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Common and distinct neural correlates of personal and vicarious reward: A quantitative meta-analysis

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Abstract

Individuals experience reward not only when directly receiving positive outcomes (e.g., food or money), but also when observing others receive such outcomes. This latter phenomenon, known as *vicarious reward*, is a perennial topic of interest among psychologists and economists. More recently, neuroscientists have begun exploring the neuroanatomy underlying vicarious reward. Here we present a quantitative whole-brain meta-analysis of this emerging literature. We identified 25 functional neuroimaging studies that included contrasts between vicarious reward and a neutral control, and subjected these contrasts to an activation likelihood estimate (ALE) meta-analysis. This analysis revealed a consistent pattern of activation across studies, spanning structures typically associated with the computation of value (especially ventromedial prefrontal cortex) and mentalizing (including dorsomedial prefrontal cortex and superior temporal sulcus). We further quantitatively compared this activation pattern to activation foci from a previous meta-analysis of *personal* reward. Conjunction analyses yielded overlapping VMPFC activity in response to personal and vicarious reward. Contrast analyses identified preferential engagement of the nucleus accumbens in response to personal as compared to vicarious reward, and in mentalizing-related structures in response to vicarious as compared to personal reward. These data shed light on the common and unique components of the reward that individuals experience directly and through their social connections.

Keywords

vicarious reward; positive empathy; empathy; ventromedial prefrontal cortex; meta-analysis; activation likelihood estimation

Humans are physically separate, but psychologically intertwined. *Empathy*—the ability to share and understand others’ internal states—intimately connects us, such that we “co-

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experience” the feelings of those around us. Empathy often involved sharing others’ pain and suffering, but applies equally to our sharing of others’ positive states. Adam Smith, whose *Theory of Moral Sentiments* (1790/2002) paved the way for modern theories of empathy, recognized such *positive empathy*. Smith even suggested that people could re-ignite their enjoyment of, for instance, theater performances by capitalizing on shared enjoyment with others who had not seen these performances before:

We enter into the surprise and admiration which it naturally excites in him, but which it is no longer capable of exciting in us... and we are amused by sympathy with his amusement which thus enlivens our own. (Pg. 9)

Although not the center of empathy research, positive empathy has received increasing attention for years (Batson et al., 1991; Gable & Reis, 2010; Morelli, Lieberman, Telzer, & Zaki, under review; Morelli, Lieberman, & Zaki, in press; K. D. Smith, Keating, & Stotland, 1989). Scientists have demonstrated, for instance, that other-reported positive empathy tracks the health of close relationships (Gable, 2006). Further, individuals reap psychological rewards from their own prosocial behaviors, reporting higher degrees of happiness after acting prosocially, as compared to selfishly (Dunn, Aknin, & Norton, 2014). Indices of positive empathy track individuals’ tendency to engage in prosocial behaviors, which suggests that positive empathy plays a functional role in driving generosity (Harbaugh, Mayr, & Burghart, 2007; Mobbs et al., 2009; Morelli et al., in press; Zaki & Mitchell, 2013). Finally, neuroimaging studies suggest that individuals may share the positive emotional and bodily states of others during positive empathy (Jabbi, Swart, & Keysers, 2007; Mobbs et al., 2009; Morelli, Rameson, & Lieberman, 2014; Perry, Hendler, & Shamay-Tsoory, 2012).

Thus, positive empathy appears to foster both prosociality and personal well-being. That said, a number of key questions about this phenomenon remain unanswered. Recent theoretical models suggest that empathy involves experience sharing (i.e., vicariously sharing targets’ internal states), mentalizing (i.e., explicitly considering and potentially understanding others’ emotional states), and motivation to help others (Davis, 1994; Singer & Klimecki, 2014; Zaki, 2014; Zaki & Ochsner, 2012). However, the psychological structure of this first process – vicarious positive affect— remains at least partially unclear. In particular, to what extent does vicarious enjoyment share affective mechanisms with “personal” reward (i.e., positive events that occur to the self)? Neuroscientific data provide a powerful lens through which to examine this question. In particular, scientists have robustly characterized the brain systems underlying positive affect, and reward processing in particular (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Liu, Hairston, Schrier, & Fan, 2011). This literature suggests ways in which personal and vicarious reward might both overlap and dissociate.

On the one hand, the experience of valuable outcomes reliably engages neural structures such as ventromedial prefrontal cortex (VMPFC) and nucleus accumbens (NAcc). These responses, especially in VMPFC, (i) track the subjective value that individuals associate with outcomes (Bartra, McGuire, & Kable, 2013), (ii) occur irrespective of the particular qualities of rewarding stimuli (Chib, Rangel, Shimojo, & O’Doherty, 2009; D. J. Levy & Glimcher, 2011), and (iii) occur even when rewards are not the result of specific actions (I.

Levy, Lazzaro, Rutledge, & Glimcher, 2011; Wunderlich, Rangel, & O’Doherty, 2010). As such, these regions might be expected to respond even to rewarding events that occur to others. Indeed, several studies have identified brain activity in NAcc and VMPFC that track a number of classes of “social rewards” (Fehr & Camerer, 2007; Sanfey, 2007). These include positive evaluation by or consensus with others (Izuma, Saito, & Sadato, 2008; Izuma, Saito, & Sadato, 2010; Klucharev, Hytonen, Rijpkema, Smidts, & Fernandez, 2009; Zaki, Schirmer, & Mitchell, 2011), acting prosocially (Dawes et al., 2012; de Quervain et al., 2004; Moll et al., 2006; Zaki & Mitchell, 2011), observing behaviors that conform to social norms such as equity and reciprocity (Rilling et al., 2002; Tricomi, Rangel, Camerer, & O’Doherty, 2010) and—crucially—observing others receiving rewarding outcomes (Hare, Camerer, Knoepfle, & Rangel, 2010a; Mobbs et al., 2009; Morelli et al., 2014; Zaki, Lopez, & Mitchell, 2014). As such, one might expect vicarious and personal reward to resemble each other in these key structures.

