

As time goes by: Oxytocin influences the subjective perception of time in a social context



Valentina Colonnello ^{a,*}, Gregor Domes ^{a,b}, Markus Heinrichs ^{a,b}

^a Department of Psychology, Laboratory for Biological and Personality Psychology, University of Freiburg, D-79104 Freiburg, Germany

^b Freiburg Brain Imaging Center, University Medical Center, University of Freiburg, D-79106 Freiburg, Germany

ARTICLE INFO

Article history:

Received 20 October 2015

Received in revised form 2 February 2016

Accepted 17 February 2016

Keywords:

Oxytocin
Social cognition
Subjectivity
Sociability

ABSTRACT

Time perception depends on an event's emotional relevance to the beholder; a subjective time dilation effect is associated with self-relevant, emotionally salient stimuli. Previous studies have revealed that oxytocin modulates the salience of social stimuli and attention to social cues. However, whether the oxytocin system is involved in human subjective time perception is unknown. The aim of the present study was to investigate whether increased oxytocin levels would induce a time dilation effect for self-relevant, positive social cues.

In a double-blind, placebo-controlled, between-subject design, heterosexual men were administered intranasal oxytocin or placebo. After about 50 min, participants completed a time-bisection task in which they estimated lengths of exposure to happy female faces (self-relevant positive stimuli, based on sexual orientation), emotionally neutral and negative female faces (control), and happy, neutral, and negative male faces (control). Oxytocin induced a subjective time dilation effect for happy female faces and a time compression effect for happy male faces.

Our results provide evidence that oxytocin influences time perception, a primary form of human subjectivity.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Time perception in the subsecond range is crucial for adaptively navigating the world: everyday choice (Haggard, 2008), social exchange (Bernieri and Rosenthal, 1991), and action (Hagura et al., 2012) are clearly dependent on the beholder's subjective time processing. However, subjective time perception is relatively malleable. The subjective duration of an event is, in fact, dependent on its salience and emotional relevance to the beholder (Wittmann, 2015; Wittmann and van Wassenhove, 2009; Droit-Volet and Meck, 2007). For example, people experience time as dilated, or lengthened, when viewing emotionally engaging pictures (Effron et al., 2006; Droit-Volet et al., 2004).

Several models of time perception have been proposed (for reviews, see Allman et al., 2014; Buhusi and Meck, 2005). Although the debate whether the perception of time relies on dedicated or distributed intrinsic neural brain systems remains open (Ivry and Schlerf, 2008; Buhusi and Meck, 2005), evidence indicates that the

subjective sense of time is not a recent achievement in brain evolution. Specifically, cross-species research on the neurobiological foundation of temporal processing indicates that subjective time perception is strongly modulated by the activation of several phylogenetically ancient brain areas (Lewis and Miall, 2003) and by the availability of neurohormones and neuromodulators that fuel these ancient brain circuits (Sandstrom, 2007; Meck, 2006, 2005, 1987).

This evidence raises the question of oxytocin's role in time perception as being one of the early forms of subjectivity in humans. Specifically, because high brain levels of the neuropeptide oxytocin enhance the perceived salience of social stimuli (Prehn et al., 2013), and because self-relevant and emotionally relevant stimuli are perceived to last longer than non-relevant stimuli (Droit-Volet and Meck, 2007; Droit-Volet et al., 2004), it is reasonable to expect that an increase in oxytocin levels would prolong one's subjective time perception of social stimuli. Supporting the possible involvement of oxytocin on time perception, cross-species studies reveal that brain areas involved in temporal processing such as the insula and putamen (Livesey et al., 2007) have a widespread distribution of oxytocin receptors (Boccia et al., 2013; Tribollet et al., 1992). To the best of our knowledge, though, no studies have directly investigated the effects of oxytocin on subjective time perception in humans. However, human studies indicate that oxytocin

* Corresponding author. Fax: +49 761 203 3023.

