4 Asymmetric frontal brain activity predicts donating behavior: Moderation of oxytocin and parental love withdrawal effects

Renske Huffmeijer, Lenneke R. A. Alink, Mattie Tops, Marian J. Bakermans-Kranenburg, & Marinus H. van IJzendoorn.
Manuscript submitted for publication.

Abstract

Asymmetric frontal brain activity has been widely implicated in reactions to emotional stimuli, and is thought to reflect individual differences in approach-withdrawal motivation. Here, we investigate whether asymmetric frontal activity, as a measure of approach-withdrawal motivation, also predicts charitable donations after viewing a charity's (emotion-eliciting) promotional video showing a child in need, in a sample of 47 young-adult women. In addition, we explore possibilities for mediation and moderation by asymmetric frontal activity of effects of intranasally administered oxytocin and parental love withdrawal on charitable donations. Greater relative left frontal activity was related to larger donations. In addition, we found evidence of moderation: low levels of parental love withdrawal predicted larger donations in the oxytocin condition for participants showing greater relative right frontal activity. We suggest that when approach motivation is high (reflected in greater relative left frontal activity), individuals are generally inclined to take action upon seeing someone in need, and thus to donate money to actively help-out. Only when approach motivation is low (reflected in less relative left/ greater relative right activity), do empathic concerns affected by oxytocin and experiences of love withdrawal play an important part in deciding about donations.

Introduction

Donating to charity is a uniquely human form of prosocial behavior that does not directly benefit the individual who donates. As such, theories explaining charitable donating have focused on indirect or psychological benefits, such as establishing a favorable reputation (Nowark & Sigmund, 2005), or the "warm glow" people experience from doing something good or righting a perceived injustice (Andreoni, 1990; Mayo & Tinsley, 2009). Empathic concern for those in need of help may be an especially important motivator for donating to charity, predicting donations even when socio-demographic variables (age, income, and gender) and past donating behavior are taken into account (Verhaert & Van den Poel, 2011).

Various factors may contribute to (the development of) prosocial attitudes and empathy, and thus affect donating behavior. Recently, we reported on effects of intranasally administered oxytocin and experienced parental love withdrawal on monetary donations in a donating task, in which participants watched a promotional video asking them to donate some money to UNICEF, after they had just earned 50 Euros by participating in an ERP experiment (Van IJzendoorn, Huffmeijer, Alink, Bakermans-Kranenburg, & Tops, 2011). Oxytocin is a neuropeptide hormone that is increasingly shown to facilitate prosocial behavior (at least in in-group situations, De Dreu et al., 2010). Oxytocin has been found to attenuate stress responses in social situations, to influence the processing of and facilitate memory for salient social stimuli, to promote trust and generosity toward an opponent (for reviews see Heinrichs, von Dawans, & Domes, 2009, and MacDonald & MacDonald, 2010), and to increase the amount of money donated to charity (Barraza, McCullough, Ahmadi, & Zak, 2011).

However, we found that oxytocin increased donations only for those reporting lower parental use of love withdrawal. Love withdrawal is a disciplinary strategy that involves withholding signals of love and affection when a child misbehaves or fails at a task. When used excessively, it is considered psychological maltreatment (Euser, Van IJzendoorn, Prinzie, & Bakermans-Kranenburg, 2010). By using love withdrawal the parent communicates to the child that his or her love and affection for the child are conditional upon the child's compliance and success. The formation of this link between compliance or performance on the one hand and relational consequences on the other is thought to underlie both the effectiveness and emotional costs of love withdrawal (Assor, Roth, & Deci, 2004; Elliot & Thrash, 2004). Parental use of love withdrawal has been associated with fear of failure, low self-esteem, low emotional well-being, and feelings of rejection and resentment toward the parents in adolescence and young adulthood (Assor et al., 2004; Elliot & Thrash, 2004; Goldstein & Heaven, 2000; Renk, McKinney, Klein, & Oliveros, 2006; Soenens, Vansteenkiste, Luyten, Duriez, & Goossens, 2005). This may both hinder empathic concern (and its expression in donating behavior), and bias decision making in social situations away from other-oriented (e.g., empathy for a child in need) to self-oriented concerns (doing what relevant others expect, out of fear for negative reactions).

To extend our previous findings, we now turn our attention to another characteristic that has been implicated in emotional and motivational processes: asymmetric frontal cortical activity. Differences in power within the alpha band (8-12 Hz) of the electroencephalogram (EEG) over left and right frontal areas are widely used to quantify asymmetric frontal brain activity. Because greater alpha power is related to deactivation of the underlying cortical tissue (Cook, O'Hara, Uijtdehaage, Mandelkern, & Leuchtner, 1998, Laufs et al., 2003), greater alpha power over right compared to left frontal areas reflects greater activity of the left compared to right frontal cortex, whereas greater alpha power over left than right frontal areas reflects relatively greater activity of the right frontal cortex. Numerous studies have related asymmetric frontal activity to emotional processes in individuals of all ages (e.g., Coan & Allen, 2004; Davidson & Fox, 1989; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). Whereas early studies focused on emotional valence, showing a relation between greater relative left activity and a tendency to experience certain positive emotions (e.g., happiness) and between greater relative right activity and a tendency to experience certain negative emotions (e.g., fear), more recent research suggest that asymmetric frontal activity relates to motivational direction (of emotions) rather than emotional valence (for a review see Harmon-Jones, Gable, & Peterson, 2010). Frontal asymmetries seem to be best characterized as reflecting a general tendency for approach versus withdrawal, with greater left activity reflecting greater approach motivation, and greater right activity reflecting greater withdrawal motivation, although there is more evidence for the link between left frontal activity and approach than for the link between right frontal activity and withdrawal (Demaree, Everhart, Youngstrom, & Harrison, 2005; Harmon-Jones & Allen, 1997; Harmon-Jones et al., 2010). Measures of asymmetric frontal activity have been shown to track both a general trait of and state-related fluctuations in approach-withdrawal motivation, with the contributions of trait- and state-related variation estimated to be about 50% each (Coan & Allen, 2004; Hagemann, Hewig, Seifert, Naumann, & Bartussek, 2005).

