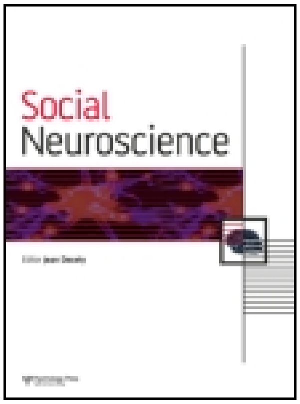

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Behavioral and neural reactions to emotions of others in the distribution of resources

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This study investigated the neural mechanisms involved in the interpersonal effects of emotions—i.e., how people are influenced by other people's emotions. Participants were allocators in a version of the dictator game and made a choice between two offers after receiving written emotional expressions of the recipients. The results showed that participants more often made a self-serving offer when dealing with an angry recipient than when dealing with a happy or disappointed recipient. Compared to disappointment, expressions of anger increased activation in regions associated with self-referential thinking (anterior medial prefrontal cortex, aMPFC) and (emotional) conflict (anterior cingulate cortex). We found increased activation in temporoparietal junction for receiving happy reactions in comparison with receiving angry or disappointed reactions. This study thus emphasizes that distinct emotions have distinct effects on people in terms of behavior and underlying neurological mechanisms.

Keywords: Interpersonal effects of emotions; fMRI; Temporoparietal junction; Medial prefrontal cortex; Dictator game.

Emotions have a significant impact on social interactions (Anderson & Guerrero, 1998; Frijda, 1986; Shaver, Wu, & Schwartz, 1992). According to social functional analyses of emotions (e.g., Keltner & Haidt, 1999; Parkinson, 1996; Van Kleef, De Dreu, & Manstead, 2010), emotions convey crucial information about the sender's feelings and intentions, which can have consequences for the behavior of receivers. Little is known, however, about the underlying neural mechanisms associated with the interpersonal effects of different emotions. In this article, we explore which brain regions are associated with the interpersonal effects of different emotions. Specifically, we focused on two of the most often expressed negative emotions in social interactions, anger and disappointment (Lelieveld, Van Dijk, Van Beest, & Van Kleef, 2012; Lelieveld, Van Dijk, Van Beest, Steinel, & Van Kleef, 2011) and compared their effects to the most often expressed positive emotion, happiness (Sauter, 2010).

Previous research has often used economic games, such as the ultimatum game (Güth, Schmittberger, & Schwarze, 1982), to study the neural mechanisms in social interactions. In this game, two players have to decide on how to distribute a certain amount of chips. One of the players, the allocator, makes a "take it or leave it" offer to the other player, the recipient, by offering a proportion of the chips. If the recipient accepts, the money will be distributed accordingly. If the recipient rejects, both players do not receive anything. Prior functional magnetic resonance imaging

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(fMRI) studies showed receiving unfair proposals is associated with increased activation in the insula, anterior cingulate cortex (ACC), and dorsolateral prefrontal cortex (DLPFC) (Rilling & Sanfey, 2011; Sanfey, 2007 for reviews). Ruz and Tudela (2011) used this paradigm to investigate whether angry and happy facial expressions from trustworthy or untrustworthy proposers influenced neural responses in recipients. Consistent with the hypothesis that communicated emotions matter, there was increased activation in the ACC when participants received offers from untrustworthy relative to trustworthy allocators and there was also increased activation in the bilateral insula when the untrustworthy allocators expressed anger. Together, these results show that recipients show elevated activation in neural regions implicated in processing unfairness when interaction partners express negative emotions.

Studies focusing on neural responses in allocators (instead of recipients) indicate that mentalizing about other people's thoughts and actions results in activation in the medial prefrontal cortex (MPFC), such as when considering whether to trust another individual (McCabe, Houser, Ryan, Smith, & Trouard, 2001). MPFC activation has been associated with strategic bargaining considerations (Rilling & Sanfey, 2011) and with mentalizing about others' intentions (Frith & Frith, 2003, 2006). However, these studies mainly focused on situations where people do not have any information about their interaction partner. To the best of our knowledge, no prior study has examined neural effects of communicated emotions on allocators.

Taken together, expressed emotions may greatly influence neural activation in bargaining. Yet, to date, studies focused on communicated emotions on recipients (Ruz & Tudela, 2011) or on mentalizing about strategic intentions with unknown others (McCabe et al., 2001). No study to date has examined the effects of communicated emotions on allocators using fMRI. The goal of this study was to test these effects in healthy adults using two conditions: (1) the comparison of negative and positive communicated emotions and (2) the effects of different types of negative emotions (anger vs. disappointment).