E-mail address: valentina.colonnello@psychologie.uni-freiburg.de
(V. Colonnello).

plays a central role in facilitating the processing of social stimuli (Meyer-Lindenberg et al., 2011; Heinrichs et al., 2009). For example, intranasal administration of oxytocin enhances positive evaluations of social stimuli (Colonnello et al., 2013; Theodoridou et al., 2009), increases emotion recognition (Lischke et al., 2012; Schulze et al., 2011), sharpens self-other perceptual distinction (Colonnello et al., 2013), and fosters feelings of comfort and personal confidence (Colonnello and Heinrichs, 2014; Panksepp, 2009). In addition, high oxytocin levels affect the recognition of sex- and relationship-related words (Heinrichs et al., 2004; Unkelbach et al., 2008), facilitate the processing of positive versus negative words (Di Simplicio et al., 2008), and increase covert attention toward happy faces (Domes et al., 2013).

Building upon this body of empirical work, we hypothesized that oxytocin would influence subjective time perception during a classic time-bisection task. Specifically, we predicted that increased oxytocin levels following intranasal administration would lengthen subjective time perception in heterosexual men when viewing self-relevant stimuli with evolutionarily basic, positive, hedonic valence as compared to placebo (i.e., photos of happy, smiling females with direct gazes). Smiling female faces are generally perceived by heterosexual men as being more attractive than neutral and happy male facial expressions (Tracy and Beall, 2011) and as signaling positive mating value (Thornhill and Gangestad, 1999); they also increase the activation of heterosexual men's brain reward circuitry (Kranz and Ishai, 2006). We therefore compared heterosexual males' responses to female and male faces displaying happy, neutral, or negative emotions.

2. Methods

2.1. Participants

Participants were 84 heterosexual males aged 22–31 ($M = 25$; $SD = 2$) years recruited among non-psychology students from the University of Freiburg, Germany via flyers and local advertisements. Each participant was randomly assigned to either the oxytocin ($n = 42$) or placebo ($n = 42$) treatment group in a placebo-controlled, double-blind, between-subject experimental design. Exclusion criteria were self-reported medical or psychiatric disorders, medication use, and history of substance abuse. Participants refrained from alcohol and exercise for 24 h immediately prior to testing, and avoided caffeinated drinks and smoking during the final 2 h of that period.

Female participants were not tested because interactions between oxytocin and hormonal fluctuation during menstrual phases are still unclear.

Prior to treatment, participants completed the following tests to control for possible baseline differences in personality characteristics between substance groups: Autism Spectrum Quotient (AQ, Baron-Cohen et al., 2001), Wortschatz test of verbal intelligence (WST; Schmidt and Metzler, 1992); Adult Attachment Scale (AAS; Collins and Read, 1990); Social Interaction Anxiety Scale (SIAS; Mattick and Clarke, 1998); State-Trait Anxiety Inventory—trait anxiety (STA1; Spielberger et al., 1983); State-Trait Anger Expression Inventory (STAXI-T; Spielberger, 1991); Freiburg Personality Inventory—openness scale (FPI; Fahrenberg et al., 1984); Interpersonal Reactivity Index (IRI; Davis, 1983); Twenty-Item Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994).

Finally, forms A and B of the 12-item Multidimensional Mood Questionnaire (MDBF, Steyer et al., 1994) were used prior to substance administration and immediately before the experimental task to control for any affective state differences at baseline and following substance administration. The two forms of the MDBF questionnaire were presented in counterbalanced order for sub-

Table 1

Mean and SD of the psychological characteristics of the participants. AQ=Autism Quotient; WST=Wortschatz-Test, verbal IQ test; AAS-C=Adult Attachment Scale-Close; AAS-D=Adult Attachment Scale-Depend; AAS-A=Adult Attachment Scale-Anxious; SIAS=Social Interaction Anxiety Scale; STA1-T=State Trait Anxiety Inventory - Trait Anxiety; STAXI-T=State-Trait-Anger Expression/Regulation Inventory; FPI=Freiburg Personality Inventory - Openness scale; IRI=Interpersonal Reactivity Index; TAS-20=Twenty-Item Toronto Alexithymia Scale.

	Placebo M(SD)	Oxytocin M(SD)	t(78)	p
AQ	17.1(6.1)	15.8(5.9)	1	.3
WST	34.6(2.8)	34.2(3.5)	.6	.5
AAS-C	18.9(4.9)	19.7(3.9)	-.7	.5
AAS-D	20.5(3.4)	20(3.4)	.5	.6
AAS-A	9.7(3.7)	10.4(3.8)	-.7	.8
SIAS	19.5(12.2)	21.9(11.8)	-.9	.4
STA1	37.2(6.9)	37.5(8.2)	-.1	.9
STAXI-T	17.8(3.7)	18.1(5)	-.4	.7
FPI	7.6(2.1)	8.2(2.1)	-.1	.2
IRI	57.1(7.1)	55.5(11)	.8	.4
TAS-20	46.7(11)	47.1(11.2)	-.3	.8

stance (placebo and oxytocin) and session (before/after substance administration).