As a measure of approach-withdrawal motivation, asymmetric frontal activity may be expected to relate to donating behavior when individuals are confronted with a charity's promotional material (typically showing the precarious situation of those in need) and asked for a donation. Higher approach motivation and a greater tendency to experience approach-related emotions, associated with greater relative left frontal activity, may well cause an individual to donate more money to actively help-out those in need. Thus, we expect that asymmetric frontal activity will predict monetary donations to UNICEF in the context of our donating task.

Because asymmetric frontal activity both reflects a trait-like motivational tendency to react in a certain (predictable) way in emotionally evocative situations, and is susceptible to state-related changes, it has been suggested that frontal asymmetries may serve as moderators or mediators of behavior (Coan & Allen, 2004). Therefore, we will also investigate whether frontal alpha asymmetry mediates or moderates the effect of oxytocin administration and parental love withdrawal that we have found previously (Van IJzendoorn et al., 2011).

For mediation to occur, asymmetric frontal activity should not only be related to donating behavior, but also be affected by oxytocin, parental love withdrawal, or both. Many effects of oxytocin on socio-emotional information processing, e.g. increased processing of facial expressions (Domes et al., 2010; Huffmeijer et al., 2011a), and behavior, e.g. increases in trust and generosity (Zak, Kurzban, & Matzner, 2005; Zak, Stanton, & Ahmadi, 2007), may be linked to approach motivation, suggesting that oxytocin might increase relative left frontal activity. Also, oxytocin has been found to have anxiolytic effects in social situations (Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003), and anxiety has been related to increased relative right frontal activity (e.g., Thibodeau, Jorgensen, & Kim, 2006). Experiences of parental love withdrawal might also relate to frontal alpha asymmetry. Experiences of parental love withdrawal have been related to fear of failure, i.e. anxiety in performance situations (e.g., Elliot & Thrash, 2004; Soenens et al., 2005). Within the current study, measures of frontal alpha asymmetry were collected before and after participants performed a computerized feedback task (i.e. in a performance situation). Because relative right frontal activity may be related to anxiety primarily within anxiety-provoking situations (Crost, Pauls, & Wacker, 2008), within the current context parental love withdrawal might be related to relative right frontal activity.

In case of moderation, on the other hand, effects of oxytocin and parental love withdrawal would depend on an individual's level (direction and degree) of asymmetric frontal activity. Effects of oxytocin and concerns related to experiences of parental love withdrawal might, for example, exert less influence over decision making in the donating task for those showing greater relative left frontal activity, who may be expected to respond positively to a request for a donation after seeing an individual in need because of a high level of approach motivation.

To summarize, the current study examines whether asymmetric frontal brain activity, as a measure of approach-withdrawal motivation, predicts donations to charity after viewing a promotional video of a child in need. We expect that greater relative left frontal activity, reflecting higher approach motivation, predicts larger donations. In addition, we explore the possibility that asymmetric frontal brain activity mediates or moderates the combined effect of oxytocin and parental love withdrawal on donating behavior.

Method

Participants

A total of 59 female undergraduate students, aged 18-30 years (M = 20.54, SD = 2.89), participated in the study. Two participants did not complete the donating task (because they did not participate in the second session, in which this task took place), nine participants contributed insufficient EEG data because of excessive ocular or motion artifacts, and data collection for one participant was disturbed by loud noise. The final sample thus consisted of 47 female undergraduate students, aged 18-30 years (M = 20.45, SD = 2.80). Exclusion criteria included colorblindness, smoking, alcohol and drug abuse, neurological and psychiatric disorders, pregnancy, breastfeeding, and use of medication (except oral contraceptives). The study was approved by the ethics committee of the Leiden University Medical Center, and informed consent was obtained from participants at the beginning of the experiment.

Procedure

Participants completed a questionnaire measuring parental use of love withdrawal during an introductory course in child and family studies. The questionnaire was administered to 391 18-30 year old female undergraduate students who were willing to participate in an ERP experiment. Participants for this experiment were selected stratified from the pool of 391 students, based on their scores on the maternal version of the questionnaire: Half of the participants were selected randomly from the group scoring in the upper quartile of the questionnaire (n = 23 for the current sample), and half of the participants were selected randomly from the group scoring in the other three quartiles (n = 24 for the current sample), resulting in a normal distribution of love-withdrawal scores (see below).