When comparing the interpersonal effects of negative and positive emotions, previous research has shown that negative emotions, such as anger, arouse strong negative sentiments in targets, hurt interpersonal relations, and often lead to conflict (Clark, Pataki, & Carver, 1996; Van Kleef et al., 2010). Since people strive to maintain positive mood states, they tend to avoid others who express negative emotions (Clark & Isen, 1982). Happiness, in contrast, encourages contact and happy people are seen as highly affiliative (Knutson, 1996). Happiness thus leads to more liking, which in turn leads to closeness and increased perspective taking (Frantz & Janoff-Bulman, 2000; Fredrickson, 1998). The first goal is therefore to test for neural effects of angry and happy communicated emotions on allocators.

Besides the general difference of valence in positive versus negative affect, research has revealed differential effects within the domain of negative emotions (Van Kleef, De Dreu, & Manstead, 2006). The second goal of the current research was to compare neural responses following anger and disappointment (Lelieveld et al., 2011, 2012). In negotiation settings, anger alerts others to possible negative consequences (e.g., conflict escalation), which may lead these others to concede to avoid impasse (e.g., Sinaceur & Tiedens, 2006; Van Kleef, De Dreu, & Manstead, 2004a, 2004b). However, communicating anger can also elicit low offers. Previous research has shown that when angry bargainers have low power, opponents do not have to fear the consequences of impasse, in which case communicating anger may backfire (Van Dijk, Van Kleef, Steinel, & Van Beest, 2008). In both situations (i.e., whether anger elicits high or low offers), anger tends to evoke a concern for own outcomes, that is, observers of anger expressions try to maximize their own outcomes (either by conceding less when facing a low-power bargainer or by conceding more to avoid impasse when facing a high-power bargainer). Disappointment, on the other hand, tends to evoke a social responsibility for the other (see Lelieveld et al., 2011, 2012). A key question now concerns whether these different behavioral responses to anger and disappointment are associated with different neural reactions.

To explore whether different communicated emotions would have different effects on mentalizing and emotional conflict areas (such as the MPFC and ACC), participants were allocators in a dictator game (Forsythe, Horowitz, Savin, & Sefton, 1994). The dictator game is similar to the ultimatum game, such that an allocator makes an offer to a recipient. However, in the dictator game, recipients cannot reject the offer, but have to accept any offer. Recipients in this game thus have low power. An advantage of using this game is that it allowed us to investigate the effects of specific emotions, without interference of strategic motivations (e.g., participants did not need to consider whether a low offer would be rejected). While playing the dictator game, participants received written comments from the interaction partners on a prior bargaining offer, which could display anger, disappointment, or happiness with the prior offer.

METHOD

Participants

Twenty-six healthy right-handed paid volunteers between ages 18 and 25 (17 females, 9 males[1]; $M_{\text{age}} = 21.00$, SD = 4.72) participated in the fMRI experiment. None of them had any history of neurological or psychiatric disorder and all were medication free. All procedures were approved by the medical ethical committee of the Leiden University Medical Center (LUMC).

Procedure

Before inviting participants to a scanning session, they first participated in a preliminary study. This study was used to create an interpersonal context for the emotional reaction they later received. Thirty-one participants read a scenario where they negotiated for a company. All participants were told that they would bargain with another person over the distribution of 10 chips, which represented money. Participants could choose between two predetermined distributions to divide the 10 chips. One option represented a 6–4 distribution in favor of the participant and the other option represented a 5–5 distribution. We expected most of the participants to choose the 6–4 distribution. Only these participants ($N = 26$) were invited to participate in the second phase of our experiment, 1 week later.[2] Reviews on ultimatum offers have shown that in general offers of 40% of the total are accepted (Camerer & Thaler, 1995; Güth, 1995; Straub & Murnighan, 1995; Tompkinson & Bethwaite, 1995). Happy reactions to 6–4 offers may therefore not be perceived as unusual. At the same time, a 6–4 offer is not a fair distribution, which ensures the credibility of the angry and disappointed reactions (see the section “Emotion manipulation”).

A week after the first phase, the remaining 26 participants were invited to a scanning session. Upon arrival, participants learned that they were going to play a similar game with new anonymous age and gender-matched partners. We told participants that their offer (the 6–4 distribution) was shown to 60 new recipients who had given a reaction upon receiving the offer. We emphasized that recipients did not know that this reaction would be sent back to the participant. This was done to ensure that participants trusted the emotional reactions to be nonstrategic (i.e., not aimed to influence the participants; see Van Kleef et al., 2004a). In reality, the 60 reactions were preprogrammed (see the section “Emotion manipulation”). On each trial participants read one of the 60 reactions. Subsequently, they played a version of the dictator game (Forsythe et al., 1994; Güroğlu, Van Den Bos, & Crone, 2009), in which participants were allocators and had to divide 10 chips. The participants learned that the recipient had to accept any distribution they would make. Participants could now choose between a 7–3 distribution (i.e., seven chips for themselves and three for the other) and a 5–5 distribution. We did not include a 6–4 distribution to ensure that a desire to stick with their first offer did not influence our results.