All participants gave written informed consent prior to participation in the study. The experimental procedures were approved by the institutional Review board (IRB) of the University of Freiburg, Germany.

2.2. Time-bisection task

2.2.1. Stimuli

Stimuli were 48 photographs of 8 faces (4 female, 4 male) displaying either a neutral or emotional (happiness, sadness, anger, disgust, or fear) expression. Two additional photographs of neutral faces (one male, one female) were used in the training phase. All photographs were obtained from the FACES database (Ebner et al., 2010). Prior to presentation, photographs were converted to gray scale and non-facial attributions (hair and ears) were covered with an elliptical mask.

2.2.2. Procedure

After completing the set of baseline personality and affective state measures, each participant received a single intranasal dose of either oxytocin (24 IU of Syntocinon® Nasal Spray, Novartis, Basel, Switzerland) or placebo (containing the same vehicle but no neuropeptide; see Heinrichs et al., 2003). Approximately 50 min afterwards, all participants completed the time-bisection task that consisted of a training and test phase.

For both phases, participants were seated in front of a computer monitor (~50 cm distance) and keyboard, and stimuli were displayed center screen in a pseudo-random order for emotion, sex, and duration. As soon as a stimulus disappeared from the screen, participants identified the duration of its display by pressing either "s" (short) or "l" (long) on the keyboard.

Only standard short (400 ms) and long (1600 ms) durations were used during the training phase. During training, each stimulus was presented 3× per standard duration. During testing, each photograph was presented four times per standard duration (400 and 1600 ms) and four times at each of five intermediate durations (600, 800, 1000, 1200, and 1400 ms). Each participant thus viewed 6 stimuli during training and 336 stimuli during testing. A black screen appeared during the 500-ms interval between each photo's presentation. Participants received immediate error feedback only during the training phase. The test lasted about 15 min.

Presentation® software (Neurobehavioral Systems Inc., Albany, CA, USA, <http://www.neurobs.com/>) was used for presenting stimuli and recording participants' responses. After presentation of the last stimulus, participants responded to an open question about

possible side effects. Using a dichotomous scale, each participant also indicated which substance he thought he had received.

2.3. Statistical analysis

Preliminary data screening revealed that one placebo-treated participant and two oxytocin-treated participants presented fixed response patterns. In addition, one placebo-treated participant scored in the clinical range on the AQ scale. Their data were therefore excluded from analysis, leaving our final sample with 40 placebo-treated and 40 oxytocin-treated participants.

Any baseline differences in personality characteristics between the substance groups were analyzed using the independent *t*-test.

To test whether the participants were able to recognize changes in presentation durations accurately, we performed a repeated-measures ANOVA with the substance group (placebo and oxytocin) as a between-subject factor, and duration (400, 500, 800, 1000, 1200, 1400, 1600), emotion (happiness, neutral, anger, sadness, disgust, and fear) and sex (female and male) as within-subject factors. To increase the statistical power, the following analyses were conducted after averaging across durations. Data on the proportion of long responses and *d* scores (differences between each emotion *z* score and the neutral *z* score per each emotion and sex, as in Efron et al., 2006) were analyzed using repeated-measures ANOVA with the substance group as a between-subject factor, and emotion (happiness, neutral, anger, sadness, disgust, and fear) and sex (female and male) as within-subject factors. To analyze whether the specific expressions led to time dilation or time contraction compared to neutral facial expressions, the *d* scores (averaged for durations) for each emotion and for each substance group were compared to zero using one-sample *t*-tests. Positive values indicate a time dilation, while negative values indicate a time contraction relative to the neutral control expressions.

MDBF scores were analyzed using repeated-measures analysis of variance (ANOVA) with substance group (placebo or oxytocin) as a between-subject factor and time (pre- or post-substance administration) as a within-subject factor.

The χ^2 test was applied to analyze participants' treatment guesses.

The data were analyzed using Statistica 8 (Statsoft INC: Tulsa, OK, USA).