By contrast, other brain structures are strong candidates for dissociation between these reward-types. Two such examples bear emphasis. First, dorsal striatum often responds to rewarding events, but in a manner specific to decision-making and action planning (Rangel & Hare, 2010; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011). Second, vicarious sharing of others’ rewards often requires *understanding* the extent to which others value a particular outcome, especially when observers and social targets’ preferences diverge. For instance, an ice cream-loving observer can simply savor frozen desserts themselves, but might need to engage in *mentalizing*—or inferences about others’ mental states. Mentalizing produces activity in a system of brain regions including dorsomedial prefrontal cortex (DMPFC), temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), and posterior cingulate cortex (PCC) involved more broadly in projecting one’s self outside of the present moment and location (Buckner & Carroll, 2007; Lieberman, 2010; Mitchell, 2009; Spreng, Mar, & Kim, 2009; Zaki & Ochsner, 2012). To the extent that vicarious, but not personal, reward involves mentalizing, these regions might be engaged preferentially by vicarious reward.

Over the last 10 years, the neuroscientific study of vicarious reward has experienced considerable growth, and in many cases supported the foregoing predictions. Here, we take a step towards more formally organizing this information through a quantitative, whole-brain, coordinate-based meta-analysis. Specifically, we employed an activation likelihood estimate (ALE) meta-analysis, surveying 25 functional magnetic resonance imaging (fMRI) studies that included contrasts between vicarious reward and a neutral control condition. We then quantitatively compared the results of this analysis (i.e., patterns of brain activity consistently associated with vicarious reward) to the results of a recent meta-analysis of personal reward (Bartra et al., 2013). This allowed us to isolate brain regions that were common to both vicarious and personal reward, as well as regions preferentially engaged by each type of reward.

Materials and Methods

We conducted two coordinate-based meta-analyses of task-based fMRI studies of vicarious and personal reward in order to understand the spatial signature of activation foci for these

two sets of studies. We also assessed the overlap and dissociation between vicarious and personal reward using conjunction and contrast analyses.

Study Selection for Vicarious Reward

We initially identified candidate studies by searching Google Scholar for combinations of key words including: “vicarious,” “reward,” “fMRI,” and “empathy.” We identified additional studies by examining papers that cited a seminal paper on vicarious reward (Mobbs et al., 2009). We further extended this corpus of studies to identify other studies that examined vicarious reward, but framed it as another phenomena (e.g., observational learning), and to catalogue various types of vicarious rewards (e.g., monetary, social, sensory, emotional). Thus, follow-up searches included terms including “observational learning,” “donation,” “win,” “gain,” “money,” “reputation,” “social reward,” “touch,” “taste,” “smell,” “happiness,” “joy,” and “positive” combined with the original search terms.

We selected a final set of studies for inclusion in our analysis using a number of criteria. We required that all studies employ fMRI to measure BOLD signal in healthy human adults. Further, studies qualified only if participants directly observed, imagined, or saw a cue indicating that another person received a reward *outcome*. Therefore, we excluded studies that focused on the *anticipation* of vicarious reward or simply depicted targets experiencing positive emotion (e.g., smiling faces). We also excluded any studies in which participants competed with, disliked, or envied the target receiving rewards (Cikara & Fiske, 2011; Dohmen, Falk, Fliessbach, Sunde, & Weber, 2011; Dvash, Gilam, Ben-Ze’ev, Hendler, & Shamay-Tsoory, 2010; Fareri & Delgado, 2014). We also did not include studies in which the participant and target shared rewarding outcomes (e.g., (Fareri, Niznikiewicz, Lee, & Delgado, 2012) so as not to confound personal and vicarious reward.

We also required that studies include whole-brain analysis comparing a vicarious reward condition to a neutral condition (e.g., no reward) or baseline (e.g., fixation), with the exception of one study that did not have a baseline condition (i.e., (Kätsyri, Hari, Ravaja, & Nummenmaa, 2013). Therefore, all region of interest (ROI) analyses were excluded. All included studies utilized a binary contrast (rather than a parametric or correlational analysis) statistically thresholded by the authors of the original papers. These studies included the observation of social targets experiencing a variety of reward types, including pleasant touch, tastes, and smells, monetary payoffs, positive social feedback (e.g., praise), and positive emotional events (e.g., getting engaged). Social distance between the participant and target varied across studies, ranging from strangers (Morelli et al., 2014) to friends and ingroup members (e.g., (Braams et al., 2013; Molenberghs et al., 2014; Varnum, Shi, Chen, Qiu, & Han, 2014) to family (Telzer, Fuligni, Lieberman, & Galván, 2013; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010).

Because many studies did not report coordinates from whole-brain contrasts of vicarious reward compared to control conditions in published tables, we obtained the remaining included contrasts from personal correspondence with study authors (when possible). However, not all authors could supply their whole-brain coordinates (Albrecht, Volz, Sutter, Laibson, & Von Cramon, 2010; Albrecht, Volz, Sutter, & von Cramon, 2013; Canessa, Motterlini, Alemanno, Perani, & Cappa, 2011; Canessa et al., 2009; Cooper, Dunne, Furey,

& O'Doherty, 2012; Harbaugh et al., 2007; Kawamichi et al., 2013; Mitchell, Schirmer, Ames, & Gilbert, 2011; Mobbs et al., 2009; Moll et al., 2006; Suzuki et al., 2012). For all included publications, we selected the most relevant contrast from the study. However, one publication included two separate studies (Morrison, Björnsdotter, & Olausson, 2011), so we selected one contrast from each study. Thus, the final set of 24 publications included a total of 25 studies, 25 analysis contrasts, 575 participants, and 358 activation foci. See Appendix A for a full list of included studies, task descriptions, reward stimuli, and contrasts.

Study Selection for Personal Reward

Drawing from a recent meta-analysis on subjective value (Bartra et al., 2013), we selected studies that closely paralleled the criteria used for vicarious reward contrasts. As a first step, we queried an online database created by Bartra and colleagues (<http://kl.rewardstudies.appspot.com/>) for studies demonstrating a positive effect of reward outcomes. This query produced a list of 79 studies including the sample size and coordinates (in MNI space) for each study. Using additional study information provided by the authors, we then selected studies from this initial list that included whole-brain binary contrasts comparing reward outcomes to no reward control conditions. Therefore, we excluded studies with (a) only region of interest (ROI) analyses, (b) parametric or correlational analyses, or (c) contrasts comparing relatively larger rewards to smaller rewards. We also excluded any studies that might involve vicarious reward – such as erotic pictures, happy faces, and shared reward outcomes. Resulting contrasts included several reward types, including primary rewards (e.g., food, drinks), monetary payoffs, and positive feedback. The final set of 42 studies (Appendix B) included a total of 42 analysis contrasts, 805 participants, and 495 activation foci.