In each trial, participants were paired with a different, anonymous player. Each trial started with a fixation, after which the participants were presented with the emotional reaction for a period of 3 s. Subsequently, they had 6 s to make a decision between the two distributions (see Figure 1). The 60 trials were divided over two blocks of 5 min each. Trials were presented in pseudo-random order with a jittered inter-stimulus interval (min. = 0.55 s, max. = 4.95 s, $M = 1.54$ s).

Before the task started, participants learned that at the end of the experiment the computer would randomly select 10 trials. They learned that they would receive the earnings of these trials. Participants also learned that the offers were redelivered to the recipients and that their earnings would be contingent on the decisions they made (see also Güroğlu, Van Den Bos, Rombouts, & Crone, 2010). At the end of the session, participant’s pay-off was presented (see also

[1] Although there is evidence that suggests that men and women process emotions differently (Lithari et al., 2010; Wager, Luan Phan, Liberzon, & Taylor, 2003), we observed no significant gender effects in this study.

[2] Because we only included participants who chose the 6–4 option and not the 5–5 option, one might wonder whether we, thereby, may have excluded individuals who have a tendency to act prosocially. However, because we created a business setting where participants were focused on profits and on maximizing the outcomes for the company, even individuals who act prosocially may have chosen the 6–4 option. This is supported by the results from a social value orientation measure, which measured whether participants were prosocials (who maximize joint outcomes and minimize differences in outcomes for the self and another person) or proselfs (who maximize individual outcomes). We assessed participants’ social value orientation with the nine-item version of the decomposed games measure (for more information, see Van Lange, De Bruin, Otten, & Joireman, 1997)—a measure that has been demonstrated to have good internal consistency (Liebrand & Van Run, 1985), test–retest reliability (Van Lange & Semin-Goossens, 1998), and construct validity (Parks, 1994). Using the criterion of at least six consistent choices, 12 participants were classified as prosocial (46.2%) and 13 as proself (50.0%). One participant (3.8%) did not make at least six consistent choices and was therefore unclassifiable. These results show that we had an almost equal number of prosocials and proselfs in our experiment.

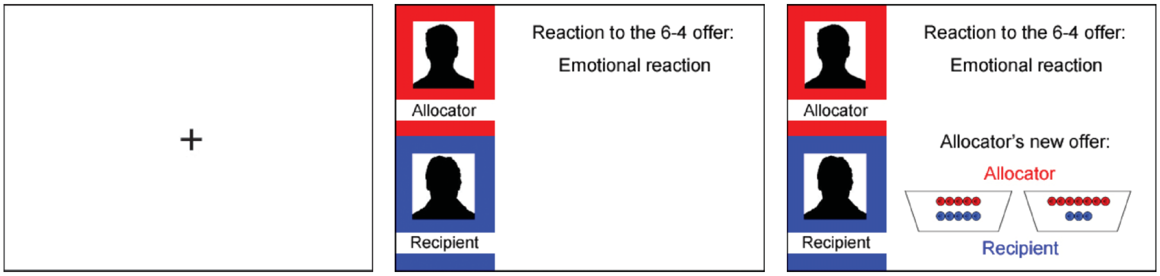

Figure 1. Visual display and timing of the events in the scanner task in milliseconds (ms). After a jittered fixation cross, a screen displayed the emotional reaction of the recipient (here "emotional reaction") for 3000 ms. We measured activation at the onset of the emotional reaction. Subsequently, the screen displayed two offers each containing red and blue coins, which indicated the share for the allocator and the recipient, respectively (here 5–5 vs. 7–3). The left panel displays the name of the allocator in red (here "allocator") and the name of the recipient in blue (here "recipient"). The decision screen was response terminated with a maximum response time of 6000 ms. After the response, the decision screen remained on the screen until 6000 ms after the onset of the decision screen.

Güroğlu et al., 2009) and participants were paid and probed for suspicion. None of them expressed any doubts concerning the cover story.