3. Results

There were no differences in personality traits between oxytocin and placebo substance groups (all $p > .05$; Table 1).

Analysis of the proportion of long responses indicated a main effect of duration, $F(6,468) = 1148.87$, $p < .0001$, $\eta_p^2 = .94$, with no differences between substance groups in sensitivity to changes in presentation of durations: substance \times duration, $F(6,468) = .65$, $p = .69$, $\eta_p^2 = .008$.

Analysis of the proportion of long responses averaged for durations revealed a significant main effect of emotion $F(5,390) = 3.07$, $p = .01$, $\eta_p^2 = .04$: The presentation of sadness was perceived as lasting shorter than that of other emotions. We also observed a significant main effect of sex, $F(1,78) = 6.99$, $p = .01$, $\eta_p^2 = .08$; The presentation of female faces was perceived as lasting shorter than that of the male faces.

The main effect of substance, $F(1,78) = .29$, $p = .59$, $\eta_p^2 = .004$, and the interactions between substance and emotion, $F(5,390) = .31$, $p = .90$, $\eta_p^2 = .004$, substance and sex, $F(1,78) = .27$, $p = .60$, $\eta_p^2 = .003$, emotion and sex, $F(5,390) = 1.55$, $p = .17$, $\eta_p^2 = .02$ were not significant. We detected no significant three-way substance \times emotion \times sex interaction: $F(5,390) = 1.46$, $p = .20$, $\eta_p^2 = .02$.

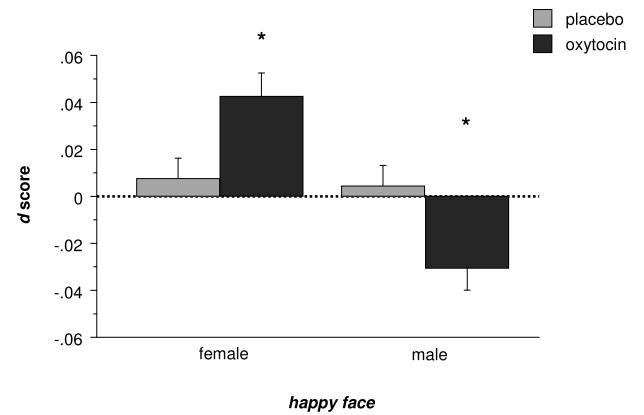


Fig. 1. Mean \pm SE scores of for happy male and female faces in the two substance groups.

* $p < .05$.

Table 2

Mean and SD of the *d* scores for the emotions and sex in the two substance group.

* $p < .05$.

	Placebo M(SD) Male	Oxytocin M(SD)	Placebo M(SD) Female	Oxytocin M(SD)
Happiness	.005 \pm .05	-.03 \pm .06*	.008 \pm .05	.043 \pm .06*
Sadness	.002 \pm .07	.0007 \pm .06	-.033 \pm .06	-.014 \pm .05
Anger	-.004 \pm .06	-.006 \pm .05	-.021 \pm .05	-.026 \pm .04
Disgust	.030 \pm .06	.020 \pm .05	.009 \pm .06	.020 \pm .06
Fear	.010 \pm .08	-.011 \pm .06	-.005 \pm .06	.008 \pm .06

As the analysis of the *d* scores revealed, the substance groups differed in their perceived duration of happy female and male faces (Fig. 1), substance \times emotion \times sex interaction: $F(4,312) = 4.13$, $p = .0028$, $\eta_p^2 = .05$. No differences between substance groups were revealed with respect to the other emotions (Table 2). The main effect of substance, $F(1,78) = .10$, $p = .75$, $\eta_p^2 = .0013$, was not significant, while the main effect of emotion, $F(4,312) = 17.04$, $p < .001$, $\eta_p^2 = .18$, was significant: The presentation of sadness was perceived as lasting shorter than the presentation of other emotions. The interaction emotion \times sex, $F(4,312) = 13.91$, $p < .001$, $\eta_p^2 = .15$, was significant: The presentation of male disgust faces was perceived as lasting longer than the presentation of the female disgust faces. The main effect of sex, $F(1,78) = .46$, $p = .49$, $\eta_p^2 = .006$, and the interaction substance \times emotion, $F(4,312) = .59$, $p = .66$, $\eta_p^2 = .007$, and substance \times sex, $F(1,78) = 2.94$, $p = .09$, $\eta_p^2 = .04$, were not significant.

