimura M, Frith CD (2014): Activity in the nucleus accumbens and amygdala underlies individual differences in prosocial and individualistic economic choices. *J Cognit Neurosci* 26:1861–1870.
- Hayden BY, Heilbronner SR, Pearson JM, Platt ML (2011): Surprise signals in anterior cingulate cortex: Neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *J Neurosci* 31:4178–4187.
- Hertz U, Palminteri S, Brunetti S, Olesen C, Frith C, Bahrami B (2017): Neural Computations Underpinning The Strategic Management Of Influence In Advice Giving. *bioRxiv* 121947.
- Hu J, Blue PR, Yu H, Gong X, Xiang Y, Jiang C, Zhou X (2016): Social status modulates the neural response to unfairness. *Soc Cogn Affect Neurosci* 11:1–10.
- Hughes BL, Beer JS (2011): Orbitofrontal cortex and anterior cingulate cortex are modulated by motivated social cognition. *Cerebr Cortex* bhr213.
- Hughes BL, Beer JS (2013): Protecting the self: The effect of social-evaluative threat on neural representations of self. *J Cognit Neurosci* 25:613–622.
- Insel TR, Fernald RD (2004): How the brain processes social information: Searching for the social brain. *Annu Rev Neurosci* 27: 697–722.
- Izuma K, Saito DN, Sadato N (2008): Processing of social and monetary rewards in the human striatum. *Neuron* 58:284–294.
- Izuma K, Saito DN, Sadato N (2010): Processing of the incentive for social approval in the ventral striatum during charitable donation. *J Cognit Neurosci* 22:621–631.
- Izuma K (2013): The neural basis of social influence and attitude change. *Curr Opin Neurobiol* 23:456–462.
- Jankowski KF, Takahashi H (2014): Cognitive neuroscience of social emotions and implications for psychopathology: Examining embarrassment, guilt, envy, and schadenfreude. *Psychiatry Clin Neurosci* 68:319–336.
- Jones DC (2001): Social comparison and body image: Attractiveness comparisons to models and peers among adolescent girls and boys. *Sex Roles* 45:645–664.
- Kang P, Lee Y, Choi I, Kim H (2013): Neural evidence for individual and cultural variability in the social comparison effect. *J Neurosci* 33:16200–16208.
- Kätsyri J, Hari R, Ravaja N, Nummenmaa L (2012): The opponent matters: Elevated fMRI reward responses to winning against a human versus a computer opponent during interactive video game playing. *Cerebr Cortex* bhs259.
- Kedia G, Mussweiler T, Mullins P, Linden DE (2014a): The neural correlates of beauty comparison. *Soc Cogn Affect Neurosci* 9: 681–688.
- Kedia G, Mussweiler T, Linden DE (2014b): Brain mechanisms of social comparison and their influence on the reward system. *NeuroReport* 25:1255.
- Kirk U, Downar J, Montague PR (2011): Interoception drives increased rational decision-making in meditators playing the ultimatum game. *Front Neurosci* 5.
- Kirk U, Gu X, Sharp C, Hula A, Fonagy P, Montague PR (2016): Mindfulness training increases cooperative decision making in economic exchanges: Evidence from fMRI. *Neuroimage* 138:274–283.
- Kishida KT, Yang D, Quartz KH, Quartz SR, Montague PR (2012): Implicit signals in small group settings and their impact on the expression of cognitive capacity and associated brain responses. *Philos Trans R Soc Lond B Biol Sci* 367:704–716. doi: 10.1098/rstb.2011.0267
- Krämer UM, Jansma H, Tempelmann C, Münte TF (2007): Tit-for-tat: The neural basis of reactive aggression. *Neuroimage* 38:203–211.
- Krishnan A, Woo C-W, Chang LJ, Ruzic L, Gu X, López-Solà M, Jackson PL, Pujol J, Fan J, Wager TD (2016): Somatic and vicarious pain are represented by dissociable multivariate brain patterns. *Elife* 5:e15166.