Emotion manipulation

The emotion statements were pretested in a pilot study involving 21 participants, none of whom participated in the main study. We created 90 emotional statements that reflected happiness, anger, and disappointment. The emotional reactions were adapted from previous research on the effects of emotional communication on negotiation behavior (e.g., Sinaceur & Tiedens, 2006; Van Dijk et al., 2008; Van Kleef et al., 2004a, 2004b, 2006). We tested 30 statements designed to reflect anger, 30 designed to reflect disappointment, and 30 designed to reflect happiness. The order of the statements was randomized across participants. For each statement, participants were asked to indicate on 7-point scales to what extent they felt it reflected anger, disappointment, and happiness (1 = *not at all*, 7 = *to a great extent*). We then selected the statements that had the highest scores on the emotions that they were intended to reflect and the lowest scores on the emotions that they were not intended to reflect (e.g., the selected angry statements had the highest anger scores and at the same time the lowest disappointment and happiness scores). We selected 20 statements for each emotion, all with different wordings. All selected statements were rated higher on the emotions they were supposed to express than on the emotions they were not supposed to express according to paired-samples *t*-tests ($4.63 < ts < 36.77$, all $ps < .001$). In addition, all emotional statements were presented in the same font, color, and on the same location on the screen. Moreover, we counted all words and letters of each emotional statement. We performed paired-samples *t*-tests to see whether the amount of words or letters differed across emotion conditions. The results showed that across conditions (anger vs. happiness vs. disappointment) emotional expressions did not differ in terms of number of words ($ps > .47$, overall $M = 8.13$, SD = 2.13) or number of letters ($ps > .11$, overall $M = 40.78$, SD = 11.14). Examples of emotional reactions depicting anger were "I feel really angry after receiving this offer," "The other person really makes me angry," "This annoying person really pisses me off," and "I am starting to get really furious about now." Examples of reactions depicting disappointment were "This really disappoints me," "I expected more from the other person," "The other person really disappoints me, he could have given me more," and "I am really disappointed in the other person." Examples of reactions depicting happiness were "I am really happy with this offer," "This guy really makes me happy," "The other person made my day," and "This is perfect, I am really satisfied."

fMRI data acquisition

Scanning was performed on a 3.0T Philips Achieva scanner at the LUMC. Functional data were acquired using a T2*-weighted echo-planar imaging (EPI) sequence (echo time/T_E = 30 ms, repetition time/T_R = 2200 ms, slice matrix = 80 × 80, slice thickness = 2.75 mm, slice gap = 0.28 mm gap, field of view = 220 mm) during two fMRI runs with 150 volumes each. A high-resolution T2-weighted high-resolution anatomical scan (same slice prescription as EPI) was collected at the end of the scan session. Responses were made with the left and right index fingers using a response box attached to the upper leg.

fMRI data analysis

Data preprocessing and analyses were conducted with SPM5 software (http://www.fil.ion.ucl.ac.uk/spm/software/spm5) implemented in MATLAB (Mathworks, Sherborn, MA, USA). All functional images were realigned and slice time corrected using the middle slice as reference. Then, they were spatially normalized to EPI templates and spatially smoothed with a Gaussian kernel (6 mm, full-width at half-maximum). The maximum amount of motion observed was 1.25 mm. To investigate the interpersonal effects of the communicated emotions, we tested a model that investigated the effects of the different emotions when participants received the emotional reaction. For this reason, a canonical hemodynamic response function was convolved at the onset of the presentation of the emotional reaction (impulse function: zero duration). The presentation of the emotional reaction could communicate one of three emotions: anger, disappointment, or happiness. The proposed offer could be of two levels: a 7–3 or a 5–5 distribution. These conditions resulted in a 3 (emotion: happiness vs. anger vs. disappointment) × 2 (distribution: 7–3 vs. 5–5) full factorial design. The analyses were carried out using the general linear model in SPM5. Contrast parameter images were computed for each individual. The resulting contrast images were submitted to second-level group analyses. At the group level, whole brain contrasts between conditions were computed by performing one-tailed *t*-tests on these images, treating participants as a random effect. The results were considered significant at an uncorrected threshold of $p < .001$, with an extent threshold of 10 continuous voxels [Table 1 reports which results remained significant with a false discovery rate (FDR) threshold].

