Breastfeeding is a dynamic biological and social process based on hormonal regulation involving oxytocin. While there is much work on the role of breastfeeding in infant development and on the role of oxytocin in socio-emotional functioning in adults, little is known about how breastfeeding impacts emotion perception during motherhood. We therefore examined whether breastfeeding influences emotion recognition in mothers. Using a dynamic emotion recognition task, we found that longer durations of exclusive breastfeeding were associated with faster recognition of happiness, providing evidence for a facilitation of processing positive facial expressions. In addition, we found that greater amounts of breastfed meals per day were associated with slower recognition of anger. Our findings are in line with current views of oxytocin function and support accounts that view maternal behaviour as tuned to prosocial responsiveness, by showing that vital elements of maternal care can facilitate the rapid responding to affiliative stimuli by reducing importance of threatening stimuli.

Breastfeeding is a dynamic process that is characterised by physical, hormonal, and psychosocial effects in both mothers and infants. In particular, exclusive breastfeeding duration has been shown to play a vital role in bonding between mother and child through the promotion of positive affect and sensitive maternal behaviours. Critically, exclusively breastfeeding mothers report lower stress, negative moods, and anxiety than formula-feeders, and this anxiolytic impact is further evidenced through stronger cardiac vagal tone modulation, reduced heart rate reactivity, blood pressure and reduced hypothalamic-pituitary-adrenal axis activity to psychosocial stress. Reduced blood pressure has also been associated with the percentage of meals still breastfed. At the hormonal level, lactation requires oxytocin, a neurohormone synthesised in the paraventricular and supraoptic nuclei of the hypothalamus. Milk let-down is a process in which infant suckling induces release of oxytocin into the bloodstream through the neurohypophysis, stimulating the extraction of milk through contraction of myoepithelial cells in the mammary gland. Oxytocin is simultaneously released into the brain via projections from the paraventricular nucleus, allowing for the hormone to have a direct influence on behaviour. Reduced blood pressure during breastfeeding has been well-documented in saliva and plasma of mothers during the feeding process. Furthermore, breastfeeding mothers have higher levels of oxytocin in general as compared to formula-feeders, making increased levels of oxytocin a characteristic trait of lactating mothers.

Oxytocin is well-known for its peripheral role in the female reproductive system; however research over the last two decades has demonstrated that it also plays a critical role in affiliative and prosocial behaviour. Intranasal oxytocin administration increases the salience of eyes in faces, enhances trust, generosity, social memory, and emotion recognition in humans. There is accumulating evidence that oxytocin might foster affiliative behaviour through both the perceptual enhancement of positive emotional cues and the perceptual reduction of negative, threatening cues. This may be due to a mechanism in which oxytocin promotes the facilitation of approach-behaviours and reduces the tendency of withdrawal-behaviours. Neuroimaging studies suggest this might be due to an attenuation of the amygdala as well as a reduction in functional coupling to regions of the brainstem in response to threatening scenes.

As breastfeeding mothers exhibit an extended release of oxytocin, the current study investigated whether breastfeeding experience promotes enhanced socio-emotional perception. Using a dynamic facial expression recognition task, we explored whether breastfeeding behaviour, as indexed through both exclusive breastfeeding duration and current breastfeeding exposure (percentage of infant’s diet still breastfed), is associated with
individual differences in emotion processing in mothers. Based on theoretical accounts that assign a primary role to breastfeeding and oxytocin in maternal sensitivity and prior empirical work relying on intranasal administration of oxytocin, we hypothesised that a greater exposure to breastfeeding would be associated with greater sensitivity to happy expressions while reducing sensitivity to expressions of threat (especially anger). As the majority of the aforementioned breastfeeding studies examined outcomes of exclusive breastfeeding duration, we used this index as our main variable of interest. Furthermore, focusing our investigation on differences in exclusive breastfeeding allowed us to examine variation within a group of breastfeeding mothers rather than coarsely contrasting formula feeding mothers to breastfeeding mothers.

Results
Breastfeeding characteristics. Out of 62 mothers included in our sample, the great majority (53 mothers: 85.5%), were still breastfeeding their infants on a daily basis. All mothers breastfed exclusively for at least 3 months (range = 91–213 days; M = 159.21, SD = 28.91) (Table 1). Using correlations, we examined the possibility that empathic concern, positive or negative affect, infant positive affect (smiling and laughter), maternal education, or parity impact breastfeeding behaviour. The duration of exclusive breastfeeding did not relate to any of these measures (all p-values > .18). However, the percentage of breastfed meals per day related to maternal education (r[62] = .32, p = .007), infant age (r[62] = -.346, p = .006), and exclusive breastfeeding duration (r[62] = .662, p < .001). Therefore years of maternal education and infant age were included as regression predictors in all analyses.