The one-group *t*-test analysis on the *d* scores to test whether specific emotion induced a lengthening or shortening of time perception compared to neutral faces confirmed that the placebo group perceived both female, $t(39) = .99$, $p = .33$, $d = .32$, and male, $t(39) = .54$, $p = .59$, $d = .17$, happy faces as lasting as long as their neutral controls. In contrast, the oxytocin group perceived that happy female faces remained on-screen longer than neutral female faces did $t(39) = 4.36$, $p = .0001$, $d = 1.40$ and happy male faces appeared for less time than male neutral faces, $t(39) = -3.48$, $p = .001$, $d = 1.15$.

Exposure to the male disgust emotion induced an experience of time dilation: placebo: $t(39) = 3.00$, $p = .005$, $d = .96$; oxytocin = $t(39) = 2.51$, $p = .02$, $d = .80$. Exposure to female disgust faces induced a time dilation effect in the oxytocin, $t(39) = 2.12$, $p = .04$, $d = .68$ but not in the placebo, $t(39) = .97$, $p = .34$, $d = .31$, substance group. However, as mentioned above, the direct contrast between the substance groups' *d* scores was not significant (Table 2). In addition, angry female faces induced a time contraction effect in both substance groups: placebo: $t(39) = -2.53$, $p = .016$, $d = .81$; oxytocin = $t(39) = -4.37$, $p < .0001$, $d = 1.40$, while sadness displayed by female faces induced a time contraction in the placebo,

$t(39) = -3.27, p = .002, d = 1.04$, but not in the oxytocin, $t(39) = -1.83, p = .07, d = .59$, group, in conjunction with absence of significant differences between substance groups (Table 2). No alterations in time perception were found with respect to male sad faces, placebo: $t(39) = .17, p = .87, d = .054$; oxytocin: $t(39) = .08, p = .93, d = .026$; angry male faces placebo: $t(39) = -.40, p = .69, d = .22$; oxytocin: $t(39) = -.83, p = .41, d = .26$; or fear faces: male placebo: $t(39) = .78, p = .44, d = .25$; male oxytocin: $t(39) = 1.15, p = .26, d = .37$; female: placebo: $t(39) = -.50, p = .61, d = .16$; female oxytocin: $t(39) = .83, p = .41, d = .27$.

3.1. Affective state measures

With respect to changes in affective state, we observed a main effect of session, $F(1,78) = 5.98, p = .017, \eta_p^2 = .07$, with a decrease in calmness levels following substance administration ($M \pm SE$, pre-test: $16.8 \pm .28$; post-test: $16.2 \pm .31$) for the calmness scores. The main effect of substance, $F(1,78) = .044, p = .83, \eta_p^2 = .0005$, and substance \times session interaction, $F(1,78) = .057, p = .81; \eta_p^2 = .0007$, were not significant.

We observed no significant main effect of substance in the mood change scores $F(1,78) = .11, p = .73, \eta_p^2 = .001$, session, $F(1,78) = .45, p = .50, \eta_p^2 = .006$, or substance \times session interaction, $F(1,78) = .77, p = .38, \eta_p^2 = .01$. The main effect of substance in the alertness scores, $F(1,78) = .62, p = .43, \eta_p^2 = .008$; session, $F(1,78) = 2.32, p = .13, \eta_p^2 = .03$, and substance \times session interaction, $F(1,78) = .18, p = .67, \eta_p^2 = .002$, were not significant.

Participants reported no side effects, nor did we detect any significant effect of belief on substance allocation, $\chi^2 = 2.00, p = .14$.