TABLE 1
Brain regions revealed by whole brain contrasts

				MNI coordinates			
Anatomical region	*L/R*	*Voxels*	*Z*	x	y	z	*FDR*
Happiness > [anger and disappointment]							
TPJ	L	503	4.48	−51	−60	45	**
			4.47	−45	−72	45	**
			4.39	−54	−45	48	**
	R	538	4.38	60	−54	42	**
			4.38	54	−69	30	**
			4.35	51	−60	45	**
DLPFC	L	129	4.72	−33	21	48	**
			3.82	−24	15	51	*
			3.43	−21	24	60	*
	R	259	4.36	39	18	48	**
			4.14	21	30	54	*
			4.13	27	21	54	*
Precuneus	L/R	201	4.04	9	−72	45	*
			3.90	9	−54	39	*
			3.82	−9	−55	48	*
[Anger and disappointment] > happiness							
Visual cortex	L/R	1418	5.37	−18	−105	3	**
			5.22	−12	−93	−9	**
			4.70	−27	−90	−12	**
Anger > disappointment							
Anterior MPFC	L/R	105	3.88	6	54	−18	
			3.49	−6	39	−15	
			3.42	−9	57	3	
Anterior cingulate	L	10	3.32	−9	42	9	
	L	26	4.04	−9	18	21	
Posterior cingulate	L	18	3.89	−9	−15	42	
Disappointment > anger							
Visual cortex	L/R	171	4.65	−18	−105	−3	
				−21	−90	−15	
				−33	−93	−9	

Notes: MNI coordinates for main effects and peak voxels were reported at $p < .001$ uncorrected, at least 10 continuous voxels (voxels size was 3.0 mm × 3.0 mm × 3.0 mm).

*The results remained significant with an FDR-corrected threshold of $p < .05$, with an extent threshold of 10 continuous voxels.

**The results remained significant with an FDR-corrected threshold of $p < .01$, with an extent threshold of 10 continuous voxels.

To examine similarities across contrasts, we computed conjunction analyses, using the minimum statistic approach (Nichols, Brett, Andersson, Wager, & Poline, 2005). These analyses identified clusters that were significantly engaged at our threshold in both contrasts that we examined.

Using the MARSBAR toolbox for SPM5 (Brett, Anton, Valabregue, & Poline, 2002), we extracted parameter estimates from the regions that were identified in the whole brain analyses to further characterize patterns of activity.

RESULTS

Behavioral results

The dependent variable of interest was the number of times participants chose the 7–3 option after receiving an angry, disappointed, or happy emotional reaction. A repeated-measures analysis of variance with emotion (anger vs. disappointment vs. happiness) as a repeated-measures variable and percentage of 7–3 choice as the dependent variable yielded a main effect of emotion, $F(1, 25) = 324.73$, $p < .001$, $\eta^2 = 0.93$. Least significant difference (LSD) post hoc tests showed that participants more often chose the 7–3 option when dealing with angry recipients (74.6%, SD = 6.03) than when dealing with disappointed (43.7%, SD = 5.96, $p < .001$) or happy recipients (50.6%, SD = 6.35, $p < .05$). The percentage of 7–3 offers to disappointed or happy recipients did not differ ($p = .44$). Thus, anger elicited lower offers than disappointment or happiness did.

fMRI results

Reactions to positive versus negative emotions

The first set of analyses investigated regions that showed increased activation when receiving positive relative to negative emotional reactions by testing the happiness > [anger and disappointment] contrast (on whole brain level). This analysis revealed increased activation in the bilateral temporoparietal junction (TPJ) and DLPFC (see Table 1 and Figure 2a). To examine whether this response was different for