DEER-T performance. In our analysis, we tested the hypothesis that greater exposure to breastfeeding would be associated with greater sensitivity to happy expressions and reduced sensitivity to threatening expressions (especially anger). As a first step, co-regressions were conducted analysing FAs (anger, fear) and RTs respectively. With this information, forced-entry multiple regressions were conducted analysing FAs (anger, fear) and RTs (anger, fear, happiness). Exclusive breastfeeding duration, percentage of breastfed meals, infant age, and maternal education were entered as predictors. No predictors remained significant for FAs, suggesting that after including variance from other factors, FAs to anger and fear no longer related to the percentage of breastfed meals (all β-values < -.187, p-values > .240). Additionally, the percentage of breastfed meals no longer predicted the RT to fear (β < -.200, p > .343).

A significant impact of breastfeeding exposure remained for RTs to anger and happiness. The percentage of breastfed meals was the strongest predictor for the reaction time to anger (Table 2, Figure 1), in which the higher the percentage, the slower the RT to anger. Exclusive breastfeeding duration was the strongest predictor for the speed of processing happy facial expressions (Table 3, Figure 2). Specifically, our analysis revealed an acceleratory effect of exclusive breastfeeding on the RT to happiness, providing evidence for a facilitation of processing positive emotional signals. Note that all p-values reported here are uncorrected and would not survive a conservative Bonferroni correction.

Discussion
In the current study, we examined whether breastfeeding exposure affects emotion recognition in mothers. Using a dynamic emotional face recognition task, we found that faster recognition of happiness was associated with longer exclusive breastfeeding duration in mothers. Furthermore, a greater percentage of currently breastfed meals was associated with slower reaction times toward anger. Thus, our data show that breastfeeding behaviour is related to an increased sensitivity to positive emotional cues and a decreased sensitivity to negative, threat-related cues. This pattern of results is in line with existing accounts of oxytocin function, according to which oxytocin is considered to enhance approach tendencies and inhibit withdrawal tendencies in an effort to facilitate prosocial behaviour. Moreover, these findings generally support the notion that breastfeeding behaviour might be associated with what has been referred to as a positivity bias in emotion perception. Critically, these findings cannot be explained by other variables such as maternal education, maternal mood, parity, or infant temperament, suggesting that variation in breastfeeding itself accounts for differences in emotion processing in motherhood.

Our findings support the view according to which maternal behaviour is tuned to prosocial responsiveness and bonding, and its vital elements can facilitate the rapid and accurate responding to affiliative cues. In this context, it is important to note that the mothers in the current study showed this bias in their emotion recognition in response to unfamiliar persons. This suggests that the breastfeeding behaviour, while certainly having specific effects on the relationship

### Table 1 | Infant and maternal characteristics

| Descriptives | Pearson’s r |
|--------------|-------------|
| **Range**    | **M(SE)**   | **EBF** | **%BFM** |
| **EBF duration (days)** | 91–213 | 159.21 (3.67) | .662*** |
| **Breastfed meals (%)** | 0–100 | 63.75 (4.23) | .662*** |
| **Maternal**  |  |  |  |
| **Age (years)** | 22–42 | 32.33 (0.53) | .135 .201 |
| **Education (years)** | 10–26 | 15.28 (0.42) | -.016 .340** |
| **Other children (count)** | 0–2 | 0.53 (0.07) | -.131 -.035 |
| **PANAS**    |  |  |  |
| **Positive affect** | 19–38 | 14.75 (0.31) | -.174 -.128 |
| **Negative affect** | 21–39 | 30.48 (0.81) | .228 .201 |
| **IRI**      |  |  |  |
| **Empathetic concern** | 10–20 | 14.75 (0.31) | .063 -.019 |
| **Perspective taking** | 7–20 | 13.49 (0.39) | .009 .039 |
| **Personal distress** | 5–17 | 11.36 (0.38) | -.116 .029 |
| **Infant**   |  |  |  |
| **Age (days)** | 166–226 | 195.79 (2.45) | .660 -.346** |
| **IBQ-R**    | 2.50–5.89 | 4.23 (0.11) | -.185 -.122 |

Note: EBF = Exclusive breastfeeding duration; PANAS = Positive and Negative Affect Schedule; IRI = Interpersonal Reactivity Index, IBQ-R = Revised Infant Behaviour Questionnaire; **p < .01; ***p < .001.

