Shaping internal working models : parental love withdrawal, oxytocin, and asymmetric frontal brain activity affect socio-emotional information processing

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3 The impact of oxytocin administration and maternal love withdrawal on event-related potential (ERP) responses to emotional expressions with performance feedback

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Abstract

This is the first experimental study on the effect of oxytocin administration on the neural processing of facial stimuli conducted with female participants that uses event-related potentials (ERPs). Using a double-blind, placebo-controlled within-subjects design, we studied effects of 24 IU of intranasal oxytocin on ERPs to pictures combining performance feedback with emotional facial expressions in 48 female undergraduate students. Participants also reported on the amount of love withdrawal they experienced from their mothers. Findings of more positive vertex positive potential (VPP) and late positive potential (LPP) amplitudes after oxytocin compared to placebo administration suggest that oxytocin increased attention to the feedback stimuli (LPP) and enhanced the processing of emotional faces (VPP). Lower maternal love withdrawal was related to larger increases in VPP amplitude after oxytocin administration. Significant associations with LPP amplitude suggest that higher maternal love withdrawal relates to the allocation of attention toward the motivationally most relevant combination of negative feedback with a disgusted face.

Introduction

The way oxytocin affects our social behavior, thinking, and perception is the subject of a rapidly increasing number of scientific investigations (e.g., see Heinrichs, von Dawans, & Domes, 2009; MacDonald & MacDonald, 2010). Although quite a few studies have focused on the effects of oxytocin on the processing of social stimuli, the vast majority of these studies have been conducted with male participants, in some cases using fMRI methodology, and the lack of studies in this area focusing on women is striking (but see Domes et al., 2010; Riem et al., 2011). The present study concerns women, and describes effects of oxytocin and perceived parenting on their event-related potential (ERP) responses to feedback stimuli combining performance feedback with emotional facial expressions.

Oxytocin is a neuropeptide that is synthesized in magnocellular neurons of the supraoptic (SON) and paraventricular (PVN) nuclei of the hypothalamus that project to the posterior pituitary from which oxytocin is released into the bloodstream. In addition, neurons in the PVN project to various limbic, mid- , and hindbrain structures (e.g., hippocampus, amygdala, and nucleus accumbens) containing oxytocin receptors. Within the brain, oxytocin can act both as a neurotransmitter and as a neuromodulator (Landgraf & Neumann, 2004; Suske & Gallagher, 2009). In mammals, oxytocin is well known for its role in parturition and lactation, is involved in regulation of the hypothalamic-pituitary-adrenal axis, and facilitates reproductive and maternal behavior, infant attachment, and social behavior (Carter, 2003; Insel, 1992; Parker, Buckmaster, Schatzberg, & Lyons, 2005).

A growing body of research suggests that in humans oxytocin also plays a role in mother-infant bonding as well as in parenting behavior (e.g., Bakermans-Kranenburg & Van IJzendoorn, 2008; Campbell, 2008; Feldman, Weller, Zagoory-Sharon, & Levinde, 2007; Naber, Van IJzendoorn, Deschamps, Van Engeland, & Bakermans-Kranenburg, 2010), and that early interpersonal experiences may be important for shaping the oxytocin system (Feldman, Gordon, & Zagoory-Sharon, 2010; Heim et al., 2008). Many studies have addressed the influence of oxytocin on social stress, perception, cognition, and decision making in adults. Oxytocin has been found to attenuate stress responses in social situations, to promote trust and generosity toward an opponent (at least in in-group situations, De Dreu et al., 2010), and to influence the processing of and facilitate memory for salient social stimuli; for reviews see Heinrichs et al. (2009), and MacDonald and MacDonald (2010). It is well known that elevations of oxytocin levels in blood (in which it has a half-life of only a few minutes) do not adequately reflect the time-range of its neurobehavioral effects, but little is known about oxytocin in other fluids (McEwen, 2004). As an addition to our study, we therefore measured oxytocin levels in saliva samples collected during the experiment to investigate whether and how long oxytocin levels would be elevated in saliva after intranasal oxytocin administration.

Of particular relevance for the current study are effects of oxytocin on the processing of faces and facial expressions. On a behavioral level, oxytocin has been found to improve recognition memory for faces, both when oxytocin is administered before (Rimmele, Hediger, Heinrichs, & Klaver, 2009) and after (Savaskan, Ehrhardt, Schulz, Walter, & Schächinger, 2008) the initial learning stage, suggesting an effect of oxytocin on memory consolidation. Oxytocin may facilitate memory encoding specifically for positive facial expressions (Guastella, Mitchell, & Mathews, 2008b). Results of several studies describe facilitative effects of oxytocin on the processing of facial expressions that may underlie improvements in memory, although there is some inconsistency regarding differential effects for different emotional expressions, complicated by differences in study designs and outcome measures. For example, Fisher-Shofty, Shamay-Tsoory, Harari, and Levkovitz (2010) found that participants were more accurate at recognizing fear, but not other emotions (happiness, sadness, surprise, and disgust) after oxytocin compared to placebo administration, whereas Di Simplicio, Massey-

Chase, Cowen, and Harmer (2009) found that oxytocin improved recognition of positive emotions (i.e., a reduction in misclassifications of positive emotions as negative ones) and slowed reaction times for fearful expressions. On a cognitive level, oxytocin has been found to improve the ability to make inferences about the mental state of another from the eye-region of the face (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007b). Interestingly and in accordance with the latter finding, oxytocin increased both the number of fixations and the total time of fixation at the eye-region of faces in a study by Guastella, Mitchell, and Dadds (2008a), suggesting that oxytocin increases attention to the eye-region of faces.

Taken together, behavioral studies suggest that oxytocin facilitates the processing of faces and facial expressions, possibly via attentional mechanisms. The neural circuitry underlying the cognitive-behavioral effects has been the topic of a number of investigations using fMRI to image brain activity. These studies typically find reductions of amygdala activation in response to facial expressions (regardless of valence) after oxytocin compared to placebo administration, which has been suggested to reflect reduced arousal resulting from a reduction in uncertainty about the meaning of social stimuli due to more efficient processing or processing biases induced by oxytocin (Domes et al., 2007a; but see Domes et al., 2010, for contrasting effects in females). In addition to reduced amygdala activity, reduced functional coupling between the amygdala and regions of the brainstem that mediate fearful behavior and arousal has been observed after oxytocin administration (Kirsch et al., 2005). A slightly more complicated picture is presented by Gamer, Zurowski, and Büchel (2010), who distinguished between different subregions of the amygdala. They found that oxytocin decreased activity in anterior parts of the amygdala when viewing fearful faces, but increased activity in these parts in response to happy faces. Increased activity in the posterior amygdala and enhanced coupling between the posterior amygdala and superior colliculus were related to increases in reflexive eye-movements toward the eye-region of the facial stimuli after oxytocin compared to placebo administration, in accordance with the role of both these regions in reflexive shifting of attention.

