Psychological Medicine (2013), **43**, 1747–1753. © Cambridge University Press 2012
doi:10.1017/S0033291712002565

ORIGINAL ARTICLE

Intranasal oxytocin increases covert attention to positive social cues

G. Domes[1,2]*, M. Sibold[1], L. Schulze[3], A. Lischke[4,5], S. C. Herpertz[5] and M. Heinrichs[1,2]

[1] *Department of Psychology, University of Freiburg, Germany*
[2] *Freiburg Brain Imaging Center, University Medical Center, University of Freiburg, Germany*
[3] *Department of Educational Sciences and Psychology, Freie Universität Berlin, Germany*
[4] *Department of General Psychiatry, University of Heidelberg, Germany*
[5] *Department of Psychiatry and Psychotherapy, University of Rostock, Germany*

Background. The neuropeptide oxytocin (OT) has positive effects on the processing of emotional stimuli such as facial expressions. To date, research has focused primarily on conditions of overt visual attention.

Method. We investigated whether a single intranasal dose of OT (24 IU) would modulate the allocation of attentional resources towards positive and negative facial expressions using a dot-probe paradigm in a sample of 69 healthy men. Attentional capacity for these facial cues was limited by presentation time (100 or 500 ms). In addition, we controlled for overt visual attention by recording eye movements using a remote eye tracker.

Results. Reaction times (RTs) in the dot-probe paradigm revealed a pronounced shift of attention towards happy facial expressions presented for 100 ms after OT administration, whereas there were no OT-induced effects for longer presentation times (500 ms). The results could not be attributed to modulations of overt visual attention as no substance effects on gazes towards the facial target were observed.

Conclusions. The results suggest that OT increased covert attention to happy faces, thereby supporting the hypothesis that OT modulates early attentional processes that might promote prosocial behavior.

Received 6 March 2012; Revised 26 September 2012; Accepted 9 October 2012; First published online 12 November 2012

Key words: Attention, awareness, eye tracking, facial emotions, neuropeptides, oxytocin.

Introduction

In recent years, oxytocin (OT), a nine-amino-acid neuropeptide, has become a major focus of research in biological psychology (Taylor, 2006; Heinrichs & Domes, 2008; Heinrichs *et al*. 2009; Meyer-Lindenberg *et al*. 2011; Kumsta & Heinrichs, 2012). Several studies have shown that OT has beneficial effects on social interactions and associated cognitive processes including the recognition of facial emotions. For example, OT is reported to improve recognition of mental states using cues from the eye region (Domes *et al*. 2007*b*) and from full facial expressions (Fischer-Shofty *et al*. 2010; Lischke *et al*. 2012*a*). On the neural level, OT seems to dampen activity in the amygdala (Kirsch *et al*. 2005; Domes *et al*. 2007*a*; Baumgartner *et al*. 2008), a structure involved in both emotion processing and social attention (Davis & Whalen, 2001).

* Address for correspondence: G. Domes, Ph.D., Department of Psychology, Laboratory for Biological and Personality Psychology, University of Freiburg, Stefan-Meier-Strasse 8, D-79104 Freiburg, Germany.
(Email: domes@psychologie.uni-freiburg.de)

As attention has been considered a crucial factor in emotion processing itself (Vuilleumier, 2005), the effects of OT on facial emotion processing might be mediated by modulation of attention. For instance, previous studies on OT and face processing have reported an increased number of saccades towards the eye region (Guastella *et al*. 2008; Gamer *et al*. 2010), suggesting that OT modulates overt visual attention during the processing of social cues. However, whereas Guastella *et al*. (2008) used neutral faces only, the OT-induced increase in post-stimulus saccades to the eye region reported by Gamer *et al*. (2010) was not affected by emotional expression. A recent study using very brief presentations of facial stimuli in a backward-masking paradigm provided the first evidence that the effects of OT on emotion recognition are not completely due to conscious evaluation of the presented stimulus (Schulze *et al*. 2011). This points to the possibility that OT-induced modulations of covert attention affect facial emotion processing with limited awareness.

