



## Review

# The Ultimatum Game and the brain: A meta-analysis of neuroimaging studies



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## ABSTRACT

Social decision-making tasks involve psychological processes key to effective functioning in a complex, social world. The Ultimatum Game (UG) is a widely studied social decision-making task, which models responses to fairness. A number of neuroimaging studies have investigated the UG to identify neural correlates of unfairness and decisions to reject versus accept an offer. We present the first quantitative summary of neuroimaging studies in social decision-making with a meta-analysis of 11 fMRI studies of the UG, including data from 282 participants. Effect-Size Signed Differential Mapping was used to estimate effect sizes from statistical parametric maps and reported peak information before meta-analysing them. Consistent activations were seen in the anterior insula, anterior cingulate cortex (ACC), supplementary motor area (SMA) and cerebellum in response to unfair offers. Robust activations in the ACC, SMA and putamen were seen when deciding to reject rather than accept UG offers. These are consistent with models of motivational conflict during the UG decision-making process, a response to norm violations, with a possible role for the reward system.

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## 1. Introduction

Social interactions often require a balance between emotional and ‘rational’, cognitive motivations. Examples of this conflict can be seen in everyday life, for example in managing workplace relationships or taking decisions to trust others. The conflict between emotional and cognitive motivation has been studied using social decision-making tasks (Rilling and Sanfey, 2011; Stallen and Sanfey, 2013). Social decision-making tasks are an important model of the interplay between social and emotional cognition and reasoned, self-interest judgments, and are believed to involve psychological processes key to effective functioning in the complex, social world.

The Ultimatum Game (UG) is a task often used to study social decision-making, with its origins in behavioural economics. In the game one player acts as proposer and another acts as responder. The proposer is given a sum of money and chooses how much to split this with the responder. The proposer is typically given a range of options as to how to split the sum, but in all cases must offer *something*. The responder can either accept the division of money, in which case both players receive the amount proposed, or they can reject it, in which case neither player receives any money at all.

According to Rational Choice and Expected Utility Theory, a rational responder in the UG should accept any amount offered by the proposer, as this will represent a gain. Knowing this, a rational proposer should offer the lowest amount allowed by the rules, typically 10% of the total sum (Glimcher et al., 2009). However, evidence shows that people do not behave in this way, with proposers typically offering fairer amounts, and responders typically rejecting unfair offers. Indeed, studies suggest that while people accept fair, or close to fair, offers (40–50%), rejection rates gradually increase as the offer becomes lower (Civai et al., 2012; Corradi-Dell’Acqua et al., 2013; Güth et al., 1982; Rilling and Sanfey, 2011). This has been interpreted as being a result of social influences on decision-making. This is supported by the consistent finding that when the same offers are made in a control condition, typically where it is clear the offer has been computer-generated, rejection rates fall close to zero (Civai et al., 2010; Sanfey et al., 2003). Thus it is suggested that responders are punishing violations of social norms despite the cost incurred to them, which has been argued to be an adaptive mechanism (Boyd et al., 2003; Rand et al., 2013).

Sanfey et al. (2003) were the first to investigate the neural basis of motivational conflicts during decision-making in the UG. They argue that the decision to forego a financial gain is a response to the negative emotion elicited by unfair treatment. In order to investigate this, neural activity following receipt of unfair offers was contrasted with activity following fair offers. In this study, offers of 30% or below of the total stake were considered unfair. The authors discussed increased activations seen in the anterior cingulate cortex (ACC), anterior insula, and the dorsolateral prefrontal cortex (DLPFC). They suggest that anterior insula activity was predictive of the decision to reject an unfair offer, and argued that this area not only represented the negative emotion associated with unfairness, but also drove the decision to reject unfair offers.

Follow-up studies have similarly investigated fairness in the UG, with others reporting differences in activation associated with the decision to reject versus accept an offer. In the imaging literature there is some variation in the threshold below which offers are considered unfair, ranging from 20% to 40% of the total stake (see Table 1 for the definition of unfair for each of the included studies in the present analysis). This lack of consensus represents a challenge for the field, as an “unfair” offer in one study may not engage the same processes as an “unfair” offer in another study. Indeed, it has been reported that responses to 30% offers are dependent on the context in which they are presented, with lower rejection rates when there are more offers of 10–20% than 40–50%, and vice versa (Wright et al., 2011). An aim of the current analysis was to see if

**Table 1**  
Details of included studies. For studies whose t-maps were not available, the reported results were thresholded as follows: Sanfey et al. (2003) –  $p < 0.001$ , cluster size  $\geq 10$  voxels; Kirk et al. (2011) –  $p < 0.05$ , FDR-corrected, extend threshold  $> 10$  voxels; Harlé and Sanfey, 2012 – corrected for cluster-wise significance:  $p < 0.05$ , cluster size  $\geq 5$ .

| Study                            | No. of participants | Data                               | Analysis software      | Definition     |        | Behavioural data                              |   | Meta-analysis |          |
|----------------------------------|---------------------|------------------------------------|------------------------|----------------|--------|---|---|---------------|----------|
|                                  |                     |                                    |                        | Unfair (mean)  | Fair   |   |   | Fairness      | Response |
| Sanfey et al. (2003)             | 19                  | Reported peak coordinates<br>t-map | Brain Voyager<br>SPM 2 | 10–30% (18%)   | 50%    | Graphically measured                          | ✓ |               |          |
| Halko et al. (2009)              | 23                  | Reported peak coordinates<br>t-map | SPM 2                  | 8–17% (10.4%)  | 33–42% | Actual data                                   | ✓ |               |          |
| Kirk et al. (2011)               | 40                  | Reported peak coordinates<br>t-map | SPM 5                  | 10–20% (15%)   | 30–50% | Graphically measured                          | ✓ |               |          |
| Baumgartner et al. (2011)        | 18                  | Reported peak coordinates<br>t-map | Brain Voyager v1.1     | 20–30% (15%)   | 40–50% | Actual data                                   | ✓ |               |          |
| Harlé and Sanfey (2012)          | 38                  | Reported peak coordinates<br>t-map | SPM 8                  | 10–30% (20%)   | 50%    | Graphically measured                          | ✓ |               | ✓        |
| Civai et al. (2012)              | 19                  | t-map                              | SPM 8                  | 10–20% (15%)   | 50%    | Actual data                                   | ✓ |               | ✓        |
| Corradi-Dell’Acqua et al. (2013) | 23                  | t-map                              | SPM 8                  | 10–20% (15%)   | 50%    | Graphically measured                          | ✓ |               | ✓        |
| Guo et al. (2013)                | 21                  | t-map                              | SPM 5                  | 10–40% (21.7%) | 50%    | Actual data (error bars graphically measured) | ✓ |               | ✓        |
| Tomasino et al. (2013)           | 17                  | t-map                              | SPM 5                  | 10% (10%)      | 30%    | Actual data                                   | ✓ |               | ✓        |
| Vieira et al. (2013)             | 35                  | t-map                              | AFNI                   | 20–33%         | 40–50% | N/A   | ✓ |               | ✓        |
| Wei et al. (2013)                | 29                  | t-map                              | SPM 8                  | 10–20%         | 40–50% | N/A   | ✓ |               | ✓        |

this variation in definition of “unfair” had a modulatory effect on the neuroimaging results.

Neuroimaging studies have investigated variables such as the context of gain or loss (Guo et al., 2013; Tomasi et al., 2013), variations across the lifespan (Harlé and Sanfey, 2012) and the influence of competition (Halko et al., 2009) and emotional states (Grecucci et al., 2013; Harlé et al., 2012) on UG behaviour.