Participants were asked to come to our laboratory for two experimental sessions, separated by approximately four weeks. To minimize influences of diurnal variations in oxytocin levels, all sessions took place in the afternoon (starting between 12.00 and 15.00). Here, we report on the second session, which ended with the donating task. Participants were instructed to abstain from alcohol and excessive physical activity during the 24 hours before the start of each session, and from caffeine on the day of the session.

Concerning the administration of oxytocin, participants were told that they would receive oxytocin during one session and a placebo during the other, and that the order was not known even to the experimenter. This message was repeated at the beginning of the second session. Participants were not informed about the effects of oxytocin under investigation, only about the possible side effects they might experience (as required by the ethics committee).

At the start of each session, participants received a nasal spray containing either 24 IU of oxytocin or a placebo (saline solution). All participants received both substances once, either the placebo during the first session and oxytocin during the second, or oxytocin during the first session and the placebo during the second. The order of administration was unknown to both the participant and the experimenter and counterbalanced across participants. Thus, half of the participants received oxytocin during the second session (n = 22 for the current sample) and half a placebo (n = 25 for the current sample). Participants were then fitted with an electrode net after which their EEG was recorded during two 2-min resting periods (the first with eyes opened, the second with eyes closed). Participants then completed a 1-hr task (for ERP data collection, results presented elsewhere) after which their EEG was again recorded during two 2-min resting periods (again, the first with eyes opened, the second with eyes closed).

Donating to UNICEF

After completion of the last EEG measurements of the second session, participants were paid 50 Euros for participation. They were then left alone and were shown a 2-min UNICEF promotional video, showing a child from a resource-limited country (Bangladesh), forced to work in a stone pit instead of going to school, due to poverty. Immediately following the video a text appeared on screen, asking the participant to donate some money. A money box had been positioned next to the video screen. The money box was filled with several coins to enhance credibility (see Van IJzendoorn, Bakermans-Kranenburg, Pannebakker, & Out, 2010, for a similar task). Because the distribution of donations was somewhat skewed, a square root transformation was used in all analyses. Donated money was transferred to the UNICEF bank account after data collection.

EEG measurement

During EEG data collection, participants were seated in a comfortable chair facing a computer screen (distance approximately 50 cm), in a dimly lit, sound-attenuated room. A white fixation cross was presented on a black background at the center of the screen during resting measurements with eyes opened. Participants were instructed to 'just relax' and keep their eyes focused on the cross as much as possible. Participants' EEG was acquired during the four resting periods using 129-channel hydrocel geodesic sensor nets, amplified using a NetAmps300 amplifier, low-pass filtered at half (i.e., 125 Hz) the digitization rate of 250 Hz and recorded using NetStation software (Electrical Geodesics, Inc.). Impedances were kept below 50 kΩ. Further processing of the raw EEG was conducted offline using Brain Vision Analyzer 2.0 software (Brain Products). The EEG was filtered with a passband range of 0.1-40 Hz (-3 dB, 48 dB/octave) and rereferenced to the average of activity in all channels. Each two-minute recording was divided into 119 2-s segments, with one second overlap between segments, and corrected for ocular artifacts using ICA. Segments containing residual artifacts were removed (segments were removed if the slope at any point during the segment exceeded 100 μV/ms, and if the difference between the maximum and minimum activity exceeded 300 μV within the entire segment or was less then 0.5 μV within any 100 ms period) and a short term Fourier transform (0.5 Hz resolution, 100% Hamming window) was computed to obtain power values (μV^2) for the remaining segments. Power values were averaged across all segments within each resting period, and then averaged across the frequency range of 8-12 Hz to obtain measures of power within the alpha band within each resting period. To normalize data distribution the natural logarithm (ln) of these values was computed.

Ln-transformed values were averaged across sets of eight electrodes to yield measures of left-frontal (20, 23, 24 [F3], 26, 27, 28, 33 [F7], 34), right-frontal (2, 3, 116, 117, 118, 122 [F8], 123, 124 [F4]), left-central (30, 36 [C3], 37, 40, 41, 42, 45, 46), right-central (87, 93, 102, 103, 104 [C4], 105, 108, 109), left-posterior (52 [P3], 53, 58 [P7], 59, 60, 61, 64, 65), and right-posterior (78, 85, 86, 90, 91, 92 [P4], 95, 96 [P8]) alpha activity. As a measure of asymmetry, laterality indices were computed separately for frontal, central and posterior sites by subtracting left alpha activity from right alpha activity (ln[right alpha] – ln[left alpha]). A zero value on this measure thus represents no alpha asymmetry, whereas more positive values result from greater alpha power over right compared to left cortical areas and therefore represent greater relative left frontal activity. Similarly, more negative values represent greater relative right frontal activity. Because no effects involving time (resting periods before vs. after the ERP experiment) or condition (eyes open vs. closed) were found (all Fs ≤ 2.89, ps $> .05$) in an ANOVA with drug (placebo vs. oxytocin), time and condition as independent variables, asymmetry values were averaged across the four baseline periods for statistical analyses.