### Table 2 | Summary of multiple regression analyses for variables predicting reaction time to anger, $R^2 = .161, N = 62$

| Variable | B | SE B | $\beta$ | t-Value | p-value |
|----------|---|------|---------|---------|---------|
| (Constant) | 42.23 | 7.21 | - | 5.86 | .000 |
| EBF (in days) | -0.05 | 0.03 | -0.30 | -1.60 | .115 |
| Breastfed meals (%) | .07 | .03 | .53 | 2.54 | .014 |
| Infant age | .03 | .03 | .13 | 0.86 | .392 |
| Maternal education | -.01 | .18 | -.01 | -0.05 | .961 |
between infant and mother3–5, is also linked to more general emotion sensitivity towards happiness32 while decreasing recognition of fear  

Figure 1 | Current breastfeeding behaviour and anger recognition. Partial regression plot in which the percentage of currently breastfed meals predicts RT to anger, $\beta = .53, p = .014$. RT increases with a larger percentage of breastfed meals. Panel on the right depicts snapshots at five time points during a dynamic morph from neutral to anger. Note: This image is not covered by the CC BY-NC-ND licence. Photographs are from the NimStim Face Stimulus Set. Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. (http://www.macbrain.org/resources.htm).

Table 3 | Summary of multiple regression analyses for variables predicting reaction time to happiness, $R^2 = .142, N = 62$

| Model                     | B     | SE B | $\beta$ | t     | p-value |
|---------------------------|-------|------|---------|-------|---------|
| (Constant)                | 54.41 | 6.44 |         | 8.44  | .000    |
| EBF (in days)             | -.06  | .03  | -.42    | -2.25 | .029    |
| Breastfed meals (%)       | .03   | .20  | .24     | 1.17  | .246    |
| Infant age                | -.03  | .03  | -.15    | -1.06 | .293    |
| Maternal education        | -.19  | .16  | -.16    | -1.15 | .254    |

and anger in facial expressions33. This is also seen during administration of selective serotonin reuptake inhibitors (SSRIs), which exert anxiolytic effects34. Oxytocin itself exerts anxiolytic effects in both mice35 and humans36. It has close ties to the serotonergic system, and facilitates serotonin secretion in the raphe nucleus35. Moreover, breastfeeding involves skin-to-skin contact and pleasant touch, which has been found to influence emotion regulation, attention, joint engagement, and pain analgesia37,38. In this context, it should be emphasized that breastfeeding is a highly complex and dynamic biological and psychological process, and more systematic research is required to understand what exactly underpins the effects observed in the current study. Therefore, we would like to stress that our study is only a first step. Future work using a systematic assessment of hormonal, genetic, neural, and behavioural variables in mothers will be vital in order to achieve a more detailed and possibly more mechanistic understanding of the effects of breastfeeding on socio-emotional processing.

Another important issue raised by the current data is the question why exclusive breastfeeding duration is associated with recognition of happy faces, while current breastfeeding exposure relates to differences in anger recognition. One possibility is that there might be differences in emotion perception due to chronic (exclusive breastfeeding) versus acute (current breastfeeding) effects of breastfeeding exposure. More specifically, while long-term breastfeeding might lead to changes in receptor affinities or distributions (perhaps in the oxytocinergic system), more acute effects of breastfeeding might have the greatest impact on arousal systems important for threat detection, such as the amygdala and brainstem regions. To our knowledge, there is currently no research that has directly assessed this issue by comparing between current breastfeeding behaviour and exclusive breastfeeding duration. However, animal research confirms that chronic oxytocin exposure is capable of changing oxytocin receptor distributions39, and most imaging studies indicate that acute oxytocin administration seems to primarily target reactivity of the amygdala15,20,27,40. In future work it will be important to distinguish between long-term and short-term effects of breastfeeding.
Relatedly, it is unclear whether the positive and negative biases found in the current sample persist after the cessation of breastfeeding. Our study was not designed to directly address this question as only nine mothers in the current sample had ceased breastfeeding. However, an exploratory correlation analysis conducted with the nine mothers that had stopped breastfeeding revealed an association between exclusive breastfeeding duration and reaction time to happy expressions ($r[9] = -0.624, p = 0.037$, one-tailed), similar to the mothers that were still breastfeeding. This suggests that some of the effects may persist after the cessation of breastfeeding, but clearly more work is needed to directly test this possibility. Finally, one limitation of the current study is that, as stated in the results section, we did not control for multiple comparisons and only report uncorrected results. However, it is important to note that the current study tested and provides support for a specific a priori hypothesis formulated on the basis of previous work19–24.