Across studies, there is an apparent consistency in the areas involved in social decision-making in the UG, and there have been a number of reviews published which summarise neuroimaging studies of social decision-making (Lee and Harris, 2013; Rilling and Sanfey, 2011; Rilling et al., 2008; Stallen and Sanfey, 2013). However, it has been documented that neuroimaging studies are typically under-powered (Button et al., 2013), leading to increased risks of both type I and type II errors. As such, meta-analyses of neuroimaging studies have become increasingly important. To date there has been no attempt at a quantitative analysis of neuroimaging findings in this field.

Social cognitive deficits are well recognised in psychiatric disorders, and have specifically been emphasised in schizophrenia as being a domain requiring urgent research to improve treatment options (Green et al., 2004). Social decision-making is an area of social cognition which is increasingly investigated, and by providing evidence for brain regions consistently involved in this domain, meta-analysis represents an important step in the development of psychopharmacological treatments. To date the UG is the most studied social decision-making task with functional imaging, hence our decision to review it here.

Popular methods of fMRI meta-analysis include activation likelihood estimation (ALE) and multi-level kernel density analysis (MKDA). These methods base their meta-analytic results on coordinates which have been reported by individual studies to have passed the statistical threshold for significance set by those studies. Whilst the results of such analyses provide an informative summary of statistically significant fMRI results across a number of studies in a field, these methods do not include subthreshold results and therefore do not necessarily address the problem of low power inherent in fMRI. A further limitation of these techniques is that they do not produce a statistical measure of effect-size or its variance.

In this analysis, we use Effect-Size Signed Differential Mapping (ES-SDM), a neuroimaging meta-analytic method that can combine reported peak information (coordinates and *t*-values) from some studies, with original statistical parametric maps (SPMs) from others, thus allowing a comprehensive inclusion of information from these studies (Radua et al., 2012). The main advantage of an effect-size-based meta-analysis is the ability to produce a more precise estimate of the effect size than is seen in the individual studies included in the meta-analysis alone. Other relevant advantages are the possibility to assess the between-study heterogeneity and the potential publication bias. Here, we not only use these tools but also assess whether findings are replicable using the so-called jack-knife analyses.

Typically, for the UG, contrasts of interest are those comparing neural activity associated with receiving an unfair offer compared to a fair offer, or activity associated with choosing to reject rather than accept an offer, although not all studies report both of these contrasts. We present findings from the analysis of both of these contrasts, termed the Fairness and Response contrast, respectively. Where appropriate, additional data has been obtained from the authors. There are four possible outcomes in the UG: acceptance or rejection of a fair offer, and acceptance or rejection of an unfair offer. Fig. 1 illustrates how these possible outcomes are positioned in each of the contrasts reported in this meta-analysis.

There are different interpretations of UG neuroimaging results. These place different emphasis on the role of negative emotions

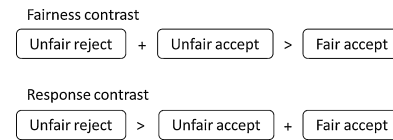


Fig. 1. Contrast diagram. NB: No 'Fair reject' as the frequency of this outcome was negligible.

and the idea of violations of social norms. As mentioned above, it has been suggested that UG rejection behaviour is driven by negative emotion elicited by unfair treatment, and that this is associated with anterior insula activation (Rilling et al., 2008; Sanfey et al., 2003). An alternative interpretation is that anterior insula responses are not driven by negative emotion per se, but by detection of violations of social norms, and that the decision to reject the unfair offer is a rejection of this norm violation (Civai et al., 2012; Corradi-Dell'Acqua et al., 2013). Additionally, a role for reward has been proposed. It has been suggested that reward pathways may be involved in the punishment of norm violations, as well as overcoming negative emotions to accept unfair offers (De Quervain et al., 2004; Tabibnia et al., 2008). These explanations need not be mutually exclusive, and while a meta-analysis will not be able to select between these interpretations, we will discuss our findings in the context of these models. Here, in order to identify areas most robustly associated with unfairness and rejection behaviour, we present results from a meta-analysis of functional neuroimaging studies investigating the Ultimatum Game.

## 2. Methods

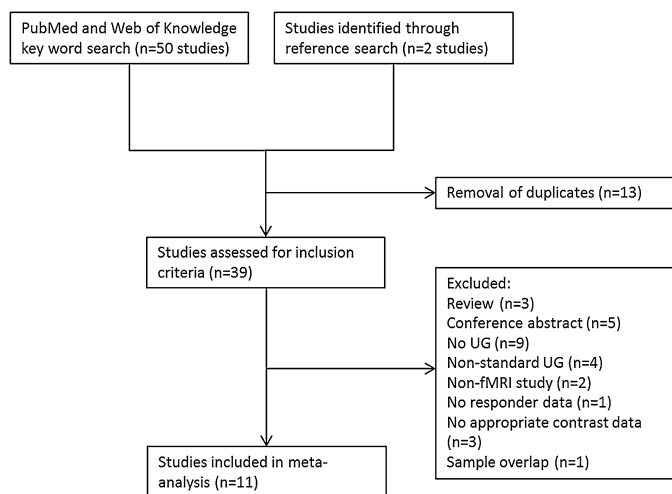
### 2.1. Literature search

A literature search was carried out using the PubMed and Web of Knowledge databases, entering the search terms “Ultimatum Game” AND (“fMRI” OR “functional magnetic resonance imaging”) in March 2014. Further papers were identified by searching reference sections in papers returned by the original search. We included studies that (1) reported fMRI results from whole brain thresholds, i.e. excluding those results *only* obtained after applying small-volume corrections, (2) included healthy participants, (3) used a single-shot rather than iterated version of the Ultimatum Game, (4) reported data from participants acting as Responders rather than Proposers, (5) reported data from versions of the Ultimatum Game which can be considered equivalent to the standard version of the game (for example, where a study investigated differences between a ‘gain’ or ‘loss’ context, we only included data from the ‘gain’ context). In order to adhere to typical meta-analysis standards, we excluded studies with sample overlap with an already-included study. Eleven studies met these inclusion criteria (see Fig. 2).

Our primary interest was in the Fairness (Unfair offer vs Fair offer) activation contrasts in participants playing a standard version-equivalent of the Ultimatum Game. Where these contrasts were not reported, authors were contacted asking for the relevant data. Authors were also asked to provide data for the Response contrast (Accept vs Reject) where available, as well as behavioural data in the form of offer rejection rate. Statistical parametric maps (*t*-maps) were requested from all studies included in the meta-analysis in order to increase the precision and accuracy of the results (for details, see Section 2.2).

### 2.2. Effect Size-Signed Differential Mapping (ES-SDM)

The meta-analysis was carried out using Effect Size-Signed Differential Mapping (ES-SDM) software. ES-SDM is a weighted, voxel-based meta-analytic method which has been validated and



**Fig. 2.** Flow chart showing study selection for the meta-analysis.

used in a number of structural and functional MRI meta-analyses (Aoki et al., 2013; Fusar-Poli, 2012; Hart et al., 2012; Richlan et al., 2011; Nakao et al., 2011). ES-SDM recreates voxel-level maps of effect sizes and their variances, and allows the inclusion of both peak information (coordinates and  $t$ -values) and statistical parametric maps (Radua et al., 2012). The conversion from  $t$ -statistics to effect size is carried out using standard statistical techniques. Where statistics are only available for reported peak coordinates, the effect size is exactly calculated at this peak and estimated in the remaining voxels depending on their distance from these peaks, using an unnormalised Gaussian kernel, which is multiplied by the effect size of the peak. This method of estimation is similar to the estimation of activation likelihood used in ALE, but the use of effect sizes in the calculation has been shown to increase the accuracy of estimation of the true signal compared to alternative methods (Radua et al., 2012). Additionally, the inclusion of statistical parametric maps in a meta-analysis has been shown to substantially increase the sensitivity of voxel-based meta-analyses. For example, in the ES-SDM validation study, sensitivity increased from 55% to 73% with the inclusion of just one SPM and to 87% with the inclusion of two SPMS (Radua et al., 2012). Unlike other methods, ES-SDM allows both negative and positive values in the same map, which, along with the use of effect size and variance maps, allows for standard meta-analytic measures to be calculated, such as between-study heterogeneity. Full details of the ES-SDM method and its validation are presented elsewhere (Radua et al., 2012).