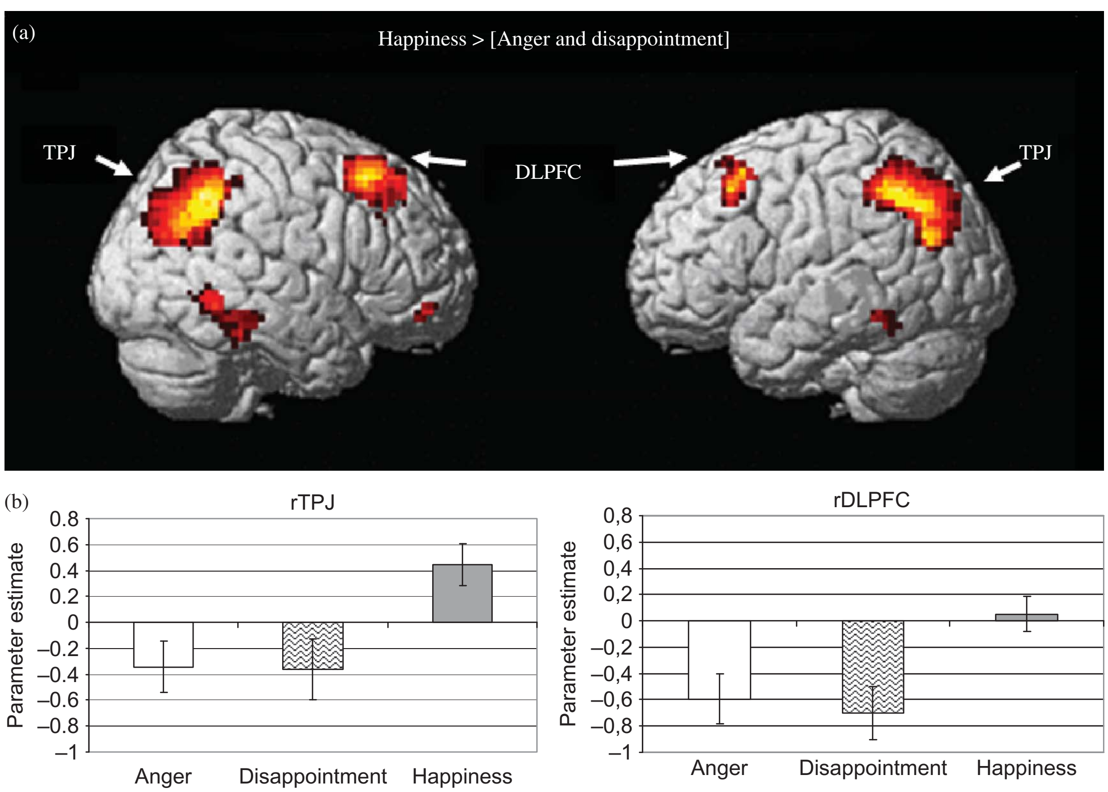

Figure 2. (a) Whole brain results for regions which were active in the happiness > [anger and disappointment] contrast (threshold at $p < .001$, uncorrected). Activation was detected in the bilateral TPJ (MNI coordinates: $x = -51$, $y = -60$, $z = 45$ and $x = 60$, $y = -54$, $z = 42$) and in the bilateral DLPFC (MNI coordinates: $x = -33$, $y = 21$, $z = 48$ and $x = 39$, $y = 18$, $z = 48$). (b) Contrast values of activation in right TPJ and right DLPFC for the three emotion conditions.

the happiness relative to the anger or disappointment trials, separate analyses were performed for happiness > anger and happiness > disappointment. These analyses resulted in similar patterns of activation. To test whether these effects are the same across the happiness > anger contrast and the happiness > disappointment contrast, we also computed a conjunction analysis. This analysis revealed that the happiness > anger contrast and the happiness > disappointment contrast showed similar activation in bilateral TPJ (left TPJ: MNI coordinates: $x = -45$, $y = -54$, $z = 39$, $t = 3.76$, $k = 162$ voxels, right TPJ: MNI coordinates: $x = 42$, $y = -57$, $z = 33$, $t = 3.93$, $k = 189$ voxels) and bilateral DLPFC (left DLPFC: MNI coordinates: $x = -36$, $y = 21$, $z = 51$, $t = 4.25$, $k = 27$ voxels, right DLPFC: MNI coordinates: $x = 39$, $y = 21$, $z = 45$, $t = 4.50$, $k = 99$ voxels). We only found increased activation in the visual cortex for the reversed contrast ([anger and disappointment] >happiness).

For illustrational purposes, we displayed Region of Interest (ROI) patterns (see Figure 2b) for activation in the right TPJ and right DLPFC. As can be seen in the figure, r-TPJ and r-DLPFC activation was higher for receiving happy reactions than for receiving angry or disappointed reactions. Similar patterns of activation were observed for left TPJ and left DLPFC.

Reactions to anger versus disappointment

The second set of analyses examined which regions showed increased activation when receiving angry reactions relative to receiving disappointed reactions by testing the anger > disappointment contrast at the onset of the emotion expression. This analysis revealed increased activation in the anterior medial prefrontal cortex (aMPFC) and several regions in the ACC and posterior cingulate cortex (PCC) (see Table 1 and Figure 3). We did not find increased activation for the reversed contrast (disappointment > anger). A conjunction analysis of anger > disappointment and anger > happiness did not result in significant overlapping clusters, showing that the difference in neural activity was specific for comparing anger with disappointment.

DISCUSSION

This study investigated the interpersonal effects of emotions in social interactions. The results showed that participants more often chose self-serving offers in the dictator game when interaction partners expressed anger than when they expressed disappointment or happiness. These findings are consistent with previous studies, which have shown that in situations where individuals have more power than their counterpart (such as the dictator game used in our study), people offer less to angry than to happy recipients (see Van Dijk et al., 2008). When anger is communicated by a low-power bargainer, opponents do not have to fear the negative consequences of communicating anger (e.g., conflict escalation and impasse) and make lower offers. Moreover, our findings replicate previous results from negotiation studies, which show that people make more generous offers to disappointed than to angry bargainers (Lelieveld et al., 2012).