Altered attention towards social information is associated with several clinical conditions such as

anxiety, autism spectrum disorders (ASD) and Williams syndrome. Whereas people with ASD usually show reduced interest in social interactions, those with Williams syndrome display a 'hypersociability' (Jones *et al*. 2000) characterized by increased approach behavior towards strangers (Jarvinen-Pasley *et al*. 2010). These differences in social phenotype seem to be reflected in gaze behavior: autistic individuals display reduced attentional capture by facial stimuli and avoidance of eye gaze (Riby & Hancock, 2009; Kliemann *et al*. 2010) whereas individuals with Williams syndrome show enhanced gazing towards facial picture components, the eye regions of faces and happy facial expressions (Riby & Hancock, 2009; Dodd & Porter, 2010; Porter *et al*. 2010; Moore *et al*. 2012). Notably, both syndromes have recently been linked to alterations in the OT system (Campbell *et al*. 2011; Dai *et al*. 2012; Pobbe *et al*. 2012).

In anxiety, the main body of evidence suggests a bias towards threat despite some variability in results across studies and differential influences of timing and threat intensity (Mogg & Bradley, 2002; Bar-Haim *et al*. 2007; for a recent review see Shechner *et al*. 2012). However, results from a recent study suggest the existence of subgroups in social anxiety disorder, with patients displaying either a heightened vigilance or avoidance of social threat (Calamaras *et al*. 2012). Using the dot-probe paradigm, Cooper & Langton (2006) investigated attentional capture by angry and happy facial stimuli in a healthy sample and showed biased attention towards angry faces exclusively for short presentation times, suggesting the involvement of initial covert attentional shifts.

In the present study we used a facial dot-probe task to investigate whether a single dose of OT modulates the allocation of attentional resources to negative and positive social cues (i.e. angry and happy faces). We varied the degree of overt attentional processes using two different presentation times (100 and 500 ms). We also controlled for eye movements indicating overt attention shifts using a remote eye tracker. We expected that OT would enhance the salience of positive rather than negative social stimuli (Unkelbach *et al*. 2008; Di Simplicio *et al*. 2009; Marsh *et al*. 2010), as reflected by attentional preference for happy compared to angry faces after OT treatment.

Method

Participants

Sixty-nine male participants (mean ± S.D. age: 24.0 ± 3.1 years) were randomly assigned to receive a single intranasal dose of OT ($n = 35$) or placebo ($n = 34$). An exclusively male sample was investigated because of empirical evidence suggesting sex differences in responding to intranasal OT (Domes *et al*. 2010; Lischke *et al*. 2012*b*). Participants had no physical or mental illness according to self-report and also according to results from a standardized screening protocol. All participants had normal or corrected-to-normal vision, were non-smokers and free of any medication. There were no significant differences between the groups regarding age (OT: 24.5 ± 3.5 years; placebo: 23.6 ± 2.7 years; $t_{67} = 1.27$, $p = 0.21$), general intellectual abilities (IQ; OT: 105.7 ± 6.2; placebo: 105.7 ± 4.2; $t_{67} = -0.02$, $p = 0.98$) and self-reported psychopathology [Symptom Checklist (Franke, 1995); OT: 0.34 ± 0.27; placebo: 0.34 ± 0.26; $t_{67} = -0.06$, $p = 0.95$]. All participants gave written informed consent and were paid for participation. The study was part of a larger project (cf. Schulze *et al*. 2011) and was approved by the ethical committee of the Medical Faculty of the University of Rostock.

Administration of OT

OT was administered intranasally (Born *et al*. 2002) following a standardized protocol used in previous studies (Domes *et al*. 2007*a*, *b*, 2010). In brief, 45 min prior to the start of the dot-probe task, participants self-administered six puffs of Syntocinon® nasal spray (Novartis, Switzerland; three puffs per nostril, containing 4 IU OT each) or a placebo under the supervision of the researcher.

Dot-probe task

The dot-probe task (MacLeod *et al*. 1986) is a well-established paradigm for investigating the attentional preference to one of two stimuli presented for a short period of time. In brief, two stimuli are presented simultaneously, one of which is a target stimulus of higher salience, for example an emotional compared to a neutral face. Reaction to a subsequently appearing probe is generally faster if the probe location is congruent with that of the target stimulus compared to the control stimulus.