### 2.3. Analyses

Meta-analytic effect-sizes were voxelwise divided by their standard errors to obtain ES-SDM  $z$ -values. As these  $z$ -values may not follow a standard normal distribution, a null distribution was empirically estimated for each meta-analytic brain map. Specifically, null distributions were obtained from 50 whole brain permutations (which, multiplied by the number of voxels, resulted in about 4-million values per null distribution); previous simulation work has found that permutation-derived ES-SDM thresholds are already very stable with even only 5 whole-brain permutations (Radua et al., 2012). Voxels with  $p$ -value  $< 0.001$  were considered as significant, but those from clusters with less than 10 voxels or with peaks with SDM  $z$ -values  $< 1$  were discarded in order to reduce the false positive rate. While this threshold is not strictly family-wise correction for multiple comparisons, previous research has found that it has an optimal sensitivity while correctly controlling the false positive rate at  $< 0.05$  or even  $< 0.01$  (Radua et al., 2012).

In order to assess the potential impact of the variation in definition of unfair offer (See Table 1), we carried out a meta-regression analysis on effect size values at peak voxels of significant clusters using the metareg module in Stata Statistical Software (Harbord and Higgins, 2008; StataCorp, 2011). Heterogeneity was also assessed in areas of significant activation. Jack-knife sensitivity analyses were conducted to examine the robustness of the main meta-analytic output. This was carried out by removing one study at a time and repeating the analysis. In order to assess publication bias, effect size estimates were extracted for peak voxels of significant clusters from the meta-analysis for each study. Using these, funnel plots were created and visually inspected, and Egger regression tests carried out (Egger et al., 1997). We used the Egger regression test as a quantitative method of assessing asymmetry in the funnel plots. Evidence of bias is indicated if the intercept of a regression line of effect size/standard error against  $1/\text{standard error}$  significantly deviates from zero.

In addition, we assessed the rejection rate of the responder from each study included in the meta-analysis in order to explore the variation in response trends across studies. Where behavioural data was supplied by corresponding authors on individual studies, this data was incorporated into this analysis ( $n = 4$ ). Where this data was unavailable from corresponding authors, graphical behavioural data was digitally measured using the GNU imaging manipulation program (v2.6.1) (Mattis and Kimball, 2008).

## 3. Results

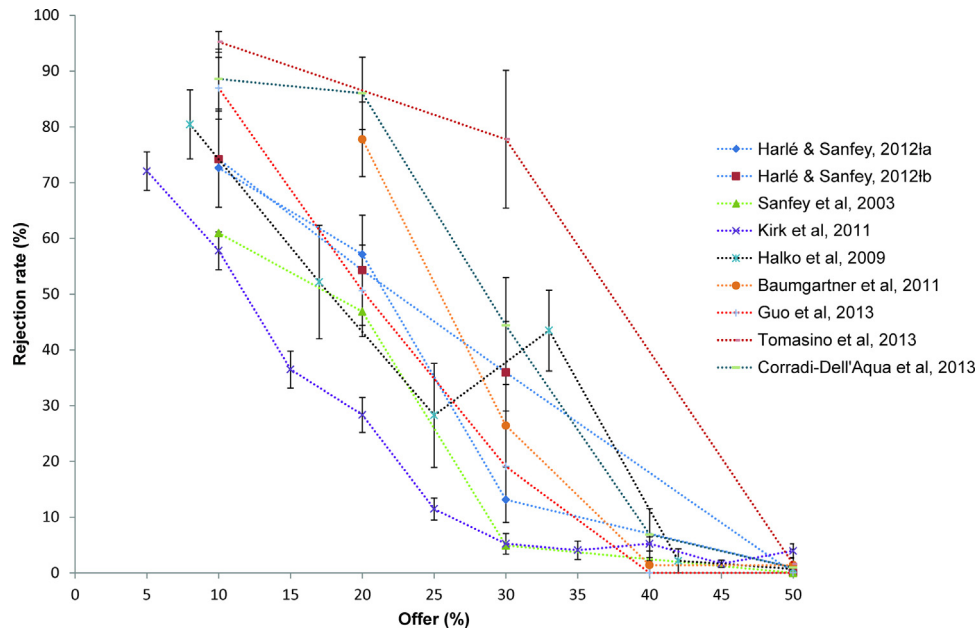
### 3.1. Included studies

See Table 1 for details of included studies. 11 studies were identified for inclusion in the 'Fairness' meta-analysis (Unfair offer  $>$  Fair offer) (Baumgartner et al., 2011; Civai et al., 2012; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Halko et al., 2009; Harlé and Sanfey, 2012; Kirk et al., 2011; Sanfey et al., 2003; Tomasino et al., 2013; Vieira et al., 2013; Wei et al., 2013). These included a total of 282 participants. The authors of eight studies were able to provide  $t$ -maps for use in the meta-analysis (Baumgartner et al., 2011; Civai et al., 2012; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Halko et al., 2009; Tomasino et al., 2013; Vieira et al., 2013; Wei et al., 2013). Five studies were able to provide statistical parametric maps for the 'Response' meta-analysis (Reject  $>$  Accept), which included data from 100 participants (Civai et al., 2012; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Tomasino et al., 2013; Wei et al., 2013). Six studies were able to provide data for contrasts which were not reported in their publications (Baumgartner et al., 2011; Civai et al., 2012; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Tomasino et al., 2013; Wei et al., 2013).

The inclusion of this many statistical parametric maps is a strong asset to the current analysis. The results of the meta-analyses will be less biased towards the reported peaks of studies for which we were unable to obtain  $t$ -maps. Additionally, the increased statistical power afforded by the inclusion of a high percentage of  $t$ -maps (Radua et al., 2012) in the analysis enables the detection of areas of activation which may not have reached statistical significance in any one study alone. As such, the potential exists to highlight new areas for study in the social decision-making field.

### 3.2. Behavioural results

Offers were converted to percentages of the total money available, to enable comparison across studies. Fig. 3 illustrates the mean rejection rate at each offer level for individual studies included in the meta-analysis.



**Fig. 3.** Responder rejection rates from behavioural data of the included studies. NB: *Civai et al. (2012)* and *Wei et al. (2013)* not included due to rejection rates not being given for individual offers. *Vieira et al. (2013)* not included because data not available. †Data from *Harlé and Sanfey (2012)* reported separately for two participant groups, a Young (18–27) and b Older (55–78). Error bars: ±1 SEM (standard error of the mean).

3.2.1. Results of fairness meta-analysis

This meta-analysis included all 11 studies comprising 282 participants. Participants showed spatially large activations in: (a) bilateral mid/anterior cingulate cortex (aMCC/ACC), extending to the left anterior supplementary motor area (SMA); (b) bilateral insula; and (c) right cerebellum. Additionally, there was a smaller cluster of activation in the left inferior parietal lobule (*Table 2; Fig. 4(A)*).

3.2.2. Fairness contrast heterogeneity, sensitivity and publication bias analyses

Significant between-study heterogeneity was limited to a small area in the cingulate gyrus. Jack-knife sensitivity analyses showed that the main findings were highly replicable across combinations of datasets. However, the activations in the clusters encompassing the left insula appear more robust than those of the right insula. In addition, clusters in the cerebellum and aMCC/ACC appear more robust than the inferior parietal lobule (see *Fig. 5(A)*). Three clusters (left precentral gyrus, left postcentral gyrus, right insula)

showed evidence of publication bias using Egger regression (see Supplementary Fig. S1). It should be noted that the publication bias analyses would not have survived multiple comparison correction, but we chose to report the conservative figure here.