In conclusion, our results provide evidence that mothers who exclusively breastfeed for longer durations show an increased sensitivity to positive facial expressions. Moreover, mothers with an increased percentage of daily breastfed meals show a decreased sensitivity to anger. The finding that such emotional biases occur in the context of the psychological and biological processes associated with breastfeeding is testament for a need to better understand the impact that maternal behaviours in general and breastfeeding in particular have on socio-emotional functioning during motherhood.

Methods

Participants. 62 healthy women of European descent ($M_{age} = 32.33$ years, $SD = 4.17$) participated in the study. All were mothers of 5- to 7-month-old infants ($M_{age} = 6.43$ months, $SD = .63$). All mothers were on maternity leave up to the point of testing. All gave informed consent and were compensated with travel money and a toy for their infant. Procedures were approved by the ethics committee of the Leipzig University Medical School and were conducted in accordance with the Declaration of Helsinki.

Questionnaires. We obtained information concerning maternal characteristics (age, years of education, number and age of other children, immigration history, highest academic/professional qualification) as well as the following information concerning breastfeeding: the duration a mother exclusively breastfed her child, at what age the child was introduced to other foods, and/or at what age the mother stopped breastfeeding, through an in-house questionnaire, a table was provided in which mothers could describe a feeding schedule over the course of a typical day. Based on this information, the frequency and percentage of breastfed meals per day was calculated. Durations provided in months were converted into days. If mothers were still exclusively breastfeeding, infants’ age on testing day was used as exclusive breastfeeding duration to be as specific as possible. In addition, the Infant Behaviour Questionnaire in its revised form (IBQ-R), the Interpersonal Reactivity Index (IRI), and the Positive and Negative Affect Schedule (PANAS) were administered in order to investigate potential influences of infant temperament, maternal affect, and maternal empathy on both emotion recognition performance and breastfeeding behaviour. The IBQ-R is commonly used instrument to assess infant temperament through parental report. It includes subscales assessing infant expression of smiling and laughing, approach tendency, perceptual sensitivity, cuddliness, fear, rate of recovery from distress, and many others. Garststein and Rothbart (2003) provide evidence supporting the instrument’s high reliability and validity. The IRI (Davis, 1983) uses a multidimensional approach to assess empathy in adults. It assesses the tendency one has to take the point of view of others (PT), the tendency to experience feelings of sympathy and compassion for those less fortunate (EC), the tendency to experience feelings of distress in response to discomfort in others (PD), and the tendency to transpose oneself into fictional situations such as novels or movies (FS). The IRI has also been reported to be a reliable and valid instrument that assesses empathy in adults (Davis, 1983). The PANAS measures affect on two subscales in adults: positive affect (i.e., enthusiasm and alertness), and negative affect (i.e., aversive mood states and general distress). Watson and colleagues (1988) report high reliability and validity of the PANAS.

The dynamic emotional expression recognition task (DEER-T). Emotion recognition was measured using the DEER-T, which has been used to study emotion recognition in various populations and is described in detail elsewhere. Neutral colour photographs of twelve Caucasian actors (six women) were morphed to create six dynamic expressions: angry, happiness, fear, sadness, disgust, and neutrality. Images were taken from the NimStim set, which is freely available to the scientific community at http://www.macbrain.org/resources.htm. Stimuli were displayed as dynamically morphing from neutral into a full-blown emotion over the course of 3000 milliseconds. Six labelled response keys corresponded to the emotions. To reduce memory load, an illustration of the keys in relation to finger positions was displayed on the monitor below the presented stimuli. Participants were instructed to press the key of the corresponding emotion as quickly and accurately as they could. Stimuli were presented on a 13-inch laptop.

Performance on the DEER-T was assessed using reaction time (RT), hits, and false alarms (FAs). RTs were analysed for correct answers only. Hits refer to the correct response frequency for a particular emotion, while FAs refer to the frequency a
participant responded with an emotion when it was incorrect. RTs were square-root transformed to form for positive skew. Data was analysed with IBM SPSS Statistics (Version 19).