- Laird AR, Fox PM, Price CJ, Glahn DC, Uecker AM, Lancaster JL, Turkeltaub PE, Kochunov P, Fox PT (2005): ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Hum Brain Mapp* 25:155–164.
- Lamichhane B, Adhikari BM, Brosnan SF, Dhamala M (2014): The neural basis of perceived unfairness in economic exchanges. *Brain Connectivity* 4:619–630.
- Lamm C, Decety J, Singer T (2011): Meta-analytic evidence for common and distinct neural networks associated with directly

- experienced pain and empathy for pain. *Neuroimage* 54: 2492–2502.
- Latané B (1966): Studies in social comparison—Introduction and overview. *J Exp Soc Psychol* 1:1–5.
- Le Bouc R, Pessiglione M (2013): Imaging social motivation: distinct brain mechanisms drive effort production during collaboration versus competition. *The Journal of Neuroscience* 33:15894–15902.
- Lieberman MD, Eisenberger NI (2008): The pains and pleasures of social life: A social cognitive neuroscience approach. *Neuro-Leadership J* 1:1–9.
- Ligneul R, Obeso I, Ruff CC, Dreher J-C (2016): Dynamical representation of dominance relationships in the human rostromedial prefrontal cortex. *Curr Biol* 26:3107–3115. doi:10.1016/j.cub.2016.09.015
- Limongi R, Sutherland SC, Zhu J, Young ME, Habib R (2013): Temporal prediction errors modulate cingulate–insular coupling. *Neuroimage* 71:147–157.
- Lindner M, Hundhammer T, Ciaramidaro A, Linden DE, Mussweiler T (2008): The neural substrates of person comparison—an fMRI study. *Neuroimage* 40:963–971.
- Lindner M, Rudolf S, Birg R, Falk A, Weber B, Fließbach K (2014): Neural patterns underlying social comparisons of personal performance. *Soc Cogn Affect Neurosci* nsu087.
- Ligneul R, Girard R, Dreher J-C (2017): Social brains and divides: the interplay between social dominance orientation and the neural sensitivity to hierarchical ranks. *Sci Rep* 7.
- Liu X, Hairston J, Schrier M, Fan J (2011): Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neurosci Biobehav Rev* 35:1219–1236.
- Logothetis NK (2008): What we can do and what we cannot do with fMRI. *Nature* 453:869.
- Luo Y, Feng C, Wu T, Broster LS, Cai H, Gu R, Luo Y-j (2015): Social comparison manifests in event-related potentials. *Sci Rep* 5.
- McClure SM, York MK, Montague PR (2004): The neural substrates of reward processing in humans: The modern role of FMRI. *Neuroscientist* 10:260–268.
- Menon V, Uddin LQ (2010): Saliency, switching, attention and control: A network model of insula function. *Brain Struct Funct* 214:655–667.
- Meshi D, Morawetz C, Heekeren HR (2013): Nucleus accumbens response to gains in reputation for the self relative to gains for others predicts social media use. *Front Hum Neurosci* 7:439.
- Mischkowski D, Crocker J, Way BM (2016): From painkiller to empathy killer: Acetaminophen (paracetamol) reduces empathy for pain. *Soc Cogn Affect Neurosci* 11:1345–1353.
- Mitchell J, Heatherton T (2009): Components of a social brain. *Cognit Neurosci* IV:951–958.
- Mobbs D, Hassabis D, Yu R, Chu C, Rushworth M, Boorman E, Dalgleish T (2013): Foraging under competition: The neural basis of input-matching in humans. *J Neurosci* 33:9866–9872.
- Modirrousta M, Fellows LK (2008): Dorsal medial prefrontal cortex plays a necessary role in rapid error prediction in humans. *J Neurosci* 28:14000–14005.
- Montague PR, Lohrenz T (2007): To detect and correct: Norm violations and their enforcement. *Neuron* 56:14–18.
- Moore WE, Merchant JS, Kahn LE, Pfeifer JH (2014): ‘Like me?’: Ventromedial prefrontal cortex is sensitive to both personal relevance and self-similarity during social comparisons. *Soc Cogn Affect Neurosci* 9:421–426.