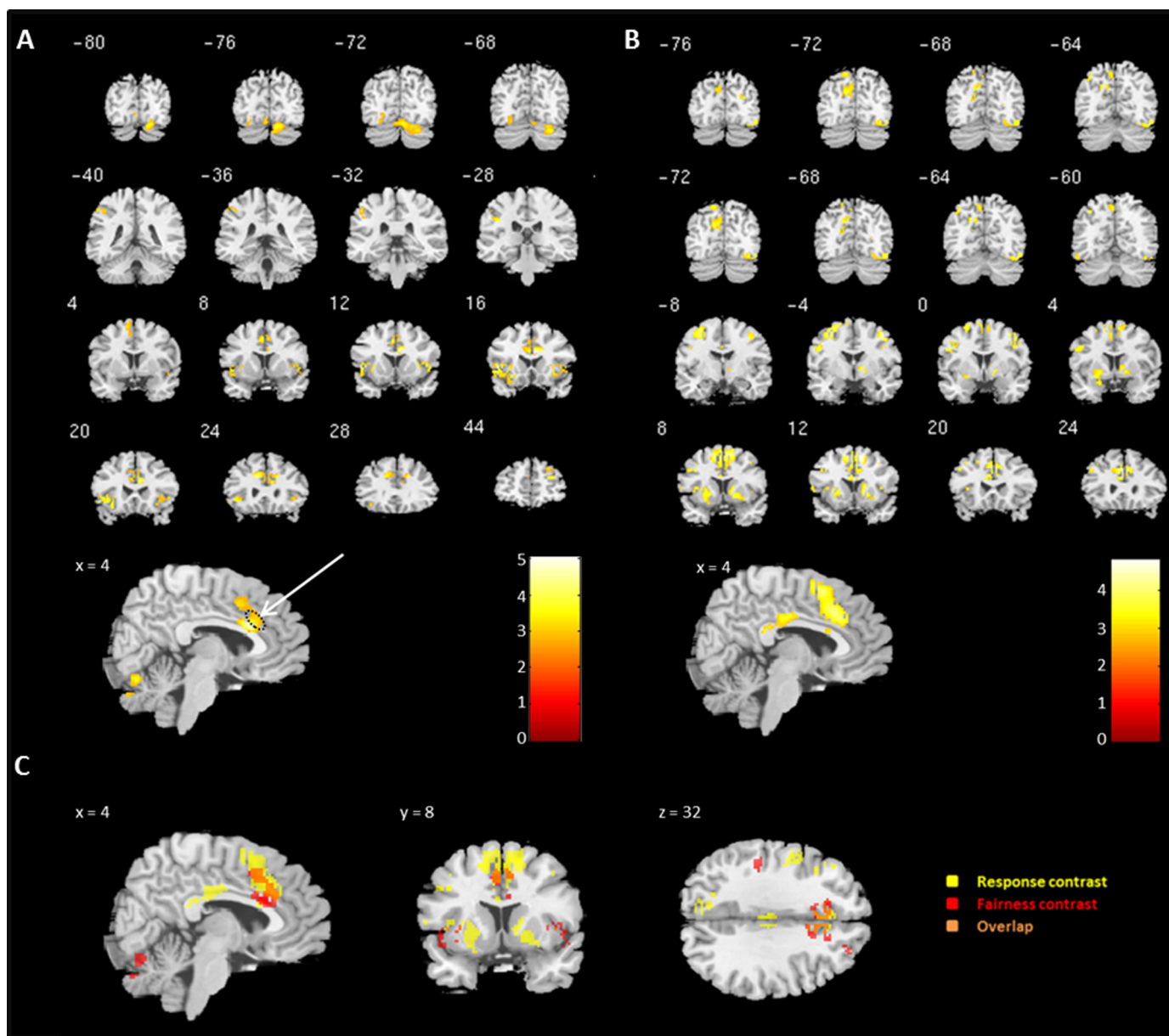
Supplementary Fig. S1 related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2014.10.014>.

3.2.3. Results of response meta-analysis

This meta-analysis only included five studies comprising 100 participants, but we could retrieve the statistical parametric maps from all of these studies. Statistical parametric maps highly increase statistical power (*Radua et al., 2012*), enabling the detection of a number of robust activation clusters. The results of the response contrast meta-analysis showed increased activation in: (a) SMA, extending to the anterior midcingulate cortex (aMCC); (b) right middle frontal gyrus; (c) bilateral lentiform nucleus. Other, less significant, clusters included the bilateral fusiform gyrus, inferior parietal lobule, and the posterior cingulate (*Table 3; Fig. 4(B)*).

**Table 2**  
Meta-analytic results for the Fairness contrast ( $n = 11, k \geq 25$ ).

| Peak voxel<br>Region      | Talairach |     |     | Hedge's g | SDM z-value | p-Value   | Cluster       |   |
|---------------------------|-----------|-----|-----|-----------|-------------|-----------|---------------|---|
|                           | x         | y   | z   |           |             |           | No. of voxels | Breakdown   |
|                           |           |     |     |           |             |           |               |   |
| Anterior cingulate cortex | 6         | 16  | 26  | 0.33      | 5.142       | <0.000001 | 678           | Bilateral mid/anterior cingulate gyrus<br>Left supplementary motor area |
| L precentral gyrus        | -42       | 14  | 6   | 0.29      | 4.698       | 0.000002  | 349           | Left insula<br>Left inferior frontal gyrus<br>Left claustrum            |
| R cerebellum (uvula)      | 26        | -68 | -26 | 0.28      | 3.731       | 0.000077  | 566           | Right cerebellum  |
| L postcentral gyrus       | -38       | -28 | 30  | 0.22      | 3.626       | 0.000125  | 123           | Left inferior parietal lobule   |
| R insula                  | 40        | 12  | 8   | 0.33      | 3.606       | 0.000125  | 220           | Right insula  |
| L lingual gyrus           | -26       | -70 | -8  | 0.19      | 3.132       | 0.000904  | 88            | Left cerebellum   |



**Fig. 4.** (A) Fairness contrast results, with small area of between-study heterogeneity labelled on sagittal slice with a dotted outline and arrow. (B) Response contrast results. (C) Fairness and Response contrasts binarised; orthogonal views to highlight overlap. Colour bars represent  $z$  values. (For interpretation of the references to colour in text, the reader is referred to the web version of this article.)

### 3.2.4. Response contrast heterogeneity, sensitivity and publication bias analyses

There was no significant between-study heterogeneity. Jack-knife sensitivity analyses showed that the main findings were replicable across combinations of datasets, with the most robust findings being in the left aMCC, left SMA and right lentiform nucleus (see Fig. 5(B)). There was no evidence of publication bias in all but one cluster, as assessed by the Egger regression test (right superior frontal gyrus) (Egger et al., 1997).