Studies employing fMRI thus associate oxytocin with alterations in amygdala activity in response to facial expressions, reflecting arousal and attentional strategies. It is important to note, however, that virtually all of the fMRI studies described above were conducted with male participants (as were the vast majority of cognitive-behavioral studies). Results obtained with male participants may not be directly applicable to women, because of sex differences in circulating levels of oxytocin (women tend to have higher levels than men) and because of the regulatory influence of sex hormones, particularly estrogen, on the oxytocin system (Suske & Gallagher, 2009). To our knowledge, only one study focusing on the effects of oxytocin on neural responses to face stimuli has been conducted with female participants. Using fMRI to measure activity in response to happy, fearful, and angry faces, Domes et al. (2010) found that, in contrast to typical results in men, oxytocin increased activity in the left amygdala in response to fearful faces. They also found increased activity in brain areas associated with the processing of faces and facial expressions, including the superior temporal cortex (for fearful faces), inferior frontal gyrus (for happy and angry faces), and

fusiform gyrus (for happy and fearful faces), suggesting heightened processing of emotional facial expressions after oxytocin compared to placebo administration.

The current study is not only one of the first to investigate effects of oxytocin on the processing of facial stimuli in women, but also the first to study ERP responses to these facial stimuli. In the late 1980s and early 1990s a couple of studies were conducted on the influence of oxytocin on ERP components sensitive to vigilance and arousal, elicited by series of briefly presented auditory stimuli (Fehm-Wolfsdorf, Bachholz, Born, Voigt, & Fehm, 1988; Geenen et al., 1988; Pietrowski, Braun, Fehm, Pauschinger, & Born, 1991). Little or no effects of oxytocin were found, which may be due to the non-social nature of the tasks and stimuli employed (in all three studies) as well as intravenous injection of oxytocin (in Geenen et al., 1988 and Pietrowski et al., 1991), as oxytocin is unlikely to cross the blood-brain barrier in substantive amounts (McEwen, 2004). In a recent study, intranasally administered oxytocin enhanced suppression of alpha and beta rhythms in the EEG while participants viewed point-light displays of a human figure walking away from or toward the participant, suggesting that oxytocin facilitates the allocation of resources toward this type of social task (Perry et al., 2010).

In the current study we focus on two components of the ERP that are sensitive to variations in the extent of processing of facial stimuli and the allocation of attentional resources. The vertex positive potential (VPP) is a positive deflection in the ERP that peaks at frontocentral electrode sites, roughly between 140 and 180 ms after stimulus onset. Evidence suggests that the VPP and N170, a negative going occipitotemporal right hemisphere dominant component, represent two sides of the same generator dipoles in occipitotemporal cortex (Joyce & Rossion, 2005). Both components have been associated with the configural processing of faces, with larger amplitudes indicating more extensive processing, and show larger amplitudes in response to emotional compared to neutral expressions (Luo, Feng, He, Wang, & Luo, 2010). VPP and N170 are often found to be sensitive to intensity, but not valence of emotional expressions (Luo et al., 2010; Sprengelmeyer & Jentzsch, 2006), although larger amplitudes in response to negative (often fearful) compared to positive (often happy) expressions have been observed in some studies (Ashley, Vuillemier, & Swick, 2004; Krombholz, Schaefer, & Boucsein, 2007; Williams, Palmer, Liddell, Song, & Gordon, 2006). If oxytocin increases attention toward (parts of) faces and facilitates the processing and encoding of facial expressions, oxytocin should also increase the amplitude of the VPP.

Whereas the VPP reflects a relatively early, automatic stage of processing, the late positive potential (LPP), a centroparietally distributed, positive-going modulation of the ERP beginning about 300-400 ms after stimulus onset, is thought to reflect the allocation of attention toward emotionally and motivationally significant stimuli (Hajcak, Dunning, & Foti, 2009; Pastor et al., 2008). Evidence suggests that occipital, posterior parietal, and inferotemporal areas are involved in generating the LPP (Keil et al., 2002; Sabatinelli, Lang, Keil, & Bradley, 2007). The amplitude of the LPP is more positive for emotional stimuli, both pleasant and unpleasant, compared to neutral stimuli and may be influenced by both automatic

(e.g., capture of attention by unpleasant stimuli) and controlled (e.g., direction of attention toward non-threatening parts of a stimulus) processes (Cacioppo, Crites, & Gardner, 1996; Hajcak et al., 2009; Hajcak, MacNamera, & Olvet, 2010; Pastor et al., 2008). If oxytocin increases the allocation of attention toward faces or facial expressions, this should lead to more positive LPP amplitudes.

Besides oxytocin, other factors may affect ERPs in response to our facial feedback stimuli. Previously we reported on effects of maternal use of love withdrawal on the VPP and N400 components of the ERP (Huffmeijer, Tops, Alink, Bakermans-Kranenburg, & Van IJzendoorn, 2011). Love withdrawal is a disciplinary strategy that involves withholding 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, and in particular maternal, use of love withdrawal has been associated with low self-esteem, low emotional well-being, feelings of resentment toward the parents, and fear of failure 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, 2005b). It is less clear, however, whether the use of love withdrawal also affects the deeper level of information processing in the brain.

Because parental use of love withdrawal is thought to affect psychological functioning through the establishment of a link between performance and compliance on the one hand and relational consequences, including intense emotional expressions, on the other, emotional information and expressions within the context of performance situations may be more relevant for, more attended by, and processed to a larger extent by persons who have experienced high levels of maternal love withdrawal compared to those who have experienced less love withdrawal. Our previous findings of a more negative N400 and a more positive VPP with higher levels of maternal love withdrawal were consistent with this idea (Huffmeijer et al., 2011). We expect that this increase in vigilance for and attention to facial expressions will not only result in a more positive VPP amplitude, but also in a more positive LPP.

To summarize, in the present study we investigate relations between oxytocin and maternal use of love withdrawal on the one hand and the VPP and LPP on the other. We controlled our analyses for fear of failure, which has been related to both love withdrawal (e.g., Elliot & Thrash, 2004; Soenens et al., 2005b) and ERPs to feedback stimuli (Tops & Wijers, 2011). We expect that oxytocin will increase the amplitudes of both the VPP and LPP. We also expect higher maternal use of love withdrawal to be related to more positive VPP and LPP amplitudes. In addition, there may be variations in the effects of oxytocin with the amount of love withdrawal experienced by the participants. Oxytocin is well known to have anxiolytic effects, particularly in social situations (Heinrichs, Baumgartner,

Kirschbaum, & Ehlert, 2003; Heinrichs & Domes, 2008). If anxiety about the relational consequences of performance underlies increased attention toward and increased processing of facial expressions for those reporting higher love withdrawal and if oxytocin reduces this anxiety, then attention toward and processing of facial expressions, and thereby VPP and LPP amplitudes, should increase less or even decrease with increasing love withdrawal after oxytocin administration.