- Muscattell KA, Morelli SA, Falk EB, Way BM, Pfeifer JH, Galinsky AD, Lieberman MD, Dapretto M, Eisenberger NI (2012): Social status modulates neural activity in the mentalizing network. *Neuroimage* 60:1771–1777.
- Mussweiler T, Rüter K, Epstude K (2004): The man who wasn’t there: Subliminal social comparison standards influence self-evaluation. *J Exp Soc Psychol* 40:689–696.
- Nieuwenhuis S, Slagter HA, Geusau V, Alting NJ, Heslenfeld DJ, Holroyd CB (2005): Knowing good from bad: Differential activation of human cortical areas by positive and negative outcomes. *Eur J Neurosci* 21:3161–3168.
- Northoff G, Heinzel A, De Greck M, Bermpohl F, Dobrowolny H, Panksepp J (2006): Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *Neuroimage* 31: 440–457.
- Olson JM, Herman CP, Zanna MP (2014): Relative deprivation and social comparison: The Ontario symposium. New York: Psychology Press. 272 p.
- Op de Macks ZA, Bunge SA, Bell ON, Kriegsfeld LJ, Kayser AS, Dahl RE (2016): The effect of social rank feedback on risk taking and associated reward processes in adolescent girls. *Soc Cogn Affect Neurosci* 12:240–250.
- Palminteri S, Justo D, Jauffret C, Pavlicek B, Dauta A, Delmaire C, Czernecki V, Karachi C, Capelle L, Durr A, Pessiglione M (2012): Critical roles for anterior insula and dorsal striatum in punishment-based avoidance learning. *Neuron* 76:998–1009.
- Peyron R, Laurent B, Garcia-Larrea L (2000): Functional imaging of brain responses to pain. A review and meta-analysis (2000). *Neurophysiol Clin/Clin Neurophysiol* 30:263–288.
- Qiu J, Yu C, Li H, Jou J, Tu S, Wang T, Wei D, Zhang Q (2010): The impact of social comparison on the neural substrates of reward processing: An event-related potential study. *Neuroimage* 49:956–962.
- Rangel A, Camerer C, Montague PR (2008): A framework for studying the neurobiology of value-based decision making. *Nat Rev Neurosci* 9:545–556.
- Rilling JK, Sanfey AG (2011): The neuroscience of social decision-making. *Annu Rev Psychol* 62:23–48.
- Roalf DR (2010): It’s not fair!: Behavioral and neural evidence that equity influences social economic decisions in healthy older adults.
- Rotge J-Y, Lemogne C, Hinfray S, Huguet P, Grynszpan O, Tartour E, George N, Fossati P (2015): A meta-analysis of the anterior cingulate contribution to social pain. *Soc Cogn Affect Neurosci* 10:19–27.
- Ruff CC, Fehr E (2014): The neurobiology of rewards and values in social decision making. *Nat Rev Neurosci* 15:549–562.
- Rushworth MF, Behrens TE (2008): Choice, uncertainty and value in prefrontal and cingulate cortex. *Nat Neurosci* 11:389.
- Rushworth MF, Noonan MP, Boorman ED, Walton ME, Behrens TE (2011): Frontal cortex and reward-guided learning and decision-making. *Neuron* 70:1054–1069.
- Rutledge RB, de Berker AO, Espenhahn S, Dayan P, Dolan RJ (2016): The social contingency of momentary subjective well-being. *Nat Commun* 7:11825.
- Sanfey AG (2007): Social decision-making: Insights from game theory and neuroscience. *Science* 318:598–602.
- Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, Cohen JD (2003): The neural basis of economic decision-making in the ultimatum game. *Science* 300:1755–1758.
- Santesso DL, Dillon DG, Birk JL, Holmes AJ, Goetz E, Bogdan R, Pizzagalli DA (2008): Individual differences in reinforcement learning: Behavioral, electrophysiological, and neuroimaging correlates. *Neuroimage* 42:807–816.