### 3.3. Comparison of Fairness and Response activations

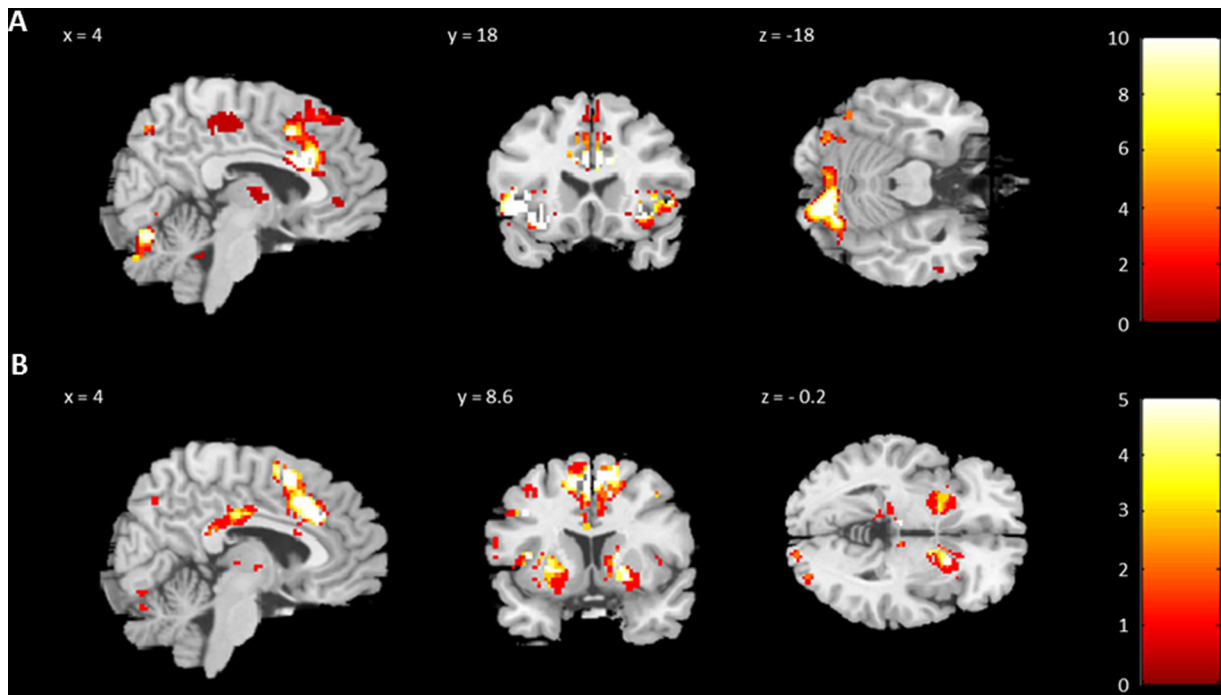
The meta-analytic output maps were binarised in order to assess the overlap of regions activated both by Fairness and Response contrasts (see Fig. 4(C)). Common activation of areas in the bilateral aMCC and right SMA were found.

### 3.4. Meta-regression to assess the influence of unfair offer definition

In order to assess the influence of the variation of unfair offer definitions across studies on the meta-analytic results, we carried out a meta-regression of the effect size of the peak voxel at each significant cluster. We first calculated the mean unfair offer in each study (range: 10–26.5%, mean: 17.4%), then used these values in the meta-regression. In no cluster across the two contrasts did the mean unfair offer modulate effect size at its peak voxel.

## 4. Discussion

We present the first meta-analysis of neuroimaging studies of the Ultimatum Game (UG). The UG is a widely used social decision-making task, which models behaviour in response to fairness considerations. By examining the neural correlates of



**Fig. 5.** Binarised maps of Jack-knife analyses. Colour bars represent number of overlapping jack-knife maps. (A) Fairness contrast and (B) response contrast. (For interpretation of the references to colour in text, the reader is referred to the web version of this article.)

responders in the UG, we aim to build upon the growing body of literature which looks to elucidate the mechanisms by which humans incorporate social and self-interested considerations on a neural level. The results of this meta-analysis indicate that there is a consistent activation of the bilateral mid-anterior insula, aMCC/anterior cingulate cortex (ACC), medial supplementary motor area (SMA), and cerebellum in response to unfairness in the Ultimatum Game (UG). When making the decision to reject rather than accept an offer, activations were seen bilaterally in the aMCC and SMA, bilateral lentiform nucleus, and the right middle frontal gyrus. The results from the Response contrast were most robust in the left aMCC and left SMA. Based on the results of these analyses, there appears to be common activations in response to unfairness and during the decision to reject rather than accept an offer. This overlap occurs in the aMCC and the SMA.

The purpose of the analysis was not to select between the different models used to explain UG behaviour and its neural correlates, but to provide a robust, quantitative definition of the brain regions consistently activated in the relevant contrasts. In so doing, we have discussed the role of each region in relation to the model of norm violations, reward, or affective processing, as appropriate.

Studies have previously found the anterior insula to be involved in processing negative emotional states, such as anger and disgust (Damasio et al., 2000; Phillips et al., 1997). The activation of this region in response to unfair offers in the UG is often interpreted as processing and representing the negative emotional state induced by unfair treatment by a social entity (Halko et al., 2009; Sanfey et al., 2003). The consistent finding that anterior insula activation is not seen in low, control-condition offers (non-social) is evidence that this is not simply a negative emotional response to low

**Table 3**  
Meta-analytic results for the response contrast ( $n=5$ ,  $k \geq 25$ ).

| Peak voxel<br>Region          | Talairach |     |     | Hedge' g | SDM z-value | p-Value   | Cluster       |  |
|-------------------------------|-----------|-----|-----|----------|-------------|-----------|---------------|--|
|                               | x         | y   | z   |          |             |           | No. of voxels | Breakdown  |
| Left superior frontal gyrus   | 10        | 12  | 52  | 0.53     | 4.895       | <0.000001 | 1285          | Bilateral anterior supplementary motor area (SMA)<br>Bilateral anterior midcingulate cortex (aMCC) |
| Right middle frontal gyrus    | 38        | -4  | 50  | 0.47     | 4.437       | 0.000001  | 169           |  |
| Right lentiform nucleus       | 16        | 10  | 2   | 0.43     | 4.090       | 0.000045  | 256           | Right caudate body<br>Right lentiform nucleus  |
| Left inferior parietal lobule | -36       | -60 | 46  | 0.42     | 3.955       | 0.000077  | 101           | Left inferior parietal lobule<br>Left superior parietal lobule                                     |
| Right fusiform gyrus          | 42        | -66 | -14 | 0.41     | 3.917       | 0.000093  | 163           |  |
| Left cingulate gyrus          | -2        | -22 | 34  | 0.41     | 3.875       | 0.000113  | 148           | Bilateral posterior mid cingulate  |
| Left lentiform nucleus        | -20       | 14  | 6   | 0.40     | 3.832       | 0.000139  | 287           |  |
| Left precuneus                | -18       | -68 | 20  | 0.40     | 3.541       | 0.000434  | 170           | Left precuneus<br>Left cuneus  |
| Left fusiform gyrus           | -50       | -56 | -16 | 0.36     | 3.415       | 0.00061   | 46            |  |
| Right middle occipital gyrus  | 30        | -78 | 20  | 0.36     | 3.398       | 0.000746  | 29            | Right cuneus   |
| Right insula                  | 38        | 10  | 6   | 0.35     | 3.340       | 0.000928  | 33            |  |
| Left precuneus                | -12       | -70 | 50  | 0.34     | 3.238       | 0.001308  | 92            |  |

monetary reward (Civai et al., 2012; Corradi-Dell'Acqua et al., 2013; Harlé et al., 2012; Sanfey et al., 2003). Some studies report that the strength of anterior insula activation in response to unfair offers is predictive of the decision to reject such an offer (Kirk et al., 2011; Sanfey et al., 2003). Indeed, Sanfey et al. (2003) examined this on a trial by trial basis and concluded that this supported "... the hypothesis that neural representations of emotional states guide human decision-making" (p. 1757).