Method

Participants

A total of 59 female undergraduate students, aged 18-30 years (M = 20.54, SD = 2.89), took part in the ERP experiment. Two participants completed only one session, and data of nine other participants could not be analyzed because of excessive ocular or motion artifacts (n = 6), or low error rates (n = 3). The final sample thus consisted of 48 female undergraduate students, aged 18-30 years (M = 20.46, SD = 2.71). Excluded and included participants did not differ significantly in age, maternal love withdrawal, and fear of failure (all ts(57) ≤ 0.75, ps > .10). They were paid 50 Euros for participation. Exclusion criteria included colorblindness, smoking, alcohol and drug abuse, neurological and psychiatric disorders, pregnancy, breastfeeding, and use of medication (except oral contraceptives [use of oral contraceptives was recorded as a background variable]). The study was approved by the ethics committee of the Leiden University Medical Center.

Procedure

Participants completed questionnaires on maternal use of love withdrawal and fear of failure during an introductory course in child and family studies. The questionnaires were administered to 391 18-30 year old women who were willing to participate in an EEG experiment. Within this sample of 391 students, the distribution of scores on the love withdrawal questionnaire was skewed toward the right, indicating that in this pool of students high maternal love withdrawal is (relatively) underrepresented. To ensure an acceptable coverage of the full range of scores on the love withdrawal questionnaire within the sample of students taking part in the EEG experiment, participants for this experiment were selected stratified from the pool of 391 students: Half of the participants were selected randomly from the group scoring in the upper quartile of the questionnaire (n = 24), and half of the participants were selected randomly from the group scoring in the other three quartiles (n = 24). This resulted in a normal distribution of love withdrawal scores (see below under *Questionnaires*). Participants were asked to come to our laboratory for two experimental sessions with double-blind administration of oxytocin and placebo, 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). 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 the session took place.

Informed consent was obtained at the beginning of the first session. Concerning the administration of oxytocin, participants were told that they would receive oxytocin during one session and a placebo during the other, but that the order was not known even to the experimenter. This message was repeated at the beginning of the second session. When participants were asked, at the end of the second session, which substance they thought they had taken during that session their guesses were not significantly better than chance. 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 (T0), a saliva sample was collected and participants completed a number of questionnaires. The participants then received 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 counterbalanced across participants and unknown to both the participant and the experimenter. Participants were then fitted with an electrode net after which they completed a flanker task (with a short break after the fourth block). The first experimental block of the flanker task began approximately 45 minutes after oxytocin or placebo administration. Halfway through (T1, approximately 1¼ hours after nasal spray administration) and after completion of the task (T2, approximately 2¼ hours after nasal spray administration) saliva samples were collected and participants completed several questionnaires. Data regarding questionnaires other than those measuring Fear of Failure and Love Withdrawal, and a post-task questionnaire will be presented elsewhere.

Questionnaires

To assess the level of fear of failure, participants filled out the 9-item Concern over Mistakes-subscale of the Multidimensional Perfectionism Scale (Frost, Marten, Lahart, & Rosenblate, 1990). Participants rated their agreement with nine statements (e.g., "People will probably think less of me when I make a mistake") on a 5-point scale ranging from 1 (completely disagree) to 5 (completely agree). The average score on the fear of failure questionnaire was 22.90 (SD = 6.56). Both skewness (0.24) and kurtosis (-0.22) were acceptable and a Shapiro-Wilks test indicated that the distribution within the current sample was not significantly different from the normal distribution (W = .98, p > .50). Cronbach's alpha was .88 for the current sample.

To measure maternal use of love withdrawal, the participants completed a questionnaire containing 11 items. This questionnaire contained 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 (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). The average score on the love withdrawal questionnaire was 25.21 (SD = 7.35). Both skewness (0.13) and kurtosis (-0.71) were acceptable and a Shapiro-Wilks test indicated that the distribution within the current sample was not significantly different from the normal distribution (W = .98, p > .50). Internal consistency of this questionnaire was adequate; Cronbach's alpha was .83 for the current sample. Reliability and validity of the CRPBI and its subscales have been well established (for information see Locke & Prinz, 2002; Schludermann & Schludermann, 1983, 1988) and various subscales, including the Withdrawal of Relations scale, are frequently used to study both the antecedents and consequences of parental use of psychologically controlling strategies like love withdrawal (e.g., Elliot & Thrash, 2004; Soenens et al., 2005a, 2005b).

At the end of the second session, participants completed a post-task questionnaire that included five questions about their motivation during the task and four about their evaluations of their own performance. Questions were answered on 5-point scales (e.g., ranging from "I performed much better than others" to "I performed much worse than others").

Experimental task

During each session, participants completed eight 72-trial blocks of a modified Eriksen flanker task (Eriksen & Eriksen, 1974), preceded by a 72-trial practice block. Target stimuli consisted of a row of five arrows (7.4° x 1.4° visual angle), presented for 50 ms, all pointing in the same direction (congruent targets), or with the middle arrow pointing in the opposite direction (incongruent targets). Target stimuli were preceded by a fixation cross, presented in black for 1000 ms and then in red for 800-1200 ms. The participants had to indicate, as fast as possible, whether the middle arrow pointed left or right by pressing the corresponding button on a response pad. To ensure participants would indeed react as fast they could and consequently would commit a substantial number of errors, response deadlines were employed. Because reaction times are generally faster to congruent than to incongruent targets, separate deadlines were used for both target types. New response deadlines were calculated after every block based on the participants' mean reaction times during that block.

Following each response (600-1000 ms after target stimulus offset) a feedback stimulus was presented for 1500 ms. A photograph of a happy or a disgusted face (18.8° x 21.2°) was presented in green if the participant's response was correct or in red if the participant made an error, resulting in four categories of feedback stimuli: green-happy, red-disgust (congruent), green-disgust and red-happy (incongruent). We chose to present disgusted facial expressions, rather than e.g., angry ones, because we anticipated that responses to these expressions would be most relevant for our understanding of the consequences of parental love withdrawal. Parental use of love withdrawal as a punishment triggers feelings of shame and rejection in the child (e.g., Elliot & Thrash, 2004). These same emotions are most likely to be activated by photographs of disgusted faces (Elison, 2005). Photographs were selected from Ekman's (Ekman & Friesen, 1976) standard set of prototypical facial expressions. If the participant's reaction time exceeded the response deadline the text 'too late' (6.8° x 0.9°) appeared on screen. Only ERPs

time-locked to the four categories of feedback stimuli (faces) were analyzed, because ERPs time-locked to 'too late' contained excessive artifacts (due to blinks, and eye and head movements). To make sure the participants would stay involved in the task, they could earn points during the last four blocks.