For the present study, angry, happy and neutral facial expressions of 40 participants (20 male/20 female) were selected from the Karolinska Directed Emotional Faces (KDEF; Lundqvist *et al*. 1998). Each trial started with a fixation cross with a randomized duration of 750 to 1500 ms. A pair of angry/neutral, happy/neutral or neutral/neutral expressions of the same person was then presented for 100 ms *versus* 500 ms (short *versus* long presentation condition). The two faces (295 × 400 pixels, 12.2 × 16.5° visual angle) were presented with an offset of ± 200 pixels (8.3° visual angle) from the screen center. Immediately

https://doi.org/10.1017/S0033291712002565 Published online by Cambridge University Press

following picture presentation, the dot probe (10×10 pixels, 0.4° visual angle) was presented at the location of one of the facial expressions. In emotional trials (one facial expression being angry or happy), the probe appeared at the location of the emotional face (congruent) and at the location of the neutral face (incongruent) in the other half of the trials. Participants were asked to indicate the location of the probe as quickly as possible by pressing one of two buttons. Correct answers and reaction times (RTs) to the dot probes were recorded.

In total, 240 trials were presented, resulting in a total duration of approximately 20 min. The experiment was run on a Windows PC with a 20-inch TFT display (40.8×30.6 cm, 1024×768 pixels) using Presentation version 12.1 (Neurobehavioral Systems, USA).

Eye tracking

To disentangle the role of overt and covert shifts of attention, saccades on primes and probes were assessed using a remote infrared eye tracker (ViewPoint PC-60 Quick Clamp, Arrington Research, USA). The viewing distance was kept constant at 55 cm using a head rest. Gaze data were collected with 60-Hz temporal resolution and a typical gaze position accuracy of 0.25–1.0° visual angle. Eye tracking data were analyzed with an in-house script written in MATLAB version 7.1 (Mathworks, USA). Raw data were corrected for blinks using a moving average calculation to interpolate missing data. A saccade towards a specific prime or probe was defined as a horizontal translation exceeding a threshold of $\pm 5^\circ$ visual angle from the central position during presentation of the particular stimulus. The cumulative number of saccades on primes and probes was then calculated for the different experimental conditions.

Statistical analysis

RT data from erroneous responses and RTs <300 ms and >1500 ms were excluded from the statistical analysis. Errors and outliers accounted for 4.2% of the data and did not differ between groups ($p > 0.10$). The remaining RTs were averaged for each condition.

Enhanced capture of attention by emotional compared to neutral facial expressions in both groups was tested within a two-way ANOVA with group as the between-subject factor and probe location (congruent *versus* incongruent) as the within-subject factor. Attentional preferences for specific emotional facial expressions were then calculated by subtracting RTs within congruent trials from RTs within incongruent trials. These bias scores were subject to a three-way ANOVA with group as the between-subject factor and presentation duration (100 ms *versus* 500 ms) and prime valence (angry *versus* happy) as within-subject factors.

Saccades during primes were analyzed for the long presentation condition only, as stimulus-associated saccades usually have a latency of about 200 ms and thus were not likely to be detectable during the 100-ms presentation of primes. Saccades during primes were subject to a three-way ANOVA with the between-subject factor group and direction (to or away from the emotional prime) and prime valence (happy *versus* angry) as within-subject factors. Saccades during probes were analyzed with a corresponding five-way ANOVA adding prime duration (100 ms *versus* 500 ms) and target location (congruent *versus* incongruent) as within-subject factors.

Table 1. *Average reaction times (in ms) for the different conditions in the facial dot-probe paradigm*

		Placebo		Oxytocin	
		Mean	S.D.	Mean	S.D.
100 ms					
Happy	Congruent	432	61	446	58
	Incongruent	428	51	457	66
Angry	Congruent	425	52	452	55
	Incongruent	432	53	452	65
500 ms					
Happy	Congruent	428	53	441	53
	Incongruent	434	51	444	58
Angry	Congruent	424	51	438	59
	Incongruent	428	57	448	58

S.D., Standard deviation.