ALE Analyses

Basic Meta-Analyses—We conducted meta-analyses of both vicarious and personal reward using the Activation Likelihood Estimation (ALE) algorithm (version 2.3) (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009; Turkeltaub et al., 2012) in MNI space. We converted any coordinates originally reported in Talairach space to MNI space. According to the ALE method, significant coordinates for a given study were represented as three-dimensional Gaussian probability distributions. The Gaussian distribution widths represent spatial uncertainty associated with neuroimaging results (e.g., that may result from sample size). Computing the voxel-wise union of these probability distributions across voxels resulted in a modeled activation (MA) map for each study. The MA map can be conceptualized as a summary of that study, mapping the likelihood that a veridical activation exists in any given voxel. Aggregation of the MA maps across studies produced an ALE map for vicarious reward, as well as personal reward. We then assessed voxel-wise spatial convergence across studies with permutation-based statistics. Specifically, voxel-wise ALE values were compared to a null distribution that did not exhibit spatial contingency. A single value in this null distribution was created by randomly spatially sampling each MA map once, and then taking the union of the resulting values. This process was then repeated to create a null distribution.

Original ALE values were then compared to the null distribution to calculate a p -value per voxel. Specifically, each voxel-wise p -value was computed by dividing the number of values in the null distribution greater than or equal to the given ALE value at that voxel by the total number of values in the null distribution. In order to correct for false positive inflation as a result of multiple comparisons from a statistical test at each voxel, we used a cluster-level correction that compared significant cluster sizes in the original data to cluster sizes in ALE maps generated from 10,000 sets of randomly distributed foci. We implemented a cluster-level threshold of $p < 0.05$, and a cluster-forming threshold of $p < 0.01$. The resulting clusters represented regions that exhibit non-random spatial convergence across the studies included in each meta-analysis (i.e., for vicarious or personal reward).

Overlap Analysis—To assess brain regions related to both vicarious and personal reward, we conducted a minimum-statistic conjunction analysis (Caspers, Zilles, Laird, & Eickhoff, 2010; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010). This analysis assessed the intersection of statistically thresholded (i.e., cluster corrected) ALE-maps for vicarious and personal reward (with matched statistical parameters, described above).

Contrast Analyses—To identify brain regions that differentially related to vicarious versus personal reward, we conducted ALE contrast analyses (Eickhoff et al., 2011). Differences were computed at each voxel between statistically thresholded vicarious reward and personal reward ALE maps. These difference values were then compared, on a voxel-wise basis, to a null distribution at each voxel. This null distribution reflected ALE scores from datasets in which the group for a given set of study coordinates (i.e., vicarious or personal reward) was shuffled. New group datasets retained the size of the initial groups. ALE difference maps were then iteratively created for each shuffled dataset, creating a volume of null distributions. The input maps for the contrast analyses are described above for the single-study ALE meta-analyses and used a cluster-level threshold of $p < 0.05$ and a cluster-forming threshold of $p < 0.01$. In order to correct for multiple comparisons in the statistical difference map, we additionally used a conservative, whole-brain FDR correction of $p < 0.01$ (pID) and cluster extent of 128 mm^3 (Laird et al., 2005). The cluster extent value was computed based on the minimum volume that would guarantee at least one significant voxel in a given cluster. ALE contrast analysis thus allowed for the assessment of brain regions that were associated with vicarious reward more than personal reward, and personal reward more than vicarious reward.

GingerALE's contrast analysis relies on a permutation null-distribution created from difference maps computed from uneven groups with the same size as the original groups. Thus, the current results should be robust to uneven group size in the original meta-analyses. Extreme group size differences can still lead to unreliable results when (1) the size difference between two sets of studies is more than four-fold and (2) the smaller group has less than 12 experiments. However, our meta-analysis of vicarious reward (i.e. smaller group) includes 25 studies. The size difference between the vicarious and personal reward meta-analysis is less than two-fold (i.e., 25 vs. 42 studies). Thus, our contrast analysis should still be robust against the uneven number of studies.

Results

All analyses referred to in this section can be accessed at <http://neurovault.org/collections/73/>. We used Connectome Workbench to visualize ALE results on three-dimensional cortical renderings and coronal slices using a standard MNI brain (Marcus et al., 2011).

Vicarious Reward Meta-Analysis

Our meta-analysis of vicarious reward revealed consistent activation foci across 25 studies in ventromedial prefrontal cortex (VMPFC), medial prefrontal cortex (MPFC), dorsomedial prefrontal cortex (DMPFC), posterior superior temporal sulcus (pSTS), and amygdala, as well as the inferior parietal lobule (IPL), anterior insula (AI), dorsal anterior cingulate cortex (dACC), subgenual anterior cingulate cortex (sgACC), and other areas (Figure 1; Table 1).

Personal Reward Meta-Analysis

We included a personal reward meta-analysis primarily as a tool for examining similarities and differences between personal and vicarious reward. This meta-analysis largely replicated the findings of the original paper on personal reward (Bartra et al., 2013). In particular, this analysis revealed significant clusters in VMPFC, bilateral NAcc, bilateral ventral tegmental area (VTA), and bilateral amygdala. (Figure 2; Table 2). In addition, significant peaks and subpeaks appeared in MPFC, posterior cingulate cortex (PCC), AI, dACC, sgACC, and other areas. The consistency in these results and those presented by Bartra et al. (2013) suggested that we could reliably use this data for the ALE conjunction and contrast analyses.

Overlap Between Vicarious and Personal Reward

An ALE conjunction analysis revealed overlap between personal and vicarious reward in a number of structures including VMPFC, MPFC, and bilateral amygdala, as well as AI, dACC, sgACC, and other areas (Figure 3; Table 3).

Dissociations Between Vicarious and Personal Reward

A number of regions distinguished between vicarious and personal reward. In particular, vicarious reward, as compared to personal reward, preferentially activated DMPFC and pSTS (Figure 4A; Table 4). In contrast, personal reward, as compared to vicarious reward, preferentially activated bilateral NAcc and other areas (Figure 4B; Table 4).