A different interpretation of anterior insula activation is that it is involved in representing a deviation from expected norms, in this case, the violation of social norms (Civai et al., 2012; Corradi-Dell'Acqua et al., 2013). Civai et al. (2012) and Corradi-Dell'Acqua et al. (2013) report that anterior insula is activated in response to unequal offers regardless of whether responders are making decisions on behalf of themselves or a third party. Citing investigations of galvanic skin response during a similar study (Civai et al., 2010), these authors have suggested that responding to third-party offers diminishes the emotional response elicited by unfair offers, despite no observed reduction in rejection rate. Supporting the interpretation that anterior insula activity represents deviation from expected norms, the study by Civai et al. (2012) reported that when participants responded to unequal offers in both directions – i.e. both advantageous and disadvantageous – for themselves or a third party, they rejected inequality on behalf of a third party regardless of advantageousness, while only rejecting disadvantageous inequality in the self-trials. Interestingly, not only was the anterior insula activated in response to both self and third-party inequality, but increased activation was *not* observed in disadvantageous unequal compared to advantageous unequal offers to the self. Furthermore no correlation was found between strength of anterior insula activation and rejection rate. This suggests that the role of the insula upon receipt of an unfair offer goes beyond representing negative emotions.

The activations seen in the medial prefrontal and cingulate cortices have been interpreted as representing the control and monitoring of conflict between emotional and cognitive motivations (Baumgartner et al., 2011; Sanfey et al., 2003). The fact that there is overlap in these areas in both the Fairness and Response analyses presented here appears to support this interpretation. Referring to Fig. 1, it is clear that the Fairness contrast encompasses the decision to both accept and reject unfair offers; the Response contrast represents the cognitive, motivational conflict involved in rejecting an unfair offer. As such both contrasts would be expected to identify a conflict between emotional and cognitive motivations. It should be noted that while these results appear to be in line with the conflict monitoring/resolution model of ACC/mPFC function, there is debate as to the validity of this model (Fellows and Farah, 2005; Grinband et al., 2011; Holroyd, 2013). Grinband et al. (2011) suggest that mPFC activation (including mid-anterior cingulate) in conflict resolution paradigms is better explained in relation to reaction/response time, with greater activation seen with longer response times. Few studies report reaction times in the UG, so a meta-regression was not possible, and there is inconsistency between those that do (Harlé and Sanfey, 2012; Tomasino et al., 2013; Van der Veen and Sahibdin, 2011). While the findings of the current analysis confirm the role of this area in social decision-making and the UG, we are unable to resolve the debate with this data.

Reports that the aMCC/mPFC are activated more in response to unfair offers to the self than to third parties, and that this activation is negatively correlated with rejection rate, supports the argument that these areas are involved in overcoming the motivation to sanction norm violations in favour of self-interest following receipt of an unfair offer (Civai et al., 2012; Corradi-Dell'Acqua et al., 2013). In a recent review, Apps and colleagues (Apps et al., 2013) argue that the midcingulate cortical gyrus is intimately involved in the

processing of social information, specifically when predicting and monitoring the outcomes of decisions during social interactions. The results from the Fairness and Response contrasts support this. Nachev et al. (2005) argue that the rostral and caudal regions of the pre-SMA, seen in the present analyses, are functionally distinct in free-choice action planning, with the overall role being to resolve competition between two incompatible action plans. The authors suggest that alterations in planned action will be represented in the pre-SMA, and this interpretation can be applied to decision to reject unfair offers (rather than act in economic self-interest), which is on the same side of both the Fairness and Response contrast.

Interestingly, activation in the dorsolateral prefrontal cortex (DLPFC) was not present in the Fairness contrast, despite this being reported in a number of studies (Baumgartner et al., 2011; Guo et al., 2013; Güroğlu et al., 2011; Harlé and Sanfey, 2012; Sanfey et al., 2003). Meta-analysis seeks to identify consistency in activation across studies. As the DLPFC encompasses a large area, the fact that it is minimally present in this contrast may reflect the disparate regions within this area being activated in different studies. Right DLPFC activation was, however, present in the Response contrast, although sensitivity analyses show the robustness of this finding was less than cingulate and medial prefrontal regions. Studies employing repetitive transcranial magnetic stimulation (rTMS) have shown that disruption to the right DLPFC results in reduced rejection rates of unfair offers (Baumgartner et al., 2011; Knoch et al., 2008, 2006). Baumgartner et al. (2011) further reported reduced connectivity to the posterior ventromedial PFC (vmPFC), but no differences in activity of, nor connectivity with, the anterior insula. rTMS did not affect participants' fairness ratings of different offers (Knoch et al., 2008, 2006). With anterior insula response to inequality still intact with disrupted right DLPFC, it suggests that DLPFC connectivity to the vmPFC may be key in *implementing* the costly, normative decision to reject unfair offers. It should be noted, however, that vmPFC activity was not seen in the current analysis, and we were unable to look at connectivity as it was not reported in the included studies. A limitation of ES-SDM, other neuroimaging meta-analytic methods and reporting of imaging results is that there are no standards in place for the meta-analysis of functional connectivity data.

Despite the finding of increased activation in the anterior putamen in the Response contrast analysis, little attempt has been made in the included studies to interpret this, although the reward system has been discussed in relation to its activation upon receipt of a fair offer (Tabibnia et al., 2008). Kirk et al. (2011) cite a study which reported putamen activation in a non-social, decision-making investment game when it was revealed that an alternative decision by the participant could have earned an alternative reward to that which they actually earned (Lohrenz et al., 2007). This is termed the "fictive error", which could plausibly explain the activations seen following offers which were later rejected – as these were mostly unfair offers. This interpretation does not elucidate the degree to which this activation is due to social processing. An interpretation which involves social processing draws on the idea of altruistic punishment, the costly punishment of social norm violation. It has been suggested that while the experience of disadvantageous inequality is in itself negative, the opportunity to resolve this inequality is rewarding (De Quervain et al., 2004; Yu et al., 2013), leading to activation of the putamen and related striatal structures. A recent review (Bhanji and Delgado, 2014) discusses the evidence for non-social reward pathways being involved in social reward. The evidence suggests there is no distinct social reward pathway, but social rewards, such as sanctioning norm violators, can activate reward areas despite monetary loss (Crockett et al., 2013; De Quervain et al., 2004). Considering the positioning of the possible responses (see Fig. 1), it is clear that putamen activation is only seen when acceptance of an unfair offer is not on the same side of the



contrast as rejection of an unfair offer. This provides some support for the idea of rejecting an unfair offer being inherently rewarding.

This meta-analysis has highlighted the involvement of another region not discussed in the UG literature: the cerebellum. A recent meta-analysis of cerebellar function highlights a region, close to those activated in our analysis, as being involved in negative emotion (Keren-Happuch et al., 2014). Activity of this area in the Fairness contrast fits with the theory that the cerebellum has a general cognitive-affective role (Keren-Happuch et al., 2014; Schmahmann and Caplan, 2006), but it is unclear from this analysis whether it plays a specific part in the social decision-making aspect of the UG. Referring again to Fig. 1, the difference between contrasts is the positioning of the decision to accept an unfair offer. The finding of cerebellar activity when both responses to unfair offers are on the same side of the contrast (Fairness) supports an affective processing role for the cerebellum; be this due to negative emotion elicited by unfair treatment, or to inequality aversion. There is large cerebellar-cortical connectivity, and investigation beyond the scope of this meta-analysis is needed to elucidate the role of the cerebellum in social decision-making.

A strength of the current study is that we were able to obtain statistical parametric maps for 8 of the 11 studies included in the analysis. However, there remains the possibility of bias towards the areas of peak coordinates reported in the remaining 3 studies. Running the analysis with just those studies for which we had *t*-maps produced results similar (though expectably slightly less significant) to those reported here, so any bias introduced appears to be minimal. The Response contrast consisted of only five studies, so the results from this contrast should be treated with some caution. However, it must be noted that we could retrieve the statistical parametric maps from all of these studies, thus highly increasing the statistical power (Radua et al., 2012). As with all meta-analyses, inclusion criteria needed to be strict to limit heterogeneity, and as such many fMRI studies in the UG field were necessarily not included in the analyses. This may add an additional unintentional level of bias to the findings reported here.