Results

Attentional preference

For raw RTs, a significant main effect of probe location was present (Table 1). RTs to probes at incongruent locations were significantly longer ($F_{1,67} = 7.15$, $p = 0.009$). The group × location interaction did not reach significance ($F_{1,67} = 0.66$, N.S.), indicating that subjects in both groups showed an attentional bias towards emotional cues. The subsequent ANOVA on attentional bias scores revealed a significant three-way interaction of group, duration and emotional valence ($F_{1,67} = 6.66$, $p = 0.012$). Follow-up two-way ANOVAs were calculated for each presentation duration and showed a specific effect of OT for the short

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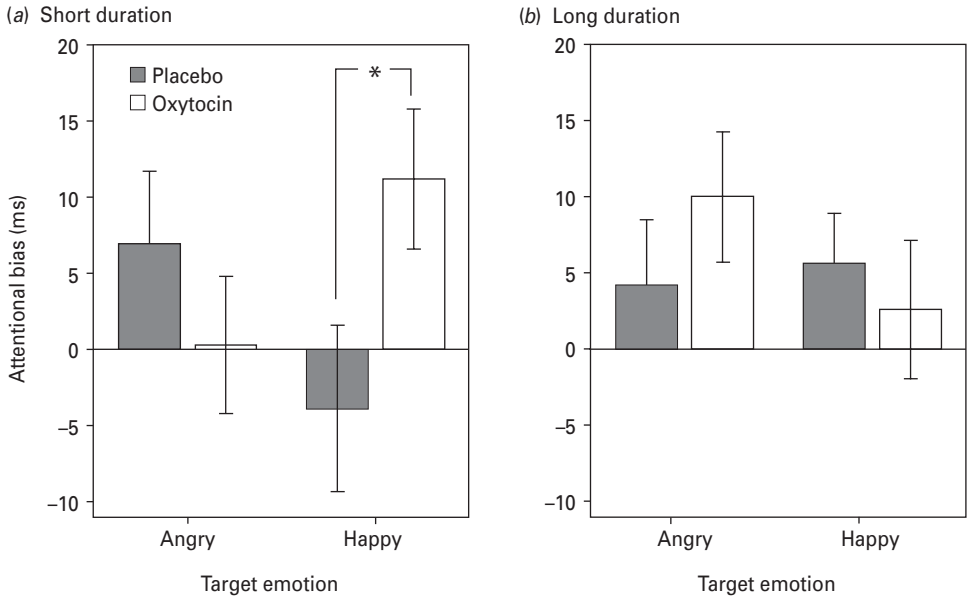

Fig. 1. Effects of intranasal oxytocin on attentional bias for facial expressions presented with either (*a*) short duration (100 ms) or (*b*) long duration (500 ms). Error bars represent the standard error of the mean. * $t_{67}=2.11$, $p<0.05$.

presentation condition (Fig. 1); the group × emotion interaction was significant ($F_{1,67}=4.81$, $p<0.05$), with the OT group showing enhanced attention to happy facial expressions ($t_{67}=2.11$, $p<0.05$). An additional ANOVA for the number of correct responses revealed no significant effects on detection rates for probes associated with OT administration (all $p>0.10$). However, detection rates were high on average, as expected, and even higher for trials with long presentation of primes, as indicated by a significant main effect of prime duration ($F_{1,67}=17.30$, $p<0.001$; Table 2).

Eye tracking

Eye tracking data from three participants of the OT group and two of the placebo group were removed because of poor calibration or hardware malfunction. For the remaining participants, the ANOVA revealed a single main effect for saccades during presentation of primes: in general, there were more saccades on emotional primes compared to neutral primes ($F_{1,62}=19.26$, $p<0.001$). All other effects were not significant. During the presentation of probes, saccades were much more likely on probes than off probes ($F_{1,62}=74.78$, $p<0.001$), and occurred more frequently after primes presented with a short duration compared to primes presented with a long duration ($F_{1,62}=10.33$, $p<0.005$). In addition, following long primes, there were more saccades on probes at the incongruent location ($F_{1,62}=9.41$, $p<0.004$). All other effects were not significant (all $p>0.10$).