ERPs

Participants' EEG was acquired during performance of the flanker task 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 0.5-30 Hz (-3 dB, 12 dB/octave [high-pass filter], -3 dB, 48 dB/octave [low-pass filter]) and rereferenced to the average of activity in all channels. Segments extending from 200 ms before to 800 ms after the onset of each feedback stimulus were extracted, corrected for ocular artifacts using ICA, and averaged per condition (green-happy, green-disgust, red-happy, red-disgust) after removal of segments containing residual artifacts (whole segments were removed if the difference between the maximum and minimum activity exceeded 60 μV in the vertical EOG channel (channel 8-channel 126) or 40 μV in the horizontal EOG channel (channel 128-channel 125), and individual channels were removed from a segment if the difference between the maximum and minimum activity in that channel during that segment exceeded 150 μV). For each of the four resulting ERPs a 200 ms pre-stimulus baseline was subtracted from all data points. There were no significant differences between the placebo and oxytocin conditions in the percentage of trials that were free of artifacts for each of the four stimulus types (green-happy: M = 96%, SD = 6% [placebo], M = 95%, SD = 7% [oxytocin]; green-disgust: M = 96%, SD = 6% [placebo], M = 95%, SD = 7% [oxytocin]; red-happy: M = 92%, SD = 7% [placebo], M = 91%, SD = 10% [oxytocin]; red-disgust: M = 93%, SD = 7% [placebo], M = 91%, SD = 12% [oxytocin]; all ts(47) ≤ 0.89, ps > .10).

The VPP and LPP were measured directly from the ERPs time-locked to the onset of the feedback stimuli. The VPP was defined as the average amplitude in the 140-180 ms post-stimulus interval at electrode Cz. The LPP was defined as the average amplitude in the 400-800 ms post-stimulus interval averaged across 11 centroparietal electrodes (31, 53, 54, 55 [CPz], 61, 62 [Pz], 78, 79, 80, 86 and Cz).

Salivary oxytocin

For each sample at least 1mL of unstimulated saliva was collected into 1.8 mL cryotubes using the passive drool method. Samples were immediately frozen and were stored at -20 degrees Centigrade until batch assay. Level of oxytocin in saliva was assayed using a commercially available kit as per the method previously described (Grewen, Davenport, & Light, 2010; Holt-Lunstad, Birmingham, & Light, 2008). Prior to the enzyme immunoassay procedure, in keeping with the manufacturer's strong recommendation, an extraction step was performed based on instructions accompanying the EIA kit currently available in February

2011 (ADI-900-153, Enzo Life Science, Plymouth Meeting, PA). The result of this extraction was to concentrate the sample 3.2 times, increase precision and reduce matrix interference. OT extraction efficiency was 93%, which was determined by spiking with a known amount of hormone and extracting this known amount along with the other samples. OT levels in extracted saliva were then quantified using the OT EIA, in which the endogenous OT hormone competes with added OT linked to alkaline phosphatase for OT antibody binding sites. After overnight incubation at 4 degrees C., the excess reagents were washed away and the bound OT phosphatase was incubated with substrate. After 1 hour this enzyme reaction, which generates a yellow color, was stopped and the optical density (OD) was read on a Sunrise plate reader (Tecan, Research Triangle Park, NC). The intensity of the color at 405nm is inversely proportional to the concentration of OT. The hormone content (in pg/mL) was determined by plotting the intensity of OD of each sample against a standard curve. Following correction for extraction, the lower limit of sensitivity was 1.25 pg/mL. Less than 1% of the samples fell below the lower level of sensitivity (4 out of 348). These values were subsequently replaced with the lowest detectable level of 1.25 pg/mL. The intra- and inter-assay coefficients of variation were 7.35% and 8.51% respectively. The manufacturer reports that cross-reactivity with similar mammalian neuropeptides is less than 1%.

Among the 48 participants included in our final sample, for one participant one oxytocin value (T1, placebo condition) was considered an outlier ($z > 3.29$) within this time point and condition. For statistical analysis this value was replaced by the highest value occurring at this time point and condition among the remaining participants. In addition, values of one participant at T1 and another participant at T2 of the oxytocin condition fell too far outside the normal curve to be considered reliable. These values were replaced by the mean value of the respective time point and condition across the remaining participants. To normalize data distribution, we computed the natural logarithm of the raw values.

Analyses

Statistical analyses were performed using SPSS 17 software. Variations in task performance across conditions and participants were evaluated using repeated measures general linear model (GLM) analyses with error percentages, percentages of late responses, number of points earned during the task, and reaction times as dependent variables, drug (placebo vs. oxytocin) as within subjects factor, order of administration (placebo first vs. oxytocin first) as between subjects factor, and maternal use of love withdrawal (LWm) and fear of failure (FoF) as covariates. The analysis of reaction time included target type (congruent vs. incongruent) as additional within subjects factor. Because the post-task questionnaire provided ordinal data, logit ordinal regression analyses were performed with answers on each of the 9 post-task questions as dependent variables and drug condition (placebo vs. oxytocin administered during the second session) and LWm as predictors (including the interaction term of the centered predictors). To test whether oxytocin levels in saliva increased after oxytocin administration, a

repeated measures GLM analysis was performed with drug (placebo vs. oxytocin) and time (T0, T1, T2) as within subjects factors and order of administration as a between subjects factor. Greenhouse-Geisser corrections were performed when necessary. Analyses of VPP and LPP amplitude respectively were performed using repeated measures GLM analyses with drug (placebo vs. oxytocin), color (green vs. red) and facial expression (happy vs. disgusted) as within subjects factors, order of administration (placebo first vs. oxytocin first) as a between subjects factor, and LWm and FoF as covariates.

Results

Behavioral data

Maternal use of love withdrawal and fear of failure were significantly correlated ($r = .34$, $p < .05$). An overview of behavioral data during the placebo and oxytocin conditions is presented in Table 1. There were no significant effects of any of the independent variables (drug, LWm, FoF, and order of administration) on participants' error percentages, percentages of late responses, and the number of points they earned during the task (all Fs ≤ 2.24, all ps > .10). Participants responded significantly faster to congruent targets than to incongruent targets (main effect of target type), $F(1,45) = 30.61$, $p < .01$. In addition, reaction times were significantly faster during the first session than during the second session (an interaction between drug and order of administration, which was significant here, is the same as a main effect of session), $F(1,45) = 28.19$, $p < .01$, and the difference between reaction times to congruent and incongruent targets was smaller during the second compared to the first session, $F(1,45) = 4.13$, $p < .05$. No other significant effects on reaction time were found (all Fs ≤ 3.13, all ps > .05).