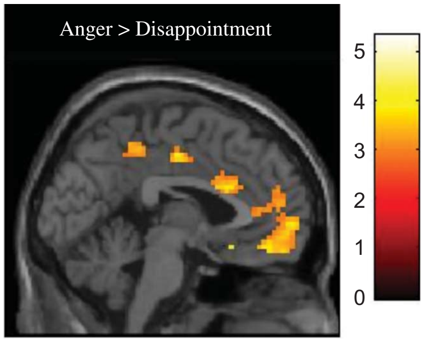

Figure 3. Whole brain results for regions which were active in the anger > disappointment contrast (based on recommendations from Lieberman & Cunningham (2009), only for illustrational purposes, we chose a threshold at $p < .005$, uncorrected, with a 10 voxel extent threshold) from a sagittal perspective. Activation was detected in the aMPFC (MNI coordinates: $x = 6$, $y = 54$, $z = -18$), two regions of the ACC (MNI coordinates: $x = -9$, $y = 42$, $z = 9$ and $x = -9$, $y = 18$, $z = 21$), and in the PCC (MNI coordinates: $x = -9$, $y = -15$, $z = 42$).

Positive and negative emotions

Our results showed that for receiving happy reactions, we found more activation in the bilateral TPJ, a region which in prior studies was associated with a variety of social cognitive tasks such as perspective taking (Ruby & Decety, 2001), action understanding (Kret, Pichon, Grèzes, & De Gelder, 2011; Samson, Apperly, Chiavarino, & Humphreys, 2004), and empathy (Lamm, Batson, & Decety, 2007), than for receiving angry or disappointed reactions. It is possible that the recipient's happiness encouraged participants to take the perspective of the recipient. This is in line with behavioral research that showed that happiness encourages contact (Knutson, 1996) and leads to more closeness and increased perspective taking (Frantz & Janoff-Bulman, 2000; Fredrickson, 1998).

Receiving angry and disappointed reactions also resulted in less activation in the DLPFC, an area involved in cognitive control (e.g., Brass, Derrfuss, Forstmann, & Von Cramon, 2005) and the regulation of thought and action (Miller & Cohen, 2001), compared to receiving happy reactions. Moreover, in several economic games, the DLPFC has been associated with the inhibition of selfish impulses (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Rilling et al., 2007). TPJ and DLPFC are also active when individuals receive trust in a trust game (Van Den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2011). Receiving trust and receiving happy reactions possibly activate a similar brain network, but exactly how these regions are associated with positive emotions should be tested further in future research. Possibly, expressions of happiness elicit similar feelings and responses as a trust cue. Indeed, prior behavioral research showed that people displaying happiness are seen as more honest, reliable, and trustworthy (Stouten & De Cremer, 2010).

Anger versus disappointment

We also investigated the difference in neural reactions to anger and disappointment. For receiving angry reactions, we found increased activation in the aMPFC in comparison with disappointment, which in previous research has been implicated in strategic bargaining (i.e., maximizing own outcomes and defecting in a trust game, see Van Den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2009, 2011) and making self-relevant decisions (Schmitz & Johnson, 2006; for a review, see Northoff et al., 2006). This interpretation is supported by the behavioral results that show that participants more often chose the 7–3 option when the recipient expressed anger than when the recipient expressed disappointment. These results are in line with earlier behavioral research by Lelieveld et al. (2011, 2012), who showed that anger evokes a concern for own outcomes, whereas disappointment evokes a concern for the outcomes of others. Although other research has also implicated the aMPFC in mentalizing and the attribution of mental states to other people (e.g., Amodio & Frith, 2006), the current results and previous behavioral results (Lelieveld et al., 2011, 2012) support the importance of the aMPFC in self-referential thinking and maximizing own outcomes (see also Denny, Kober, Wager, & Ochsner, 2012). Future research should investigate when the processing of others' emotions is associated with mentalizing in economic games (Rilling et al., 2008) and when with self-referential thinking (Denny et al., 2012).

We also found increased activation in several regions of the ACC after participants received angry reactions (relative to disappointed reactions). Especially the rostral ACC, which has been implicated in conflict monitoring (Botvinick, 2007) and emotional conflict (Egner, Etkin, Gale, & Hirsch, 2008; Ochsner, Hughes, Robertson, Cooper, & Gabrieli, 2009; Ruz & Tudela, 2011), was activated more when recipients expressed anger. Anger may have elicited more (emotional) conflict than disappointment. This accords with behavioral research showing that anger evokes more conflict in others (e.g., Barsade, 2002; Friedman et al., 2004; Kopelman, Rosette, & Thompson, 2006; Van Dijk et al., 2008; Van Kleef & Côté, 2007) than disappointment (Lelieveld et al., 2011). Ruz and Tudela (2011) also found that the ACC was involved in observing conflictive emotional displays, which provides further support for its role in the interpersonal effects of emotions.