4. Discussion

To our knowledge, the present study is the first to demonstrate that oxytocin administration does indeed influence human subjective time perception. As expected, we observed that high levels of oxytocin induced time dilation, or a prolonged perception of time, in conjunction with self-relevant social stimuli with positive hedonic valence. In addition, a time contraction for happy male faces was detected following oxytocin administration. Compared to placebo, oxytocin selectively induced a time dilation effect when participants viewed photographs of smiling women, but time perception was compressed when photographs of happy men were being viewed. Of note, on the self-report affective measure, substance administration had no effect on change in alertness scores. However, the oxytocin may have induced a transient change in arousal during the presentation of happy female and male faces. In the light of the classic pacemaker-accumulator models of time perception (Droit-Volet and Meck, 2007), it is possible to interpret the time dilation for happy female faces observed following to oxytocin administration as an oxytocin-induced transient increase in arousal due to the exposure to emotionally engaging stimuli and associated acceleration of internal clock speed. In turn, the time contraction for happy male faces may be due to a decrease in arousal and deceleration of the internal clock speed (Droit-Volet and Meck, 2007). Thus, our results are consistent with studies indicating that oxytocin is a facilitator of salience attribution to social stimuli (Prehn et al., 2013), and they are in line with previous studies showing that oxytocin enhances the recognition of sex-related stimuli (Unkelbach et al., 2008) and arousal to sexual cues (Burri et al., 2008). These effects are particularly intriguing because they suggest that under the present experimental conditions, oxytocin is not increasing the salience of positive hedonic stimuli in an unspecific manner; instead, it is only enhancing the salience of positive stimuli that may be personally relevant to the beholder. The oxytocin effect thus occurred in the absence of changes in sensitivity

to negative emotions: compared to placebo, oxytocin did not influence the time perception of sadness or fear. In addition, oxytocin did not alter the time perception of faces displaying disgust, which are considered relevant warning signals (Oaten et al., 2009), and it did not increase sensitivity to angry, potentially threatening faces.

Of note, previous bisectional studies of time perception using emotional faces have found that faces expressing anger generally induce time dilation compared to neutral faces (Tipples, 2008; Droit-Volet et al., 2004). As we observed no time dilation effect in response to angry faces, *prima facie*, our results would appear to contradict those studies. However, discordant study results may occur due to differences in procedures and participant-recruiting criteria. In the present study, our participants were asked to wait about 50 min before completing the task, which induced a significant reduction in their calmness levels. Furthermore, participants in previous studies viewed a smaller set of emotions, which might have affected the salience of the presentation of angry faces. Furthermore, in most of the previous studies, participants were women or mixed samples of men and women. Thus it would be interesting and perhaps illuminating to extend our study by directly comparing men and women in the time-perception task and specifically investigating potential interactions between oxytocin and time perception as a function of sexual orientation and gender, using a smaller set of stimuli. It is possible that heterosexual women, as well as homosexual and bisexual individuals, would display a different pattern of responses, especially considering Thienel et al. (2014) study indicating that oxytocin administration influences social stimulus processing differently in heterosexual and homosexual men.

The present results indicate that in humans, time perception—an evolutionarily primary aspect of subjectivity—is influenced by the ancient, subcortically synthesized neurohormone oxytocin. The alteration in time perception following oxytocin administration occurred on the implicit behavioral level and in the absence of any consciously detected differences in affective state. Although we tested healthy men, our results point toward oxytocin's involvement in creating a neurobiological framework for the appreciation of positive hedonic social stimuli.

Role of the funding

Source: This work was supported by grants from the Deutsche Forschungsgemeinschaft to M.H. (He5310/1-1).

Conflicts of interest

None.

Authors contribution

V.C. conceived the study, V.C., G.D. and M.H. designed the study, interpreted the results, and wrote the manuscript.

Acknowledgments

We are grateful to Nicole Frank, Rob Falkenstein, Jonas Schmidt, Thea Günther, Judith Großmann, Sebastian Neusius, and Nicolas Conze for help in data collection. V.C. was supported by a research fellowship from the Alexander von Humboldt Foundation.

References

- Allman, M.J., Teki, S., Griffiths, T.D., Meck, W.H., 2014. Properties of the internal clock: first-and second-order principles of subjective time. *Annu. Rev. Psychol.* **65**, 743–771.