Parental use of love withdrawal

Participants completed an 11-item questionnaire, containing all five items of the Withdrawal of Relations subscale of the Children's Report of Parental Behavior Inventory (CRPBI; Beyers & Goossens, 2003; Schludermann & Schludermann, 1988), two items that were adapted from this same questionnaire, and four items adapted from the Parental Discipline Questionnaire (PDQ; Hoffman & Saltzstein, 1967; Patrick & Gibbs, 2007). Participants rated how well each of the 11 statements described their mother and father separately (e.g., "My mother is a person who, when I disappoint her, tells me how sad I make her") on a 5-point scale ranging from 1 (not at all) to 5 (very well). Scores for maternal and paternal love withdrawal were summed, and the resulting scale was normally distributed. Cronbach's alpha was .87 for the current sample.

Analyses
Statistical analyses were performed using SPSS 17 software. To evaluate effects (simple, mediation, moderation) of frontal alpha asymmetry on donating behavior, a series of hierarchical linear regression analyses was performed. In all regression analyses, continuous predictors were centered on their respective means, and contrast codes were used for drug (placebo vs. oxytocin).

Results

Descriptives
Among the 47 participants included in the current sample, 37 donated some money (80%), and the average amount of money donated was 2.77 Euros (SD = 2.83, range 0.00 - 15.00). As described above, a square root transformation was computed to normalize data distribution, and transformed values were used in all analyses. The average score on the love withdrawal questionnaire was 48.06 (SD = 12.75), average values for frontal, central and posterior alpha asymmetry were -0.05 (SD = 0.17), -0.10 (SD = 0.26), and 0.07 (SD = 0.27) respectively. Posterior alpha asymmetry was significantly correlated with both frontal (r = -.45, p < .01) and central alpha asymmetry (r = .39, p < .01), whereas frontal and central asymmetry were not significantly related (r = .16, p > .10).

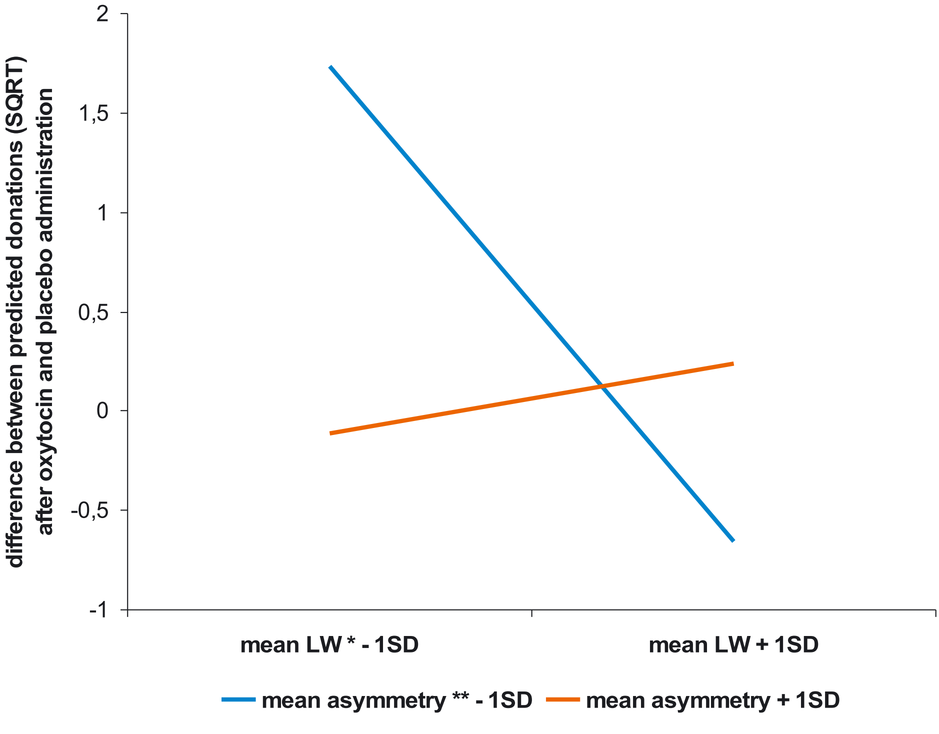
To confirm our previous result that the interaction between drug and love withdrawal predicted donating behavior in the current sample of 47 students, a hierarchical regression analysis was performed with drug (placebo vs. oxytocin) entered in the first step, love withdrawal in the second step, and the interaction between drug and love withdrawal in the third step. As expected, the model was significant (F(3,43) = 2.91, p < .05, R^2 = .17) and only the interaction term significantly predicted donating (β = .32, p < .05; other $|\beta s| \leq .16$, ps > .10).

Frontal alpha asymmetry and donating

Simple effect. Frontal alpha asymmetry and donating behavior were significantly and positively correlated (r = .30, p < .05). More positive values, and thus greater relative left frontal activity, were related to larger donations to UNICEF.

Mediation. To test whether frontal alpha asymmetry mediated effects of oxytocin and love withdrawal on donating behavior, we first examined if frontal alpha asymmetry was predicted by oxytocin, love withdrawal, or both. We therefore conducted a hierarchical regression analysis with frontal alpha asymmetry as the dependent variable, in which drug (placebo vs. oxytocin) was entered as a predictor in the first step, love withdrawal in the second, and the interaction term in the third step. No significant effects were found (all $|\beta s| \leq .10$, $ps > .50$; model: $F(3,43) = 0.15$, $p > .50$ $R^2 = .01$), thus ruling out mediation.