Love withdrawal significantly predicted answers on three of the post-task questions. Participants reporting higher love withdrawal rated their performance worse in general ($p < .01$), were less satisfied with their performance ($p < .01$), and rated their performance less favorably compared to others ($p < .05$). No significant effects of drug or interactions between drug and LWm were found (all ps > .10).

Table 1
Summary of behavioral data

Measure	Placebo	Oxytocin
Points earned	1024 (677)	1195 (485)
Percentage errors	17 (7)	15 (6)
Percentage late responses	12 (2)	12 (2)
Reaction time congruent targets (in ms)	312 (30)	315 (23)
Reaction time incongruent targets (in ms)	352 (38)	359 (31)

Note: Each cell in the table includes the mean, with the standarddeviation between brackets.

Salivary oxytocin

The (ln-transformed) average levels of oxytocin at the different time-points during the placebo and oxytocin condition are plotted in Figure 1. The GLM analysis revealed significant main effects of drug, $F(1,46) = 257.98$, $p < .01$, and time, $F(1.65,76.00) = 77.31$, $p < .01$, qualified by a significant interaction between drug and time, $F(2,92) = 99.87$, $p < .01$. As can be seen in Figure 1, average levels of oxytocin were virtually the same in both conditions before nasal spray administration (T0, $M = 1.85$ [placebo condition], $M = 1.84$ [oxytocin condition]) and markedly increased only after oxytocin administration.

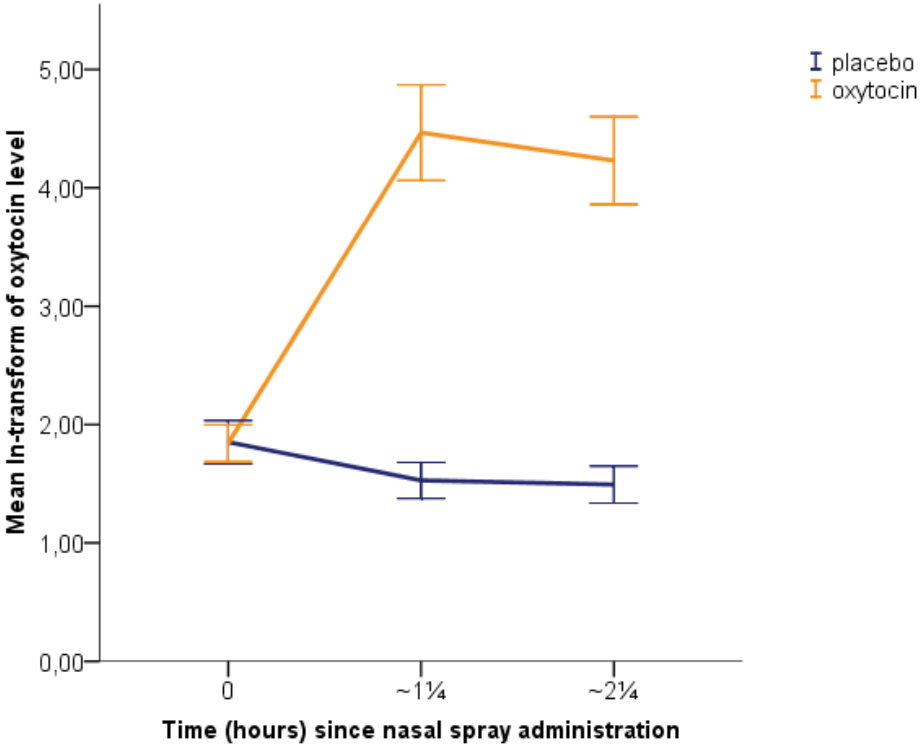

Figure 1. Mean (ln-transformed) levels of salivary oxytocin before (T0), approximately 1¼ hours after (T1), and approximately 2¼ hours after (T2) administration of nasal spray containing 24 IU of oxytocin or a placebo. Vertical bars represent 95% confidence intervals.

ERPs: VPP

Grand average ERPs at Cz time-locked to the onset of the feedback stimuli are presented in Figure 2, illustrating the VPP. Figure 3 presents the scalp voltage-distribution of this component.

The GLM analysis on VPP amplitude revealed a significant main effect of drug, $F(1,44) = 8.84$, $p < .01$, reflecting more positive VPP amplitudes in the oxytocin compared to the placebo condition. Importantly, the interaction between drug and LWm was significant as well, $F(1,44) = 7.33$, $p < .05$. Lower LWm was associated with larger increases in VPP amplitude after oxytocin compared to placebo administration, whereas this effect was smaller or absent for participants with higher scores on LWm. Oxytocin thus heightened processing of the happy and disgusted faces primarily for those reporting lower love withdrawal, as can be seen in Figure 2. An extended description of the results of this analysis can be found in the Supplementary Material. Here we focus only on findings relating to oxytocin and maternal love withdrawal.

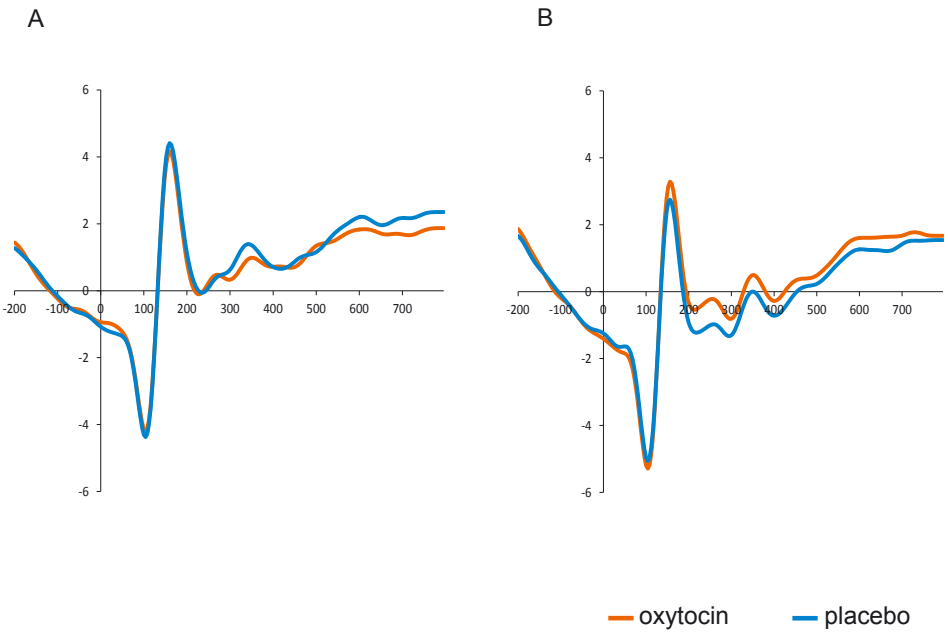

Figure 2. Grandaverage ERPs at Cz, illustrating the VPP. A: ERPs to feedback stimuli for participants reporting high maternal use of love withdrawal. B: ERPs to feedback stimuli for participants reporting low maternal use of love withdrawal. Participants were divided into groups for displaying purposes only. Participants reporting lower maternal use of love withdrawal showed a more positive response to the feedback stimuli after oxytocin compared to placebo administration between 140 and 180 ms after stimulus onset (VPP). ERPs were low-pass filtered at 15 Hz for displaying purposes.