- Bagby, R.M., Parker, J.D., Taylor, G.J., 1994. The twenty-item Toronto Alexithymia Scale—I: item selection and cross-validation of the factor structure. *J. Psychosom. Res.* 38, 23–32.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., Clubley, E., 2001. The autism-spectrum quotient (AQ): evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *J. Autism Dev. Dis.* 31, 5–17.
- Bernieri, F.J., Rosenthal, R., 1991. Interpersonal coordination: behavior matching and interactional synchrony. In: Feldman, R.S., Rime, B. (Eds.), *Fundamentals of Nonverbal Behavior*. Cambridge University Press, Cambridge England, pp. 401–432.
- Boccia, M.L., Petrusz, P., Suzuki, K., Marson, L., Pedersen, C.A., 2013. Immunohistochemical localization of oxytocin receptors in human brain. *Neuroscience* 253, 155–164.
- Buhusi, C.V., Meck, W.H., 2005. What makes us tick? Functional and neural mechanisms of interval timing. *Nat. Rev. Neurosci.* 6, 755–765.
- Burri, A., Heinrichs, M., Schedlowski, M., Kruger, T.H., 2008. The acute effects of intranasal oxytocin administration on endocrine and sexual function in males. *Psychoneuroendocrinology* 33, 591–600.
- Collins, N.L., Read, S.J., 1990. Adult attachment, working models, and relationship quality in dating couples. *J. Pers. Soc. Psychol.* 58, 644–663.
- Colonnello, V., Heinrichs, M., 2014. Intranasal oxytocin enhances positive self-attribution in healthy men. *J. Psychosom. Res.* 77, 415–419.
- Colonnello, V., Chen, F.S., Panksepp, J., Heinrichs, M., 2013. Oxytocin sharpens self-other perceptual boundary. *Psychoneuroendocrinology* 38, 2996–3002.
- Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. *J. Pers. Soc. Psychol.* 44, 113–126.
- Di Simplicio, M., Massey-Chase, R., Cowen, P.J., Harmer, C.J., 2008. Oxytocin enhances processing of positive versus negative emotional information in healthy male volunteers. *J. Psychopharmacol.* 23, 241–248.
- Domes, G., Sibold, M., Schulze, L., Lischke, A., Herpertz, S.C., Heinrichs, M., 2013. Intranasal oxytocin increases covert attention to positive social cues. *Psychol. Med.* 43, 1747–1753.
- Droit-Volet, S., Meck, W.H., 2007. How emotions colour our perception of time. *Trends Cogn. Sci.* 11, 504–513.
- Droit-Volet, S., Brunot, S., Niedenthal, P., 2004. Brief report: perception of the duration of emotional events. *Cogn. Emot.* 18, 849–858.
- Ebner, N.C., Riediger, M., Lindenberger, U., 2010. Faces—a database of facial expressions in young, middle-aged, and older women and men: development and validation. *Behav. Res. Methods* 42, 351–362.
- Effron, D.A., Niedenthal, P.M., Gil, S., Droit-Volet, S., 2006. Embodied temporal perception of emotion. *Emotion* 6, 1–9.
- Fahrenberg, J., Hampel, R., Selg, H., 1984. Das Freiburger Person-Lichkeitsinventar (FPZ und FPI-R), Handbuch, (The Freiburg Per-Sonality Inventory (FPI and FPI-R). Manual), 4th ed. Hogrefe, Gottingen.
- Haggard, P., 2008. Human volition: towards a neuroscience of will. *Nat. Rev. Neurosci.* 9, 934–946.
- Hagura, N., Kanai, R., Orgs, G., Haggard, P., 2012. Ready steady slow: action preparation slows the subjective passage of time. *Proc. Biol. Sci.* 279, 4399–4406.
- Heinrichs, M., Meinlschmidt, G., Wippich, W., Ehlert, U., Hellhammer, D.H., 2004. Selective amnesia effects of oxytocin on human memory. *Physiol. Behav.* 83, 31–38.
- Heinrichs, M., von Dawans, B., Domes, G., 2009. Oxytocin, vasopressin, and human social behavior. *Front. Neuroendocrinol.* 30, 548–557.
- Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biol. Psychiatry* 54, 1389–1398.
- Ivry, R.B., Schlerf, J.E., 2008. Dedicated and intrinsic models of time perception. *Trends Cogn. Sci.* 12, 273–280.
- Kranz, F., Ishai, A., 2006. Face perception is modulated by sexual preference. *Curr. Biol.* 16, 63–68.
- Lewis, P.A., Miall, R.C., 2003. Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Curr. Opin. Neurobiol.* 13, 250–255.