Table 2. *Average number of correct responses for the different conditions in the dot-probe paradigm*

		Placebo		Oxytocin	
		Mean	S.D.	Mean	S.D.
100 ms					
Happy	Congruent	18.8	2.8	19.2	1.3
	Incongruent	18.9	1.5	19.2	0.9
Angry	Congruent	18.5	2.1	19.2	0.9
	Incongruent	18.7	1.8	19.2	0.9
500 ms					
Happy	Congruent	19.4	1.2	19.6	0.7
	Incongruent	19.1	1.4	19.4	0.9
Angry	Congruent	19.4	1.0	19.6	0.7
	Incongruent	19.3	1.0	19.7	0.6

S.D., Standard deviation.

Discussion

In the present study, the administration of OT resulted in an attentional preference towards happy faces when stimuli were presented with a short duration of 100 ms. This suggests that intranasal OT promotes the attentional preference for briefly presented positive social cues. The specificity of OT effects for facial cues of positive social interaction is in line with previous research in humans (Unkelbach *et al*. 2008; Di Simplicio *et al*. 2009; Marsh *et al*. 2010), and also with a large body of animal research emphasizing the crucial role of OT in prosocial behavior (e.g. Young, 2009;

https://doi.org/10.1017/S0033291712002565 Published online by Cambridge University Press

Keebaugh & Young, 2011). Of note, a recent study using a comparable paradigm with sad and angry facial stimuli showed increased disengagement from briefly presented angry faces (Ellenbogen *et al*. 2012). Although in the present study, the effect for angry facial expressions was not significant, the two studies are in accordance with the hypothesis that OT might shift attention towards positive rather than negative social stimuli.

To our knowledge this is the first study to show that OT selectively enhances covert attention for positive emotional cues and thereby might promote prosocial behavior. Our results provide an explanation for previously reported OT effects on behavioral and neural responses to facial emotional expressions in the absence of changes in overt attentional processing (Domes *et al*. 2010; Alvares *et al*. 2012; Lischke *et al*. 2012*a*). For example, Lischke *et al*. (2012*a*) studied OT effects on gazes to the eye region of dynamically presented faces of varying emotional expression. Although OT generally improved recognition of the specific emotion, it did not affect gazing behavior as measured by eye tracking. The authors concluded that the beneficial effects of OT on emotion recognition are not mediated by changes in overt visual attention. The results from a recent study by Leknes *et al*. (2012) found an OT-induced enhancement of emotional attention that was associated with an overall increase in pupil dilation irrespective of the type of expression.

However, in most of these studies visual attention was guided explicitly towards facial emotional expressions and often included cognitive evaluation of the particular expression. The dot-probe paradigm used in our study allowed for investigation of covert attention as the emotional stimuli are not task-relevant *per se* and not located in the center of visual attention. Furthermore, for the short presentation condition, stimuli were presented too briefly to allow for overt gaze shifts towards them. Notably, OT-induced modulation of covert attention concurs with the recently reported lower detection threshold for very briefly presented emotional facial expressions in a backward-masking paradigm (Schulze *et al*. 2011).

The present study has some limitations, such as the exclusively male sample, the between-subject design and the use of faces as the only stimuli, which could be subject to improvement in replication studies investigating sex differences (Domes *et al*. 2010; Lischke *et al*. 2012*b*) and the specificity of our findings. In addition, it should be noted that the size of the OT-induced effects on attentional biases as revealed by RTs were, although significant, relatively small. However, together with previous studies reporting effects of OT on neural activity using functional magnetic resonance imaging (for an overview, see Meyer-Lindenberg *et al*. 2011), the present results point to the possibility that OT modulates the neural circuitry underlying the early attentional orienting and processing of emotional stimuli (Tamietto & de Gelder, 2010). This assumption could be investigated in future studies using experimental paradigms that focus on different aspects of attention, such as overt *versus* covert or temporal attention, to better understand the role of OT in the context of human emotion processing.