Discussion

Positive empathy and vicarious reward are topics of widespread interest in psychology, economics, and—increasingly—neuroscience. Here we organize extant information about the neural structure of vicarious reward through a quantitative meta-analysis of neuroimaging data examining this phenomenon. We found that vicarious reward engages ventromedial prefrontal cortex (VMPFC), a region commonly implicated in the computation of subjective value (Bartra et al., 2013; Hare, Camerer, Knoepfle, & Rangel, 2010b). This is consistent with both animal and human neuroscience suggesting that the VMPFC aggregates cues from multiple sensory modalities, along with contextual information about an

organism's current drives, to produce high-order representations of value. These representations, in turn, support decision-making even over seemingly incommensurate choices (Grabenhorst & Rolls, 2011; Izquierdo, Suda, & Murray, 2004; D. J. Levy & Glimcher, 2011; Strait, Blanchard, & Hayden, 2014). These data also fit with recent findings that the VMPFC is involved in computing value even when outcomes are decoupled from specific motor acts (Gläscher, Hampton, & O'Doherty, 2009; I. Levy et al., 2011). Our data demonstrate that VMPFC responds consistently not only when individuals receive valuable outcomes themselves, but also when they observe others receiving such outcomes. This suggests that the integrative value signal computed in VMPFC might be "person-invariant," flexible not only with respect to the reward modality, but also the individual receiving that reward (cf. Zaki et al., 2014).

The personal and vicarious reward meta-analyses also showed overlap in the amygdalae, regions that are typically activated by motivationally relevant and emotionally impactful stimuli (Adolphs, 2010; Ewbank, Barnard, Croucher, Ramponi, & Calder, 2009; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). The amygdalae process emotional aspects of reward, such as valence (e.g., positive vs. negative) and relative value (e.g., small vs. large), and also update the value of expected outcomes in concert with the VMPFC (Gottfried, O'Doherty, & Dolan, 2003; Murray, 2007). Thus, the amygdalae's response to both personal and vicarious reward could reflect the salience of rewarding stimuli for the self or for others. Although past work relates amygdala dysfunction to reduced empathy in psychopathy and autism spectrum disorders (Baron-Cohen et al., 2000; Blair, 2008), these findings suggest that vicarious reward, and positive empathy more broadly, may rely on the amygdala to generate affective responses to others' positive outcomes.

We also document robust dissociations between vicarious and personal reward. One such difference is that, although personal reward consistently engaged NAcc, vicarious reward did not. This finding could occur for a number of reasons. First, we focused on reward *outcomes*, whereas NAcc activity is often instead linked to reward *anticipation* (Knutson, Fong, Adams, Varner, & Hommer, 2001) or reward prediction errors (comparisons of outcomes to expectations; e.g., Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008). However, the personal reward meta-analysis we examined likewise compared rewarding and neutral outcomes, and did yield consistent engagement of NAcc in response to personal reward. This suggests that a focus on outcome alone does not explain the lack of NAcc activity in studies of vicarious reward.

Alternatively, personal rewards may activate the NAcc more strongly because they are a direct result of the participants' action (Elliott, Newman, Longe, & William Deakin, 2004; Sescousse, Caldú, Segura, & Dreher, 2013; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004), whereas vicarious reward tasks typically involve passive observation of reward receipt. In fact, the majority of the studies in the vicarious reward meta-analysis did not directly involve the participant and only asked that participants observe others receive rewards – which may explain the lack of NAcc activation across studies. However, a few studies in this meta-analysis asked participants to win rewards for another person (Braams et al., 2013; Jung, Sul, & Kim, 2013; Varnum et al., 2014), linking participants' direct actions to others' rewarding outcomes. Due to the limited number of studies, however, we could not

determine if vicarious reward tasks that involve direct action (vs. passive observation) increase NAcc activity during vicarious reward. Although we cannot resolve why personal reward engages NAcc more than vicarious reward, this comparison generates novel and interesting empirical predictions that can be explored in future research.

Vicarious reward could also lack psychological features that are (i) involved in personal reward and (ii) related to NAcc function. One such candidate is affective intensity. NAcc activity is often linked to the positive arousal, or excitement, that accompanies anticipating, learning about, and receiving rewards (Knutson, Katovich, & Suri, 2014; Rutledge, Skandali, Dayan, & Dolan, 2014). Such reactions often diminish with psychological distance, which renders cognitive and affective reactions more abstract (Fujita, Henderson, Eng, Trope, & Liberman, 2006; Tamir & Mitchell, 2011). Thus, an observer witnessing a target receive rewards might compute the value of those rewards as they would with personally received outcomes (e.g., in VMPFC), but not experience the same level of excitement they would upon receiving rewards themselves, thus diminishing activity in NAcc.

This idea, though speculative, dovetails with prior work. First, three studies have documented NAcc activity in response to watching socially close, but not distant, targets receive rewards (Braams et al., 2013; Mobbs et al., 2009; Varnum et al., 2014), consistent with the idea that stronger affective intensity might accompany vicarious reward in socially close contexts. Second, this effect resembles similar findings on empathy for pain. A recent meta-analysis in that domain (Lamm, Decety, & Singer, 2011) found overlap between vicarious and personal pain in areas associated with higher-order pain representations (e.g., anterior cingulate cortex and anterior insula), but less consistent overlap in regions associated with perceptions of pain location and intensity. Our data suggest that vicarious reward might likewise include more abstract (e.g., valuation) psychological features of personal reward, but may not elicit positive arousal and increased NAcc activity when observing distant others receive rewards (Knutson et al., 2014). Future research should directly assess this prediction by examining whether self-reported positive arousal or excitement (i) distinguishes between personal and vicarious reward, and (ii) explains differential NAcc responses to these two phenomena.

Vicarious reward also produced consistent patterns of engagement not found in response to personal reward. Interestingly, this pattern included areas that are often associated with mentalizing (i.e., dorsomedial prefrontal cortex and posterior superior temporal sulcus) and mirroring (Mitchell, 2009; Puce & Perrett, 2003). As described above (see Introduction), this activity might represent a “layer” of inference necessary for vicarious, but not personal, reward: an observer’s decision as to whether outcomes are in fact valuable to social targets. When observer and target preferences diverge, this can be considered an affective analogue of a false belief task, because observers must simultaneously hold in mind both their and a target’s value representation. Interestingly, like classic false belief tasks (Saxe & Powell, 2006; Wellman, Cross, & Watson, 2001) reasoning about others’ preferences—especially when they are different from observers’ own—recruits activity in the inferior parietal lobe (Janowski, Camerer, & Rangel, 2012; Silani, Lamm, Ruff, & Singer, 2013). Further, one recent paper documented functional coupling between another region involved in

mentalizing, the pSTS, and VMPFC in response to vicarious, but not personal reward (Hare et al., 2010b). These suggest that VMPFC commonly responds to vicarious and personal reward, but uniquely integrates information from regions involved in social cognition when processing vicarious reward. Our aggregated data across studies provides converging support for this idea.