Note that our results did not reveal brain regions specifically associated with the interpersonal effects of disappointment. Although we expected disappointment to activate brain regions associated with mentalizing and a concern for others, we did not find such effects. Like happiness, disappointment elicited more generous offers, but happiness and disappointment did not activate similar brain regions. This is interesting in light of the observation that although behavioral responses to these two emotions are similar, the behavior might be associated with different neural mechanisms. TPJ activation seems to be restricted to receiving positive emotional reactions. Future research should try to identify regions that are specifically associated with interpersonal disappointment.

Our results also did not reveal activation in the anterior insula, a region often associated with negative emotional states. This region has often been implicated in studies of emotion, in particular involvement in the evaluation and representation of specific negative emotional states (Calder, Lawrence, & Young, 2001; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). These studies focused on the intrapersonal effects of emotions (how one's own emotions affect one's brain regions). This study, however, focused on the interpersonal effects of emotions and investigates how others' emotions affect one's brain regions. One study that also focused on the interpersonal effects of emotions (see Ruz & Tudela, 2011) found activation in the anterior insula for receiving angry reactions, but only when it was expressed by an untrustworthy person. Possibly, the insula is more responsive to the additive effect of different negative emotions rather than to anger per se.

The model that we tested was locked at the onset of the presentation of the emotional reaction. Because the two distributions that participants could choose from were the same for each trial, regions that were activated during the presentation of the emotional reaction may have also reflected participant's choice. With the current design, it is thus hard to discern whether the results found are linked to the presentation of the emotional state of the opponents, the decision stage or a mixture of both. Future research could vary the distributions that allocators in the dictator game can choose from, so that participants do not know beforehand which choice they have. This way, it is clearer that the brain regions activated during the presentation of the emotion reflect the communicated emotion of the opponent. However, even when distributions are varied, it may remain difficult to disentangle the activation related to stimulus presentation and the decision made, especially since we do not know at which point the decision is made. Future research may consider using electroencephalographic measurements to address this issue, where the time lines of activations are easier to follow (with, of course, the disadvantage that it is difficult to locate the source of activations).

It is also possible to test a model which is locked at the onset of the choice. Because the emotional reaction and the choice followed each other within a short period of time (i.e., 3000 ms), it is possible that the hemodynamic response at these time points overlaps. In the earlier described study by Ruz and Tudela (2011), this problem was circumvented by jittering the decision screen. Future research using our design, where the effects of communicated emotions on the offers of allocators in the dictator game are investigated, could jitter the onset of the decision screen. This enables researchers to investigate brain regions specific to the emotional expression and brain regions specific to the offer. Another possibility is to test a model where the observations within each emotional condition are divided depending on the choice made by the participants. Our study did not have enough statistical power to perform such analyses. Future research could use more trials (i.e., more emotional reactions) to further explore the interaction between the emotional reaction and the choice participants made.

Taken together, the current research investigated how distinct emotions influenced other people in a social interaction. We used the dictator game to examine these interpersonal effects of emotions in the fMRI scanner. Whereas previous studies mainly focused on brain activation of *recipients* in ultimatum and dictator games (see Güroğlu et al., 2010; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004; Sanfey et al., 2003), this study is one of the first that investigated brain regions of *allocators*. Moreover, the (simulated) recipients in the dictator game expressed their emotion by means of typed messages. Previous work on the neural mechanisms associated with the interpersonal effects of emotions manipulated the emotions by means of pictures of emotional faces (e.g., Ruz & Tudela, 2011). This study thus not only extends previous research by creating an interpersonal setting where emotions are based on previous behavior, but also by looking at the interpersonal effects of emotions using a different type of emotion manipulation. We do not expect that our results are restricted to verbal emotional reactions. Previous behavioral research has used various settings and different manipulations to compare effects of communicated emotions. Findings obtained with verbal manipulations of emotional expressions (Van Kleef et al., 2004a, 2004b) are similar to findings obtained with nonverbal manipulations by means of pictures (e.g., Pietroni, Van Kleef, De Dreu, & Pagliaro, 2008) and face-to-face interaction (e.g., Sinaceur & Tiedens, 2006).

This study demonstrated that people respond differently to discrete emotions. By providing a broader and more differentiated view of the behavioral and neural reactions to discrete emotions of others, this work may contribute to a better understanding of how different emotions affect other people.

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