Moderation. To test for potential moderating effects of frontal alpha asymmetry, a hierarchical regression analysis was performed with donation as the dependent variable, in which drug (placebo vs. oxytocin) was entered in the first step, love withdrawal and frontal alpha asymmetry in the second step, all two-way interactions of the (centered) variables (drug*love withdrawal, drug*frontal alpha asymmetry, love withdrawal*frontal alpha asymmetry) in the third step, and the three-way interaction (drug*love withdrawal*frontal alpha asymmetry)



* mean LW: mean score on the love withdrawal questionnaire across participants
** mean asymmetry: mean frontal alpha asymmetry score across participants. Note that mean asymmetry - 1 SD reflects relative right frontal activity (M - 1SD = -0.05 - 0.17 = -0.22), whereas mean asymmetry + 1 SD reflects relative left frontal activity (M + 1SD = -0.05 + 0.17 = 0.12).

Figure 1. Differences between the predicted donations (square root transformation) to a charity after oxytocin versus placebo administration (oxytocin - placebo) as a function of frontal alpha asymmetry and love withdrawal. For those showing greater relative right frontal activity, lower love withdrawal was associated with larger donations after oxytocin compared to placebo administration.

in the fourth step. The final model was significant ($F(7,39) = 3,71$, $p < .01$, $R^2 = .40$). As in the analyses described above, the main effect of frontal alpha asymmetry ($\beta = .30$, $p < .05$) and the interaction between drug and love withdrawal ($\beta = .27$, $p < .05$) were significant. These effects were, however, qualified by a significant three-way interaction between drug, love withdrawal and frontal alpha asymmetry ($\beta = -.32$, $p < .05$). No other effects were significant (all $|\beta s| \leq .22$, $ps > .10$). To further explore the three-way interaction, we divided the participants into groups showing above average (more positive values, reflecting greater relative left / less relative right activity, $n = 23$) and below average (more negative values, reflecting greater relative right / less relative left activity, $n = 24$) frontal alpha asymmetry, and then conducted separate hierarchical regression analyses for each group with donation as the dependent variable, and predictors drug (placebo vs. oxytocin) entered in the first step, love withdrawal in the second, and the interaction term in the third step. For the group showing greater relative right / less relative left activity, the model was significant ($F(3,20) = 8.40$, $p < .01$, $R^2 = .56$), and the interaction between drug and love withdrawal significantly predicted donations ($\beta = .68$, $p < .01$; other $|\beta s| \leq .24$, $ps > .10$), whereas for the group showing greater relative left / less relative right activity no significant effects were found (all $|\beta s| \leq .32$, $ps > .10$; model: $F(3,19) = 0.91$, $p > .10$, $R^2 = .13$). As can be seen in Figure 1, lower love withdrawal was associated with larger donations after oxytocin (compared to placebo) administration for those showing greater relative right frontal activity.

Controlling for central and posterior alpha asymmetry

Because we found some significant correlations between alpha asymmetry at frontal, central, and posterior electrode sites, we repeated the analyses (with donation as dependent variable) described above under *Simple effect* and *Moderation* twice, once with central and once with posterior alpha asymmetry replacing frontal alpha asymmetry. Neither central ($r = .17$, $p > .10$) nor posterior alpha asymmetry ($r = -.06$, $p > .50$) was significantly correlated with donations, and in regression analyses no significant effects involving central (all $|\beta s| \leq .19$, $ps > .10$) or posterior alpha asymmetry (all $|\beta s| \leq .15$, $ps > .10$) were found. Finally, we performed a regression analysis (with donation as the dependent variable) in which central and posterior alpha asymmetry were entered as predictors in the first step to control for potential effects of central and posterior alpha asymmetry on donating behavior, before entering drug (placebo vs. oxytocin, step 2), love withdrawal and frontal alpha asymmetry (step 3), and the two- (step 4) and three-way interaction terms (step 5) of these three variables. The final model was significant ($F(9,37) = 2.78$, $p < .05$, $R^2 = .40$), and both the main effect of frontal alpha asymmetry ($\beta = .33$, $p < .05$) and the interaction between drug, love withdrawal, and frontal alpha asymmetry ($\beta = -.31$, $p < .01$) remained significant. Neither central ($\beta = -.02$, $p > .50$), nor posterior alpha asymmetry ($\beta = .08$, $p > .50$) significantly predicted donations. The interaction between drug and love withdrawal just failed to reach significance ($\beta = .27$, $p = .05$) and no other significant effects were found (all $|\beta s| \leq .22$, $ps > .10$).

Discussion

Asymmetric frontal brain activity significantly predicted donating behavior. As was expected, greater relative left frontal activity / less relative right frontal activity was associated with larger donations to UNICEF after viewing a promotional video showing a child in need. This finding is in line with the idea that higher approach motivation and a greater tendency to experience approach-related emotions, associated with greater relative left frontal activity, would cause an individual to donate more money to actively help-out those in need.