Taken together, our analyses reveal several dissociations between personal and vicarious reward that warrant further exploration. In particular, thinking more deeply about why these differences occur can generate novel predictions and exciting new research directions. For example, future studies could explore exactly which features of vicarious reward might engage some parts of the “valuation network,” but not other parts of this network. Similarly, future work could examine whether some components of the mentalizing network serve a functionally distinct purpose during vicarious reward processing, while other regions might be generally responsive to mental state evaluation.

This meta-analysis surveys a burgeoning research enterprise, and as such is subject to certain limitations. In particular, the limited number of studies directly assessing vicarious reward meant that we did not have the power to explore patterns of activation specific to particular vicarious reward features, such as anticipation and prediction errors. Likewise, we are as of yet unable to formally dissociate between different classes of vicarious reward (e.g., watching others receive monetary versus primary rewards), levels of abstraction in vicarious reward cues, or social closeness as a moderator of vicarious reward. As the neuroscientific literature in this domain grows, scientists will be able to better parse the processes that constitute vicarious reward, and map each to potentially dissociable brain circuitry. Nonetheless, even at this early stage, our analyses demonstrate clear and theoretically compelling patterns of brain activity consistently associated with socially-mediated reward experiences.

Conclusions

The neuroscientific study of vicarious reward has grown quickly in recent years. Here we demonstrate consistency in patterns of brain activity that accompany the experience of vicarious reward. Like another recent meta-analysis examining vicarious and personal pain (Lamm et al., 2011), we document both overlap and dissociation between vicarious and personal reward. These data suggest inferences about the psychological structure of vicarious positive affect, and empathy more broadly.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Appendix A

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
Bellebaum, C., Jokisch, D., Gizewski, E., Forsting, M., & Daum, I. (2012). The neural coding of expected and unexpected monetary performance outcomes: Dissociations between active and observational	Participants had to learn by observing the performance and outcomes of another subject. For each trial, they observed	Money	Observational feedback learning task: Reward outcome > Non-reward outcome	Personal correspondence

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
learning. <i>Behavioural Brain Research</i> , 227(1), 241–251.	another subject choose between two stimuli and receive monetary feedback, such as monetary reward (20 cents) or non-reward (neither reward nor punishment).			
Braams, B. R., Güro lu, B., de Water, E., Meuwese, R., Koolschijn, P. C., Peper, J. S., & Crone, E. A. (2013). Reward-related neural responses are dependent on the beneficiary. <i>Social Cognitive and Affective Neuroscience</i> , nst077.	Participants could win money for their best friend in a gambling task.	Money	Friend gain > Fixation	Personal correspondence
Burke, C. J., Tobler, P. N., Baddeley, M., & Schultz, W. (2010). Neural mechanisms of observational learning. <i>Proceedings of the National Academy of Sciences</i> , 107(32), 14431–14436.	Participants could learn by observing the performance and outcomes of another subject. During the gain sessions, they observed another subject choose between two stimuli and receive a reward (10 points) or non-reward (0 points).	Points	Full observational learning during gain session: 10-point gain > 0-point gain	Personal correspondence
Chester, D. S., Powell, C. A., Smith, R. H., Joseph, J. E., Kedia, G., Combs, D. J., & DeWall, C. N. (2013). Justice for the average Joe: The role of envy and the mentalizing network in the deservingness of others' misfortunes. <i>Social Neuroscience</i> , 8(6), 640–649.	Participants observed that non-enviable targets had been accepted into a prestigious student program (i.e., good fortune).	Acceptance into student program	Good fortune for low envy targets > Baseline	Personal correspondence
Hamilton, J. P., Chen, M. C., Waugh, C. E., Joormann, J., & Gotlib, I. H. (2014). Distinctive and common neural underpinnings of major depression, social anxiety, and their comorbidity. <i>Social Cognitive and Affective Neuroscience</i> , nsu084.	Participants passively listened to positive affective statements (praise) directed at another person.	Positive social feedback	Healthy controls only: Other positive > Baseline	Personal correspondence
Hare, T. A., Camerer, C. F., Knopfle, D. T., &	Participants made donations	Money	For all amounts except \$0: Forced	Personal correspondence

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
Rangel, A. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. <i>Journal of Neuroscience</i> , 30(2), 583–590. doi: 30/2/583 [pii] 0.1523/JNEUROSCI.4089-09.2010	to different charities. In forced donation trials subjects were instructed how much they had to donate in that trial (\$0 – \$100 in \$5 increments) and had to move a slider to the mandated amount (i.e. forced response).		response > Fixation	
Hooker, C. I., Verosky, S. C., Miyakawa, A., Knight, R. T., & D'Esposito, M. (2008). The influence of personality on neural mechanisms of observational fear and reward learning. <i>Neuropsychologia</i> , 46(11), 2709–2724.	Participants learned object-emotion associations by observing whether a woman reacted with a happy or neutral expression to a neutral object.	Object	Learn happy > Learn neutral	Table 6
Izuma, K., Saito, D. N., & Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. <i>Neuron</i> , 58(2), 284–294.	Participants saw blocks of all positive words showing what others thought of another person (i.e. high social reputation) or saw no feedback about the other person (i.e. no social reputation).	Positive social feedback	Other high social reputation > Other no social reputation	Personal correspondence
Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. <i>Neuroimage</i> , 34(4), 1744–1753.	Participants saw videos of people drinking pleasant and neutral liquids.	Juice	Pleasant > Neutral	Personal correspondence
Jung, D., Sul, S., & Kim, H. (2013). Dissociable neural processes underlying risky decisions for self versus other. <i>Frontiers in Neuroscience</i> , 7.	Participants were asked to perform a gambling task on behalf of another person (decision-for-other condition). These decisions sometimes resulted in a person winning either 10 points or 90 points. Points were converted to money.	Points/Money	Other Win > Fixation	Personal correspondence