It is notable that very few neuroimaging meta-analyses address the issue of publication bias. Publication bias analysis in neuroimaging is an area which requires further consideration in the field as a whole, as interpretation of its results are not as straightforward as in traditional meta-analyses. Firstly, there is a relatively low plausibility of a whole-brain analysis not being published due to a low effect in a particular voxel. Secondly, voxels whose effect failed to survive multiple comparisons in an individual study will have an estimated effect size of zero in a coordinate-based, voxel-wise meta-analysis (i.e. in the absence of a statistical parametric map). Studies with small sample sizes will more likely have small effects not reaching significance. Ultimately, this will affect the standard analysis of a funnel plot. However, we have reported the results of the publication bias analysis here to stay in line with standard meta-analysis methods and because the majority of our data included whole brain statistical parametric maps. Furthermore, we do not believe publication bias is any less of an issue as it is in other fields. With these limitations in mind, Egger regression analyses revealed asymmetry in the funnel plots of the peak voxel of 3 clusters in the Fairness contrast, and 1 in the Response contrast. Visual inspection of these funnel plots suggest that some relatively smaller studies reporting small effects at these voxels are not included in the analysis (see Supplementary Fig. 1).

## 5. Conclusion

This study presents the first meta-analysis of functional neuroimaging studies investigating social decision-making. Specifically, Fairness and Response contrasts in the Ultimatum Game.

Consistent activations were seen in the anterior insula, aMCC, ACC, and mPFC in response to unfair compared to fair offers. These activations are consistent with a model of norm violations. This analysis has also identified a potential role for the cerebellum in social decision-making. Robust findings of activation in the aMCC, mPFC and putamen were seen during the decision to reject as compared to accept UG offers. This is most parsimoniously explained by conflict during the decision-making process, with a possible role for the reward system, which may have a social element to it.

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## References

- Aoki, Y., Inokuchi, R., Nakao, T., Yamasue, H., 2013. Neural bases of antisocial behavior: a voxel-based meta-analysis. *Soc. Cogn. Affect. Neurosci.*, <http://dx.doi.org/10.1093/scan/nst104>.
- Apps, M.A.J., Lockwood, P.L., Balsters, J.H., 2013. The role of the midcingulate cortex in monitoring others' decisions. *Front. Neurosci.* 7, 251, <http://dx.doi.org/10.3389/fnins.2013.00251>.
- Baumgartner, T., Knösch, D., Hotz, P., Eisenegger, C., Fehr, E., 2011. Dorsolateral and ventromedial prefrontal cortex orchestrate normative choice. *Nat. Neurosci.* 14, 1468–1474, <http://dx.doi.org/10.1038/nn.2933>.
- Bhanji, J.P., Delgado, M.R., 2014. The social brain and reward: social information processing in the human striatum. *Wiley Interdiscip. Rev. Cogn. Sci.* 5, 61–73, <http://dx.doi.org/10.1002/wcs.1266>.
- Boyd, R., Gintis, H., Bowles, S., Richerson, P.J., 2003. The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. U. S. A.* 100, 3531–3535, <http://dx.doi.org/10.1073/pnas.0630443100>.
- Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. *Nat. Rev. Neurosci.* 14, 365–376, <http://dx.doi.org/10.1038/nrn3475>.
- Civai, C., Corradi-Dell'Acqua, C., Gamer, M., Rumiati, R.I., 2010. Are irrational reactions to unfairness truly emotionally-driven? Dissociated behavioural and emotional responses in the Ultimatum Game task. *Cognition* 114, 89–95, <http://dx.doi.org/10.1016/j.cognition.2009.09.001>.
- Civai, C., Crescentini, C., Rustichini, A., Rumiati, R.I., 2012. Equality versus self-interest in the brain: differential roles of anterior insula and medial prefrontal cortex. *Neuroimage* 62, 102–112, <http://dx.doi.org/10.1016/j.neuroimage.2012.04.037>.
- Corradi-Dell'Acqua, C., Civai, C., Rumiati, R.I., Fink, G.R., 2013. Disentangling self- and fairness-related neural mechanisms involved in the Ultimatum Game: an fMRI study. *Soc. Cogn. Affect. Neurosci.* 8, 424–431, <http://dx.doi.org/10.1093/scan/nss014>.
- Crockett, M.J., Apergis-Schoute, A., Herrmann, B., Lieberman, M.D., Lieberman, M., Müller, U., Robbins, T.W., Clark, L., 2013. Serotonin modulates striatal responses to fairness and retaliation in humans. *J. Neurosci. Off. J. Soc. Neurosci.* 33, 3505–3513, <http://dx.doi.org/10.1523/JNEUROSCI.2761-12.2013>.
- Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L.B., Parvizi, J., Hichwa, R.D., 2000. Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat. Neurosci.* 09, 1049–1056.
- De Quervain, D.J.-F., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A., Fehr, E., 2004. The neural basis of altruistic punishment. *Science* 305, 1254–1258, <http://dx.doi.org/10.1126/science.1100735>.
- Egger, M., Davey Smith, G., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple, graphical test. *BMJ* 315, 629–634.
- Fellows, L.K., Farah, M.J., 2005. Is anterior cingulate cortex necessary for cognitive control? *Brain J. Neurol.* 128, 788–796, <http://dx.doi.org/10.1093/brain/awh405>.
- Fusar-Poli, P., 2012. Voxel-wise meta-analysis of fMRI studies in patients at clinical high risk for psychosis. *J. Psychiatry Neurosci.* JPN 37, 106–112, <http://dx.doi.org/10.1503/jpn.110021>.
- Glimcher, P.W., Camerer, C.F., Fehr, E., Poldrack, R.A., 2009. *Neuroeconomics: Decision Making and the Brain*, first ed. Academic Press, London, UK.
- Greucci, A., Giorgetta, C., Van't Wout, M., Bonini, N., Sanfey, A.G., 2013. Reappraising the ultimatum: an fMRI study of emotion regulation and decision making. *Cereb. Cortex* 23, 399–410, <http://dx.doi.org/10.1093/cercor/bhs028>.
- Green, M.F., Kern, R.S., Heaton, R.K., 2004. Longitudinal studies of cognition and functional outcome in schizophrenia: implications for MATRICS. *Schizophr. Res.* 72, 41–51, <http://dx.doi.org/10.1016/j.schres.2004.09.009>.
- Grinband, J., Savitskaya, J., Wager, T.D., Teichert, T., Ferrera, V.P., Hirsch, J., 2011. The dorsal medial frontal cortex is sensitive to time on task, not response