Moreover, frontal alpha asymmetry moderated the interactive effect of oxytocin and parental love withdrawal on donating behavior that we had observed previously (Van IJzendoorn et al., 2011). The predictive value of the interaction between oxytocin and parental love withdrawal (larger donations after oxytocin compared to placebo administration for those reporting lower love withdrawal) increased with decreasing relative left / increasing relative right frontal activity. Lower love withdrawal was associated with larger donations after oxytocin compared to placebo administration only for those showing relative right frontal activity. Thus, it seems that effects of oxytocin on prosocial attitudes and behavior, and concerns related to experiences of parental love withdrawal only affect decisions about donating for individuals whose response to emotional material is characterized by withdrawal rather than approach, as suggested by their pattern of frontal brain activity. We tentatively suggest that those showing greater relative left frontal activity are likely to donate money in response to promotional material showing an individual in need, irrespective of how their empathic responding is affected by oxytocin administration or experiences of love withdrawal, because approach-related tendencies motivate them to take action, and thus to donate money. For those less inclined to donate out of approach motivation (i.e., those showing less relative left / greater relative right frontal activity), empathic and other concerns affected by oxytocin and experiences of love withdrawal may play a more important part in deciding whether and how much money they donate.

The most obvious feature of the interaction between oxytocin and parental love withdrawal, both when ignoring differences in asymmetric frontal brain activity (see Figure 1, cf. Van IJzendoorn et al., 2011) and when focusing on individuals showing les relative left/ greater relative right frontal activity (see Figure 1), is the increase in donations after oxytocin (vs. placebo) administration for individuals reporting lower love withdrawal. However, a closer look at Figure 1 reveals that at the higher end of the love withdrawal continuum oxytocin actually seems to decrease donations relative to placebo for those showing less relative left / greater relative right frontal activity. An interpretation of these seemingly opposing effects of oxytocin would necessarily be speculative and is beyond the scope of the current paper (but see Van IJzendoorn et al., 2011, for some suggestions). Nevertheless, it is important to note that although individuals showing less relative left / greater relative right frontal activity appear to be more sensitive to influences of oxytocin and parental love withdrawal on (processes involved in) decision making in the donating task, these influences are not necessarily unidirectional. Compared to those showing greater relative left frontal activity, individuals showing greater relative right frontal activity may show both larger increases and smaller increases or even decreases in donations after oxytocin compared to placebo administration, depending on their experiences of parental love withdrawal.

There is a striking similarity between this observation and findings concerning the model of differential susceptibility of individuals to environmental influences throughout development, showing that children with certain neurobiological dispositions (as evident from genetic, neuroendocrine, or behavioral measures) both benefit more from a favorable caregiving environment and are more affected by negative caregiving experiences (for an overview see Ellis, Boyce, Belsky, Bakermans-Kranenburg, & Van IJzendoorn, 2011). The differential susceptibility model has been contrasted with diathesis-stress or dual-risk models that focus on the added negative effects of unfavorable circumstances for some individuals, assuming no differential effects of favorable circumstances (see Ellis et al., 2011). Interestingly, a diathesis-stress model has also been proposed for the role of relative right frontal brain activity in depression (Davidson, 1998).

There are, of course, substantial differences between the differential susceptibility literature and our current study (but see Bakermans-Kranenburg & Van IJzendoorn, 2011). Nevertheless, a recurrent observation in studies of the interplay between neurobiological characteristics and external factors or experiences is that certain characteristics are associated with a greater sensitivity to (influences of) external factors and experiences, and that effects of this heightened sensitivity can go both ways: Depending on the level of the external variable or experiences under consideration, the more susceptible or sensitive individual can be both worse and better off, show both more and less desirable behavior, or, as in our current study, show both similar but larger and opposite effects of oxytocin, compared to the less sensitive individual. Thus, however associative the link between our current results and differential susceptibility theory may be, this type of interaction between neurobiological characteristics, experiences, and external factors deserves attention in future studies.

As the approach-withdrawal model was devised specifically to explain the role of asymmetric frontal brain activity in emotional processes (e.g., see Demaree et al., 2005; Harmon-Jones et al., 2010), including affective reactions to emotional film fragments and photographs (e.g., Perry, Bentin, Bartal, Lamm, & Decety, 2010; Tomarken, Davidson, & Henriques, 1990), showing a UNICEF promotional video of a child in need may be an important component of the current experimental setup. Showing such a video activates emotional systems (by eliciting emotional reactions such as empathy, see for example Burt & Strongman, 2004) and may thus be particularly suited to study the influences of individual characteristics (in this case frontal asymmetries and parental love withdrawal) and substances (in this case oxytocin) involved in emotional processes on donating behavior.