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
Kätsyri, J., Hari, R., Ravaja, N., & Nummenmaa, L. (2013). Just watching the game ain't enough: striatal fMRI reward responses to successes and failures in a video game during active and vicarious playing. <i>Frontiers in Human Neuroscience</i> , 7.	Participants watched a pre-recorded gameplay video (vicarious playing) and observed another player's successes (wins) and failures (losses).	Video game wins	Vicarious play: Win > Loss	Personal correspondence
Korn, C. W., Prehn, K., Park, S. Q., Walter, H., & Heekeren, H. R. (2012). Positively biased processing of self-relevant social feedback. <i>The Journal of Neuroscience</i> , 32(47), 16832–16844.	Participants observed others receive desirable feedback about their personality traits.	Positive social feedback	Other desirable feedback > Fixation	Personal correspondence
Meffert, H., Gazzola, V., den Boer, J. A., Bartels, A. A., & Keysers, C. (2013). Reduced spontaneous but relatively normal deliberate vicarious representations in psychopathy. <i>Brain</i> , 136(8), 2550–2562.	Participants watched videos of others' hands receiving loving or neutral touch.	Loving touch	Healthy controls only: Observe loving touch > Observe neutral touch	Personal correspondence
Meshi, D., Morawetz, C., & Heekeren, H. R. (2013). Nucleus accumbens response to gains in reputation for the self relative to gains for others predicts social media use. <i>Frontiers in Human Neuroscience</i> , 7.	Participants observed others receive positive feedback about their personality traits or no feedback.	Positive social feedback	Other high positive feedback > Other no feedback	Personal correspondence
Molenberghs, P., Bosworth, R., Nott, Z., Louis, W. R., Smith, J. R., Amiot, C. E., Decety, J. (2014). The influence of group membership and individual differences in psychopathy and perspective taking on neural responses when punishing and rewarding others. <i>Human Brain Mapping</i> .	Participants gave monetary rewards or nothing (neutral) to in-group members during a trivia game.	Money	Reward in-group > Neutral in-group	Personal correspondence
Morelli, S. A., Rameson, L. T., & Lieberman, M. D. (2014). The neural components of empathy: Predicting daily prosocial behavior. <i>Social Cognitive and Affective Neuroscience</i> , 9(1), 39–47. doi: 10.1093/scan/nss088	Participants were asked to empathize with photos of others' happy events (e.g., getting engaged) and to view others' neutral events (e.g., ironing).	Positive emotional events	Happy empathize > Neutral	Table 1

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
Morrison, I., Björnsdotter, M., & Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. <i>The Journal of Neuroscience</i> , 31(26), 9554–9562. Morrison	Participants observed brush strokes on another person's arm at two different speeds: 3 cm/s (pleasant) and 30 cm/s (neutral).	Pleasant touch	Study 1: Seen 3 > Seen 30	Table 1
Morrison, I., Björnsdotter, M., & Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. <i>The Journal of Neuroscience</i> , 31(26), 9554–9562.	Participants observed brush strokes on another person's arm at two different speeds: 3 cm/s (pleasant) and 30 cm/s (neutral).	Pleasant touch	Study 2: Seen 3 > Seen 30	Table 2
Perry, D., Hender, T., & Shamay-Tsoory, S. G. (2012). Can we share the joy of others? Empathic neural responses to distress vs joy. <i>Social Cognitive and Affective Neuroscience</i> , 7(8), 909–916.	Participants read sentences depicting everyday positive emotional events occurring to a fictional character.	Positive emotional events	Other positive > Fixation	Personal correspondence
Spunt, R. P., & Lieberman, M. D. (2012). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. <i>Neuroimage</i> , 59(3), 3050–3059. doi: S1053-8119(11)01166-9 [pii] 10.1016/j.neuroimage.2011.10.005	Participants watched video clips of others' experiencing positive emotions and were asked to imagine why they felt that way. They also did a shape matching task which served as a neutral condition.	Positive emotional events	Positive Why task > Shape matching	Personal correspondence
Telzer, E. H., Masten, C. L., Berkman, E. T., Lieberman, M. D., & Fuligni, A. J. (2010). Gaining while giving: An fMRI study of the rewards of family assistance among White and Latino youth. <i>Social Neuroscience</i> , 5(5–6), 508–518."	Participants choose whether to accept or reject a payment option that affected their own and their family's endowment. One type of payment included a noncostly-donation to the family (e.g., YOU -\$0.00 FAM +\$3.00).	Money	Noncostly donation > Fixation	Personal correspondence
Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galván, A. (2013). Ventral striatum	Participants choose whether to accept or reject a	Money	Noncostly donation > Control	Personal correspondence

Paper	Task Description for Relevant Conditions	Type of Reward	Contrast	Source of Coordinates
activation to prosocial rewards predicts longitudinal declines in adolescent risk taking. <i>Developmental Cognitive Neuroscience</i> , 3, 45–52.	payment option that affected their own and their family's endowment. One type of payment included a noncostly-donation to the family (e.g., YOU -\$0.00 FAM +\$3.00). For the control condition, YOU and FAM were presented without a financial gain or loss.			
Tricomi, E., Rangel, A., Camerer, C. F., & O'Doherty, J. P. (2010). Neural evidence for inequality-averse social preferences. <i>Nature</i> , 463(7284), 1089–1091.	Inequality was created by recruiting pairs of subjects and giving one of them a large monetary endowment (i.e. high-pay player). This high-pay player then evaluated monetary transfers from the experimenter to the other participant (i.e. low-pay player).	Money	High-pay player: Payments to low-pay player > Control	Personal correspondence
Varnum, M. E., Shi, Z., Chen, A., Qiu, J., & Han, S. (2014). When "Your" reward is the same as "My" reward: Self-construal priming shifts neural responses to own vs. friends' rewards. <i>Neuro Image</i> , 87, 164–169.	Experimenters manipulated participants' self-construal (independent vs. interdependent). Participants then played a game in which they could win money for a friend during a gambling game.	Money	Interdependent prime for main task: Friend win > Neutral	Personal correspondence
Wicker, B., Keysers, C., Plailly, J., Royet, J., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in My Insula: The common neural basis of seeing and feeling disgust. <i>Neuron</i> , 40(3), 655–664.	Participants watch videos of other people smelling pleasant odors.	Pleasant odors	Observation of pleasure > Neutral	Personal correspondence

Appendix B

List of articles included in the meta-analysis of personal reward:

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Highlights

- We compare quantitative meta-analyses of personal and vicarious (vic.) reward.
- Vic. reward studies activate regions related to value computation and mentalizing.
- Vic. and personal reward studies commonly activate ventromedial PFC.
- Personal as compared to vic. reward preferentially engages nucleus accumbens.
- Vic. versus personal reward preferentially engages regions related to mentalizing.