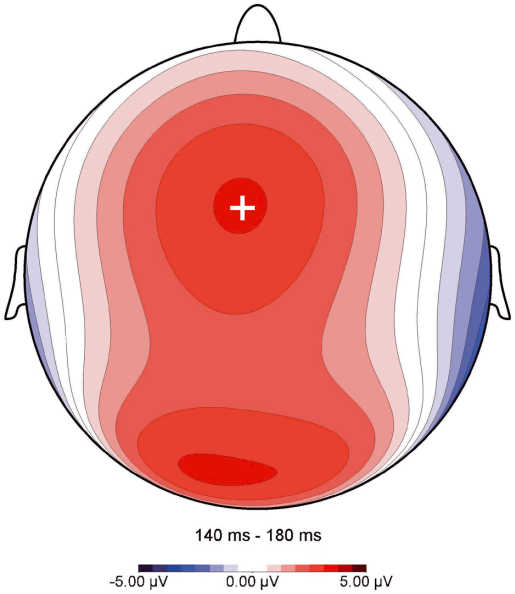

Figure 3. Scalp voltage distribution of the VPP: Voltage distribution of the ERP (averaged over all feedback stimuli) across the 140-180 ms post-stimulus interval. The maximum of the VPP is marked with '+'.

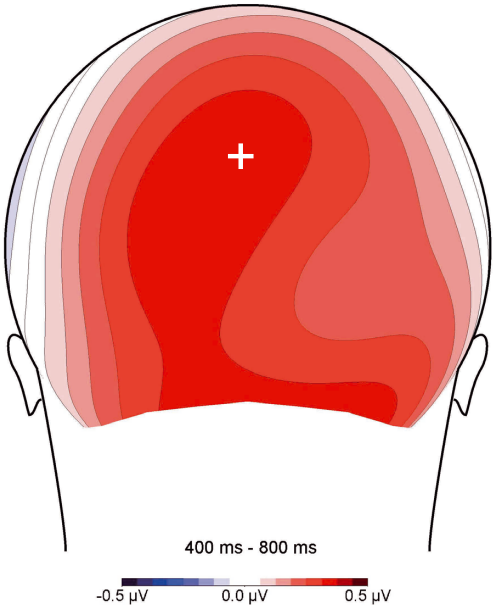

Figure 4. Scalp voltage distribution of the effect of oxytocin on LPP amplitude: Distribution of the ERP in the oxytocin condition minus the ERP in the placebo condition (averaged over all categories of feedback stimuli) across the 400-800 ms post-stimulus interval. The maximum is marked with '+'.

ERPs: LPP

The GLM analysis on LPP amplitude revealed a significant main effect of drug, $F(1,44) = 6.81$, $p < .05$, reflecting more positive LPP amplitudes in the oxytocin compared to the placebo condition. The effect of oxytocin is illustrated in Figure 4, showing the broad posterior distribution of the oxytocin effect. In contrast to the VPP, we did not find a significant interaction effect between drug and LWm on LPP amplitude, $F(1,44) = 2.15$, $p > .10$. Significant interaction effects were found between facial expression and LWm, $F(1,44) = 4.20$, $p < .05$, and between color and facial expression, $F(1,44) = 7.06$, $p < .05$, that were both further qualified

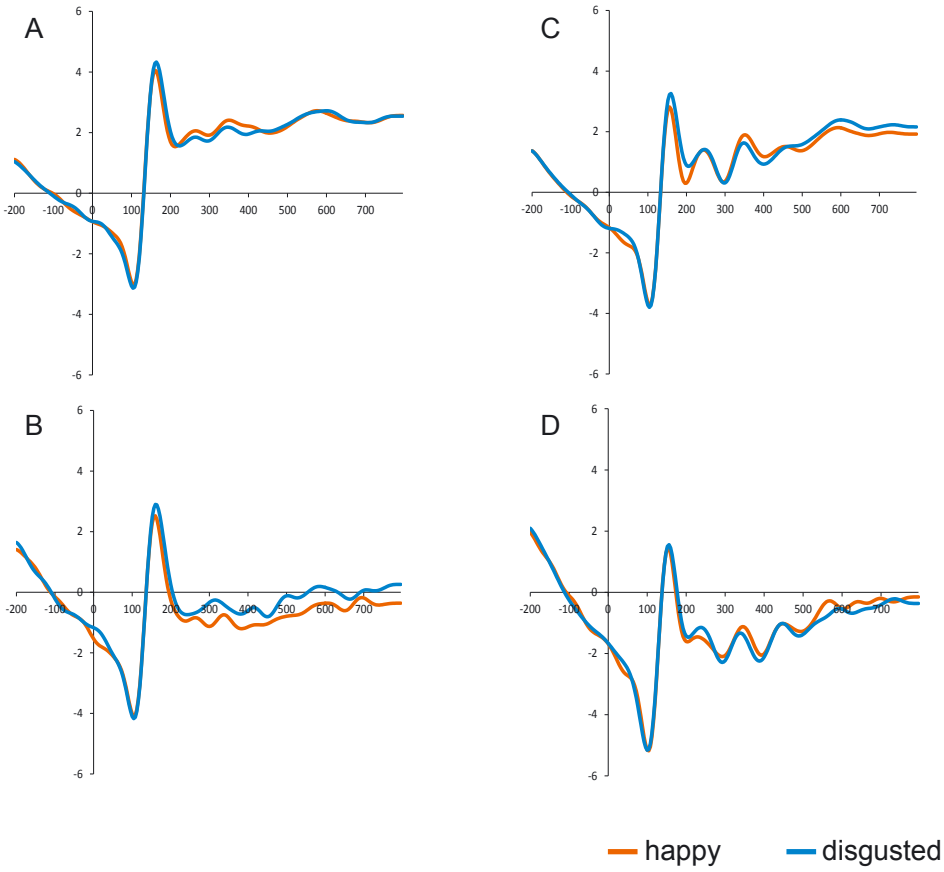

Figure 5. Grandaverage ERPs at CPz, illustrating the LPP. A and B: ERPs to green (A) and red (B) feedback stimuli for participants reporting high maternal use of love withdrawal. C and D: ERPs to green (C) and red (D) feedback stimuli for participants reporting low maternal use of love withdrawal. Participants were divided into groups for displaying purposes only. Participants reporting higher maternal use of love withdrawal showed a larger difference between responses to disgusted and happy faces (more positive for disgust) for red compared to green stimuli in the time interval ranging from 400 to 800 ms after stimulus onset at centroposterior electrode sites (LPP). ERPs were low-pass filtered at 15 Hz for displaying purposes.