A factor to consider when interpreting our results is that all our participants were female. We included only women in this study because of the considerable differences between males and females in the oxytocin system (Suske & Gallagher, 2009), because the effects of oxytocin in women are less frequently studied than those in men, and because the ERP experiment focused on effects of maternal use of love withdrawal with daughters (see Huffmeijer et al, 2011a; Huffmeijer, Tops, Alink, Bakermans-Kranenburg, & Van IJzendoorn, 2011b). Nevertheless, it would be interesting to study the same processes in men. Future studies could also include behavioral or questionnaire measures of approach-withdrawal motivation (such as the BIS/BAS Scales; Carver & White, 1994), to test our interpretation of the effects of asymmetric frontal activity on donating behavior in terms of approach-withdrawal motivation. Importantly though, our results were specific to frontal alpha asymmetry and not affected by the inclusion of central and posterior alpha asymmetry, increasing confidence in our findings. Finally, because measures of frontal alpha asymmetry have been found to be composed of both a trait level of asymmetry and state-induced variation (Coan & Allen, 2004; Hagemann et al., 2005), future studies could include multiple measures (taken on multiple occasions) of frontal alpha asymmetry to evaluate the respective contributions of trait-related and state-related factors.

In conclusion, greater left compared to right frontal brain activity predicted larger donations after viewing a video of a child in need. Moreover, asymmetric frontal activity moderated effects of oxytocin and parental love withdrawal on donating behavior. We suggest that when approach motivation is high (reflected in greater relative left frontal activity), individuals are inclined to take action upon seeing someone in need, and thus to donate more money to actively help-out. Only when approach motivation is low (reflected in less relative left/ more relative right activity), do empathic and other concerns affected by oxytocin and experiences of love withdrawal play an important part in deciding about donations. Future research, incorporating direct measures of approach-withdrawal motivation, will be necessary to test this interpretation, and to extend findings to a wider population, including men.

References

Andreoni, J. (1990). Impure altruism and donations to public goods: A theory of warm-glow giving. *The Economic Journal, 100,* 464-477.
Assor, A., Roth, G., & Deci, E.L. (2004). The emotional costs of parents' conditional regard: A self-determination theory analysis. *Journal of Personality, 72 (1),* 47-88.
Bakermans-Kranenburg, M.J., & Van IJzendoorn, M.H. (2011). Differential susceptibility to rearing environment depending on dopamine-related genes: New evidence and a meta-analysis. *Development and Psychopathology, 23,* 39-52.
Barraza, J.A., McCullough, M.E., Ahmadi, S., & Zak, P.J. (2011). Oxytocin infusion increases charitable donations regardless of monetary resources. *Hormones and Behavior, 60 (2),* 148-151.
Beyers, W., & Goossens, L. (2003). Psychological separation and adjustment to university: Moderating effects of gender, age and perceived parenting style. *Journal of Adolescent Research, 18*, 363-382.
Burt, C.D.B., & Strongman, K. (2004). Use of images in charity advertising: Improving donations and compliance rates. *International Journal of Organisational Behaviour, 8 (8),* 571-580.
Carver, C.S., & White, T.L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology, 67,* 319-333.
Coan, J.A., & Allen, J.J.B. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology, 67,* 7-49.
Cook, I.A., O'Hara, R., Uijtdehaage, S.H.J., Mandelkern, M., & Leuchtner, A.F. (1998). Assessing the accuracy of topographic EEG mapping for determining local brain function. *Electroencephalography and Clinical Neurophysiology, 107,* 408-414.
Crost, N.W., Pauls, C.A., & Wacker, J. (2008). Defensiveness and anxiety predict frontal EEG asymmetry only in specific situational contexts. *Biological Psychology, 78,* 43-52.
Davidson, R.J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition and Emotion, 12,* 307-330.
Davidson, R.J., & Fox, N.A. (1989). Frontal brain asymmetry predicts infants' response to maternal separation. *Journal of Abnormal Psychology, 98,* 127-131
De Dreu, C.K.W., Greer, L.L., Handgraaf, M.J.J., Shalvi, S., Van Kleef, G.A., Baas, M., Ten elden, F.S., Van Dijk, E.H., & Feith, S.W.W. (2010). The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science, 328,* 1408-1411.
Demaree, H.A., Everhart, D.E., Youngstrom, E.A., & Harrison, D.W. (2005). Brain lateralization of emotional processing: Historical roots and future incorporating "dominance". *Behavioral and Cognitive Neuroscience Reviews, 4 (1),* 3-20.
Domes, G., Lischke, A., Berger, C., Grossmann, A., Hauenstein, K., Heinrichs, M., & Herpertz, S.C. (2010). Effects of intranasal oxytocin on emotional face processing in women. *Psychoneuroendocrinology, 35 (1),* 83-93.

Elliot, A.J., & Thrash, T.M. (2004). The intergenerational transmission of fear of failure. *Personality and Social Psychology Bulletin, 30,* 957-971.

Ellis, B.J., Boyce, W.T., Belsky, J., Bakermans-Kranenburg, M.J., & Van IJzendoorn, M.H. (2011). Differential susceptibility to the environment: An evolutionary-neurodevelopmental theory. *Development and Psychopathology, 23,* 7-28.

Euser, E.M., Van IJzendoorn, M.H., Prinzie, P., & Bakermans-Kranenburg, M.J. (2010). Prevalence of child maltreatment in the Netherlands. *Child Maltreatment, 15 (1),* 5-17.

Fox, N.A., Henderson, H.A., Rubin, K.H., Calkins, S.D., & Schmidt, L.A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72 (1),* 1-21.