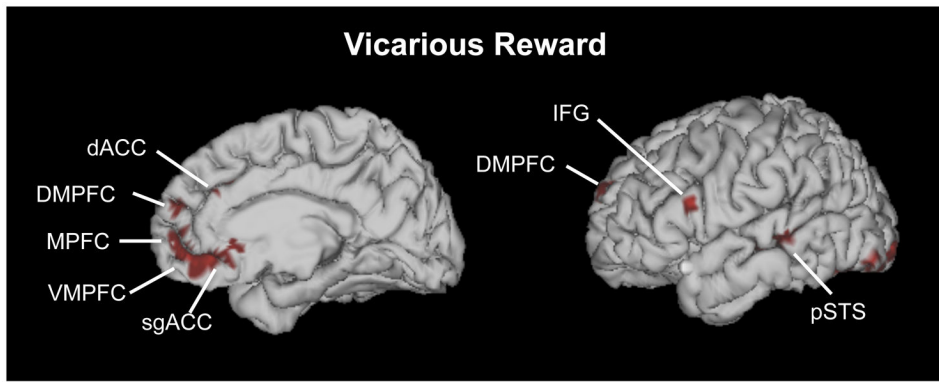


Figure 1.
Brain areas activated by vicarious reward across 25 studies

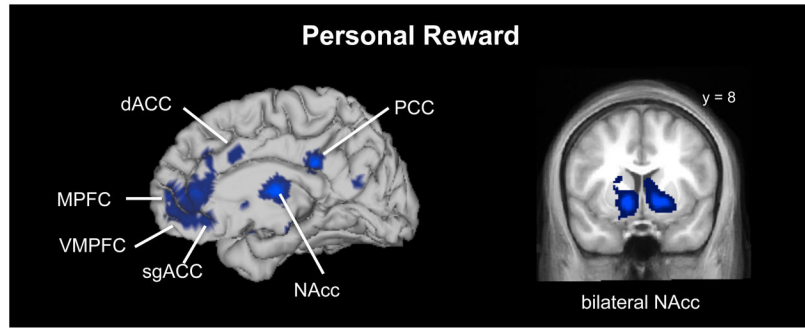


Figure 2.
Brain areas activated by personal reward across 42 studies

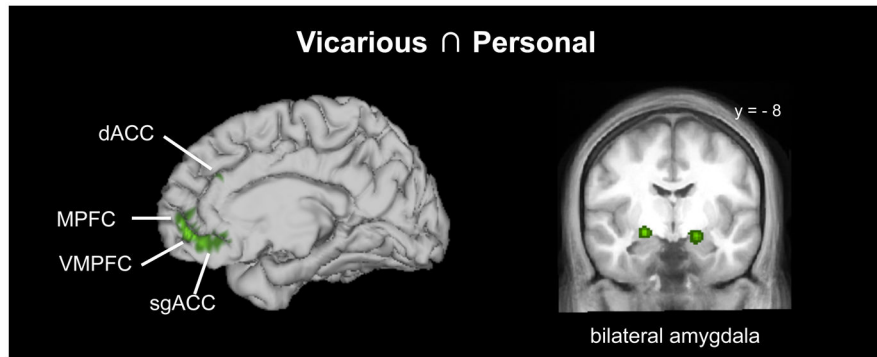


Figure 3.
Brain areas commonly activated by both vicarious and personal reward

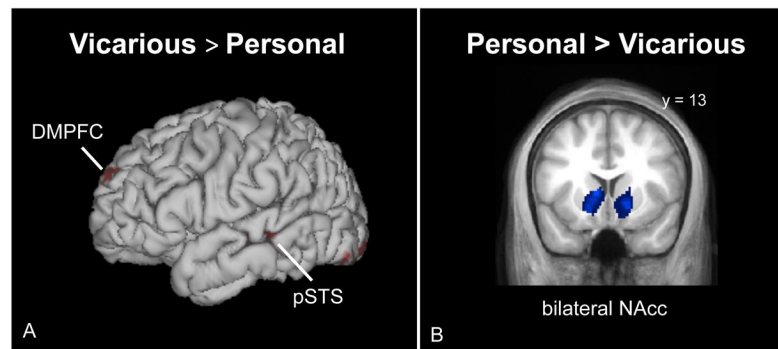


Figure 4. Brain areas activated more by (a) vicarious reward than personal reward and (b) personal reward than vicarious reward.

Table 1
Brain areas activated by vicarious reward as identified using ALE meta-analysis

Region	Size	L/R	x	y	z
Ventromedial prefrontal cortex	2752	R	2	36	-14
Ventromedial prefrontal cortex			0	50	-12
Ventromedial prefrontal cortex			0	44	-16
Medial prefrontal cortex			0	58	-6
Medial prefrontal cortex	2128	R	6	58	14
Dorsomedial prefrontal cortex		L	-6	60	24
Posterior superior temporal sulcus	880	R	56	-32	-4
Middle temporal gyrus		R	60	-38	-8
Posterior superior temporal sulcus	2136	L	-62	-38	2
Posterior superior temporal sulcus		L	-52	-36	0
Posterior superior temporal sulcus		L	-60	-28	0
Middle temporal gyrus		L	-60	-20	-6
Amygdala	736	R	24	-6	-10
Amygdala	976	L	-18	-10	-14
Hippocampus		L	-10	0	-12
Anterior insula	1816	L	-30	8	-10
Anterior insula		L	-34	16	-2
Putamen		L	-28	8	-4
Inferior parietal lobule	2232	R	38	-62	44
Inferior parietal lobule		R	30	-72	38
Inferior parietal lobule		R	46	-56	38
Dorsal anterior cingulate cortex	1392	R	12	28	26
Dorsal anterior cingulate cortex		R	12	36	20
Dorsal anterior cingulate cortex		R	4	38	24
Subgenual anterior cingulate cortex	808	L	-2	24	-6
Subgenual anterior cingulate cortex		L	-2	24	-14
Inferior frontal gyrus	960	L	-38	18	22
Inferior frontal gyrus		L	-54	18	20