by an interaction between color, facial expression and LWm, $F(1,44) = 9.54$, $p < .01$. Higher LWm was related to larger differences in LPP amplitudes in response to disgusted compared to happy faces (with LPP amplitudes in response to disgusted faces more positive than to happy ones), and to larger differences between LPP amplitudes to disgusted and happy faces when presented in red than when presented in green. That is, those reporting higher love withdrawal directed more attention toward disgusted compared to happy faces, especially when they made an error (face presented in red). Figures 5 and 6 present grandaverage ERPs at CPz and Pz time-locked to the onset of the four categories

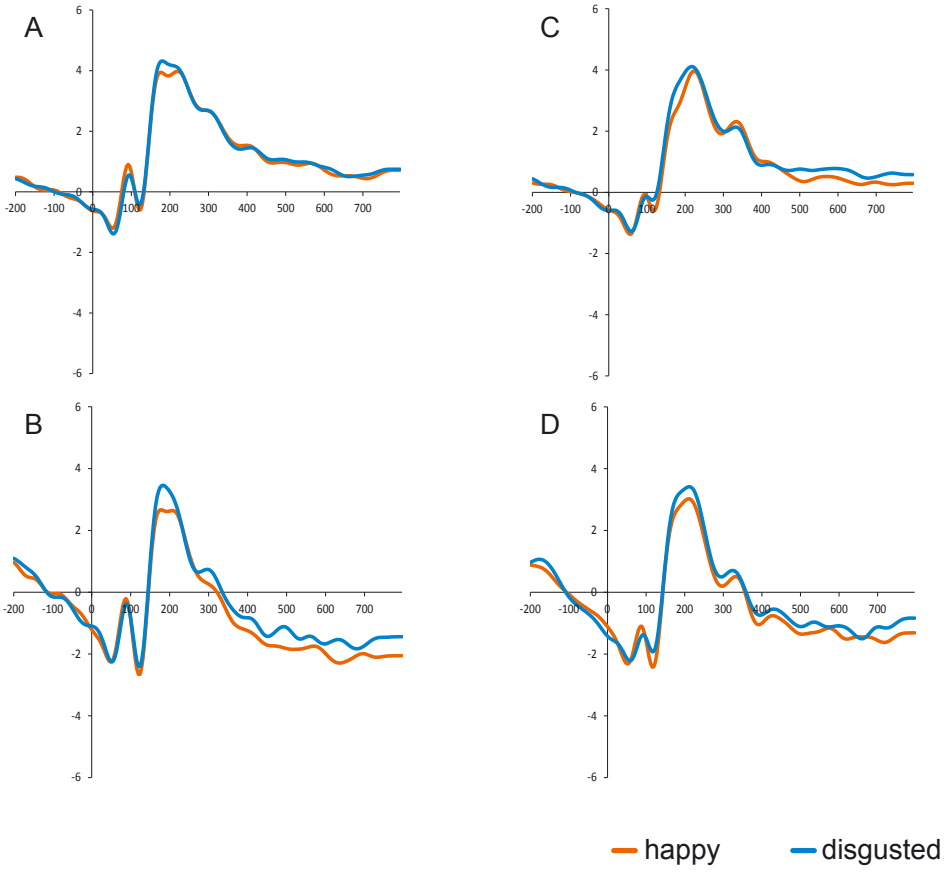

Figure 6. Grandaverage ERPs at Pz, illustrating the LPP. A and B: ERPs to green (A) and red (B) feedback stimuli for participants reporting high maternal use of love withdrawal. C and D: ERPs to green (C) and red (D) feedback stimuli for participants reporting low maternal use of love withdrawal. Participants were divided into groups for displaying purposes only. Participants reporting higher maternal use of love withdrawal showed a larger difference between responses to disgusted and happy faces (more positive for disgust) for red compared to green stimuli in the time interval ranging from 400 to 800 ms after stimulus onset at centroposterior electrode sites (LPP). ERPs were low-pass filtered at 15 Hz for displaying purposes.

of feedback stimuli, illustrating these effects. Again, an extended description of the results of this analysis can be found in the Supplementary Material.

ERPs: Fear of failure

Because no significant effects of FoF were found in any of the analyses described above, we repeated the analyses with fear of failure as the only covariate (i.e., excluding LWm from the analyses). No significant main or interactions effects involving FoF on VPP (all Fs ≤ 2.40, all ps > .10) and LPP amplitude (all Fs ≤ 3.79, ps > .05) were found.

ERPs: Use of oral contraceptives

Because the influence of oxytocin may be dependent on the use of oral contraceptives the repeated measures GLM analyses (with both LWm and FoF as covariates) described above were repeated with use of oral contraceptives (used vs. not used) as an additional between subjects factor. In the analysis with VPP amplitude as the dependent variable, all the effects described above remained significant (all Fs ≥ 4.10, ps < .05). In the analyses with LPP amplitude as the dependent variable only the interaction effect between facial expression and LWm was no longer significant, $F(1,42) = 2.38$, $p > .10$. The main effects of drug and color, and the interaction effects between color and facial expression, and between color, facial expression and LWm all remained significant (all Fs ≥ 6.29, ps < .05). Including use of oral contraceptives in the analyses thus did basically not change the outcomes.

Discussion

Oxytocin affected electrocortical responses to facial feedback stimuli, both in relatively early (VPP) and later (LPP) stages of processing, and in the absence of effects on task performance and subjective evaluations. Moreover, we demonstrated the effect of oxytocin administration on salivary oxytocin levels up to 2¼ hours after use of the nasal spray. Thus, clear elevations of oxytocin levels were observed within a time-range comparable to its neurobehavioral effects, suggesting that salivary concentrations may be a valuable biomarker for oxytocin.