- Saxe R, Powell LJ (2006): It’s the thought that counts: Specific brain regions for one component of theory of mind. *Psychol Sci* 17:692–699.

- Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, Reiss AL, Greicius MD (2007): Dissociable intrinsic connectivity networks for salience processing and executive control. *J Neurosci* 27:2349–2356.
- Servaas MN, Aleman A, Marsman J-BC, Renken RJ, Riese H, Ormel J (2015): Lower dorsal striatum activation in association with neuroticism during the acceptance of unfair offers. *Cogn Affect Behav Neurosci* 15:537–552.
- Schultz W (2006): Behavioral theories and the neurophysiology of reward. *Annu Rev Psychol* 57:87–115.
- Schultz W, Dayan P, Montague PR (1997): A neural substrate of prediction and reward. *Science* 275:1593–1599.
- Sescousse G, Li Y, Dreher J-C (2015): A common currency for the computation of motivational values in the human striatum. *Soc Cogn Affect Neurosci* 10:467–473.
- Shackman AJ, Salomons TV, Slagter HA, Fox AS, Winter JJ, Davidson RJ (2011): The integration of negative affect, pain, and cognitive control in the cingulate cortex. *Nat Rev Neurosci* 12:154.
- Shenhav A, Botvinick MM, Cohen JD (2013): The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron* 79:217–240.
- Shenhav A, Cohen JD, Botvinick MM (2016): Dorsal anterior cingulate cortex and the value of control. *Nat Neurosci* 19:1286–1291.
- Singer T (2006): The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research. *Neurosci Biobehav Rev* 30:855–863.
- Sommerville JA, Schmidt MF, Yun J. e, Burns M (2013): The development of fairness expectations and prosocial behavior in the second year of life. *Infancy* 18:40–66.
- Stapel DA, Blanton H (2004): From seeing to being: Subliminal social comparisons affect implicit and explicit self-evaluations. *J Pers Soc Psychol* 87:468–481.
- Steinbeis N, Singer T (2014): Projecting my envy onto you: Neurocognitive mechanisms of an offline emotional egocentricity bias. *Neuroimage* 102:370–380.
- Suls J, Martin R, Wheeler L (2002): Social comparison: Why, with whom, and with what effect?. *Curr Directions Psychol Sci* 11:159–163.
- Swallow SR, Kuiper NA (1988): Social comparison and negative self-evaluations: An application to depression. *Clin Psychol Rev* 8:55–76.
- Swencionis JK, Fiske ST (2014): How social neuroscience can inform theories of social comparison. *Neuropsychologia* 56:140–146.
- Tabachnik N, Crocker J, Alloy LB (1983): Depression, social comparison, and the false-consensus effect. *J Pers Soc Psychol* 45:688.
- Takahashi H, Kato M, Matsuura M, Mobbs D, Suhara T, Okubo Y (2009): When your gain is my pain and your pain is my gain: Neural correlates of envy and schadenfreude. *Science* 323:937–939.
- Taylor SE, Lobel M (1989): Social comparison activity under threat: Downward evaluation and upward contacts. *Psychol Rev* 96:569.
- Tesser A, Millar M, Moore J (1988): Some affective consequences of social comparison and reflection processes: The pain and pleasure of being close. *J Pers Soc Psychol* 54:49.
- Tricomi E, Sullivan-Toole H (2015): Fairness and inequity aversion. *AW Toga (F. d.), Brain Mapp* 3:3–8.
- Turkeltaub PE, Eden GF, Jones KM, Zeffiro TA (2002): Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *Neuroimage* 16:765–780.
- Turkeltaub PE, Eickhoff SB, Laird AR, Fox M, Wiener M, Fox P (2012): Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Hum Brain Mapp* 33:1–13.
- van den Bos W, Talwar A, McClure SM (2013): Neural correlates of reinforcement learning and social preferences in competitive bidding. *J Neurosci* 33:2137–2146.