Region	Size	L/R	x	y	z
Superior parietal lobule	1064	L	-28	-62	44
Parietal lobule		L	-34	-68	38
Supplementary motor area	680	L	-8	10	62
Fusiform gyrus	1112	L	-40	-70	-18
Fusiform gyrus		L	-44	-58	-18
Superior temporal gyrus	808	L	-32	0	-22
Thalamus	744	L	-22	-30	-2
Inferior occipital gyrus	2528	L	-26	-96	-8
Inferior occipital gyrus		L	-42	-86	-12
Inferior occipital gyrus		L	-30	-90	-16
Inferior occipital gyrus	1856	R	36	-90	-4
Inferior occipital gyrus		R	24	-94	-6
Middle occipital gyrus		R	34	-88	16

Notes: We used a cluster-level threshold of $p < 0.05$, with a cluster-forming threshold of $p < 0.01$. Peaks are listed first for each cluster with subpeaks listed in subsequent rows.

Table 2
Brain areas activated by personal reward as identified using ALE meta-analysis

Region	Size	L/R	x	y	z
Medial prefrontal cortex	10320		0	56	0
Medial prefrontal cortex			0	48	-2
Ventromedial prefrontal cortex			0	56	-14
Ventromedial prefrontal cortex		R	4	42	-16
Ventromedial prefrontal cortex			0	32	-14
Dorsal anterior cingulate cortex		R	2	38	26
Dorsal anterior cingulate cortex		R	4	32	14
Rostral anterior cingulate cortex		R	2	38	2
Nucleus accumbens	9944	R	12	10	-6
Caudate nucleus		R	12	18	2
Caudate		R	18	12	16
Putamen		R	26	18	-4
Amygdala		R	20	-2	-16
Nucleus accumbens	20904	L	-12	12	-6
Caudate		L	-14	28	0
Amygdala		L	-16	-2	-14
Anterior insula		L	-30	22	0
Anterior insula		L	-38	20	-12
Inferior frontal gyrus		L	-42	28	-6
Inferior frontal gyrus		L	-40	34	8
Inferior frontal gyrus		L	-44	38	-2
Inferior frontal gyrus		L	-46	32	0
Thalamus			0	-10	10
Thalamus		L	-12	-12	8
Thalamus		R	22	-12	14
Thalamus		R	16	-6	12
Ventral tegmental area	1864	R	6	-24	-14
Ventral tegmental area		L	-2	-22	-18

Region	Size	L/R	x	y	z
Posterior cingulate	1792		0	-32	30
Inferior frontal gyrus	2744	R	32	30	-18
Anterior insula		R	34	18	-18
Pons		L	-4	-28	-20
Dorsal anterior cingulate cortex	1104	R	6	20	30
Cuneus	1344	R	4	-62	20
Cuneus		R	12	-68	10
Posterior cingulate		R	6	-52	22

Notes. We used a cluster-level threshold of $p < 0.05$, with a cluster-forming threshold of $p < 0.01$. Peaks are listed first for each cluster with subpeaks listed in subsequent rows.

Brain areas commonly activated by vicarious and personal reward as identified using ALE conjunction analysis

Table 3

Region	Size	L/R	x	y	z
Ventromedial prefrontal cortex	2128		0	34	-14
Ventromedial prefrontal cortex			0	52	-12
Ventromedial prefrontal cortex		R	2	40	-14
Medial prefrontal cortex			0	58	-6
Amygdala	56	R	22	-6	-14
Amygdala	568	L	-18	-8	-14
Putamen	272	L	-26	8	-6
Anterior insula	200	L	-30	18	-2
Anterior insula	8	L	-34	10	-14
Hippocampus		L	-10	0	-12
Dorsal anterior cingulate cortex	120	R	4	38	24
Dorsal anterior cingulate cortex	16	R	12	24	28
Subgenual anterior cingulate cortex	24	R	0	28	-14

Notes. Both input images were cluster-level thresholded at $p < 0.05$, with a cluster-forming thresholded at $p < 0.01$. Peaks are listed first for each cluster with subpeaks listed in subsequent rows.

Brain areas activated more by (a) vicarious reward than personal reward and (b) personal reward than vicarious reward in ALE contrast analyses

Table 4

Region	Size	L/R	x	y	z
<i>Vicarious Reward > Personal Reward</i>					
Dorsomedial prefrontal cortex	536	L	-12	61	26
Dorsomedial prefrontal cortex		L	-14	56	26
Middle temporal gyrus	672	L	-58	-20	-4
Posterior superior temporal sulcus		L	-60	-27	-1
Angular gyrus	128	L	-30	-60	40
Cerebellum	1832	L	-28	-90	-16
Cerebellum		L	-33	-89	-17
Cerebellum		L	-22	-90	-18
Fusiform gyrus		L	-24	-92	-11
Fusiform gyrus		L	-40	-84	-12
Fusiform gyrus		L	-30	-94	-12
Superior occipital gyrus	1096	R	32	-64	40
Middle occipital gyrus		R	32	-70	36
Middle occipital gyrus	256	R	39	-87	11
Middle occipital gyrus		R	34	-90	12
<i>Personal Reward > Vicarious Reward</i>					
Nucleus accumbens	2712	R	15	17	-5
Nucleus accumbens		R	12	16	-14
Caudate		R	12	24	6
Caudate		R	16	19	8
Thalamus	7568	L	-6	-10	11
Thalamus		R	8	-10	12
Thalamus		R	14	-6	14
Nucleus accumbens		L	-9	5	1
Nucleus accumbens		L	-14	13	-7
Caudate		L	-6	10	18
Inferior frontal gyrus	264	R	38	24	-10

Notes. The input maps for the contrast analyses are described above for the single-study ALE meta-analyses and used a cluster-level threshold of $p < 0.05$ and a cluster-forming threshold of $p < 0.01$. In order to correct for multiple comparisons in the statistical difference map, we additionally used a conservative, whole-brain FDR correction of $p < 0.01$ (pID) and cluster extent of 128 mm^3 . Peaks are listed first for each cluster with subpeaks listed in subsequent rows.

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