Goldstein, M., & Heaven, P.C.L. (2000). Perceptions of the family, delinquency, and emotional adjustment among youth. *Personality and Individual Differences, 29,* 1169-1178.

Hagemann, D., Hewig, J., Seifert, J., Naumann, E., & Bartussek, D. (2005). The latent state-trait structure of resting EEG asymmetry: Replication and extension. *Psychophysiology, 42,* 740-752.

Harmon-Jones, E., & Allen, J.J.B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: Covariation of putative indicators related to risk for mood disorders. *Journal of Abnormal Psychology, 106 (1),* 159-163.

Harmon-Jones, E., Gable, P.A., & Peterson, C.K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology, 84,* 451-462.

Heinrichs, M., Baumgartner, T., Kirschbaum, C., & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry, 54,* 1389-1398.

Heinrichs, M., Dawans, B. von, & Domes, G. (2009). Oxytocin, vasopressin, and human social behavior. *Frontiers in Neuroendocrinology, 30,* 548-557.

Hoffman, M.L., & Saltzstein, H.D. (1967). Parent discipline and the child's moral development. *Journal of Personality and Social Psychology, 5 (1),* 45-57.

Huffmeijer, R., Alink, L.R.A., Tops, M., Grewen, K.M., Light, K.C., Bakermans-Kranenburg, M.J., & Van IJzendoorn, M.H. (2011a). The impact of oxytocin administration and maternal love withdrawal on event-related potential (ERP) responses to emotional expressions with performance feedback. Manuscript submitted for publication.

Huffmeijer, R., Tops, M., Alink, L.R.A., Bakermans-Kranenburg, M.J., & Van IJzendoorn, M.H. (2011b). Love withdrawal is related to heightened processing of faces with emotional expressions and incongruent emotional feedback: Evidence from ERPs. *Biological Psychology, 86,* 307-313.

Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., Salek-Haddadi, A., & Kleinschmidt, A. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. *PNAS, 100,* 11053-11058.

MacDonald, K., & MacDonald, T.M. (2010). The peptide that binds: A systematic review of oxytocin and its prosocial effects in humans. *Harvard Review of Psychiatry, 18,* 1-21.

Mayo, J.W., & Tinsley, C.H. (2009). Warm glow and charitable giving: Why the wealthy do not give more to charity? *Journal of Economic Psychology, 30,* 490-499.

Nowark, M.A., & Sigmund, D. (2005). Evolution of indirect reciprocity. *Nature, 437,* 1291-1298.

Patrick, R.B., & Gibbs, J.C. (2007). Parental expression of disappointment: Should it be a factor in Hoffman's model of parental discipline? *The Journal of Genetic Psychology, 168 (2),* 131-145.

Perry, A., Bentin, S., Bartal, I.B.A., Lamm, C., & Decety, J. (2010). "Feeling" the pain of those who are different from us: Modulation of EEG in the mu/ alpha range. *Cognitive, Affective & Behavioral Neuroscience, 10 (4),* 493-504.

Renk, K., McKinney, C., Klein, J., & Oliveros, A. (2006). Childhood discipline, perceptions of parents, and current functioning in female college students. *Journal of Adolescence, 29,* 73-88.

Schludermann, E.H., & Schludermann, S.M. (1988). Children's Report of Parent Behavior (CRPBI-108, CRPBI-30) for older children and adolescents (Tech. Rep.). Winnipeg, Manitoba, Canada: University of Manitoba, Department of Psychology.

Soenens, B., Vansteenkiste, M., Luyten, P., Duriez, B., & Goossens, L. (2005). Maladaptive perfectionistic self-representations: The mediational link between psychological control and adjustment. *Personality and Individual Differences, 38,* 487-498.

Suske, D.H., & Gallagher, L. (2009). Dopaminergic-neuropeptide interactions in the social brain. *Trends in Cognitive Sciences, 13 (1),* 27-35.

Thibodeau, R., Jorgensen, R.S., & Kim, S. (2006). Depression, anxiety, and resting frontal EEG asymmetry: A meta-analytic review. *Journal of Abnormal Psychology, 115 (4),* 715-729.

Tomarken, A.J., Davidson, R.J., & Henriques, J.B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology, 59 (4),* 791-801.

Van IJzendoorn, M.H., Bakermans-Kranenburg, M.J., Pannebakker, F., & Out, D. (2010). In defence of situational morality: Genetic, dispositional and situational determinants of children's donating to charity. *Journal of Moral Education, 39 (1),* 1-20.

Van IJzendoorn, M.H., Huffmeijer, R., Alink, L.R.A., Bakermans-Kranenburg, M.J., & Tops, M. (2011). The impact of oxytocin administration on charitable donating is moderated by experiences of parental love withdrawal. *Frontiers in Developmental Psychology, 2,* 258.

Verhaert, G.A., & Van den Poel, D. (2011). Empathy as added value in predicting donation behavior. *Journal of Business Research, 64 (12),* 1288-1295.

Zak, P.J., Kurzban, R., & Matzner, W.T. (2005). Oxytocin is associated with human trustworthiness. *Hormones and Behavior, 48,* 522-527.

Zak, P.J., Stanton, A.A., & Ahmadi, S. (2007). Oxytocin increases generosity in humans. *PLoS ONE, 11,* e1128.