The results of the present study also have clinical implications. Several studies have provided initial evidence that OT might be a promising option in the treatment of mental disorders with social impairments (Guastella *et al*. 2009, 2010; Pedersen *et al*. 2011). Given the role of biased social attention in different clinical syndromes such as anxiety or autism (Riby & Hancock, 2009; Kliemann *et al*. 2010; Shechner *et al*. 2012), a better understanding on how OT shapes attention for social signals seems highly relevant. Future studies could investigate valence-related effects of OT on social attention in clinical populations combining an exogenous administration of OT with analyses of genetic factors and brain-imaging data. For example, in a recent study Sauer *et al*. (2012) showed that variations in the *CD38* gene important for OT secretion are associated with differences in neural responses to social stimuli, with these differences being increased following OT administration.

Furthermore, evidence from both animal and human studies suggests strong interactions of the OT and the dopaminergic system in the context of social behavior (Baskerville & Douglas, 2010; Strathearn, 2011). OT was shown to increase dopamine signaling in reward-related brain structures in rats, with the latter being associated with increased maternal behavior (Shahrokh *et al*. 2010). In our study, the automatic attentional shift towards positive social cues might reflect increased reward sensitivity after OT administration, possibly mediated by OT effects on dopaminergic mid-brain regions (Krebs *et al*. 2012).

To summarize, OT seems to shape early attentional processes in a way that might facilitate prosocial behavior. Because of the complexity of the OT system and its inter-relatedness with other neurophysiological systems, future studies should address the role of OT in social attention in health and clinical conditions following a multi-modal approach.

Acknowledgments

We thank J. Greif for assistance with the data collection. This work was supported by the German Research Foundation (DFG Do1312/2-1; He5310/1-1).

Declaration of Interest

None.

References

Alvares GA, Chen NT, Balleine BW, Hickie IB, Guastella AJ (2012). Oxytocin selectively moderates negative cognitive appraisals in high trait anxious males. *Psychoneuroendocrinology*. Published online: 20 May 2012. doi:10.1016/j.psyneuen.2012.04.018.

Bar-Haim Y, Lamy D, Pergamin L, Bakermans-Kranenburg MJ, van IJzendoorn MH (2007). Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. *Psychological Bulletin* **133**, 1–24.

Baskerville TA, Douglas AJ (2010). Dopamine and oxytocin interactions underlying behaviors: potential contributions to behavioral disorders. *CNS Neuroscience and Therapeutics* **16**, e92–e123.

Baumgartner T, Heinrichs M, Vonlanthen A, Fischbacher U, Fehr E (2008). Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron* **58**, 639–650.

Born J, Lange T, Kern W, McGregor GP, Bickel U, Fehm HL (2002). Sniffing neuropeptides: a transnasal approach to the human brain. *Nature Neuroscience* **5**, 514–516.

Calamaras MR, Tone EB, Anderson PL (2012). A pilot study of attention bias subtypes: examining their relation to cognitive bias and their change following cognitive behavioral therapy. *Journal of Clinical Psychology*. Published online: 18 May 2012. doi:10.1002/jclp.21875.

Campbell DB, Datta D, Jones ST, Batey Lee E, Sutcliffe JS, Hammock EA, Levitt P (2011). Association of oxytocin receptor (OXTR) gene variants with multiple phenotype domains of autism spectrum disorder. *Journal of Neurodevelopmental Disorders* **3**, 101–112.

Cooper RM, Langton SRH (2006). Attentional bias to angry faces using the dot-probe task? It depends when you look for it. *Behaviour Research and Therapy* **44**, 1321–1329.

Dai L, Carter CS, Ying J, Bellugi U, Pournajafi-Nazarloo H, Korenberg JR (2012). Oxytocin and vasopressin are dysregulated in Williams Syndrome, a genetic disorder affecting social behavior. *PLoS ONE* **7**, e38513.

Davis M, Whalen PJ (2001). The amygdala: vigilance and emotion. *Molecular Psychiatry* **6**, 13–34.

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

Dodd HF, Porter MA (2010). I see happy people: attention bias towards happy but not angry facial expressions in Williams syndrome. *Cognitive Neuropsychiatry* **15**, 549–567.

Domes G, Heinrichs M, Glascher J, Buchel C, Braus DF, Herpertz SC (2007*a*). Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biological Psychiatry* **62**, 1187–1190.