- Lischke, A., Berger, C., Prehn, K., Heinrichs, M., Herpertz, S.C., Domes, G., 2012. Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye-gaze unaffected. *Psychoneuroendocrinology* 37, 475–481.
- Livesey, A.C., Wall, M.B., Smith, A.T., 2007. Time perception: manipulation of task difficulty dissociates clock functions from other cognitive demands. *Neuropsychologia* 45, 321–331.
- Mattick, R.P., Clarke, J.C., 1998. Development and validation of measures of social phobia scrutiny fear and social interaction anxiety. *Behav. Res. Ther.* 36, 455–470.
- Meck, W.H., 2006. Neuroanatomical localization of an internal clock: a functional link between mesolimbic, nigrostriatal, and mesocortical dopaminergic systems. *Brain Res.* 1109, 93–107.
- Meck, W.H., 2005. Neuropsychology of timing and time perception. *Brain Cogn.* 58, 1–8.
- Meck, W.H., 1987. Vasopressin metabolite neuropeptide facilitates simultaneous temporal processing. *Behav. Brain Res.* 23, 147–157.
- Meyer-Lindenberg, A., Domes, G., Kirsch, P., Heinrichs, M., 2011. Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. *Nat. Rev. Neurosci.* 12, 524–538.
- Oaten, M., Stevenson, R.J., Case, T.I., 2009. Disgust as a disease-avoidance mechanism. *Psychol. Bull.* 135, 303–333.
- Panksepp, J., 2009. Primary process affects and brain oxytocin. *Biol. Psychiatry* 65, 725–727.
- Prehn, K., Kazzer, P., Lischke, A., Heinrichs, M., Herpertz, S.C., Domes, G., 2013. Effects of intranasal oxytocin on pupil dilation indicate increased salience of socioaffective stimuli. *Psychophysiology* 50, 528–537.
- Sandstrom, N.J., 2007. Estradiol modulation of the speed of an internal clock. *Behav. Neurosci.* 121, 422.
- Schmidt, K., Metzler, P., 1992. *Wortschatztest WST*. Beltz Verlag, Weinheim.
- Schulze, L., Lischke, A., Greif, J., Herpertz, S.C., Heinrichs, M., Domes, G., 2011. Oxytocin increases recognition of masked emotional faces. *Psychoneuroendocrinology* 36, 1378–1382.
- Spielberger, C.D., 1991. State-Trait Anger Expression Inventory. *Psychological Assessment Resources*, Lutz, FL, Revised research edition. professional manual.
- Spielberger, C.D., Gorsuch, R.L., Lushene, R., Vagg, P.R., Jacobs, G.A., 1983. *Manual for the State-trait Anxiety Inventory*. Consulting Psychologists Press, Palo Alto, CA.
- Steyer, R., Schwenkmezger, P., Notz, P., Eid, M., 1994. Testtheoretische Analysen des mehrdimensionalen Befindlichkeitsfragebogens (MDBF). *Diagnostica* 40, 320–328.
- Theodoridou, A., Rowe, A.C., Penton-Voak, I.S., Rogers, P.J., 2009. Oxytocin and social perception: oxytocin increases perceived facial trustworthiness and attractiveness. *Horm. Behav.* 56, 128–132.
- Thienel, M., Heinrichs, M., Fischer, S., Ott, V., Born, J., Hallschmid, M., 2014. Oxytocin's impact on social face processing is stronger in homosexual than heterosexual men. *Psychoneuroendocrinology* 39, 194–203.
- Thornhill, R., Gangestad, S.W., 1999. Facial attractiveness. *Trends Cogn. Sci.* 3, 452–460.
- Tipples, J., 2008. Negative emotionality influences the effects of emotion on time perception. *Emotion* 8, 127–131.
- Tracy, J.L., Beall, A.T., 2011. Happy guys finish last: The impact of emotion expressions on sexual attraction. *Emotion* 11, 1379.
- Tribollet, E., Dubois-Dauphin, M., Dreifuss, J.J., Barberis, C., Jard, S., 1992. Oxytocin receptors in the central nervous system. *Ann. N. Y. Acad. Sci.* 652, 29–38.
- Unkelbach, C., Guastella, A.J., Forgas, J.P., 2008. Oxytocin selectively facilitates recognition of positive sex and relationship words. *Psychol. Sci.* 19, 1092–1094.
- Wittmann, M., van Wassenhove, V., 2009. The experience of time: neural mechanisms and the interplay of emotion: cognition and embodiment. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 364, 1809–1813.
- Wittmann, M., 2015. Modulations of the experience of self and time. *Conscious. Cogn.* 38, 172–181.