1. Deoni, S. C. et al. Breastfeeding and early white matter development: A cross-sectional study. *NeuroImage* **82**, 77–86 (2013).

2. Heinrichs, M., Neumann, I. & Ehlert, U. Lactation and stress: Positive effects of breast-feeding in humans. *Stress* **5**, 195–203 (2002).

3. Raju, T. N. Breastfeeding is a dynamic biological process—not simply a meal at the breast. *Breastfeed. Med.* **6**, 257–259 (2011).

4. Kim, P. et al. Breastfeeding, brain activation to own infant cry, and maternal sensitivity. *J. Child Psychol. Psychiat.* **52**, 907–915 (2011).

5. Zetterstrom, R. Breastfeeding and infant-mother interaction. *Acta Paediatr.* **88**, 1–6 (1999).

6. Brandt, K. A., Andrews, C. M. & Kvale, J. Mother-infant interaction and breastfeeding outcome 6 weeks after birth. *J. Obstet. Gynaecol. Neonatal Nurs.* **27**, 169–174 (1998).

7. Groer, M. W. Differences between exclusive breastfeeders, formula-feeders, and controls: A study of stress, mood, and endocrine variables. * Biol. Res. Nurs. **15**, 105–117 (2005).

8. Mezzacappa, E. S., Kelsey, R. M. & Katkin, E. S. Breast feeding, bottle feeding, and salivary cortisol responses in breast- and formula-feeding mothers of infants. *Psychophysiology** **47**, 625–652 (2010).

9. Hahn-Holbrook, J., Holt-Lunstad, J., Holbrook, C., Coyne, S. M. & Lawson, E. T. Neuroendocrine control of milk ejection. *J. Clin. Endocrinol. Metab.* **85**, 1009–1015 (2000).

10. Lincoln, D. W. & Paisley, A. C. Neuroendocrine control of milk ejection. *J. Neuroendocrinol.** **25**, 1198–1202 (2013).

11. Landgraf, R. & Neumann, I. D. Vasopressin and oxytocin release within the brain: A dynamic concept of multiple and variable modes of neuropeptide communication. *Front. Neuroendocrinol.** **25**, 150–176 (2004).

12. Dawood, M. Y., Khan-Dawood, F. S., Wahi, R. S. & Fuchs, F. Oxytocin release and salivary oxytocin responses in breast- and formula-feeding mothers of infants. *Psychoneuroendocrinology** **38**, 2550–2557 (2013).

13. Groer, M. W. Differences between exclusive breastfeeders, formula-feeders, and controls: A study of stress, mood, and endocrine variables. *Biol. Res. Nurs.** **15**, 105–117 (2005).

14. Insel, T. R. Oxytocin—A neuropeptide for affiliation: Evidence from behavioral, receptor autoradiographic, and comparative studies. *Psychoneuroendocrinology** **17**, 3–35 (1992).

15. Heinrichs, M., von Dawans, B. & Domes, G. Oxytocin, vasopressin, and human social behavior. *Front. Neuroendocrinol.** **30**, 548–557 (2009).

16. Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. Oxytocin increases trust in humans. *Nature** **435**, 673–676 (2005).

17. Zak, P. J., Stanton, A. A. & Ahmadi, S. Oxytocin increases generosity in humans. *PLoS One** **2**, e1128 (2007).

18. Guastella, A. J., Mitchell, P. R. & Matthews, F. Oxytocin enhances the encoding of positive social memories in humans. *Biol. Psychiatry** **64**, 256–258 (2008).

19. Di Simplicio, M., Massey-Chase, R., Cowen, P. J. & Harmer, C. J. Oxytocin enhances processing of positive versus negative emotional information in healthy male volunteers. *J. Psychopharmacology** **23**, 241–248 (2009).

20. Domes, G., Steineer, A., Porges, S. W. & Heinrichs, M. Oxytocin differentially modulates eye gaze to naturalistic social signals of happiness and anger. *Psychoneuroendocrinology** **38**, 1198–1202 (2013).

21. Kirsch, P. et al. Oxytocin modulates neural circuitry for social cognition and fear in humans. *J. Neurosci.** **25**, 11489–11493 (2005).

22. Marsh, A. A., Yu, H. H., Pine, D. S. & Blair, R. J. Oxytocin improves specific recognition of positive facial expressions. *J. Psychopharmacology** **209**, 225–232 (2010).