Domes G, Heinrichs M, Michel A, Berger C, Herpertz SC (2007*b*). Oxytocin improves 'mind-reading' in humans. *Biological Psychiatry* **61**, 731–733.

Domes G, Lischke A, Berger C, Grossmann A, Hauenstein K, Heinrichs M, Herpertz SC (2010). Effects of intranasal oxytocin on emotional face processing in women. *Psychoneuroendocrinology* **35**, 83–93.

Ellenbogen MA, Linnen AM, Grumet R, Cardoso C, Joober R (2012). The acute effects of intranasal oxytocin on automatic and effortful attentional shifting to emotional faces. *Psychophysiology* **49**, 128–137.

Fischer-Shofty M, Shamay-Tsoory SG, Harari H, Levkovitz Y (2010). The effect of intranasal administration of oxytocin on fear recognition. *Neuropsychologia* **48**, 179–184.

Franke G (1995). *The Symptom Checklist by Derogatis – German Version – SCL-90-R* [in German]. Beltz: Göttingen.

Gamer M, Zurowski B, Buchel C (2010). Different amygdala subregions mediate valence-related and attentional effects of oxytocin in humans. *Proceedings of the National Academy of Sciences USA* **107**, 9400–9405.

Guastella AJ, Einfeld SL, Gray KM, Rinehart NJ, Tonge BJ, Lambert TJ, Hickie IB (2010). Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry* **67**, 692–694.

Guastella AJ, Howard AL, Dadds MR, Mitchell P, Carson DS (2009). A randomized controlled trial of intranasal oxytocin as an adjunct to exposure therapy for social anxiety disorder. *Psychoneuroendocrinology* **34**, 917–923.

Guastella AJ, Mitchell PB, Dadds MR (2008). Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry* **63**, 3–5.

Heinrichs M, Domes G (2008). Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. *Progress in Brain Research* **170**, 337–350.

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

Jarvinen-Pasley A, Vines BW, Hill KJ, Yam A, Grichanik M, Mills D, Reiss AL, Korenberg JR, Bellugi U (2010). Cross-modal influences of affect across social and non-social domains in individuals with Williams syndrome. *Neuropsychologia* **48**, 456–466.

Jones W, Bellugi U, Lai Z, Chiles M, Reilly J, Lincoln A, Adolphs R (2000). II. Hypersociability in Williams Syndrome. *Journal of Cognitive Neuroscience* **12** (Suppl. 1), 30–46.

Keebaugh AC, Young LJ (2011). Increasing oxytocin receptor expression in the nucleus accumbens of pre-pubertal female prairie voles enhances alloparental responsiveness and partner preference formation as adults. *Hormones and Behavior* **60**, 498–504.

Kirsch P, Esslinger C, Chen Q, Mier D, Lis S, Siddhanti S, Gruppe H, Mattay VS, Gallhofer B, Meyer-Lindenberg A (2005). Oxytocin modulates neural circuitry for social cognition and fear in humans. *Journal of Neuroscience* **25**, 11489–11493.

Kliemann D, Dziobek I, Hatri A, Steimke R, Heekeren HR (2010). Atypical reflexive gaze patterns on emotional faces

in autism spectrum disorders. *Journal of Neuroscience* **30**, 12281–12287.

Krebs RM, Boehler CN, Roberts KC, Song AW, Woldorff MG (2012). The involvement of the dopaminergic midbrain and cortico-striatal-thalamic circuits in the integration of reward prospect and attentional task demands. *Cerebral Cortex* **22**, 607–615.

Kumsta R, Heinrichs M (2012). Oxytocin, stress and social behavior: neurogenetics of the human oxytocin system. *Current Opinions in Neurobiology*. Published online: 3 October 2012. doi:10.1016/j.conb.2012.09.004.

Leknes S, Wessberg J, Ellingsen DM, Chelnokova O, Olausson H, Laeng B (2012). Oxytocin enhances pupil dilation and sensitivity to 'hidden' emotional expressions. *Social Cognitive and Affective Neuroscience*. Published online: 29 June 2012. doi:10.1093/scan/nss062.