- conflict or error likelihood. *Neuroimage* 57, 303–311, <http://dx.doi.org/10.1016/j.neuroimage.2010.12.027>.
- Guo, X., Zheng, L., Zhu, L., Li, J., Wang, Q., Dienes, Z., Yang, Z., 2013. Increased neural responses to unfairness in a loss context. *Neuroimage* 77, 246–253, <http://dx.doi.org/10.1016/j.neuroimage.2013.03.048>.
- Güroğlu, B., van den Bos, W., van Dijk, E., Rombouts, S.A.R.B., Crone, E.A., 2011. Dissociable brain networks involved in development of fairness considerations: understanding intentionality behind unfairness. *Neuroimage* 57, 634–641, <http://dx.doi.org/10.1016/j.neuroimage.2011.04.032>.
- Güth, W., Schmittberger, R., Schwarze, B., 1982. An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Organ.* 3, 367–388, [http://dx.doi.org/10.1016/0167-2681\(82\)90011-7](http://dx.doi.org/10.1016/0167-2681(82)90011-7).
- 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, <http://dx.doi.org/10.1016/j.neuroimage.2009.01.063>.
- Harbord, R.M., Higgins, J.P.T., 2008. *Meta-regression in Stata*. *Stata J.* 8, 493–519.
- Harlé, K.M., Chang, L.J., Van't Wout, M., Sanfey, A.G., 2012. The neural mechanisms of affect infusion in social economic decision-making: a mediating role of the anterior insula. *Neuroimage* 61, 32–40, <http://dx.doi.org/10.1016/j.neuroimage.2012.02.027>.
- Harlé, K.M., Sanfey, A.G., 2012. Social economic decision-making across the lifespan: an fMRI investigation. *Neuropsychologia* 50, 1416–1424, <http://dx.doi.org/10.1016/j.neuropsychologia.2012.02.026>.
- Hart, H., Radua, J., Mataix-Cols, D., Rubia, K., 2012. Meta-analysis of fMRI studies of timing in attention-deficit hyperactivity disorder (ADHD). *Neurosci. Biobehav. Rev.* 36, 2248–2256, <http://dx.doi.org/10.1016/j.neubiorev.2012.08.003>.
- Holroyd, C.B., 2013. Theories of anterior cingulate cortex function: opportunity cost. *Behav. Brain Sci.* 36, 693–694, <http://dx.doi.org/10.1017/S0140525X13001052>.
- Keren-Happuch, E., Chen, S.-H.A., Ho, M.-H.R., Desmond, J.E., 2014. A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. *Hum. Brain Mapp.* 35, 593–615, <http://dx.doi.org/10.1002/hbm.22194>.
- Kirk, U., Downar, J., Montague, P.R., 2011. Interoception drives increased rational decision-making in meditators playing the Ultimatum Game. *Front. Neurosci.* 5, 49, <http://dx.doi.org/10.3389/fnins.2011.00049>.
- Knoch, D., Nitsche, M.A., Fischbacher, U., Eisenegger, C., Pascual-Leone, A., Fehr, E., 2008. Studying the neurobiology of social interaction with transcranial direct current stimulation – the example of punishing unfairness. *Cereb. Cortex* 18, 1987–1990, <http://dx.doi.org/10.1093/cercor/bhm237>.
- Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V., Fehr, E., 2006. Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science* 314, 829–832, <http://dx.doi.org/10.1126/science.1129156>.
- Lee, V.K., Harris, L.T., 2013. How social cognition can inform social decision making. *Front. Neurosci.* 7, 259, <http://dx.doi.org/10.3389/fnins.2013.00259>.
- Lohrenz, T., McCabe, K., Camerer, C.F., Montague, P.R., 2007. Neural signature of fictive learning signals in a sequential investment task. *Proc. Natl. Acad. Sci. U. S. A.* 104, 9493–9498, <http://dx.doi.org/10.1073/pnas.0608842104>.
- Mattis, P., Kimball, S., 2008. Gimp, the GNU image manipulation program [WWW Document] URL: <http://www.gimp.org>
- Nachev, P., Rees, G., Parton, A., Kennard, C., Husain, M., 2005. *Volition and conflict in human medial frontal cortex*. *Curr. Biol.* 15, 122–128.
- Nakao, T., Radua, J., Rubia, K., Mataix-cols, D., 2011. *Gray matter volume abnormalities in ADHD: voxel-based meta-analysis exploring the effects of age and stimulant medication*. *Am. J. Psychiatry* 168, 1154–1163.
- Phillips, M.L., Young, A.W., Senior, C., Brammer, M., Andrew, C., Calder, A.J., Bullmore, E.T., Perrett, D.I., Rowland, D., Williams, S.C., Gray, J.A., David, A.S., 1997. A specific neural substrate for perceiving facial expressions of disgust. *Nature* 389, 495–498, <http://dx.doi.org/10.1038/39051>.
- Radua, J., Mataix-Cols, D., Phillips, M.L., El-Hage, W., Kronhaus, D.M., Cardoner, N., Surguladze, S., 2012. A new meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. *Eur. Psychiatr. J. Assoc. Eur. Psychiatr.* 27, 605–611, <http://dx.doi.org/10.1016/j.eurpsy.2011.04.001>.
- Rand, D.G., Tarnita, C.E., Ohtsuki, H., Nowak, M.A., 2013. Evolution of fairness in the one-shot anonymous Ultimatum Game. *Proc. Natl. Acad. Sci. U. S. A.* 110, 2581–2586, <http://dx.doi.org/10.1073/pnas.1214167110>.
- Richlan, F., Kronbichler, M., Wimmer, H., 2011. Meta-analyzing brain dysfunctions in dyslexic children and adults. *Neuroimage* 56, 1735–1742, <http://dx.doi.org/10.1016/j.neuroimage.2011.02.040>.
- Rilling, J.K., King-Casas, B., Sanfey, A.G., 2008. The neurobiology of social decision-making. *Curr. Opin. Neurobiol.* 18, 159–165, <http://dx.doi.org/10.1016/j.conb.2008.06.003>.
- Rilling, J.K., Sanfey, A.G., 2011. The neuroscience of social decision-making. *Annu. Rev. Psychol.* 62, 23–48, <http://dx.doi.org/10.1146/annurev.psych.121208.131647>.
- Sanfey, A.G., Rilling, J.K., Aronson, J.a., Nystrom, L.E., Cohen, J.D., 2003. The neural basis of economic decision-making in the Ultimatum Game. *Science* 300, 1755–1758, <http://dx.doi.org/10.1126/science.1082976>.
- Schmahmann, J.D., Caplan, D., 2006. Cognition, emotion and the cerebellum. *Brain J. Neurol.* 129, 290–292, <http://dx.doi.org/10.1093/brain/awh729>.
- Stallen, M., Sanfey, A.G., 2013. The cooperative brain. *Neurosci. Rev. J. Bringing Neurobiol. Neurol. Psychiatry* 19, 292–303, <http://dx.doi.org/10.1177/1073858412469728>.
- StataCorp, 2011. *Stata Statistical Software: Release 12*. StataCorp LP, College Station, TX.
- Tabibnia, G., Satpute, A.B., Lieberman, M.D., 2008. The sunny side of fairness: preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychol. Sci.* 19, 339–347, <http://dx.doi.org/10.1111/j.1467-9280.2008.02091.x>.
- Tomasino, B., Lotto, L., Sarlo, M., Civai, C., Rumiati, R., Rumiati, R.I., 2013. Framing the Ultimatum Game: the contribution of simulation. *Front. Hum. Neurosci.* 7, 337, <http://dx.doi.org/10.3389/fnhum.2013.00337>.
- Van der Veen, F.M., Sahibdin, P.P., 2011. Dissociation between medial frontal negativity and cardiac responses in the Ultimatum Game: effects of offer size and fairness. *Cogn. Affect. Behav. Neurosci.* 11, 516–525, <http://dx.doi.org/10.3758/s13415-011-0050-1>.
- Vieira, J.B., Almeida, P.R., Ferreira-Santos, F., Barbosa, F., Marques-Teixeira, J., Marsh, A.A., 2013. Distinct neural activation patterns underlie economic decisions in high and low psychopathy scorers. *Soc. Cogn. Affect. Neurosci.*, <http://dx.doi.org/10.1093/scan/nst093>.
- Wei, Z., Zhao, Z., Zheng, Y., 2013. Neural mechanisms underlying social conformity in an Ultimatum Game. *Front. Hum. Neurosci.* 7, 896, <http://dx.doi.org/10.3389/fnhum.2013.00896>.
- Wright, N.D., Symmonds, M., Fleming, S.M., Dolan, R.J., 2011. Neural segregation of objective and contextual aspects of fairness. *J. Neurosci. Off. J. Soc. Neurosci.* 31, 5244–5252, <http://dx.doi.org/10.1523/JNEUROSCI.3138-10.2011>.
- Yu, R., Calder, A.J., Mobbs, D., 2013. Overlapping and distinct representations of advantageous and disadvantageous inequality. *Human Brain Mapp.* 35, 3290–3301, <http://dx.doi.org/10.1002/hbm.22402>.