23. Parr, L. A., Modi, M., Siebert, E. & Young, L. J. Intranasal oxytocin selectively attenuates rhesus monkeys’ attention to negative facial expressions. *Psychoneuroendocrinology** **38**, 1748–1766 (2013).

24. Schulze, L., Lischke, A., Greif, J., Herpertz, S. C., Heinrichs, M. & Domes, G. Oxytocin increases recognition of masked emotional faces. *Psychoneuroendocrinology** **36**, 1378–1382 (2011).

25. Kemp, A. H. & Guastella, A. J. The role of oxytocin in human affect: A novel hypothesis. *Curr. Dir. Psychol. Sci.** **20**, 222–231 (2011).

26. Gamer, M., Zurowski, B. & Buchel, C. Different amygdala subregions mediate valence-related and attentional effects of oxytocin in humans. *Proc. Natl. Acad. Sci. U.S.A.** **107**, 9400–9405 (2010).

27. Petrovic, P., Kalisch, R., Singer, T. & Dolan, R. J. Oxytocin attenuates affective evaluations of conditioned faces and amygdala activity. *J. Neurosci.** **28**, 6607–6615 (2008).

28. Platt, B., Kamboj, S., Morgan, C. J. & Curran, H. V. Processing dynamic facial affect in frequent cannabis-users: evidence of deficits in the speed of identifying emotional expressions. *Drug Alcohol Depend.** **112**, 27–32 (2010).

29. Peeters, G. The positive-negative asymmetry: On cognitive consistency and positivity bias. *Eur. J. Soc. Psychol.** **1**, 453–474 (1971).

30. Feldman, R. Parent-infant synchrony: A biobehavioral model of mutual influences in the formation of affiliative bonds. *Monogr. Soc. Res. Child Dev.** **77**, 2–51 (2012).

31. Hrdy, S. B. Mothers and others: The evolutionary origins of mutual understanding. Cambridge, MA: Harvard University Press (2009).

32. Murphy, S. E., Downham, C., Cowan, P. J. & Harmer, C. J. Direct effects of diazepam on emotional processing in healthy volunteers. *J. Psychopharmacol.** **163**, 36–41 (2002).

33. Harmer, C. J., Shelley, N. C., Cowen, P. J. & Goodwin, G. M. Increased positive versus negative affective perception and memory in healthy volunteers following selective serotonin and norepinephrine reuptake inhibition. *Am. J. Psychiatry** **161**, 1256–1263 (2004).

34. Yoshida, M. et al. Evidence that oxytocin exerts anxiolytic effects via oxytocin receptor expressed in serotoninergic neurons in mice. *J. Neurosci.** **29**, 2259–2271 (2009).

35. De Oliveira, D. C. G., Zuardi, A. W., Graeff, F. G., Queiroz, R. H. C. & Crippa, J. A. S. Anxiolytic-like effect of oxytocin in the simulated public speaking test. *J. Psychopharmacol.** **26**, 497–504 (2012).

36. Feldman, R., Rosenthal, Z. & Eidelman, A. I. Maternal-preterm skin-to-skin contact enhances child physiologic organization and cognitive control across the first 10 years of life. *Biol. Psychiatry** **75**, 56–64 (2014).

37. Gray, L., Watt, L. & Blass, E. M. Skin-to-skin contact is analgesic in healthy newborns. *Pediatrics** **105**, e14 (2000).

38. Insel, T. R., Winslow, J. T. & Witt, D. M. Homologous regulation of brain oxytocin receptors. *Endocrinology** **130**, 2602–2608 (1992).

39. Domes, G., Heinrichs, M., Gläscher, J., Buchel, C., Braus, D. F. & Herpertz, S. C. Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biol. Psychiatry** **62**, 1187–1190 (2007).

40. Gartstein, M. A. & Rothbart, M. K. Studying infant temperament via the Revised Infant Behaviour Questionnaire. *Infant Behav. Dev.** **26**, 64–86 (2003).

41. Davis, M. H. Measuring individual differences in empathy: Evidence for a multidimensional approach. *J. Pers. Soc. Psychol.** **44**, 113–126 (1983).

42. Watson, D., Clark, L. A. & Tellegen, A. Development and validation of brief measures of positive and negative affect: The Positive and Negative Affect Schedule scales. *J. Pers. Soc. Psychol.** **54**, 1063–1070 (1988).

43. Tottenham, N. et al. The NIMStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Res.** **168**, 242–249.