Lischke A, Berger C, Prehn K, Heinrichs M, Herpertz SC, Domes G (2012*a*). Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye-gaze unaffected. *Psychoneuroendocrinology* **37**, 475–481.

Lischke A, Gamer M, Berger C, Grossmann A, Hauenstein K, Heinrichs M, Herpertz SC, Domes G (2012*b*). Oxytocin increases amygdala reactivity to threatening scenes in females. *Psychoneuroendocrinology* **37**, 1431–1438.

Lundqvist D, Flykt A, Ohman A (1998). *The Karolinska Directed Emotional Faces* (*KDEF*). Department of Neurosciences, Karolinska Hospital: Stockholm.

MacLeod C, Mathews A, Tata P (1986). Attentional bias in emotional disorders. *Journal of Abnormal Psychology* **95**, 15–20.

Marsh AA, Yu HH, Pine DS, Blair RJ (2010). Oxytocin improves specific recognition of positive facial expressions. *Psychopharmacology* **209**, 225–232.

Meyer-Lindenberg A, Domes G, Kirsch P, Heinrichs M (2011). Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. *Nature Reviews. Neuroscience* **12**, 524–538.

Mogg K, Bradley BP (2002). Selective orienting of attention to masked threat faces in social anxiety. *Behaviour Research and Therapy* **40**, 1403–1414.

Moore DJ, Heavey L, Reidy J (2012). Attentional processing of faces in ASD: a dot-probe study. *Journal of Autism and Developmental Disorders* **42**, 2038–2045.

Pedersen CA, Gibson CM, Rau SW, Salimi K, Smedley KL, Casey RL, Leserman J, Jarskog LF, Penn DL (2011). Intranasal oxytocin reduces psychotic symptoms and improves Theory of Mind and social perception in schizophrenia. *Schizophrenia Research* **132**, 50–53.

Pobbe RL, Pearson BL, Defensor EB, Bolivar VJ, Young 3rd WS, Lee HJ, Blanchard DC, Blanchard RJ (2012). Oxytocin receptor knockout mice display deficits in the expression of autism-related behaviors. *Hormones and Behavior* **61**, 436–444.

Porter MA, Shaw TA, Marsh PJ (2010). An unusual attraction to the eyes in Williams-Beuren syndrome: a manipulation of facial affect while measuring face scanpaths. *Cognitive Neuropsychiatry* **15**, 505–530.

Riby DM, Hancock PJ (2009). Do faces capture the attention of individuals with Williams syndrome or autism? Evidence from tracking eye movements. *Journal of Autism and Developmental Disorders* **39**, 421–431.

Sauer C, Montag C, Worner C, Kirsch P, Reuter M (2012). Effects of a common variant in the CD38 gene on social processing in an oxytocin challenge study: possible links to autism. *Neuropsychopharmacology* **37**, 1474–1482.

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

Shahrokh DK, Zhang TY, Diorio J, Gratton A, Meaney MJ (2010). Oxytocin-dopamine interactions mediate variations in maternal behavior in the rat. *Endocrinology* **151**, 2276–2286.

Shechner T, Britton JC, Perez-Edgar K, Bar-Haim Y, Ernst M, Fox NA, Leibenluft E, Pine DS (2012). Attention biases, anxiety, and development: toward or away from threats or rewards? *Depression and Anxiety* **29**, 282–294.

Strathearn L (2011). Maternal neglect: oxytocin, dopamine and the neurobiology of attachment. *Journal of Neuroendocrinology* **23**, 1054–1065.

Tamietto M, de Gelder B (2010). Neural bases of the non-conscious perception of emotional signals. Nature Reviews. *Neuroscience* **11**, 697–709.

Taylor SE (2006). Tend and befriend: biobehavioral bases of affiliation under stress. *Current Directions in Psychological Science* **15**, 273–277.

Unkelbach C, Guastella AJ, Forgas JP (2008). Oxytocin selectively facilitates recognition of positive sex and relationship words. *Psychological Science* **19**, 1092–1094.

Vuilleumier P (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences* **9**, 585–594.

Young LJ (2009). The neuroendocrinology of the social brain. *Frontiers in Neuroendocrinology* **30**, 425–428.