- Verdejo-García A, Verdejo-Román J, Albein-Urios N, Martínez-González JM, Soriano-Mas C (2015a): Brain substrates of social decision-making in dual diagnosis: Cocaine dependence and personality disorders. *Addiction Biol*
- Verdejo-García A, Verdejo-Román J, Rio-Valle JS, Lacomba JA, Lagos FM, Soriano-Mas C (2015b): Dysfunctional involvement of emotion and reward brain regions on social decision making in excess weight adolescents. *Hum Brain Mapp* 36:226–237.
- Votinov M, Pripfl J, Windischberger C, Sailer U, Lamm C (2015): Better you lose than I do: Neural networks involved in winning and losing in a real time strictly competitive game. *Sci Rep* 5.
- Wager TD, Atlas LY, Lindquist MA, Roy M, Woo C-W, Kross E (2013): An fMRI-based neurologic signature of physical pain. *N Engl J Med* 368:1388–1397.
- White SF, Brislin SJ, Meffert H, Sinclair S, Blair RJR (2013): Callosal-unemotional traits modulate the neural response associated with punishing another individual during social exchange: A preliminary investigation. *J Pers Disord* 27:99–112.
- White SF, Brislin SJ, Sinclair S, Blair JR (2014): Punishing unfairness: Rewarding or the organization of a reactively aggressive response? *Hum Brain Mapp* 35:2137–2147.
- Wills TA (1981): Downward comparison principles in social psychology. *Psychol Bull* 90:245.
- Woo C-W, Krishnan A, Wager TD (2014a): Cluster-extent based thresholding in fMRI analyses: Pitfalls and recommendations. *Neuroimage* 91:412–419.
- Woo C-W, Koban L, Kross E, Lindquist MA, Banich MT, Ruzic L, Andrews-Hanna JR, Wager TD (2014b): Separate neural representations for physical pain and social rejection. *Nat Commun* 5:5380.
- Wood JV (1989): Theory and research concerning social comparisons of personal attributes. *Psychol Bull* 106:231.
- Wu CC, Samanez-Larkin GR, Katovich K, Knutson B (2014a): Affective traits link to reliable neural markers of incentive anticipation. *Neuroimage* 84:279–289.
- Wu Y, Yu H, Shen B, Yu R, Zhou Z, Zhang G, Jiang Y, Zhou X (2014b): Neural basis of increased costly norm enforcement under adversity. *Soc Cogn Affect Neurosci* 9:187.
- Wu Y, Zang Y, Yuan B, Tian X (2015): Neural correlates of decision making after unfair treatment. *Front Hum Neurosci* 9:123.
- Wu H, Luo Y, Feng C (2016): Neural signatures of social conformity: A coordinate-based activation likelihood estimation meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 71:101–111.
- Wu Y, Zhang D, Elieson B, Zhou X (2012): Brain potentials in outcome evaluation: When social comparison takes effect. *Int J Psychophysiol* 85:145–152.
- Xiang T, Lohrenz T, Montague PR (2013): Computational substrates of norms and their violations during social exchange. *Journal of Neuroscience* 33:1099–1108.
- Zaki J, López G, Mitchell JP (2014): Activity in ventromedial prefrontal cortex co-varies with revealed social preferences: Evidence for person-invariant value. *Soc Cogn Affect Neurosci* 9:464–469.

- Zhen S, Yu R, Brañas-Garza P (2016): Tend to compare and tend to be fair: The relationship between social comparison sensitivity and justice sensitivity. *PloS One* 11:e0155414.
- Zheng L, Guo X, Zhu L, Li J, Chen L, Dienes Z (2015): Whether others were treated equally affects neural responses to unfairness in the Ultimatum Game. *Soc Cogn Affect Neurosci* 10:461–466.
- Zhou Y, Wang Y, Rao L-L, Yang L-Q, Li S (2014): Money talks: Neural substrate of modulation of fairness by monetary incentives. *Front Behav Neurosci* 8:150.
- Zink CF, Tong Y, Chen Q, Bassett DS, Stein JL, Meyer-Lindenberg A (2008): Know your place: Neural processing of social hierarchy in humans. *Neuron* 58:273–283. doi:10.1016/j.neuron.2008.01.025