As expected, VPP amplitudes were more positive after oxytocin compared to placebo administration, indicating that oxytocin enhanced the (configural) processing of emotional faces, regardless of the expression or feedback. These results are thus consistent with findings by Domes et al. (2010) of enhanced activity in various brain areas involved in face processing after oxytocin administration in healthy women. In addition, oxytocin interacted with maternal use of love withdrawal to affect the processing of emotional faces. Higher maternal love withdrawal was related to smaller increases in VPP amplitude after oxytocin administration compared to placebo administration. An explanation for this interaction between oxytocin administration and love withdrawal may be that participants reporting higher love withdrawal likely show near maximum

processing of facial expressions even under placebo conditions, thus limiting potential increases after oxytocin administration. If oxytocin would have caused participants with higher love withdrawal to be less anxious about (the consequences of) task performance and consequently to attend less to facial expressions, we would have expected a similar interaction effect between oxytocin administration and love withdrawal on LPP amplitude. We did, however, not observe such an interaction. In addition, although love withdrawal was related to some of the answers on the post-task questionnaire, no effects of oxytocin and, more importantly, no interaction effects between love withdrawal and oxytocin that would have supported an effect of oxytocin on the perception of the task were found for any of the questions.

Consistent with our hypothesis, LPP amplitudes were more positive after oxytocin compared to placebo administration, indicating that oxytocin enhanced attention to the feedback stimuli. The LPP is known to be strongly modulated by emotional facial expressions, which by definition are motivationally relevant, being primary sources of information about others' emotional states and intentions (Domes et al., 2007b; Haxby, Hoffman, & Gobbini, 2002). Thus, because oxytocin enhanced the processing of emotional faces (as indexed by VPP amplitude), it is tempting to speculate that the increased LPP amplitude observed here reflects the allocation of attention toward the facial expressions specifically. However, we can not rule out the possibility that oxytocin enhanced attention to faces in general or even to the feedback itself, because no neutral facial expressions were included and faces and feedback were presented simultaneously. Maternal love withdrawal was also related to LPP amplitudes, consistent with an attentional bias resulting from an association between performance and relational consequences established through the experience of love withdrawal. Higher love withdrawal was related to more positive LPP amplitudes in response to disgusted compared to happy faces, specifically when faces were presented in red (i.e., after an error). Thus, participants reporting higher love withdrawal increasingly direct attention toward disgusted (compared to happy) faces, implying that their attention is biased toward disgusted faces, specifically after they have made an error. In terms of the emotional or motivational significance of stimuli, the congruent combination of a disgusted face presented in red may well be the most relevant stimulus for participants who experienced more love withdrawal, because of its association with negative relational outcomes linked to failure.

It is interesting to speculate about the brain regions involved in the modulation of LPP amplitude. Sabatinelli et al. (2007) suggest that activity in the areas generating the LPP (inferotemporal, posterior parietal, and occipital visual areas) may result from reentrant connections from the amygdala to visual areas. The amygdala is well known to be connected to and interact with areas such as the inferior frontal gyrus, fusiform gyrus, and superior temporal areas in the processing of facial expressions (Amaral & Price, 1984; Haxby et al., 2002; Iidaka et al., 2001). The inferior frontal gyrus (and adjacent anterior insula) and superior temporal sulcus, have been found to contain mirror neurons that respond to emotional expressions and emotional prosody (Gazzola, Aziz-Zadeh, & Keysers, 2006; Wildgruber, Ackermann, Kreifelts, & Ethofer, 2006). Mirror systems are

both active when an individual performs an action and when another individual performs an action from the same class of actions or an action with a similar goal or meaning (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Mirror neurons have been found to be involved in affect mirroring, understanding others' actions, and some aspects of empathy, and areas containing mirror neurons are involved in judging the appropriateness of facial affect (Gazzola et al., 2006; Kim et al., 2005). In accordance with these social processes involving mirror neurons, oxytocin has been suggested to influence the mirror neuron system (Perry et al., 2010). In addition, it is likely that mirror neurons are involved in affect mirroring and contingency detection in mother-child interactions that are central to the development of emotional self-awareness, self-control, and empathy from infancy through adolescence (Feldman, 2007; Fonagy, Gergely, & Target, 2007; Gergely & Watson, 1996). This system is thus also a likely candidate for parenting strategies like love withdrawal to take effect.

As in our previous analyses of ERP responses under placebo conditions (Huffmeijer et al., 2011) and in contrast to Tops and Wijers (2011), who used the same experimental paradigm, we found no significant effects of fear of failure on VPP and LPP amplitudes in response to the feedback stimuli. Further research is needed to clarify whether and how fear of failure is related to ERP responses to facial feedback stimuli. Future studies could also address some of the limitations of the current study. Neutral facial expressions might be included in future experiments to distinguish between effects of oxytocin on the processing of faces in general and facial expressions in particular. Furthermore, in our study participants committed about 16% errors, and they were therefore presented with more green than red stimuli. Future studies may (additionally) use more difficult tasks resulting in higher error percentages and thus more equal numbers of green and red feedback stimuli. Furthermore, we measured maternal use of love withdrawal and fear of failure with self-report questionnaires. There are obvious limitations to the accuracy and reliability of participants' self-reports. Lastly, our participants were all female. We chose to include only women in this study, because of the considerable differences between males and females in the oxytocin system (Suske & Gallagher, 2009), and because most of the studies on the behavioral or psychological outcomes of love withdrawal focus on maternal use of love withdrawal with daughters (e.g., Elliot & Thrash, 2004; Renk et al., 2006). It would be interesting to study the same processes in men.

In conclusion, we extended previous findings relating maternal use of love withdrawal to ERPs in response to facial feedback stimuli, demonstrating not only that love withdrawal, in interaction with oxytocin, relates to the processing of emotional faces in a performance context, but also that higher maternal love withdrawal relates to the allocation of attentional resources toward the motivationally most relevant combination of negative feedback presented with a disgusted face. Furthermore, the current study is the first to describe effects of oxytocin on electrocortical responses to facial stimuli in females, using pictures combining emotional faces with performance feedback. The findings of more positive VPP and LPP amplitudes suggest that oxytocin increases attention to the facial feedback stimuli (LPP) and enhances the processing of emotional faces (VPP).

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Supplementary material

Analysis of VPP amplitude
Besides the significant main effect of drug and interaction effect between LWm and drug, we also found a significant interaction between drug and order of administration, $F(1,44) = 10.65$, $p < .01$ (this is a session effect, reflecting more positive VPP amplitudes during the first compared to the second session), a significant main effect of color, $F(1,44) = 6.34$, $p < .05$ (more positive amplitudes to green than to red stimuli), and a significant interaction between color, drug and order of administration, $F(1,44) = 5.23$, $p < .05$ (i.e., an interaction between color and session, reflecting a larger color effect during the first compared to the second session). No other effects were significant (all Fs ≤ 2.62, ps > .10).

Analysis of LPP amplitude
Besides the significant effects described in the main paper (main effect of drug, and interactions between LWm and facial expression, between color and facial expression, and between LWm, color, and facial expression), we also obtained a significant main effect of color, $F(1,44) = 6.37$, $p < .05$ (more positive amplitudes in response to green compared to red stimuli). No other effects were significant (all Fs ≤ 3.00, ps > .05).